

Species richness and diversity across rocky intertidal elevation gradients in Helgoland: testing predictions from an environmental stress model

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Abstract Environmental stress affects species richness and diversity in communities, but the precise form of the relationship is unclear. We tested an environmental stress model (ESM) that predicts a unimodal pattern for total richness and diversity in local communities across the full stress gradient where a regional biota can occur. In 2008, we measured richness and diversity (considering all macrobenthic species) across the entire intertidal range on three rocky shores on Helgoland Island, Germany. Intertidal elevation is known to be positively related to abiotic stress. Since Helgoland is between the northern and southern biogeographic boundaries for the cold-temperate NE Atlantic intertidal biota, it exhibits low stress levels for this biota at low elevations and high stress at high elevations because of long (>6 h) emersion times. Thus, we predicted a unimodal trend for richness and diversity across elevation. On all three shores, richness increased from high to middle elevations, but remained similar between middle and low elevations. Diversity followed the same trend on one shore and different trends (although also non-

unimodal) on the other two. Evenness explained the trend differences between richness and diversity. Overall, our study yielded little support for the ESM. Reasons for richness and diversity not decreasing at low elevations may be related to influences of mostly subtidal species, Helgoland's intertidal range, or sampling resolution. Our study also suggests that the ESM must be developed further to differentiate between richness and diversity. We offer recommendations to improve future ESM research using intertidal systems.

Keywords Diversity · Elevation · Environmental stress · Evenness · Richness · Rocky intertidal

Introduction

Species diversity is an important property of communities because it is often related to their functioning and potential for change (Hooper et al. 2005; Stachowicz et al. 2007; Gamfeldt and Hillebrand 2008). Diversity is a measure of how likely two randomly selected individuals in a community belong to different species. Thus, diversity is affected by two other properties of communities: richness, which is the total number of species, and evenness, which is the degree of similarity in abundance among the species (Krebs 1999).

Environmental stress is the negative forcing exerted by the abiotic environment on the performance of organisms (Heaven and Scrosati 2008) and plays a major role in determining local species diversity mediated by interspecific interactions (Menge et al. 2002; Crain and Bertness 2006). Based mostly on research done with marine benthic systems, an environmental stress model (ESM; Menge and Sutherland 1987) predicts how the local diversity and

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richness (terms that were used interchangeably) of basal species should vary with abiotic stress for a regional species pool. On marine rocky shores, the basal species are primary-space holders, that is, the sessile species that are attached to the substrate (e.g., seaweeds and filter feeders). Later developments of the ESM extended predictions to the totality of species in communities, thus including also secondary-space holders (sessile species attached to the primary-space holders) and the associated mobile species (Bruno et al. 2003). In such an updated ESM, total species richness and diversity are predicted to follow a unimodal pattern across the full stress gradient across which a regional biota can occur (Fig. 1). Such a pattern results from the interaction between stress and interspecific interactions. At the highest stress level, richness and diversity are lowest because few species are able to tolerate the conditions. At moderately lower stress levels, more species are able to survive and facilitation from some species may further help other species to occur through habitat amelioration. At intermediate stress levels, competitive exclusion among basal species occurs, but the dominant species often increase habitat complexity through their body structures, thus favouring the occurrence of many secondary species, resulting in the richness/diversity peak in the model. At lower stress levels, the increasing consumer pressure (from herbivores and/or carnivores) prevents competitive exclusions, thus allowing for more basal species to coexist, but decreasing overall richness and diversity because of the loss in biogenic habitat complexity. At the lowest stress level for the regional biota in question, consumer pressure is greatest, resulting in the loss

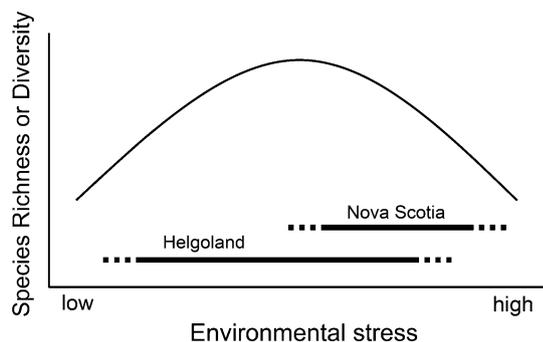


Fig. 1 Model predicting overall species richness and diversity in local communities across the full range of environmental stress across which a regional biota can occur (see the “Introduction” for a rationale). The horizontal lines for northern Nova Scotia and Helgoland indicate the approximate stress range occurring on those two coasts relative to the full stress range across which the cold-temperate biotas from the NW Atlantic and NE Atlantic, respectively, can occur. On each coast, high stress is expected at high intertidal elevations, whereas low stress is expected at low elevations. The dotted sections of each line indicate the possible variation among local shores

of a number of basal species and even of some consumer species, driving overall richness and diversity to another minimum (Menge and Sutherland 1987; Bruno et al. 2003). The unimodal richness curve for basal species between intermediate and high stress levels is also known as the intermediate disturbance hypothesis (see Menge and Sutherland 1987). An alternative version of the ESM considers that competitive exclusions among basal species may not happen at intermediate stress levels, as niche diversification leading to species coexistence may also occur (Menge and Sutherland 1987); nonetheless, total richness and diversity are still predicted to peak at intermediate stress levels, because neither consumer pressure nor abiotic stress is too great at such levels.

Despite the intended universality of the ESM, field tests of its predictions on overall richness and diversity are rare. The ideal approach would be to measure both traits in local communities covering the full stress range for a regional biota, but this is difficult to achieve for logistic reasons. Thus, most studies documenting diversity across stress gradients surveyed only selected taxonomic groups or restricted stress ranges (Locke 1996; Townsend et al. 1997; Hacker and Bertness 1999; Ohlemüller and Wilson 2000; Attrill and Rundle 2002; Chiba 2007; Lepori and Malmqvist 2009). However, knowing trends for some groups may not allow inference of community trends (Vellend 2008). A recent study tested ESM predictions by measuring richness and diversity across intertidal stress gradients in northern Nova Scotia (Canada) considering all benthic macroscopic species; overall richness and diversity increased from high to low elevations (Scrosati and Heaven 2007). In intertidal habitats, the abiotic stresses related to temperature, desiccation, irradiance, and osmotic potential increase sharply with elevation because of tides. Due to the high variation and extreme values occurring in those abiotic factors at the high intertidal zone, high elevations exhibit the most stressful conditions for intertidal biotas. Low elevations, because of their short periods of aerial exposure, offer more benign conditions (Raffaelli and Hawkins 1996). The study in Nova Scotia could not survey the entire stress gradient across which the cold-temperate rocky intertidal biota from the NW Atlantic can occur. High elevations in northern Nova Scotia adequately represent high stress, but low elevations represent only relatively intermediate stress levels for that biota because of harsh winter conditions (Bertness 2007; Scrosati and Eckersley 2007). Lower yearly levels of stress occur farther south (New England), particularly at the low intertidal zone. Thus, the negative relationship between richness/diversity and environmental stress found for Nova Scotia (Scrosati and Heaven 2007) is consistent with the ESM (Fig. 1). To test ESM predictions for lower stress ranges experienced by a regional biota, it is necessary to survey other shores.

The NE Atlantic coast also exhibits a cold-temperate intertidal biota, which extends between Norway and Spain (Lüning 1990). For this regional biota, high stress levels occur at the high intertidal zone because of its harsh conditions at low tide, the highest stress levels occurring at the northern and southern biogeographic boundaries because they represent extreme cold and heat stress for this biota, respectively. Low stress levels for this biota occur on shores between the two biogeographic boundaries, particularly at low elevations under moderate or low wave exposure (Menge and Branch 2001). The island of Helgoland, on the North Sea off the coast of Germany, lies in between those biogeographic boundaries, thus representing an adequate model system to test ESM predictions from high to low stress levels. Therefore, we used Helgoland's intertidal elevation gradient to test ESM predictions on richness and diversity. We hypothesized that species richness and diversity would follow a unimodal trend between low and high elevations in Helgoland (Fig. 1). Since evenness helps to explain potential differences between richness and diversity (Krebs 1999), we also measured the spatial trend for evenness across intertidal elevation.

Methods

Study sites

We studied the vertical trend in species richness, diversity, and evenness on 3 shores on the island of Helgoland (Fig. 2): Nord-Ost Hafen ($54^{\circ}11'00''\text{N}$, $7^{\circ}53'34''\text{E}$), Kringel ($54^{\circ}10'60''\text{N}$, $7^{\circ}53'15''\text{E}$), and Bunker ($54^{\circ}11'32''\text{N}$, $7^{\circ}52'35''\text{E}$). In situ measurements of maximum water velocity (an index of wave exposure) done with dynamometers (see design in Bell and Denny 1994) between September 2008 and July 2009 yielded values of $1.6 \pm 0.1 \text{ m s}^{-1}$ (mean \pm SE, $n = 22$, range = 0.8 – 2.8 m s^{-1}) for Nord-Ost Hafen, $2.0 \pm 0.2 \text{ m s}^{-1}$ ($n = 11$, range = 1.3 – 3.5 m s^{-1}) for Kringel, and $3.8 \pm 0.2 \text{ m s}^{-1}$

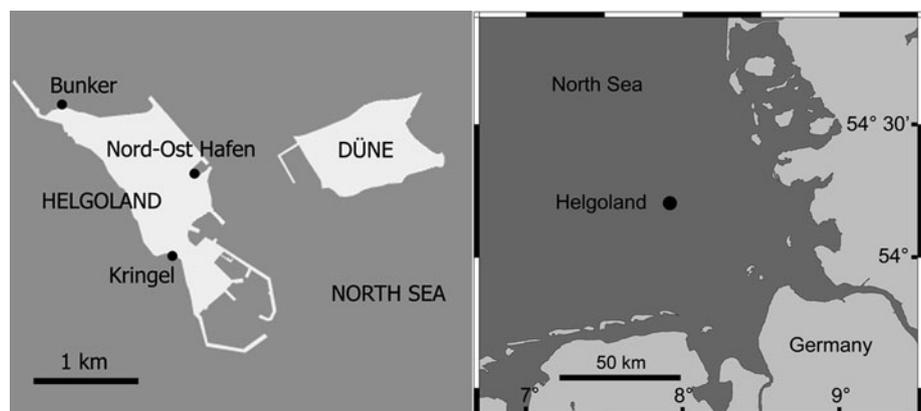
($n = 15$, range = 2.4 – 5.1 m s^{-1}) for Bunker. Since a preliminary statistical analysis did not detect significant differences in exposure between Nord-Ost Hafen and Kringel, we could not use those 3 shores to test ESM predictions across a horizontal (wave exposure) gradient as done for Nova Scotia (Scrosati and Heaven 2007).

Sampling design

We surveyed the vertical gradient of elevation on the 3 study shores between 0 m (chart datum) and an upper boundary determined using ecological indicators (the seaweed *Fucus spiralis*) to account for the fact that zones with similar emersion-related stresses are higher and wider as wave exposure increases (Harley and Helmuth 2003). This macroalga is the sessile, perennial species occurring highest on the 3 studied shores, which ensured that annual and seasonal wave regimes were integrated when determining upper intertidal boundaries using this indicator. Once we determined the upper boundary for each shore, we divided the intertidal range in three zones of equal vertical extent (high, middle, and low zones). Using a theodolite with a precision of 1 cm, we determined the upper boundary and those between zones, marking them with screws bolted to the rocky substrate. The upper boundary was 2.0 m at Nord-Ost Hafen, 1.8 m at Kringel, and 2.3 m at Bunker. Based on our wave exposure values, the upper intertidal boundary was slightly lower than expected at Kringel. This was probably so because, at the time of our study, construction above the intertidal zone was taking place there, which involved the placement of large concrete structures (tetrapods) that seem to have disturbed the uppermost intertidal reaches, apparently creating new substrate that had not yet been colonized.

On each shore, we randomly established 3 sites, which were separated 5–10 m from one another following the coastline. At each site, we delimited the position of 2 transect lines that ran from high to low elevations. In July–August 2008, we determined species richness, diversity,

Fig. 2 Map of the island of Helgoland, off the coast of Germany on the North Sea, showing the location of the 3 studied shores



and evenness for 3 quadrats (25 cm × 25 cm) that we randomly placed along each transect within each intertidal zone, avoiding the use of contiguous quadrats. Thus, we sampled 18 quadrats at each intertidal zone on each shore ($n = 162$ quadrats in total). We avoided sampling tide pools, large crevices, and steep inclines for consistency. At each quadrat, we identified all seaweeds and invertebrates (>1 mm) using field guides (Luther 1987; Janke and Kremer 1988, 2003; Kornmann and Sahling 1977, 1994) and taxonomic keys (Maggs and Hommersand 1993; Hayward and Ryland 1995). We identified most taxa to the species level, but a few taxa remained doubtful because of their small size or phenotypic overlap with similar species, even after laboratory observations under a stereomicroscope (50× magnification). For those cases, we made identifications to the lowest possible taxonomic level, as done in other field studies identifying all seaweeds and invertebrates (Kimbrow and Grosholz 2006; Russell et al. 2006; Thompson et al. 2007; Konar et al. 2009; Valdivia and Molis 2009). For each quadrat, we measured the percent cover of each species using a 25 cm × 25 cm metallic frame divided in 100 equal sections with monofilament line. We chose percent cover to quantify abundance because alternative measures (e.g., density of individuals) cannot always be determined reliably for clonal organisms (Scrosati 2005) or (e.g., biomass) would have implied destructive sampling of numerous shore areas. When an abundant algal canopy occurred, we first measured all canopy species and, then, we carefully moved the canopy away to sample understory species. Due to the multilayered structure of these assemblages, cover values did not necessarily represent use of primary substrate and total percent cover could exceed 100%. When percent cover was less than 1% for a given species, we recorded it as 0.5%.

We calculated species richness, diversity, and evenness for each quadrat. Richness (S) was the total number of species identified in the quadrat. We measured diversity using 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 (proportions were calculated using percent cover data). Simpson's diversity index ranges between 0 and almost 1 ($1 - S^{-1}$), is robust, and has a low bias toward the abundance distribution and sample size (Krebs 1999). We calculated evenness using Simpson's evenness index:

$$E_{1/D} = (DS)^{-1}.$$

Simpson's evenness index ranges between 0 and 1 and is relatively unaffected by the rare species in the quadrat and by spatial distribution (Krebs 1999; Payne et al. 2005).

Data analysis

We tested the effects of intertidal elevation on species richness, diversity, and evenness through nested analyses of variance done separately for each dependent variable (Underwood 1997). The factors were intertidal elevation (fixed, with 3 levels: low, middle, and high), shore (fixed, with 3 levels: Nord-Ost Hafen, Kringel, and Bunker), site (random) nested within shore, and transect (random) nested within site. We tested the normality and homoscedasticity assumptions using normal probability plots and Levene's tests, respectively, accepting the assumptions in all cases. When an ANOVA revealed significant main effects for elevation or shore, we compared factor levels using Tukey HSD tests. When the interaction between elevation and shore was significant, we tested for simple effects (effects of elevation at each shore and effects of shore at each elevation) by performing one-way ANOVAs followed by Tukey HSD tests. We did the analyses using *R* software (R Development Core Team 2008).

Results

Richness

We identified 62 taxa (29 seaweeds and 33 invertebrates) among the 3 shores (Table 1). Species richness varied across intertidal elevation (Table 2). Combining the 3 shores, richness was lower at the high than at the middle and low intertidal zones ($P < 0.001$), without differing between the middle and low zones ($P = 0.429$; Fig. 3a). Richness also varied among the shores (Table 2). Combining the 3 elevations, richness was lower at Kringel than at Nord-Ost Hafen and Bunker ($P < 0.001$) and lower at Bunker than at Nord-Ost Hafen ($P = 0.007$; Fig. 3b). The elevation × shore interaction was not significant (Table 2), meaning that the vertical trend in richness was similar for all shores.

Diversity

Species diversity varied across elevation (Table 2). Combining the 3 shores, diversity was similar between the high and middle intertidal zones ($P = 0.867$) and between the high and low zones ($P = 0.092$), but lower at the middle than at the low zone ($P = 0.027$; Fig. 4a). Diversity also varied among shores (Table 2). Combining the 3 elevations, diversity was higher at Nord-Ost Hafen than at Kringel ($P < 0.001$) and Bunker ($P < 0.001$) and similar between Kringel and Bunker ($P = 0.110$; Fig. 4b). The elevation × shore interaction was significant (Table 2). Diversity differed among elevations for Nord-Ost Hafen

Table 1 Abundance of taxa (mean percent cover \pm SE, $n = 18$ quadrats) at each elevation zone on each studied shore in Helgoland

Taxon	Nord-Ost Hafen			Kringel			Bunker		
	Low	Middle	High	Low	Middle	High	Low	Middle	High
Seaweeds									
<i>Blidingia</i> spp.	0.67 \pm 0.67	3.61 \pm 1.20	12.11 \pm 4.00	0.17 \pm 0.17	1.06 \pm 0.38	22.11 \pm 4.55			18.11 \pm 5.18
<i>Ceramium virgatum</i>	0.25 \pm 0.13								
<i>Chaetomorpha melangonium</i>	2.69 \pm 0.67	0.67 \pm 0.27		0.28 \pm 0.17					
<i>Chondrus crispus</i>	3.39 \pm 1.16			13.78 \pm 4.03	0.06 \pm 0.06		4.97 \pm 2.28	0.06 \pm 0.06	
<i>Cladophora rupestris</i>	13.72 \pm 3.42	3.19 \pm 1.41		2.92 \pm 1.50	0.25 \pm 0.12		1.22 \pm 0.43	0.58 \pm 0.16	1.11 \pm 0.59
<i>Cladostephus spongiosus</i>	0.33 \pm 0.33								
<i>Corallina officinalis</i>							0.33 \pm 0.18		
<i>Cystoclonium purpureum</i>	0.11 \pm 0.11								
<i>Dumontia contorta</i>				0.11 \pm 0.11					
<i>Elachista fucicola</i>	1.81 \pm 0.82	0.86 \pm 0.50	0.03 \pm 0.03	0.06 \pm 0.06	0.81 \pm 0.43	0.31 \pm 0.23	0.31 \pm 0.28	0.17 \pm 0.08	
Filamentous red alga	0.50 \pm 0.44				0.06 \pm 0.06		0.17 \pm 0.11		
<i>Fucus</i> sp.	0.50 \pm 0.35	0.39 \pm 0.24		0.06 \pm 0.06	2.39 \pm 1.07	1.22 \pm 0.78	0.17 \pm 0.11	0.72 \pm 0.67	
<i>Fucus serratus</i>	70.78 \pm 5.84	30.00 \pm 8.89		9.11 \pm 4.17	25.39 \pm 7.39	1.33 \pm 1.33	6.11 \pm 4.19	3.56 \pm 2.60	39.33 \pm 10.07
<i>Fucus spiralis</i>			0.44 \pm 0.44	1.33 \pm 1.33	82.50 \pm 4.91	77.33 \pm 7.12			50.67 \pm 9.92
<i>Fucus vesiculosus</i>		8.72 \pm 5.83	11.00 \pm 4.10		0.89 \pm 0.89	0.44 \pm 0.44		11.94 \pm 3.73	18.22 \pm 6.20
<i>Hildenbrandia rubra</i>	0.22 \pm 0.17	0.06 \pm 0.06	0.06 \pm 0.06	0.17 \pm 0.08	0.25 \pm 0.09	1.78 \pm 0.35	0.69 \pm 0.23	1.33 \pm 0.39	6.39 \pm 1.30
<i>Laminaria</i> sp.	0.06 \pm 0.06								
<i>Laminaria digitata</i>	1.22 \pm 0.87								
<i>Mastocarpus stellatus</i>	33.67 \pm 5.38	89.22 \pm 5.02	42.17 \pm 6.00	52.00 \pm 7.34	35.56 \pm 5.93	3.22 \pm 1.27	55.17 \pm 6.22	89.50 \pm 3.44	12.50 \pm 2.01
<i>Membranoptera alata</i>	0.06 \pm 0.06	0.03 \pm 0.03							
<i>Phymatolithon</i> sp.	4.17 \pm 1.15	1.17 \pm 0.30	0.08 \pm 0.06	0.67 \pm 0.25	0.14 \pm 0.11	0.11 \pm 0.11	8.61 \pm 1.80	6.89 \pm 1.84	7.83 \pm 1.94
<i>Plumaria elegans</i>	0.06 \pm 0.06								
<i>Porphyra</i> sp.	0.06 \pm 0.06	0.19 \pm 0.12	4.61 \pm 2.59	1.44 \pm 0.89	0.06 \pm 0.06	1.36 \pm 0.66			
<i>Ralfsia</i> sp.		0.17 \pm 0.08	9.36 \pm 1.65	3.75 \pm 1.33	1.44 \pm 0.45		0.78 \pm 0.42	0.22 \pm 0.09	1.25 \pm 0.79
Red alga	0.17 \pm 0.17								
<i>Rhodothamniella floridula</i>	3.89 \pm 0.93	0.53 \pm 0.39		0.03 \pm 0.03	0.08 \pm 0.06				0.33 \pm 0.24
<i>Ulva</i> sp. 1	6.75 \pm 1.64	11.94 \pm 4.46	1.67 \pm 0.68	7.31 \pm 4.09	0.03 \pm 0.03	0.08 \pm 0.06	0.17 \pm 0.07	0.17 \pm 0.06	0.03 \pm 0.03
<i>Ulva</i> sp. 3	2.83 \pm 1.54	0.67 \pm 0.32		4.22 \pm 2.92		0.22 \pm 0.22	0.81 \pm 0.78		
<i>Ulva</i> sp. 3	0.03 \pm 0.03	0.33 \pm 0.06	0.42 \pm 0.05	0.08 \pm 0.06	0.19 \pm 0.08	0.22 \pm 0.12			0.03 \pm 0.03
Invertebrates									
<i>Actinia equina</i>				0.06 \pm 0.06	0.19 \pm 0.08	0.11 \pm 0.11			
Amphipoda	1.78 \pm 0.24	0.33 \pm 0.06	0.42 \pm 0.05	0.03 \pm 0.03	0.19 \pm 0.08	0.11 \pm 0.05	0.03 \pm 0.03	0.28 \pm 0.06	0.56 \pm 0.08

Table 1 continued

Taxon	Nord-Ost Hafen			Kringel			Bunker		
	Low	Middle	High	Low	Middle	High	Low	Middle	High
Anemone		0.03 ± 0.03							
<i>Anurida maritima</i>						0.08 ± 0.05			
<i>Balanus balanus</i>	1.78 ± 0.24	0.86 ± 0.43					0.33 ± 0.17		
<i>Balanus crenatus</i>							0.03 ± 0.03		
<i>Balanus improvisus</i>	0.81 ± 0.16	1.25 ± 0.28		0.06 ± 0.06	0.67 ± 0.36		0.64 ± 0.12	0.28 ± 0.08	
<i>Carcinus maenas</i>	0.61 ± 0.09	1.47 ± 0.17	0.17 ± 0.08	0.97 ± 0.22	0.89 ± 0.20	0.14 ± 0.08	0.61 ± 0.09	0.53 ± 0.08	0.42 ± 0.18
<i>Crassostrea gigas</i>		1.25 ± 0.51	0.19 ± 0.09	0.22 ± 0.22			0.36 ± 0.24	1.56 ± 0.50	
<i>Cryptosula pallasiana</i>	0.33 ± 0.20	0.58 ± 0.20	0.06 ± 0.06				0.31 ± 0.18	0.22 ± 0.22	
<i>Dynamena pumila</i>	1.14 ± 0.37	1.72 ± 0.43	0.14 ± 0.05	0.28 ± 0.13	0.61 ± 0.29		1.72 ± 0.38	1.11 ± 0.34	0.17 ± 0.07
<i>Electra pilosa</i>	3.22 ± 1.14	0.64 ± 0.14	0.03 ± 0.03	0.22 ± 0.10			0.22 ± 0.07	0.08 ± 0.05	
<i>Elminius modestus</i>	0.33 ± 0.13	1.11 ± 0.23	1.83 ± 0.29	0.17 ± 0.07	0.94 ± 0.54	0.17 ± 0.07	0.36 ± 0.10	0.39 ± 0.10	0.31 ± 0.09
<i>Flustrellidra hispida</i>	9.50 ± 1.05	16.67 ± 1.69	0.53 ± 0.28				0.14 ± 0.08		
<i>Gibbula cineraria</i>							0.22 ± 0.12	0.03 ± 0.03	
<i>Hemigrapsus</i> sp.			0.03 ± 0.03						
Hydrozoa	0.08 ± 0.06	0.39 ± 0.22		0.03 ± 0.03			0.58 ± 0.50	0.11 ± 0.06	
Isopoda	0.14 ± 0.05	0.17 ± 0.06	0.22 ± 0.06	0.03 ± 0.03	0.19 ± 0.06	0.19 ± 0.07	0.22 ± 0.06	0.22 ± 0.07	0.39 ± 0.06
<i>Janua pagenstecheri</i>	0.86 ± 0.14	2.08 ± 0.32	0.08 ± 0.05				1.44 ± 0.28	0.75 ± 0.16	
<i>Laomedea flexuosa</i>	0.03 ± 0.03	0.31 ± 0.08	0.08 ± 0.05	0.36 ± 0.10	0.69 ± 0.24		0.36 ± 0.09	0.58 ± 0.07	0.14 ± 0.05
<i>Littorina litorea</i>	0.28 ± 0.12	0.28 ± 0.13	0.33 ± 0.14	8.89 ± 3.09	0.39 ± 0.28		2.31 ± 0.58	5.00 ± 0.82	0.56 ± 0.39
<i>Littorina obtusata</i>	0.50 ± 0.13	0.58 ± 0.09	0.50 ± 0.17	0.47 ± 0.09	0.81 ± 0.15	0.17 ± 0.06	0.61 ± 0.12	0.75 ± 0.14	0.75 ± 0.17
<i>Littorina saxatilis</i>		0.11 ± 0.05	0.31 ± 0.08	0.06 ± 0.04	0.08 ± 0.05	0.08 ± 0.05	0.08 ± 0.05	0.08 ± 0.05	0.03 ± 0.03
<i>Mytilus edulis</i>	0.19 ± 0.08	0.72 ± 0.16	0.17 ± 0.07	0.03 ± 0.03			0.17 ± 0.07	0.42 ± 0.08	0.17 ± 0.09
<i>Pilumnus hirtellus</i>		0.03 ± 0.03							
<i>Pomatoceros triqueter</i>	0.03 ± 0.03						0.03 ± 0.03		
<i>Sargatia</i> sp.				0.17 ± 0.07	0.89 ± 0.23	0.17 ± 0.08	0.06 ± 0.04	0.06 ± 0.04	0.03 ± 0.03
<i>Sargatiogeton</i> sp.				0.33 ± 0.07	1.00 ± 0.17	0.08 ± 0.06	0.14 ± 0.05	0.14 ± 0.07	0.06 ± 0.04
<i>Semibalanus balanoides</i>	0.83 ± 0.20	11.33 ± 1.75	8.11 ± 1.40	0.31 ± 0.09	1.25 ± 0.59	1.08 ± 0.41	3.08 ± 0.75	7.17 ± 1.74	7.11 ± 2.09
Spionidae				0.14 ± 0.05	0.19 ± 0.06		0.11 ± 0.05	0.11 ± 0.05	0.03 ± 0.03
<i>Spirorbis spirorbis</i>	0.14 ± 0.08						0.06 ± 0.06		
<i>Verruca stroemia</i>	10.61 ± 2.45			0.03 ± 0.03					
Worms		0.03 ± 0.03		0.08 ± 0.06			0.03 ± 0.03		0.06 ± 0.06

Blanks represent zero abundance

Table 2 Summary table for the nested ANOVAs done for species richness, diversity, and evenness

Source of variation	df	MS	F	P
Richness				
Elevation	2	11.16	42.95	4×10^{-11}
Shore	2	8.67	64.13	10^{-7}
Elevation \times shore	4	0.57	2.20	0.084
Site (shore)	15	0.15	1.13	0.337
Transect (site (shore))	9	0.12	0.92	0.510
Site (shore) \times elevation	30	0.31	2.32	0.001
Transect (site (shore)) \times elevation	12	0.21	1.53	0.092
Error	108	0.14		
Diversity				
Elevation	2	0.07	3.52	0.042
Shore	2	0.57	33.53	10^{-4}
Elevation \times shore	4	0.15	7.89	2×10^{-4}
Site (shore)	15	0.03	1.62	0.080
Transect (site (shore))	9	0.02	1.15	0.336
Site (shore) \times elevation	30	0.02	1.09	0.360
Transect (site (shore)) \times elevation	12	0.02	0.93	0.520
Error	108	0.02		
Evenness				
Elevation	2	3.96	21.16	3×10^{-7}
Shore	2	0.89	8.46	4×10^{-4}
Elevation \times shore	4	0.24	1.26	0.299
Site (shore)	15	0.12	1.14	0.330
Transect (site (shore))	9	0.13	1.27	0.263
Site (shore) \times elevation	30	0.22	2.11	0.003
Transect (site (shore)) \times elevation	12	0.15	1.47	0.114
Error	108	0.11		

($F_{2,159} = 8.83$, $P < 0.001$), Kringel ($F_{2,159} = 4.92$, $P = 0.011$), and Bunker ($F_{2,159} = 6.91$, $P = 0.002$; Fig. 4c). At Nord-Ost Hafen, diversity was higher at the low than at the high and middle intertidal zones ($P = 0.002$) and similar between the middle and high zones ($P = 0.996$). At Kringel, diversity was lower at the high than at the middle ($P = 0.019$) and low zones ($P = 0.031$) and similar between the middle and low zones ($P = 0.982$). At Bunker, diversity was lower at the middle than at the high zone ($P = 0.002$) and similar between the high and low zones ($P = 0.077$) and middle and low zones ($P = 0.313$). Diversity also varied among the 3 shores when analyzed separately for high ($F_{2,159} = 17.15$, $P < 0.001$), middle ($F_{2,159} = 8.29$, $P < 0.001$), and low elevations ($F_{2,159} = 21.86$, $P < 0.001$; Fig. 4c). At the high intertidal zone, diversity was lower at Kringel than at Nord-Ost Hafen ($P < 0.001$) and Bunker ($P < 0.001$) and similar between Nord-Ost Hafen and Bunker ($P = 0.975$). At the middle intertidal zone, diversity was lower at

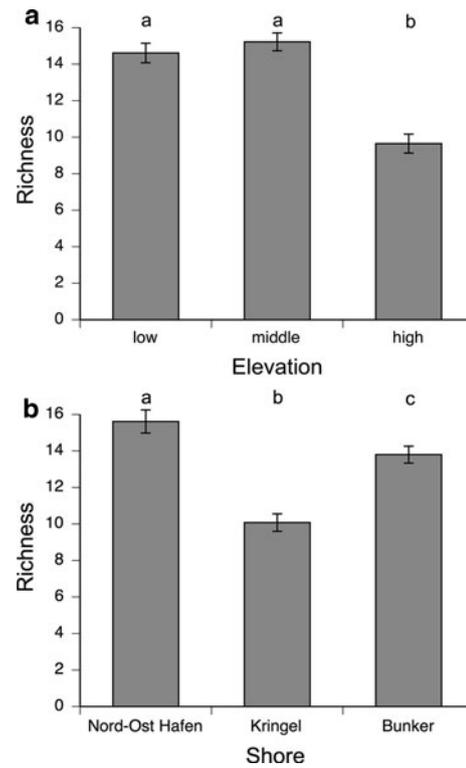


Fig. 3 Trends in species richness (mean \pm SE) across **a** intertidal elevation (with data for the 3 shores combined; main effects) and **b** the 3 studied shores (with data for the 3 elevations combined; main effects). In each graph, significant differences between means are indicated by different letters (see “Results” for P values). The elevation \times shore interaction was not significant (Table 2), so no simple effects were calculated

Bunker than at Nord-Ost Hafen ($P < 0.001$) and similar between Kringel and Bunker ($P = 0.182$) and Kringel and Nord-Ost Hafen ($P = 0.069$). At the low intertidal zone, diversity was higher at Nord-Ost Hafen than at Kringel ($P < 0.001$) and Bunker ($P < 0.001$) and similar between Kringel and Bunker ($P = 0.999$).

Evenness

Species evenness varied across elevation (Table 2). Combining the 3 shores, evenness was higher at the high than at the middle and low intertidal zones ($P < 0.001$) and lower at the middle than at the low zone ($P = 0.004$; Fig. 5a). Evenness also varied among the 3 shores (Table 2). Combining the 3 elevations, evenness was lower at Bunker than at Nord-Ost Hafen and Kringel ($P = 0.002$) and similar between Nord-Ost Hafen and Kringel ($P = 0.999$; Fig. 5b). The elevation \times shore interaction was not significant (Table 2), meaning that the vertical trend in evenness was similar for all shores.

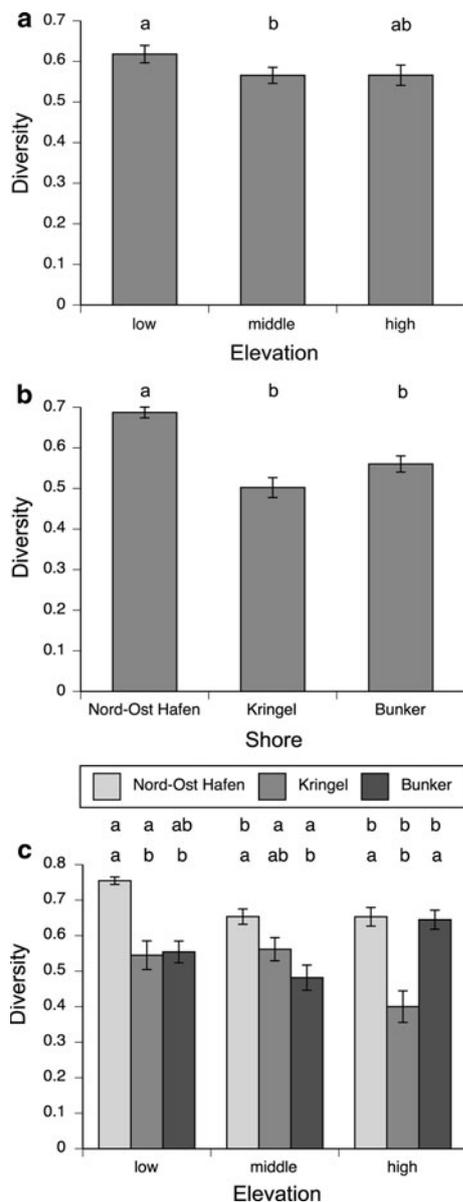


Fig. 4 Trends in species diversity (mean \pm SE) across **a** intertidal elevation (with data for the 3 shores combined; main effects), **b** the 3 studied shores (with data for the 3 elevations combined; main effects), and **c** across elevation separately for each shore (simple effects). In graphs **a** and **b**, significant differences between means are indicated by *different letters* (see “Results” for *P* values). In graph **c**, the upper row of *letters* compares means for elevations separately for each shore, while the lower row compares means for shores separately for each elevation (see “Results” for *P* values)

Discussion

Our study covered a large proportion of the types of rocky intertidal habitats on Helgoland Island. Only the open west coast could not be surveyed, because it was off limits for research during our fieldwork. The west coast faces the North Sea directly, so it is subjected to a higher degree of wave exposure than our studied shores. Other surveys of

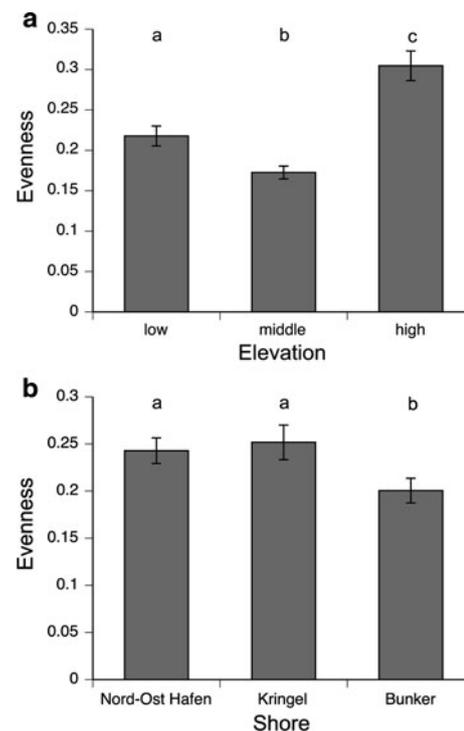


Fig. 5 Trends in species evenness (mean \pm SE) across **a** intertidal elevation (with data for the 3 shores combined; main effects) and the 3 studied shores (with data for the 3 elevations combined; main effects). In each graph, significant differences between means are indicated by *different letters* (see Results for *P* values). The elevation \times shore interaction was not significant (Table 2), so no simple effects were calculated

rocky intertidal species richness have been conducted recently on Helgoland shores (Reichert et al. 2008; Valdivia and Molis 2009), but they did not sample the entire intertidal range. Our data covering the full intertidal range indicate that neither overall richness nor diversity followed the predicted unimodal trend across elevation. Support for ESM predictions was only partial, since richness did increase from high to middle elevations but remained similar between middle and low elevations. The predicted increase in diversity from high to middle elevations only occurred at Kringel, with the opposite trend occurring at Bunker and no significant change at Nord-Ost Hafen. From middle to low elevations, diversity remained similar at Kringel and Bunker and increased at Nord-Ost Hafen. Hereafter, we discuss our findings with the goal of improving the understanding and testing of the ESM.

An important issue to consider is the domain of application of the ESM. The unimodal curve for overall richness and diversity (Scrosati and Heaven 2007) and the curves for the underlying interspecific interactions (Bruno et al. 2003) apply to the full stress gradient across which a regional biota can occur. Thus, the presence of species of other biotas might render the ESM unable to make accurate

predictions. For example, communities in transition areas between two contiguous biotas share species to some extent (Kent et al. 1997; Attrill and Rundle 2002; Gastner et al. 2009). In rocky intertidal habitats, high elevations are often only occupied by truly intertidal species, which decrease in richness toward the upper intertidal boundary without sharing the substrate with the terrestrial species (e.g., vascular plants) that occur above (Raffaelli and Hawkins 1996). Thus, ESM predictions (low richness and diversity, and abiotic stress determining dynamics) are often met at the high intertidal zone (Bertness et al. 1999, 2006; Russell et al. 2006; Scrosati and Heaven 2007; Petes et al. 2008). In contrast, because of its limited aerial exposure, the low intertidal zone includes some species that primarily belong to subtidal biotas. Thus, the overlap of intertidal and subtidal biotas at low elevations might not allow ESM predictions to apply there. It is worth noting that the few studies that have quantified overall benthic richness (primary producers plus consumers) across the full intertidal range have found that richness increases from high to low elevations. This trend has been found for southern South America (Ingólfsson 2005), the central E Pacific (Lubchenco et al. 1984), NE Pacific (Ingólfsson 2005; Konar et al. 2009), NW Atlantic (Scrosati and Heaven 2007), N Atlantic (Ingólfsson 2005), and NE Atlantic (this study). Whether this pattern is universal for rocky intertidal systems remains unknown, but it suggests that the ESM might not be a good predictive tool for transition zones between biotas.

We initially evaluated removing from analyses the species appearing to be mostly subtidal (those occurring only at low elevations; Table 1), although that was an estimate because the full vertical distribution (elevation and depth) is unknown for many of such species. In any case, a quick analysis following that routine did reveal a unimodal trend for “intertidal” richness for Nord-Ost Hafen (with a total of 33, 40, and 28 species at low, middle, and high elevations, respectively) and Bunker (30, 33, 29), but Kringel retained the original trend (32, 31, 25). However, even when the corrected richness decreased at low elevations, it is unclear whether that resulted from effects of the “subtidal” species that were in the quadrats but were ignored, or whether it truly resulted from the interaction between the environment and the “intertidal” species as predicted by the ESM (Bruno et al. 2003). The ideal test of ESM predictions using low elevations would experimentally exclude the predominantly subtidal species and then assess richness once the community readjusts. ESM predictions on richness have been tested through mensurative approaches in other aquatic systems, such as lakes (Locke 1996). Although only zooplankton species were assessed, that study found a weak unimodal richness trend across a stress gradient determined by pH changes. Overlap of

different biotas seemed not to occur in those lakes, suggesting that ESM-predicted richness patterns might indeed occur when communities from the same regional species pool are considered.

Another issue to consider relates to the interspecific interactions behind the predicted patterns in richness and diversity (summarized in the Introduction). Is there evidence in our data that interspecific interactions changed in importance across elevation as predicted by the ESM (Bruno et al. 2003)? The success or failure to find such evidence may give clues as to what aspects may be relevant to understanding our results in relation to the ESM. For example, the red alga *Mastocarpus stellatus* was the dominant basal species at middle elevations at Nord-Ost Hafen (reaching 90% cover), suggesting that this species may be competitively dominant there. This would agree with the predictions made by the ESM for intermediate stress levels (Bruno et al. 2003). The morphologically complex thallus of this alga (Dudgeon and Johnson 1992) might attract a number of small species that would otherwise be absent, resulting in total richness peaking at middle elevations, as the ESM predicted (Fig. 1). Our richness data did not show such a peak, but species size may have influenced this outcome. Because of constraints in logistics and taxonomic expertise, we restricted observations to organisms larger than 1 mm. Thus, if very small species were in fact drawn to middle elevations by *M. stellatus*, our sampling approach might have missed them, potentially explaining the lack of a unimodal pattern for our richness data. This type of limitation is a universal problem affecting intertidal diversity studies (Kimbrow and Grosholz 2006; Russell et al. 2006; Thompson et al. 2007; Konar et al. 2009; Valdivia and Molis 2009). In fact, we know of no community study, aquatic or terrestrial, that has not suffered from this drawback. Increased efforts to identify even the smallest species might thus improve the accuracy of trend determination in ESM research. The above discussion must not be taken, however, as an indication that ESM-predicted patterns in richness did occur in Helgoland but our surveys failed to detect them. For example, at Bunker, the combined cover of all morphologically complex algae (*M. stellatus* and *Fucus* spp.) actually peaked at high elevations. Then, were these algae promoting a high occurrence of very small species there, total richness would still not follow a unimodal pattern.

Another prediction of the ESM on interspecific interactions is that consumers should play larger roles as stress decreases (Bruno et al. 2003). Is there evidence in our data suggesting that consumer pressure may have been particularly strong at low elevations? Percent cover data (as well as other abundance measures, such as density and biomass) may not be accurate indicators of consumer pressure, but offer information for a basic analysis. On Helgoland rocky

shores, periwinkles (*Littorina* spp.) and green crabs (*Carcinus maenas*) are important consumers (Janke 1990; Eschweiler et al. 2009). The most abundant periwinkles, *Littorina littorea* and *L. obtusata*, feed readily on the green algae *Ulva* spp. (Janke 1990) and on the brown algae *Fucus* spp. (Watson and Norton 1981), respectively, while the mussel *Mytilus edulis* is a preferred food item for *C. maenas* (Ropes 1968). From middle to low elevations on our studied shores, the abundance of these consumers generally remained similar or decreased (Table 1). In the only case in which it clearly increased (*L. littorea* at Kringel), the abundance of its preferred food (*Ulva* spp.) also increased toward low elevations. These observations suggest that consumer pressure may not be particularly strong at the low intertidal zone relative to higher elevations. Field experiments should be done to confirm this notion, which may also contribute to explaining why overall richness and diversity did not decrease from middle to low elevations, as the ESM had predicted.

An alternative possible explanation for ESM-predicted patterns in richness and diversity not occurring in Helgoland relates to the extent of the intertidal range. For example, the change from stress being the main factor structuring communities, to species coexistence and higher richness of basal species, to competitive exclusions among basal species, to predation disrupting such exclusions occurs from high elevations down the intertidal zone on the Pacific coast of North America (Paine 1974; Kim 1997; Robles et al. 2009), where tidal ranges reach 4–5 m. On shores with smaller tidal ranges (e.g., ~2 m in Helgoland) and a similar slope, the size and/or mobility of organisms might complicate the detection, or even the occurrence, of horizontal zones representing the ecological stages described above and, consequently, changes in total richness (which have not been quantified for western North America). We suggest that ESM-predicted patterns might become increasingly evident with increasing intertidal range.

A possible solution to working on shores with a limited intertidal range might be to increase the spatial resolution of sampling. For example, on each Helgoland shore, we sampled the full intertidal range between chart datum and the upper intertidal boundary. However, we combined data for quadrats from the lower, middle, and upper thirds of the range to describe average richness and diversity for the low, middle, and high intertidal zones. This is a common approach in intertidal ecology, allowing researchers to identify broad patterns (Menge and Branch 2001; Konar et al. 2009). As discussed above, our tests did not find a unimodal richness/diversity pattern across elevation. Thus, if full ESM-predicted patterns did occur on a shore with a limited intertidal range, sampling at a higher resolution might reveal them. For example, an intertidal range of 2 m could be divided in 8 elevation zones of 25 cm in vertical

extent each, which could be sampled with 25 cm × 25 cm quadrats. This approach would require sampling almost 3 times more quadrats than a classic 3-zone study to maintain the same sampling effort at each zone. Nonetheless, future ESM tests might profit from following this approach.

A final consideration is due regarding the trends followed by richness and diversity in Helgoland. Both traits showed the same pattern across elevation at Kringel, but differences existed at Nord-Ost Hafen and Bunker. A similar situation occurred across the shores, as richness was lower at Kringel than on the other 2 shores, but diversity was similar in Kringel and Bunker. Logically, these differences were explained by evenness trends (Krebs 1999). Richness and diversity have been considered virtually as synonyms in many biodiversity studies (Whittaker et al. 2001, Wilsey et al. 2005, Stachowicz et al. 2007), but both traits may differ in spatial (or temporal) pattern mediated by evenness (Badano et al. 2002; Kimbro and Grosholz 2006; Scrosati and Heaven 2007; Wilsey and Stirling 2007). Since both richness and diversity help to understand community functioning, predicting how they vary with stress is thus important. Therefore, future ESM studies should quantify richness, diversity, and evenness simultaneously to facilitate ecological synthesis.

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References

- Attrill MJ, Rundle SD (2002) Ecotone or ecocline: ecological boundaries in estuaries. *Estuar Coast Shelf Sci* 55:929–936
- Badano EI, Molina-Montenegro MA, Quiroz C, Cavieres LA (2002) Effects of the cushion plant *Oreopolus glacialis* (Rubiaceae) on species richness and diversity in a high-Andean plant community of central Chile. *Rev Chil Hist Nat* 75:757–765
- Bell EC, Denny MW (1994) Quantifying “wave exposure”: a simple device for recording maximum velocity and results of its use at several field sites. *J Exp Mar Biol Ecol* 181:9–29
- Bertness MD (2007) Atlantic shorelines. Natural history and ecology. Princeton University Press, Princeton
- Bertness MD, Leonard GH, Levine JM, Schmidt PR, Ingraham AO (1999) Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology* 80:2711–2726
- Bertness MD, Crain CM, Silliman BR, Bazterrica MC, Reyna MV, Hidalgo F, Kongo Farina J (2006) The community structure of western Atlantic Patagonian rocky shores. *Ecol Monogr* 76:439–460
- Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. *Trends Ecol Evol* 18:119–125
- Chiba S (2007) Species richness patterns along environmental gradients in island land molluscan fauna. *Ecology* 88:1738–1746

- Crain CM, Bertness MD (2006) Ecosystem engineering across environmental gradients: implications for conservation and management. *Bioscience* 56:211–218
- Dudgeon SR, Johnson AS (1992) Thick vs. thin: thallus morphology and tissue mechanics influence differential drag and dislodgement of two co-dominant seaweeds. *J Exp Mar Biol Ecol* 165:23–43
- Eschweiler N, Molis M, Buschbaum C (2009) Habitat-specific size structure variations in periwinkle populations (*Littorina littorea*) caused by biotic factors. *Helgol Mar Res* 63:119–127
- Gamfeldt L, Hillebrand H (2008) Biodiversity effects on aquatic ecosystem functioning—Maturation of a new paradigm. *Internat Rev Hydrobiol* 93:550–564
- Gastner MT, Oborny B, Zimmermann DK, Pruessner G (2009) Transition from connected to fragmented vegetation across an environmental gradient: scaling laws in ecotone geometry. *Am Nat* 174:E23–E39
- Hacker SD, Bertness MD (1999) Experimental evidence for factors maintaining plant species diversity in a New England salt marsh. *Ecology* 80:2064–2073
- Harley CDG, Helmuth BST (2003) Local- and regional-scale effects of wave exposure, thermal stress, and absolute versus effective shore level on patterns of intertidal zonation. *Limnol Oceanogr* 48:1498–1508
- Hayward PJ, Ryland JS (1995) *Handbook of the marine fauna of north-west Europe*. Oxford University Press, New York
- Heaven CS, Scrosati RA (2008) Benthic community composition across gradients of intertidal elevation, wave exposure, and ice scour in Atlantic Canada. *Mar Ecol Prog Ser* 369:13–23
- Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* 75:3–35
- Ingólfsson A (2005) Community structure and zonation patterns of rocky shores at high latitudes: an interocean comparison. *J Biogeogr* 32:169–182
- Janke K (1990) Biological interactions and their role in community structure in the rocky intertidal of Helgoland (German Bight, North Sea). *Helgol Meeresunters* 44:219–263
- Janke K, Kremer BP (1988) *Düne, Strand und Wattenmeer: Tiere und Pflanzen unserer Küsten (Kosmos-Naturführer)*. Franckh'sche Verlagshandlung, Stuttgart
- Janke K, Kremer BP (2003) *Das Watt: alle Wichtigen Tiere und Pflanzen in ihren Lebensräumen (Kosmos-Naturführer)*. Franckh-Kosmos Verlag, Stuttgart
- Kent M, Gill WJ, Weaver RE, Armitage RP (1997) Landscape and plant community boundaries in biogeography. *Prog Phys Geog* 21:315–353
- Kim JH (1997) The role of herbivory, and direct and indirect interactions, in algal succession. *J Exp Mar Biol Ecol* 217:119–135
- Kimbro DL, Grosholz ED (2006) Disturbance influences oyster community richness and evenness, but not diversity. *Ecology* 87:2378–2388
- Konar B, Iken K, Edwards M (2009) Depth-stratified community zonation patterns on Gulf of Alaska rocky shores. *Mar Ecol* 30:63–73
- Korrmann P, Sahling PH (1977) Meeresalgen von Helgoland: benthische Grün-, Braun- und Rotalgen. *Helgol Meeresunters* 29:1–289
- Korrmann P, Sahling PH (1994) Meeresalgen von Helgoland: zweite Ergänzung. *Helgol Meeresunters* 48:365–406
- Krebs CJ (1999) *Ecological methodology*. Benjamin Cummings, Menlo Park
- Lepori F, Malmqvist B (2009) Deterministic control on community assembly peaks at intermediate levels of disturbance. *Oikos* 118:471–479
- Locke A (1996) Applications of the Menge–Sutherland model to acid-stressed lake communities. *Ecol Appl* 6:797–805
- Lubchenco J, Menge BA, Garrity SD, Lubchenco PJ, Ashkenas LR, Gaines SD, Emlet R, Lucas J, Strauss S (1984) Structure, persistence, and role of consumers in a tropical rocky intertidal community (Taboguilla Island, Bay of Panama). *J Exp Mar Biol Ecol* 78:23–73
- Lüning K (1990) *Seaweeds. Their environment, biogeography, and ecophysiology*. John Wiley, New York
- Luther G (1987) *Seepocken der deutschen Küstengewässer*. *Helgol Meeresunters* 41:1–43
- Maggs CA, Hommersand MH (1993) *Seaweeds of the British Isles: volume 1 Rhodophyta, part 3 A Ceramiales*. The Natural History Museum, London
- Menge BA, Branch GM (2001) Rocky intertidal communities. In: Bertness MD, Gaines SD, Hay ME (eds) *Marine community ecology*. Sinauer, Sunderland, pp 221–251
- Menge BA, Sutherland JP (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am Nat* 130:730–757
- Menge BA, Olson AM, Dahlhoff EP (2002) Environmental stress, bottom-up effects, and community dynamics: integrating molecular–physiological and ecological approaches. *Integ Comp Biol* 42:892–908
- Ohlemüller R, Wilson JB (2000) Vascular plant species richness across latitudinal and altitudinal gradients: a contribution from New Zealand temperate rainforests. *Ecol Lett* 3:262–266
- Paine RT (1974) Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15:93–120
- Payne LX, Schindler DE, Parrish JK, Temple SA (2005) Quantifying spatial pattern with evenness indices. *Ecol Appl* 15:507–520
- Petes LE, Mouchka ME, Milston-Clements RH, Momoda TS, Menge BA (2008) Effects of environmental stress on intertidal mussels and their sea star predators. *Oecologia* 156:671–680
- R Development Core Team (2008) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna
- Raffaelli D, Hawkins S (1996) *Intertidal ecology*. Chapman & Hall, London
- Reichert K, Buchholz F, Bartsch I, Kersten T, Giménez L (2008) Scale-dependent patterns of variability in species assemblages of the rocky intertidal at Helgoland (German Bight, North Sea). *J Mar Biol Assoc U K* 88:1319–1329
- Robles CD, Desharnais RA, Garza C, Donahue MJ, Martínez CA (2009) Complex equilibria in the maintenance of boundaries: experiments with mussel beds. *Ecology* 90:985–995
- Ropes JW (1968) The feeding habits of the green crab, *Carcinus maenas* (L.). *U S Fish Wildl Serv Fish Bull* 67:183–203
- Russell R, Wood SA, Allison G, Menge BA (2006) Scale, environment, and trophic status: the context dependency of community saturation in rocky intertidal communities. *Am Nat* 167:E158–E170
- Scrosati R (2005) Review of studies on biomass-density relationships (including self-thinning lines) in seaweeds: main contributions and persisting misconceptions. *Phycol Res* 53:224–233
- Scrosati R, Eckersley LK (2007) Thermal insulation of the intertidal zone by the ice foot. *J Sea Res* 58:331–334
- Scrosati R, Heaven C (2007) Spatial trends in community richness, diversity, and evenness across rocky intertidal environmental stress gradients in eastern Canada. *Mar Ecol Prog Ser* 342:1–14
- Stachowicz JJ, Bruno JF, Duffy JE (2007) Understanding the effects of marine biodiversity on communities and ecosystems. *Annu Rev Ecol Syst* 38:739–766
- Thompson RM, Hemberg M, Starzomski BM, Shurin JB (2007) Trophic levels and trophic tangles: the prevalence of omnivory in real food webs. *Ecology* 88:612–617

- Townsend CR, Scarsbrook MR, Dolédec S (1997) The intermediate disturbance hypothesis, refugia, and biodiversity in streams. *Limnol Oceanogr* 42:938–949
- Underwood AJ (1997) *Experiments in ecology*. Cambridge University Press, Cambridge
- Valdivia N, Molis M (2009) Observational evidence of a negative biodiversity–stability relationship in intertidal epibenthic communities. *Aquat Biol* 4:263–271
- Vellend M (2008) Effects of diversity on diversity: consequences of competition and facilitation. *Oikos* 117:1075–1085
- Watson DC, Norton TA (1981) The habitat and feeding preferences of *Littorina obtusata* (L.) and *L. mariaae* Sacchi et Rastelli. *J Exp Mar Biol Ecol* 112:61–72
- Whittaker RJ, Willis KJ, Field R (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *J Biogeogr* 28:453–470
- Wilsey B, Stirling G (2007) Species richness and evenness respond in a different manner to propagule density in developing prairie microcosm communities. *Plant Ecol* 190:259–273
- Wilsey BJ, Chalcraft DR, Bowles CM, Willig MR (2005) Relationships among indices suggest that richness is an incomplete surrogate for grassland biodiversity. *Ecology* 86:1178–1184