



Species richness and diversity in different functional groups across environmental stress gradients: a model for marine rocky shores

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We present a model predicting how the species richness and diversity within benthic functional groups should vary across the full environmental stress gradient across which a regional biota from marine rocky shores can occur. Built upon previous models, our model makes predictions for sessile species (macroalgae and filter feeders), herbivores, and carnivores. We tested some of its predictions by surveying vertical (intertidal elevation) and horizontal (wave exposure and ice scour) stress gradients in northern Nova Scotia, Canada. Because of harsh winter conditions, these coasts only depict approximately intermediate-to-high yearly levels of stress that the cold-temperate, rocky intertidal biota from the northwestern Atlantic can experience. The observed trends matched predictions for sessile species in 75% of the studied gradients, and showed a moderate agreement for herbivores and carnivores only when they were combined as mobile consumers. Agreement meant that both richness and diversity increased from the most stressful to the most benign habitats that can be found in northern Nova Scotia. Also as predicted, sessile species generally showed a faster rate of increase in richness than mobile consumers. Our model also predicted a higher overall richness for sessile species than for mobile consumers, which was true by a factor of 3. Therefore, our model may constitute a useful tool to understanding community composition as a function of abiotic stress, which may in turn facilitate studies on community functioning. Model predictions for lower stress ranges could be tested on more southern shores where the same regional biota occurs.

Species richness (the number of species in a community) is one of the main traits of communities because it influences their stability, productivity, and susceptibility to invasion (Hooper et al. 2005, Duffy et al. 2007, Gamfeldt and Hillebrand 2008). Thus, research on the factors that determine richness has been common in ecology (Field et al. 2009). Environmental stress, or the negative forcing that the abiotic environment exerts on the performance of organisms, is known to affect species richness. Based mostly on research done with marine benthic communities, an environmental stress model (ESM) predicts how the richness of the primary-space holders (sessile species attached to the substrate) should vary with stress for a regional species pool (Menge and Sutherland 1987). Predictions were later developed for the richness of secondary-space holders, which were defined as the sessile species attached to primary-space holders plus the associated mobile species (Bruno et al. 2003). Ultimately, those predictions were used to model the changes in total species richness across the stress gradient along which assemblages from a regional biota can occur (Scrosati and Heaven 2007).

For the moment, the ESM does not make predictions on species richness for different functional groups. In rocky-

shore benthic communities, the primary-space holders include primary producers and filter feeders (Menge and Sutherland 1987), but many secondary-space holders are also primary producers or filter feeders. Secondary-space holders also include herbivores and carnivores, which are mobile consumers (Bruno et al. 2003). Species richness within functional groups influences community functioning (Cardinale et al. 2006, Duffy et al. 2007, Bruno and Cardinale 2008), often through mechanisms that differ depending on the group (Long et al. 2007). However, natural patterns in species richness across functional groups have been less studied than patterns in abundance or biomass (Petchey et al. 2004a). Thus, refining the ESM towards predicting richness in functional groups might help to understanding how community functioning may vary with abiotic stress (Kimbrow and Grosholz 2006). In the present study, we develop a model predicting how richness in different functional groups might change with stress for a regional biota. Then, we test some of the predictions using rocky intertidal systems from the northwestern Atlantic coast.

To develop our model, we considered previous developments. Across the stress gradient over which a regional species pool can occur, the richness of primary-space holders

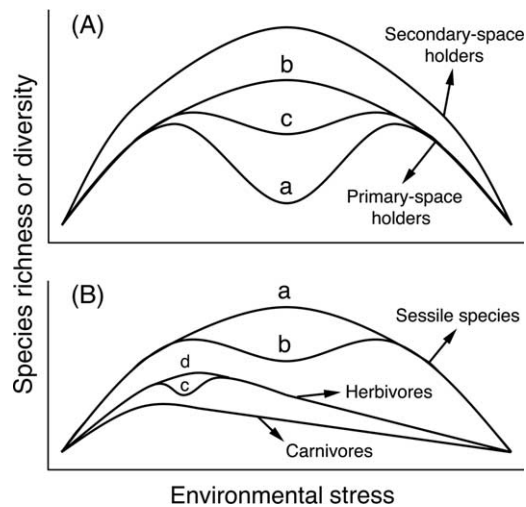


Figure 1. (A) Predicted changes in the species richness and diversity of primary-space holders across the full environmental stress gradient across which a regional species pool can occur, considering (a) strong competitive exclusion because of high recruitment, (b) niche partitioning, and (c) mild competitive exclusion because of low recruitment (from Menge and Sutherland 1987), and predicted changes in the richness of secondary-space holders (from Bruno et al. 2003). (B) Our model, showing the predicted changes in richness and diversity for sessile species, considering (a) competitive exclusion under low (or even high) recruitment or niche partitioning and (b) strong competitive exclusion under high recruitment, for herbivores, considering (c) competitive exclusion and (d) niche partitioning, and for carnivores (see the Introduction for an explanation of trends).

is predicted to follow a bimodal curve (Fig. 1A-a), when competitive exclusions occur at intermediate stress levels, or a unimodal curve (Fig. 1A-b), when niche partitioning occurs at those levels (Menge and Sutherland 1987). In the bimodal curve, the unimodal half from low to intermediate stress represents the predation hypothesis, whereas the unimodal half from intermediate to high stress represents the intermediate disturbance hypothesis (Menge and Sutherland 1987). The richness of primary-space holders is lowest under the highest stress because of the harsh conditions. As stress decreases, richness increases because conditions improve. At intermediate stress levels, richness exhibits a trough because of competitive exclusions. As stress decreases further, the increasing consumer pressure on the primary-space holders disrupts those competitive exclusions, allowing richness to increase again. At the lowest stress levels, richness decreases again because consumer pressure is too intense and eliminates many primary-space holders (Menge and Sutherland 1987). The trough in the bimodal curve is predicted to become shallower as recruitment rates decrease (Menge and Sutherland 1987; Fig. 1A-c). Now, the primary-space holders that generate the competitive exclusions under intermediate stress often cause a peak in the richness of secondary-space holders because of their structural complexity (Bruno et al. 2003). As a result, the richness of secondary-space holders is predicted to follow a unimodal curve across the full stress gradient (Fig. 1A). Although not addressed by Bruno et al. (2003), even when the curve for primary-space holders is unimodal (due to niche partitioning at intermediate stress), a unimodal curve

should also result for secondary-space holders, since neither consumer pressure nor stress is too high in the middle of the stress gradient.

In our model, we combine benthic primary producers and filter feeders into a single group termed sessile species. Thus, this group includes the primary-space holders *sensu* Menge and Sutherland (1987) and some species of secondary-space holders *sensu* Bruno et al. (2003). It is difficult to ascertain the proportion of secondary-space holders that are sessile species (as opposed to mobile consumers), as this may vary among biotas, but basic predictions can be made using Fig. 1d-ii in Bruno et al. (2003). When competitive exclusions occur among primary-space holders under intermediate stress, a unimodal richness curve for sessile species should result (Fig. 1B-a) or, at least, a bimodal curve with a shallow trough (Fig. 1B-b) due to the increased structural complexity of the dominant primary-space holders. When niche partitioning among primary-space holders occurs under intermediate stress, a unimodal curve for sessile species should result (Fig. 1B-a). With low recruitment rates, the unimodal curve (Fig. 1B-a) should also apply (Menge and Sutherland 1987).

In natural communities, species richness often decreases from basal to upper trophic levels (Duffy 2003, Petchey et al. 2004a). Thus, our model predicts a lower richness for herbivores and carnivores than for sessile species (Fig. 1B). Since mobile consumers perform poorly between moderate and high stress (Menge and Sutherland 1987, Dahlhoff et al. 2001, Petes et al. 2008, Miller et al. 2009), herbivores and carnivores should increase in richness relatively slowly from high to intermediate stress (Fig. 1B). Herbivores should decrease in richness at mild stress levels when competitive exclusions occur among them, increasing again when carnivores disrupt that phenomenon at lower stress levels (Fig. 1B-c). Towards the lowest stress levels for a regional biota, carnivore pressure should peak and decrease herbivore richness again (Fig. 1B). If competitive exclusions do not occur among herbivores (due to niche partitioning), their richness curve should be unimodal (Fig. 1B-d). Carnivore richness should peak at low stress levels and decrease towards the lowest stress levels because of competitive exclusions among carnivores (Fig. 1B). No trough is predicted for the carnivore curve because there are no higher trophic levels.

We tested the predictions of our model using rocky intertidal gradients of abiotic stress in northern Nova Scotia, Canada. The cold-temperate biota from the north-western Atlantic coast occurs between Newfoundland/southern Labrador (Mathieson et al. 1991, Adey and Hayek 2005) and Cape Hatteras, North Carolina (Searles 1984). Because of the harsh winter conditions in northern Nova Scotia (Bertness 2007, Scrosati and Eckersley 2007, Fisheries and Oceans Canada 2009), its intertidal habitats represent only moderate to high levels of overall annual stress for this regional biota. Milder yearly conditions occur farther south (e.g. New England, USA). Thus, we were only able to test approximately the intermediate-to-high range of stress that applies to this regional biota. Intertidal recruitment rates are barely known for northern Nova Scotia. For barnacles (characteristic species on these shores; Heaven and Scrosati 2008), recruitment is lower than in New England (Menge 1991, MacPherson et al. 2008, S. Cole, R. Scrosati

Table 1. Summary tables for the nested ANOVAs done separately for species richness within each functional group on the Gulf of St. Lawrence coast (SS). The significance level used for each test is indicated between parentheses besides the name of each functional group; see Materials and methods for an explanation on the selection of significance levels.

	DF	MS	F	p	ω^2
Sessile species (0.05)					
Elevation	2	300.66	25.44	0.001	60.7
Exposure	1	70.53	5.97	0.047	6.2
Elevation \times exposure	2	37.36	3.16	0.115	5.4
Site (elevation \times exposure)	6	11.82	3.31	0.005	5.2
Error	108	3.57			
Herbivores (0.01)					
Elevation	2	8.91	6.40	0.033	23.2
Exposure	1	3.01	2.16	0.192	2.5
Elevation \times exposure	2	7.26	5.22	0.049	18.1
Site (elevation \times exposure)	6	1.39	2.67	0.019	8.1
Error	108	0.52			
Carnivores (0.01)					
Elevation	2	1.23	1.97	0.220	3.7
Exposure	1	0.68	1.08	0.339	0.2
Elevation \times exposure	2	0.70	1.12	0.386	0.5
Site (elevation \times exposure)	6	0.63	3.69	0.002	1.9
Error	108	0.17			
Mobile consumers (0.05)					
Elevation	2	12.76	6.90	0.028	21.7
Exposure	1	6.53	3.53	0.109	4.7
Elevation \times exposure	2	12.31	6.65	0.030	20.8
Site (elevation \times exposure)	6	1.85	2.37	0.034	6.4
Error	108	0.78			

and J. Tam pers. comm.). In addition, the lower abundance of other dominant invertebrates and macroalgae in northern Nova Scotia compared with New England (Scrosati and Heaven 2008) suggests that lower recruitment rates are common in northern Nova Scotia. Thus, for sessile species, we considered the unimodal curve (Fig. 1B-a) instead of the bimodal curve (Fig. 1B-b). Then, according to our model (Fig. 1B), we hypothesized that the richness of sessile species, herbivores, and carnivores would increase from the most stressful to the least stressful habitats that occur in northern Nova Scotia. We also hypothesized that the rate of change in richness across our stress gradients would be highest for sessile species, followed by that for herbivores and, then, for carnivores. Lastly, we hypothesized that overall richness would be highest for sessile species, followed by that for herbivores and, then, for carnivores.

The ESM makes the same predictions for species richness and diversity (Menge and Sutherland 1987). Diversity is a measure of how likely two randomly selected individuals in a community belong to different species, and is determined by both richness and evenness, which is the degree of similarity in abundance among the species (Krebs 1999). Therefore, according to the original literature on the ESM (Menge and Sutherland 1987), our model (Fig. 1B) could in theory also be used to make predictions on functional-group diversity, besides richness. Thus, we hypothesized that species diversity within each functional group would increase from the most stressful to the least stressful habitats that occur in northern Nova Scotia.

Material and methods

We did our study at Sea Spray Shore (45°46'N, 62°8'W; hereafter SS), on the Gulf of St. Lawrence coast, and at

Tor Bay Provincial Park (45°10'N, 61°21'W; hereafter TB), on the open Atlantic coast (see Scrosati and Heaven 2008 for a map). On each shore, we sampled the full intertidal range (vertical stress gradient) between 0 m (chart datum) and an upper boundary that we determined using ecological indicators (the barnacle *Semibalanus balanoides*) to account for the fact that zones with similar emersion-related stresses occur higher on the shore, and are vertically wider, on wave-exposed shores than on sheltered shores (Harley and Helmuth 2003). This barnacle is the sessile, perennial species occurring highest on both coasts, which ensured that annual and seasonal wave regimes were integrated when determining upper intertidal boundaries. Once we determined the upper boundary, we divided the intertidal range in three zones of equal vertical extent (high, middle, and low zones). Because of tides, the abiotic stresses related to desiccation, temperature, and irradiance increase from low to high elevations (Raffaelli and Hawkins 1996). Wave exposure (which determines horizontal stress gradients; Denny and Wetthey 2001) is generally lower on the Gulf of St. Lawrence coast than on the Atlantic coast (Fisheries and Oceans Canada 2009). Thus, we selected two exposure levels for SS (sheltered and exposed) and three for TB (sheltered, intermediate, and exposed). Between the summer and autumn of 2005, maximum water velocity (an index of exposure) averaged 3.4 m s⁻¹ in sheltered sites and 5.2 m s⁻¹ in exposed sites at SS, while it averaged 4.3 m s⁻¹ in sheltered sites, 6.5 m s⁻¹ under intermediate exposure, and 7.5 m s⁻¹ in exposed sites at TB (Scrosati and Heaven 2007). The upper intertidal boundary, as defined above relative to chart datum, was 1.66 m (sheltered) and 1.70 m (exposed) at SS and 1.56 m (sheltered), 1.99 m (intermediate exposure), and 2.16 m (exposed) at TB. The Gulf of St. Lawrence coast freezes in winter (Scrosati and Eckersley

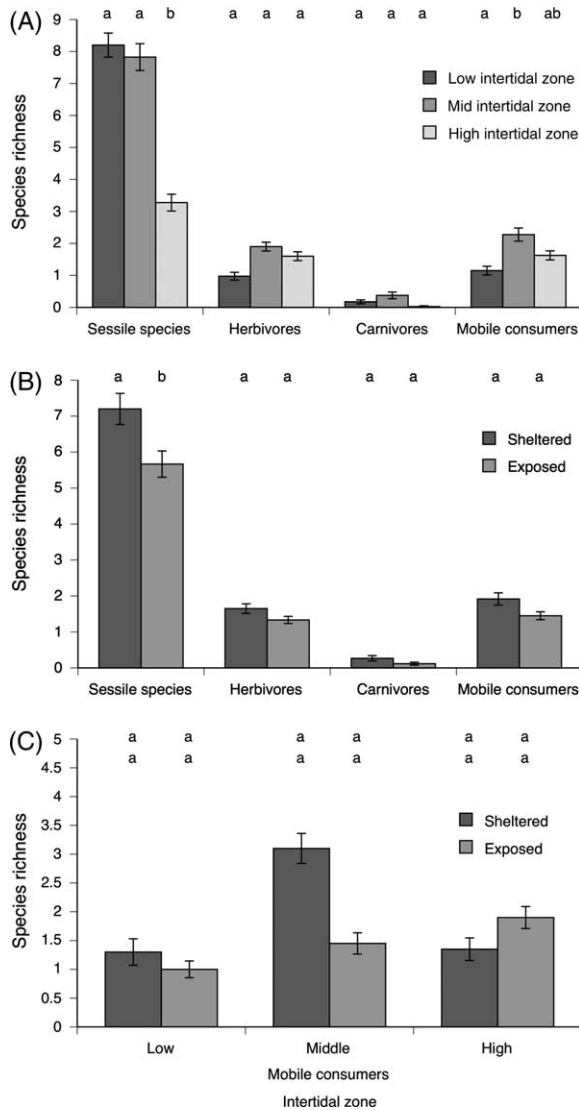


Figure 2. Main effects of (A) elevation and (B) exposure on the species richness within functional groups on the Gulf of St. Lawrence coast (SS), and (C) simple effects of elevation and exposure on the richness within mobile consumers (means \pm SE; $n = 40$ for A, $n = 60$ for B, and $n = 20$ for C). Simple effects are shown only for the group for which the elevation \times exposure interaction was significant (Table 1). In panels (A) and (B), significant differences between means for different factor levels for each functional group are indicated with different letters. In panel (C), the upper row of letters compares means for elevation levels separately for each exposure level, while the lower row compares means for exposure levels separately for each elevation.

2007), so intertidal habitats are then subjected to ice scour (Belt et al. 2009). The Atlantic coast does not experience local formation of ice on the sea surface in winter (McCook and Chapman 1997, Minchinton et al. 1997). Measurement of the damage (angle of deformation) caused by sea ice to metallic cages affixed to the rocky substrate at SS indicated that ice scour is strong (mean angle of deformation of 90°) on wave-exposed areas and milder (mean angle of 47°) on wave-sheltered areas (Scrosati and Heaven 2006). Thus, the two levels used for wave exposure at SS also represented differences in ice scour intensity. For

simplicity, for SS hereafter the term “exposed” will refer to high levels of wave exposure and ice scour, whereas the term “sheltered” will refer to low levels in those variables. Pictures showing the positive spatial relationship between wave exposure and ice scour intensity appear in Scrosati and Heaven (2007).

We measured the richness and diversity of sessile species, herbivores, and carnivores in July–August 2005. We sampled coastal ranges that are topographically complex, which determines an availability of sites that differ in exposure: sites fully facing open waters experience the highest exposures, while sites mostly facing rocky land masses a short distance away are sheltered in comparison. Sites of differing exposures are found interspersed along these coastlines. At low tide, we identified all seaweeds and invertebrates in 10 quadrats (25×25 cm) placed randomly at each of 2 sites (each one 40–50 m in extent along the shore) located at each of the 3 elevation zones at each exposure level (2 levels at SS and 3 levels at TB) on each of the 2 studied coasts (Gulf of St. Lawrence and Atlantic), thus generating data for 300 quadrats. Sites for different elevations were interspersed along the shoreline for each exposure level, contiguous sites being separated by 10–40 m. The extent of sampled coast was ca 400 m on both shores. Observational surveys along both coasts had previously indicated that our study sites are physically and biologically representative of at least several tens of km along each shore. Recent quantitative surveys on selected taxa support this notion, as the cover of fucooid algae (ecosystem engineers that affect local diversity) and their epiphytes is similar along at least 80 km of Atlantic coastline including TB (Longtin and Scrosati 2009), while the cover of fucooid algae and mussels is similar along at least 25 km of Gulf of St. Lawrence coastline including SS (Cole 2010).

We restricted sampling to intertidal sites with stable bedrock (volcanic rock at SS and metamorphose sedimentary rock at TB), surveying the natural variety of slopes and avoiding tide pools. We identified the species using field guides (Gibson 2003, Martínez 2003) and taxonomic keys (Pollock 1998, Villalard-Bohnsack 2003). For juveniles, small adults, or morphologically similar species, making accurate identifications at the species level is sometimes not possible. For such few cases (Supplementary material), we made identifications at the lowest possible taxonomic level, as normally done in studies identifying all primary producers and animals simultaneously (Kimbrow and Grosholz 2006, Russell et al. 2006, Thompson et al. 2007, Valdivia and Molis 2009). For each quadrat, we measured the percent cover of each species using a metallic frame divided in 100 equal sections with monofilament line. When cover was $< 1\%$ for a given species, we recorded it as 0.5%.

For each quadrat, species richness (S) was the total number of identified species. We measured species diversity with Simpson’s diversity index ($1 - D$):

$$1 - D = 1 - \sum (p_i)^2,$$

where p_i was the proportion of species i in the quadrat, calculated using percent cover data. Simpson’s diversity index ranges between 0 and almost 1 ($1 - S^{-1}$), is a robust diversity index, and has a low bias towards the abundance distribution and sample size (Krebs 1999).

Table 2. Summary tables for the nested ANOVAs done separately for species richness within each functional group on the Atlantic coast (TB). The significance level used for each test is indicated between parentheses besides the name of each functional group; see Materials and methods for an explanation on the selection of significance levels.

	DF	MS	F	p	ω^2
Sessile species (0.05)					
Elevation	2	385.09	46.77	<0.001	52.7
Exposure	2	92.82	11.27	0.004	11.8
Elevation \times exposure	4	26.11	3.17	0.069	5.0
Site (elevation \times exposure)	9	8.23	1.84	0.065	2.4
Error	162	4.48			
Herbivores (0.01)					
Elevation	2	2.64	6.69	0.017	3.4
Exposure	2	16.24	41.17	<0.001	23.9
Elevation \times exposure	4	3.58	9.08	0.003	9.6
Site (elevation \times exposure)	9	0.39	0.40	0.933	0
Error	162	0.99			
Carnivores (0.01)					
Elevation	2	6.07	8.03	0.008	29.0
Exposure	2	1.62	2.14	0.174	47.0
Elevation \times exposure	4	0.76	1.00	0.45	0.03
Site (elevation \times exposure)	9	0.76	3.50	0.001	13.2
Error	162	0.22			
Mobile consumers (0.05)					
Elevation	2	15.51	9.03	0.007	13.9
Exposure	2	26.41	15.38	0.001	24.8
Elevation \times exposure	4	6.41	3.73	0.047	9.4
Site (elevation \times exposure)	9	1.72	1.59	0.123	2.9
Error	162	1.08			

We tested the effects of elevation (fixed factor with 3 levels) and exposure (fixed factor with 2 levels at SS and 3 levels at TB) on species richness and diversity separately for each functional group and coast using factorial ANOVAs, considering sites as a random factor nested within the elevation \times exposure interaction (Underwood 1997, Wikström and Kautsky 2007). We assessed the normality assumption with Kolmogorov-Smirnov tests and the homoscedasticity assumption with Levene tests (Quinn and Keough 2002). When these assumptions were met, we used the traditional significance level of 0.05 for the tests. When violation of assumptions occurred, we sought solutions by transforming the data, but no transformation led to meeting the assumptions. Therefore, we ran the tests on the raw data using a conservative significance level (0.01). The ANOVA is a robust test against violation of assumptions when sample size within treatments is higher than 6, when there are >5 treatments, and when the design is balanced (Underwood 1997). All of those conditions were met in our study, but we used anyways a conservative significance level when assumptions were not met for added security, as recommended by Underwood (1997). When an ANOVA revealed main effects, we did pairwise comparisons between factor levels using Tukey HSD tests. When the elevation \times exposure interaction was significant, we tested for simple effects by running one-way ANOVAs to compare levels of a given factor separately for each level of the other factor, using the error term from the factorial ANOVA to compute F values (Howell 2002). We used Tukey HSD tests for pairwise comparisons whenever a one-way ANOVA yielded a significant result (Quinn and Keough 2002). Since the average richness of herbivores and carnivores was relatively low for each factor level (see Results), we combined the data for both functional groups into a single group termed mobile consumers. According

to our model (Fig. 1B), we hypothesized that the richness and diversity of mobile consumers would increase from the highest to the lowest stress levels found on northern Nova Scotia shores.

Results

Species richness

Sessile species

On the Gulf of St. Lawrence coast (SS), we found 27 sessile species, including 20 algae and 7 filter feeders (Supplementary material). At SS, richness varied across the elevation and exposure gradients (Table 1), increasing from high to low elevations (Fig. 2A) and from exposed to sheltered habitats (Fig. 2B). On the Atlantic coast (TB), we found 42 sessile species, including 30 algae and 12 filter feeders (Supplementary material). At TB, richness varied across the elevation and exposure gradients (Table 2), increasing from high to low elevations (Fig. 3A) but showing no significant difference between exposed and sheltered habitats, with a trough at intermediate exposures (Fig. 3B). The elevation \times exposure interaction was not significant for either SS (Table 1) or TB (Table 2).

Herbivores

On the Gulf of St. Lawrence coast (SS), we found 5 herbivores (Supplementary material). At SS, richness did not vary significantly across the elevation and exposure gradients (Table 1, Fig. 2A, B). On the Atlantic coast (TB), we found 6 herbivores (Supplementary material). At TB, richness did not vary across the elevation gradient (Table 2, Fig. 3A), but it did vary across the exposure gradient (Table 2), increasing from exposed to sheltered habitats (Fig. 3B).

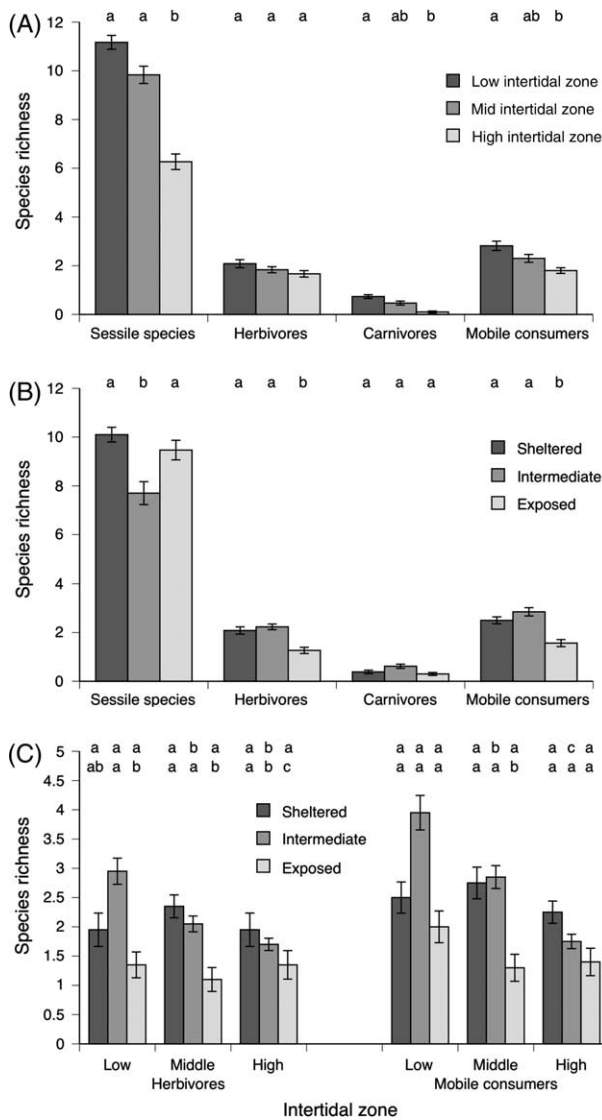


Figure 3. Main effects of (A) elevation and (B) exposure on the species richness within functional groups on the Atlantic coast (TB), and (C) simple effects of elevation and exposure on the richness of herbivores and mobile consumers (means \pm SE; $n = 60$ for A, $n = 60$ for B, and $n = 20$ for C). Simple effects are shown only for the groups for which the elevation \times exposure interaction was significant (Table 2). In panels (A) and (B), significant differences between means for different factor levels for each functional group are indicated with different letters. In panel (C), the upper row of letters compares means for elevation levels separately for each exposure level, while the lower row compares means for exposure levels separately for each elevation.

At TB, the elevation \times exposure interaction was significant (Table 2), revealing that the predicted trends of increasing richness from stressful to benign habitats occurred only in some cases (Fig. 3C).

Carnivores

On the Gulf of St. Lawrence coast (SS), we found 4 carnivores (Supplementary material). At SS, richness did not vary significantly across the elevation and exposure gradients (Table 1, Fig. 2A, B). On the Atlantic coast (TB), we found 8 carnivores (Supplementary material). At TB,

richness varied across the elevation gradient (Table 2), increasing from high to low elevations (Fig. 3A), but it did not vary across the exposure gradient (Table 2, Fig. 3B). The elevation \times exposure interaction was not significant for either SS (Table 1) or TB (Table 2).

Mobile consumers

On the Gulf of St. Lawrence coast (SS), we found 9 mobile consumers (herbivores plus carnivores; Supplementary material). At SS, richness varied across the elevation gradient (Table 1) with an unclear trend (Fig. 2A) and did not vary across the exposure gradient (Table 1, Fig. 2B). At SS, the elevation \times exposure interaction was significant (Table 1), although no clear trends emerged when simple effects were evaluated (Fig. 2C). On the Atlantic coast (TB), we found 14 mobile consumers (Supplementary material). At TB, richness varied across the elevation and exposure gradients (Table 2), increasing from high to low elevations (Fig. 3A) and from exposed to sheltered habitats (Fig. 3B). At TB, the elevation \times exposure interaction was significant (Table 2). Tests for simple effects revealed that the trends detected by the main-effect tests (Fig. 3A, B) were significant only in some cases when viewed at separate factor levels (Fig. 2C).

Rate of change in richness

On the Gulf of St. Lawrence coast (SS), the mean richness of sessile species increased in 4.9 species from high to low elevations and in 1.5 species from exposed to sheltered habitats, but changes were nonsignificant for the other functional groups (Fig. 2A). On the Atlantic coast (TB), the mean richness of sessile species increased in 4.9 species from high to low elevations but remained statistically similar across the exposure gradient (Fig. 3A). From high to low elevations at TB, mean richness increased in 0.6 species for carnivores and in 1.0 species for mobile consumers, with no significant change recorded for herbivores (Fig. 3A). From exposed to sheltered habitats at TB, mean richness increased in 0.8 species for herbivores and in 0.9 species for mobile consumers, with no significant change recorded for herbivores (Fig. 3B).

Species diversity

Sessile species

On the Gulf of St. Lawrence coast (SS), diversity varied across the elevation and exposure gradients (Table 3), increasing from high to low elevations (Fig. 4A) and from exposed to sheltered habitats (Fig. 4B). On the Atlantic coast (TB), diversity varied across the elevation and exposure gradients (Table 4), increasing from high to low elevations (Fig. 5A) but showing no significant difference between exposed and sheltered habitats, with a trough at intermediate exposures (Fig. 5B). The elevation \times exposure interaction was not significant for either SS (Table 3) or TB (Table 4).

Herbivores

On the Gulf of St. Lawrence coast (SS), diversity did not vary across the elevation and exposure gradients (Table 3,

Table 3. Summary tables for the nested ANOVAs done separately for species diversity within each functional group on the Gulf of St. Lawrence coast (SS). The significance level used for each test is indicated between parentheses besides the name of each functional group; see Materials and methods for an explanation on the selection of significance levels.

	DF	MS	F	p	ω^2
Sessile species (0.01)					
Elevation	2	8.91	50.41	<0.001	55.1
Exposure	1	3.86	21.80	0.003	11.6
Elevation \times exposure	2	1.43	8.11	0.020	7.9
Site (elevation \times exposure)	6	0.18	1.36	0.237	0.9
Error	108	0.13			
Herbivores (0.01)					
Elevation	2	1.24	6.38	0.033	17.0
Exposure	1	1.17	6.06	0.049	8.0
Elevation \times exposure	2	1.42	7.34	0.024	20.0
Site (elevation \times exposure)	6	0.19	1.88	0.092	4.4
Error	108	0.10			
Carnivores (0.05)					
Elevation	2	0.02	1.00	0.422	0
Exposure	1	0.02	1.00	0.356	0
Elevation \times exposure	2	0.02	1.00	0.422	0
Site (elevation \times exposure)	6	0.02	2.10	0.059	9.8
Error	108	0.01			
Mobile consumers (0.05)					
Elevation	2	1.50	5.69	0.041	16.0
Exposure	1	1.15	4.37	0.082	5.8
Elevation \times exposure	2	1.72	6.51	0.031	18.8
Site (elevation \times exposure)	6	0.26	1.88	0.091	4.8
Error	108	0.14			

Fig. 4A, B). On the Atlantic coast (TB), diversity did not vary across the elevation gradient (Table 4, Fig. 5A), but it did change across the exposure gradient (Table 4), increasing from exposed to sheltered habitats (Fig. 5B). The elevation \times exposure interaction was not significant for either SS (Table 3) or TB (Table 4).

Carnivores

The diversity of carnivores did not vary across the elevation and exposure gradients on either coast (Table 3–4, Fig. 4A, B, 5A, B). The elevation \times exposure interaction was not significant for either coast (Table 3–4).

Mobile consumers

On the Gulf of St. Lawrence coast (SS), diversity varied across the elevation gradient (Table 3) with an unclear general trend (Fig. 4A), but it did not change across the exposure gradient (Table 4, Fig. 4B). At SS, the elevation \times exposure interaction was significant (Table 3), but most trends viewed separately at factor levels were nonsignificant (Fig. 4C). On the Atlantic coast (TB), diversity varied across the elevation and exposure gradients (Table 4), increasing from high to low elevations (Fig. 5A) and from exposed to sheltered habitats (Fig. 5B). At TB, the elevation \times exposure interaction was not significant (Table 4).

Discussion

As predicted, the richness of sessile species was higher than for herbivores and carnivores on both coasts, clearly so by a factor of 5–7. Within sessile species, algal richness almost tripled that of filter feeders (algal predominance among temperate sessile species is common; Broitman et al. 2001),

while herbivores and carnivores were similar in their low richness values. Remarkably, the ratio between sessile species and mobile consumers was the same (3) for the Gulf of St. Lawrence coast (27:9) and the Atlantic coast (42:14). Also in good agreement with our predictions, both the richness and diversity of sessile species increased from the most stressful habitats to the most benign habitats found in northern Nova Scotia in 3 of the 4 studied gradients (75% agreement). This pattern occurred on both coasts across the vertical gradient, but only at SS across the horizontal gradient, showing little change across exposures at TB. Richness and diversity trends for herbivores and carnivores, however, agreed with our predictions only in a few cases. Such a poor fit may have been the result of both groups having low richness values in general. After combining herbivores and carnivores into mobile consumers, richness and diversity trends matched our predictions more often, showing 50% agreement (for both richness and diversity) when main effects were assessed and 18 and 55% agreement (for richness and diversity, respectively) when simple effects were determined. Our predictions on the rate of change in richness across the stress gradients were also generally supported by our data. Sessile species showed a stronger increase in richness than herbivores and carnivores in 3 of the 4 studied gradients (75% agreement), differences being very small in the remaining gradient (exposure at TB).

Overall, then, our field surveys have revealed a number of strengths in our model. The reasons behind the divergences found occasionally between predicted and observed trends for sessile species and mobile consumers are not obvious. They may simply have resulted from sampling error, considering the low richness values occurring in northern Nova Scotia, or perhaps other factors may rarely add small amounts of variation in ways yet to be recognized. Regarding mobile consumers specifically,

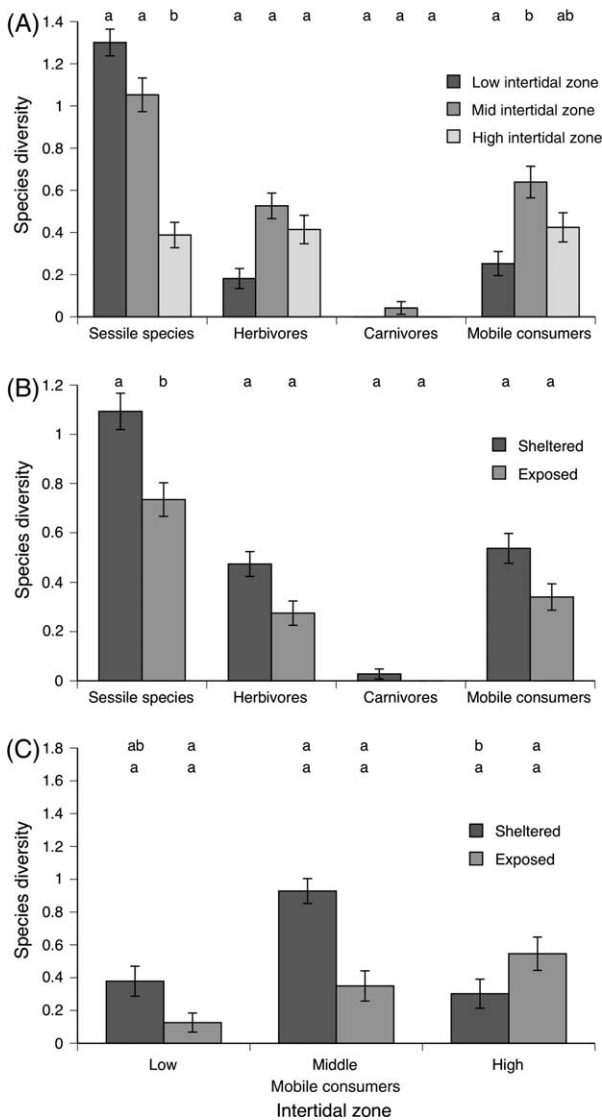


Figure 4. Main effects of (A) elevation and (B) exposure on the species diversity within functional groups on the Gulf of St. Lawrence coast (SS), and (C) simple effects of elevation and exposure on the diversity within mobile consumers (means \pm SE; $n = 40$ for A, $n = 60$ for B, and $n = 20$ for C). Simple effects are shown only for the group for which the elevation \times exposure interaction was significant (Table 3). In panels (A) and (B), significant differences between means for different factor levels for each functional group are indicated with different letters. In panel (C), the upper row of letters compares means for elevation levels separately for each exposure level, while the lower row compares means for exposure levels separately for each elevation.

possibly their degree of mobility may determine that relationships with spatial changes in abiotic stress are more difficult to establish than for sessile species. We also point out, again, that northern Nova Scotia shores exhibit only intermediate-to-high yearly levels of abiotic stress across the range applying to the cold-temperate, rocky intertidal biota from the northwestern Atlantic coast (Bertness 2007, Scrosati and Eckersley 2007, Fisheries and Oceans Canada 2009). Therefore, the predictions that our model makes between intermediate and low stress levels should be tested on more southern shores (e.g. New

England) if the northwestern Atlantic biota is used as the test system.

A couple of structural aspects of our model are worth discussing. Our field surveys missed highly mobile consumers that come and go with the tides, such as fishes and birds. The effects of such organisms on intertidal species is beginning to be understood, and they have been found to be relevant in some cases (Wootton 1997, Horn and Ojeda 1999, Norton and Cook 1999, Ellis et al. 2007). Including those very mobile species in future models of intertidal richness (including permanent as well as transient species) would constitute a useful next step. Another issue worth discussing is the possible extent of omnivory. We followed the traditional approach of separating mobile consumers into herbivores and carnivores, but species with mixed food preferences (omnivores) do exist in communities (Polis and Strong 1996, Williams and Martínez 2004). However, a recent analysis of many aquatic and terrestrial food webs has concluded that, although omnivory is common, it is mostly concentrated in trophic levels above herbivores (Thompson et al. 2007). Thus, since we considered only one carnivore group in our model (including all levels of carnivory), omnivory in that group should not affect considerably the predictions shown in Fig. 1B. In any case, future studies on food preferences should inevitably lead to increasing the level of realism of our model.

Because nature is inherently variable, our model should be considered as a flexible tool. For different rocky-shore biotas from similar environmental ranges around the world (e.g. cold-temperate biotas), variation in richness within the same relative level of stress may occur depending on whether competitive exclusions or niche partitioning occurs (Menge and Sutherland 1987), which depends on the ecological and evolutionary history of biotas. Variation may also result from human-mediated species invasions and from the harvesting of benthic species, which may affect the richness within native functional groups (Castilla 1999, Casas et al. 2004, Piazzini and Ceccherelli 2006). In addition, variation may occur depending on a combination of habitat complexity and the spatial resolution of observations (Russell et al. 2006, Firth and Crowe 2008, Kallimanis et al. 2008, Dunn and Halpin 2009), although this is not always the case (Rowe and Lidgard 2009). Therefore, we suggest that our model be tested using other rocky-shore biotas worldwide to determine its consistency and degree of variability.

The potential application of our model to benthic systems other than rocky shores would need to consider fundamental differences between the systems. For example, macroalgae and planktotrophic filter feeders mainly sustain upper trophic levels on marine rocky shores (Menge and Branch 2001, Witman and Dayton 2001), but imported detritus is key to sustaining animal species on many soft-sediment shores (Little 2000). Recent studies on benthic food web structure have used a basal group that included vascular plants, macroalgae, and detritus and a primary-consumer group that included herbivores and detritivores (Thompson et al. 2007). Thus, our model could be modified and tested in benthic systems other than rocky shores. In doing so, which is beyond the scope of our study, elements of our model might be retained due to their potential generality. For example, in benthic freshwater systems, the richness of four functional groups from basal

Table 4. Summary tables for the nested ANOVAs done separately for species diversity within each functional group on the Atlantic coast (TB). The significance level used for each test is indicated between parentheses besides the name of each functional group; see Materials and methods for an explanation on the selection of significance levels.

	DF	MS	F	p	ω^2
Sessile species (0.01)					
Elevation	2	3.18	39.89	<0.001	31.8
Exposure	2	1.39	17.45	0.001	13.5
Elevation × exposure	4	0.33	4.13	0.036	5.1
Site (elevation × exposure)	9	0.08	0.72	0.688	0
Error	162	0.11			
Herbivores (0.01)					
Elevation	2	0.06	1.03	0.394	0.02
Exposure	2	1.26	21.96	<0.001	13.4
Elevation × exposure	4	0.31	5.35	0.017	5.6
Site (elevation × exposure)	9	0.06	0.33	0.96	0
Error	162	0.17			
Carnivores (0.01)					
Elevation	2	0.03	0.66	0.539	0
Exposure	2	0.06	1.14	0.363	1.0
Elevation × exposure	4	0.04	0.69	0.618	0
Site (elevation × exposure)	9	0.05	3.82	<0.001	23.3
Error	162	0.01			
Mobile consumers (0.05)					
Elevation	2	1.00	7.08	0.014	8.2
Exposure	2	1.88	13.29	0.002	16.5
Elevation × exposure	4	0.45	3.17	0.069	5.8
Site (elevation × exposure)	9	0.14	0.86	0.566	0
Error	162	0.17			

species to top consumers decreased towards the highest values of acidity (abiotic stress) for those biotas and, in a few cases, consumer groups peaked mildly in richness at intermediate pH values (Petchey et al. 2004a). Similarly, on a soft-sediment marine shore, the richness of sessile species and mobile consumers increased from the most disturbed areas to areas of lower physical stress that were dominated by a filter feeder that acted as a foundation species (Kimbrow and Grosholz 2006), suggesting that such areas represent intermediate stress levels for that regional biota, according to Menge and Sutherland's (1987) model.

It is worth noting that gradients of nutrient supply (also termed productivity gradients) are also considered to affect species richness in communities (Kondoh 2001, Worm et al. 2002). However, the context and shape of such a relationship are not entirely clear (Pärtel et al. 2007, Svensson et al. 2007, Laanisto et al. 2008, Witman et al. 2008, Cardinale et al. 2009). Incorporating productivity gradients to our model, in addition to environmental stress gradients, might increase its predictive power as future studies clarify the productivity–richness relationship. For the time being, considering variation in environmental stress has allowed us to make several successful predictions, as shown by our data on total species richness and diversity (Scrosati and Heaven 2007) and on the richness and diversity of sessile species and, to a lesser degree, mobile consumers (this study). This is consistent with the notion that gradients of abiotic stress can explain a considerable amount of variation in community structure, particularly when such gradients occur at spatial scales across which nutrient concentration is similar (Menge 1992).

As traits used to predict community functioning, species richness and diversity offer less information than measures

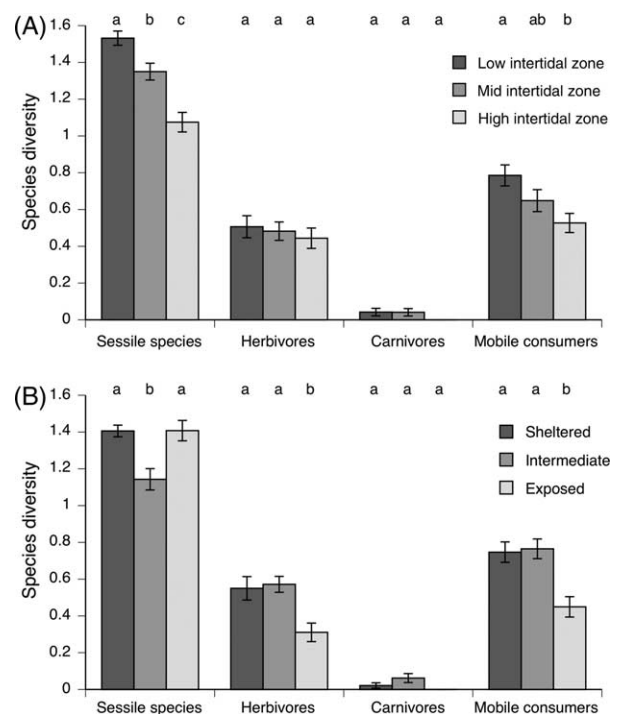


Figure 5. Main effects of (A) elevation and (B) exposure on the species diversity within functional groups on the Atlantic coast (TB) (means \pm SE; $n = 60$ for A and $n = 60$ for B). Simple effects were not calculated because the elevation \times exposure interaction was never significant (Table 4). Significant differences between means for different factor levels for each functional group are indicated with different letters.

of functional diversity, which consider differences among species even within functional groups (Petchey et al. 2004b, Valdivia et al. 2009). However, for logistic reasons, it is not always feasible to collect information on functional diversity for an entire biota for this to become a practical concept under all circumstances. Thus, species richness and diversity remain as basic primary tools to investigate the role of communities in ecosystems, especially when richness and diversity data can be obtained for different functional groups (Long et al. 2007, Bruno and Cardinale 2008). In particular, the ubiquity of abiotic stress gradients in nature has resulted in renewed calls for studies being done on them to understand the variation in community functioning across space and, considering climate change, across time (McGill et al. 2006, Smale and Barnes 2008, Algar et al. 2009). We hope that our study stimulates research on the factors that determine species richness and diversity within functional groups in nature, particularly across environmental stress gradients.

Acknowledgements – We thank Elizabeth A. MacPherson and Lindsay K. Eckersley for their field assistance and B. Klemens Eriksson and 3 anonymous reviewers for their constructive comments on our study. Funding was provided by grants from the Canada Research Chairs (CRC) program, the Canada Foundation for Innovation (CFI), the Natural Sciences and Engineering Research Council of Canada (NSERC Discovery Grant), and the Saint Francis Xavier Univ. Council for Research (UCR) to R.A.S. and by a graduate scholarship from the Univ. of Groningen (The Netherlands) to B.v.G.

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Supplementary Material

List of the species identified in rocky intertidal habitats on the Gulf of St. Lawrence coast (SS) and on the open Atlantic coast (TB) of Nova Scotia, classified by the functional groups considered for this study.

Species	Gulf of St. Lawrence coast	Atlantic coast
Sessile species (algae)		
<i>Alaria esculenta</i>		X
<i>Ascophyllum nodosum</i>	X	X
<i>Calothrix</i> sp.	X	X
<i>Ceramium</i> sp.	X	
<i>Chondrus crispus</i>	X	X
<i>Chorda filum</i>	X	
<i>Chordaria flagelliformis</i>	X	X
<i>Cladophora rupestris</i>		X
<i>Cladophora</i> sp.	X	X
<i>Corallina officinalis</i>	X	X
<i>Devaleraea ramentacea</i>		X
<i>Dictyosiphon</i> sp.	X	
<i>Dumontia contorta</i>		X
Epiphytic brown algae	X	X
Filamentous turf		X
<i>Fucus serratus</i>	X	X
<i>Fucus</i> sp.	X	X
<i>Fucus spiralis</i>		X
<i>Fucus vesiculosus</i>	X	X
Green algal crust	X	X
<i>Hildenbrandia rubra</i>	X	X
<i>Laminaria digitata</i>		X
<i>Laminaria longicuris</i>		X
<i>Laminaria saccharina</i>		X
<i>Lithothamnion</i> sp.	X	X
<i>Petalonia fascia</i>	X	
<i>Polysiphonia</i> sp.	X	X
<i>Porphyra</i> sp.		X
<i>Ralfsia</i> sp.		X
<i>Rhizoclonium tortuosum</i>		X
<i>Rhodomela</i> sp.		X
<i>Scytosiphon</i> sp.	X	X
<i>Spongomorpha aeruginosa</i>	X	X
<i>Ulva intestinalis</i>		X

Sessile species (filter feeders)		
<i>Anomia simplex</i>		X
<i>Clava multicornis</i>	X	X
<i>Crassostrea virginica</i>	X	
<i>Dynamena pumila</i>	X	X
<i>Electra</i> sp.		X
<i>Halichondria</i> sp.		X
<i>Halisarca</i> sp.		X
<i>Hiatella arctica</i>		X
<i>Membranipora</i> sp.	X	X
<i>Mytilus</i> sp.	X	X
<i>Obelia</i> sp.	X	X
<i>Semibalanus balanoides</i>	X	X
<i>Spirorbis spirillum</i>		X
Herbivores		
<i>Idotea</i> sp.	X	X
<i>Lacuna vineta</i>		X
<i>Littorina littorea</i>	X	X
<i>Littorina obtusata</i>	X	X
<i>Littorina saxatilis</i>	X	X
<i>Tectura testudinalis</i>	X	X
Carnivores		
<i>Asterias</i> sp.	X	X
<i>Cancer irroratus</i>		X
<i>Cancer</i> sp.	X	X
<i>Carcinus maenas</i>		X
<i>Coryphella</i> sp.		X
<i>Nucella lapillus</i>	X	X
<i>Pagurus</i> sp.	X	X
<i>Urticina felina</i>		X