



# Observational evidence of a negative biodiversity–stability relationship in intertidal epibenthic communities

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**ABSTRACT:** The idea that diversity begets the functioning and stability of ecosystems has been intensely examined in terrestrial habitats, yet these relationships remain poorly studied in the marine realm. Theoretical and empirical work suggest that diversity enhances the stability of communities, but decreases the stability of populations. This is because compensatory dynamics, such as when one species decreases while another increases, stabilise the community as long as species richness increases the variety of responses to the environment. In an observational field study, the temporal variability in species abundance was used as a measure of stability that was compared among 5 intertidal sites of naturally different species richness. Percent coverage of macrobenthic species was estimated every 6 mo for 2 yr. Stability in total community coverage was a negative but curvilinear function of species richness. In addition, the stability of single populations (averaged over all species) fluctuated across the species richness gradient, without showing the predicted negative pattern. We found no evidence for increasing compensatory dynamics with increasing species richness, suggesting that the variety of responses to environmental changes was unrelated to diversity. Diversity–stability relationships in natural communities may be more complex than those predicted by theory and manipulative experiments.

**KEY WORDS:** Diversity–stability hypothesis · Hard bottom · Intertidal · Marine · Portfolio effect · Species compensation · Species richness · Statistical averaging · Temporal variability

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## INTRODUCTION

The effects of biodiversity on ecosystem processes have received considerable attention because of the concern that loss of biodiversity can impair the functioning of ecosystems (reviewed by Hooper et al. 2005, Stachowicz et al. 2007). Greater species diversity represents more adaptive responses to environmental fluctuations (MacArthur 1955, Elton 1958). By this, the probability that some species maintain functioning when other species fail ensures the persistence of ecosystem properties under variable environmental conditions (Walker 1992, Yachi & Loreau 1999). Indeed, influential research in terrestrial habitats has shown that diversity is beneficial for the functioning and stability of ecosystems (e.g. Tilman 1996, Hector et al.

1999, Loreau & Hector 2001, Tilman et al. 2006). These ideas, however, remain poorly examined in aquatic ecosystems, for which there is also a need to understand the ecological consequences of species loss (Gessner et al. 2004, Hooper et al. 2005). Considering the differences between terrestrial and aquatic ecosystems (Giller et al. 2004), generalisations obtained from terrestrial habitats may not apply to marine habitats.

Stability has several meanings in ecology, including the resistance to and the resilience from disturbances, the resistance to invasions, and the temporal variability in a community property (Johnson et al. 1996, Shea & Chesson 2002). In the present study, we focus on temporal variability, expressed as the temporal variance in total species coverage of intertidal epibenthic communities, and on the role of statistical averaging (also

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called the portfolio effect) and overyielding as 2 mechanisms by which community variability decreases with increasing diversity. Statistical averaging occurs when an aggregate community property (e.g. total community abundance) is calculated by adding that property across species. If the temporal variations of species are asynchronous, adding more species will increase the probability that those fluctuations are averaged out and the variability in total abundance will decrease merely on statistical grounds (Doak et al. 1998). Nevertheless, because asynchrony among species can result from the different abilities of species to tolerate environmental changes, statistical averaging is due, in part, to ecological differences among species (Cottingham et al. 2001).

Asynchrony in species fluctuations leads to compensatory dynamics, such that the abundance of one species decreases while that of another increases; the resulting negative covariance buffers the community stability (e.g. Vasseur & Gaedke 2007). If species richness increases the variety of responses to the environment, then the presence of more species increases the probability that some species will compensate for the loss of others (Yachi & Loreau 1999, Ives et al. 2000). Increasing compensatory dynamics with increasing diversity will tend to stabilise the community, but will cause individual populations to be more unstable (Lehman & Tilman 2000).

The strength of statistical averaging effects depends on the relative abundance of species (Steiner et al. 2005). When species contribute unequally to the community abundance, the negative effect of diversity on community variability is dampened (Doak et al. 1998), as shown in terrestrial plant communities (Poley et al. 2007). Moreover, high species dominance can lead to negative and non-linear diversity–stability relationships (Lhomme & Winkel 2002).

Overyielding, increases in the mean of an aggregate property with species richness, is the second mechanism that influences the diversity–stability relationship. Overyielding comes from differences among species—if many species compete for several resources, then coexistence results in a greater proportion of space covered by the community (Tilman et al. 1997). A more diverse assemblage stands for greater variety of species traits, which can cause the average community property to increase in comparison to the property of the average population. This overyielding effect will temporally stabilise the community as species richness increases (Lehman & Tilman 2000).

Experimental manipulation of marine epibenthic diversity shows that diversity enhances community stability (reviewed by Stachowicz et al. 2007). Spatial models based on observational data, however, predict the contrary (Dunstan & Johnson 2004, 2006). This is

possible when species produce aggregate structures (e.g. aggregations of conspecifics or colonies), as a result of differential use of the space among species. These structures raise spatial refuges, leading to enhanced probabilities of survival and to more stable communities at low-diversity sites (Dunstan & Johnson 2004, 2006). Contrarily, theory predicting a positive diversity–stability relationship is based on the assumption of well-mixed communities, where aggregations of conspecifics are almost absent (Dunstan & Johnson 2006).

In an observational study, we tested the relationships between species richness and community stability. Observational studies permit the inspection of broader ranges of species richness and more realistic environmental conditions than those usually present in manipulative experiments (Stachowicz et al. 2007). We tested whether species richness is positively related to community stability (temporal variability in coverage summed across all species in a sampling unit), but negatively related to population stability (temporal variability in the coverage of individual epibenthic species). In addition, we investigated whether species richness is positively related to average community coverage (i.e. overyielding effect), and whether species richness is positively related to the occurrence of species compensation (i.e. whether species covariances become more negative as species richness increases).

## MATERIALS AND METHODS

**Study sites.** The study was conducted at 5 intertidal sites of naturally differing species richness on the rocky shore of Helgoland Island, NE Atlantic. Each site was ca. 200 m<sup>2</sup> in area, and adjacent sites were ≥100 m apart from each other. Two sites, 'barren ground' (BG) and 'semi-sheltered *Fucus* bed' (SFB), were located on the moderately exposed north-eastern shore, which is partly sheltered from wave action by a 250 m long concrete jetty running from north to south. The mid-intertidal at BG was formerly dominated by the blue mussel *Mytilus edulis* and fucoid seaweeds (Bartsch & Tittley 2004). Today, the community at BG is dominated by the encrusting coralline algae *Phymatolithon* spp. and high densities of the periwinkle *Littorina littorea*, while mussels and fucoid seaweeds have almost disappeared. During September and November 2007, the average densities of *L. littorea* were 227 and 281 ind. m<sup>-2</sup> at BG, but 16 and 90 ind. m<sup>-2</sup> at SFB (M. Molis unpubl. data). At SFB, the canopy-forming brown seaweed *Fucus serratus* extensively covers the substrate from the lower intertidal to the upper subtidal, where the understorey is dominated by *Phymatolithon* spp. and the turf-forming algae *Cladophora rupestris*,

*Chondrus crispus*, and *Corallina officinalis* (Bartsch & Tittley 2004). The third site, 'exposed *Fucus* bed' (EFB) was located at the western wave-exposed rocky shore of Helgoland. Here, the dense *F. serratus* canopy has been gradually replaced by the red algae *C. crispus* and *Mastocarpus stellatus* (Bartsch & Tittley 2004). The fourth and fifth sites were located on concrete harbour walls in the south-eastern area of Helgoland. 'Exposed mole' (EM) is a wave-exposed site, dominated by dense turfs of *C. rupestris*, patches of the barnacle *Veruca stroemia*, and *Phymatolithon* spp. The fifth site, 'sheltered harbour' (SH) is a wave-sheltered site dominated by a number of red algae such as *Phyllophora* spp., *Ceramium virgatum*, and *Bonnemaisonia hamifera* (Trailliella-phase). In addition *F. serratus* and the encrusting bryozoan *Electra pilosa* exist here in high abundance.

**Community sampling.** During March 2006, fifteen  $0.5 \times 0.5$  m plots were randomly positioned and permanently marked with stainless steel screws at each site. All sites were sampled every 6 mo between March 2006 and March 2008, except that the final sampling of SH was delayed by 1 mo. Due to time constraints, a random sub-sample of 9 fixed plots was followed throughout time. In species accumulation curves, 7 or 8 plots were enough to represent the number of species at each site (Appendix 1, Supplementary Material available at [http://www.int-res.com/articles/suppl/b004p263\\_app.pdf](http://www.int-res.com/articles/suppl/b004p263_app.pdf)). Over the 2 yr study period, 2 plots were lost at SH and EFB, and 1 plot, at EM.

For each plot, percent coverage of each macrobenthic species was estimated to the nearest 1%. Species with <1% coverage in a plot were uniformly recorded with 0.5% abundance. Due to the multilayered structure of the assemblages, total community coverage could well exceed 100%. Taxa were identified to the lowest possible taxonomic level in the field. For ambiguous taxa, sub-samples collected from adjacent areas were identified in the laboratory. Some taxa were identified to genus level, such as *Phymatolithon* spp., *Porphyra* sp. and *Ulva* spp. Small burrowing spionids were classified as the family Spionidae and small filamentous brown algae as order Ectocarpales (Appendix 2, Supplementary Material available at [http://www.int-res.com/articles/suppl/b004p263\\_app.pdf](http://www.int-res.com/articles/suppl/b004p263_app.pdf)).

**Data analysis.** Because species richness did vary over time, the gradient of species richness was defined by using species accumulation curves that were generated separately for each site, using the data for all sample dates. The maximum number of species obtained from each curve corresponded to the site-specific richness used in the analyses. Species occurring in <3 out of the 5 sample dates or contributing <1% to total community coverage were omitted from all analyses,

except for rare species with a consistent seasonal pattern (defined as the occurrence of a species during the same season across years).

The PRIMER similarity-percentages routine, SIMPER, was used to identify the species with larger contribution to the multivariate structure of each site. Bray-Curtis (BC) similarities ( $1 - BC$ ) were calculated between all pairs of samples in the entire data set. The average similarities between all pairs of within-site samples were then broken down into separate contributions from each species to the structure of each site (Clarke & Warwick 2001).

The  $\mu \sigma^{-1}$  ratio (temporal stability,  $S$ ) was used as a measure of community stability, where  $\mu$  is the temporal mean community total coverage for a time period and  $\sigma$  is its temporal standard deviation over the same interval (Tilman 1999). In comparison to the frequently used coefficient of variation ( $100 \sigma \mu^{-1}$ ), which approaches zero as stability increases,  $S$  is advantageous because its magnitude increases with stability. The stability of the  $i$ th species,  $S_i$ , was calculated by dividing its mean coverage by its standard deviation. Population stability was then calculated for each plot by averaging  $S_i$  across all species (Tilman et al. 2006).

The temporal variance in total community coverage was partitioned into the sum of all ( $N$ ) species variances and covariances. This was done by calculating an  $N \times N$  covariance matrix across time for each plot; the sum of all values in the diagonal corresponds to the summed species variances, and the sum of the off diagonals to the summed species covariances. The sum of the full covariance matrix corresponds to the net variance (i.e. summed variances plus summed covariances). The summed covariances were used as a measure of compensatory dynamics—if species compensation increases, then the summed covariances become more negative.

Regression analyses of the relationship between diversity and stability were conducted using R environment, Version 2.7.2 (R Development Core Team 2008). We conducted orthogonal polynomial regressions to assess curvilinear patterns of diversity–stability relationships. We tested up to the fourth-order fit (1 minus the number of richness levels), and we used the procedure described by Sokal & Rohlf (1995), in which the significance of each polynomial regression is tested as part of the ANOVA table. All curves were fitted using least-squares regression, and ANOVAs were applied using the general linear model routines. All measures of stability were ln transformed due to their patchy statistical distribution. The transformation assured normality and allowed the use of general linear models.

Regression analyses were also used to investigate the relationship between richness and (1) the average

total community coverage (averaged over the 5 sample dates), (2) the sum of all species variances, (3) the sum of all pair-wise species covariances, and (4) the net variance in total community coverage. Analysis 1 was done to test whether increasing species richness leads to overyielding, and Analyses 2, 3 and 4 were done to test whether increases in the variance of species abundances are offset by increasingly negative species covariances.

Statistical averaging effects depend on the way in which the temporal variance in the abundance of a species changes with the temporal mean (Tilman et al. 1998). The general tendency of the variance  $\sigma^2$  to increase with the mean  $\mu$  is described with Taylor's power function,  $\sigma^2 = c\mu^z$ , where  $c$  is a constant and  $z$  is the scaling coefficient (Taylor 1961). The value of  $z$  affects the strength of the statistical averaging, with  $1 < z < 2$  meaning that diversity dampens the community variability but increases the population variability (Tilman et al. 1998, Tilman 1999). The logarithmic transformation of  $\sigma^2 = c\mu^z$  results in a linear equation in the form of  $\log(\sigma^2) = c + z \log(\mu)$ . We fitted this regression to the most important species identified by SIMPER routines and to the entire data set, combining all species.

## RESULTS

Seventy-three taxa were identified during the study; 52 were included in the analyses (Appendix 2). Site-specific species richness was 30 at BG, 34 at EFB, 36 at EM, 40 at SFB, and 43 at SH. The total community coverage averaged over the 5 sample dates ( $\pm$ SEM) ranged from  $119 \pm 7\%$  (BG) to  $211 \pm 6\%$  (SFB). The taxa contributing most to the community structure at each site were identified using SIMPER routines (Table 1). At BG, EM, and SFB, 3 to 4 species contributed 90% to the communities; at EFB and SH, 6 and 8 species, respectively. The taxa with the highest and most consistent contributions to within-site similarities were *Phymatolithon* spp., *Fucus serratus*, and *Cladophora rupestris* (Table 1). These 3 species represented 61% of the sum of all species abundances from the 5 sample sites.

Contrary to our predictions, community stability was a negative and curvilinear function of species richness (Fig. 1). Accordingly, both the linear and cubic models fit these data significantly (Fig. 1,

Table 2). Highest community stability values were found at BG, while lowest values were found at EFB and SH. Population stability showed large fluctuations over the species richness gradient, and no clear trend of decreasing values was observed. Consequently, the linear model was insignificant, whereas the quadratic and quartic models explained significant portions of the population stability data (Fig. 1, Table 2). Population stability was highest at EM, and lowest at EFB and SH.

The average total community coverage significantly increased with site-specific species richness ( $y = -54.10 + 5.95x$ ,  $R^2 = 0.5$ ,  $F_{1,38} = 38$ ,  $p < 0.0001$ ). In addition, total community coverage increased with site diversity at each of the sample dates (separate regressions performed at each sample date,  $p \leq 0.004$ ).

The summed variances showed an oscillating pattern across the species richness gradient and a signifi-

Table 1. Dominant taxa at sites with naturally differing numbers of species. Decomposition of within-site Bray-Curtis similarities into contribution of taxa to the structure of each site (Contribution<sub>*i*</sub>). Contributions of taxa are also expressed as percent (%<sub>*i*</sub>). A value of the ratio Contribution<sub>*i*</sub>/SD  $\geq 1$  indicates that the contribution of taxon *i* to the within-site similarity is consistent across all pairs of samples. Percent coverage (averaged over plots and all sample dates) of each taxon is given (% coverage<sub>*i*</sub>). Site-specific species richness is given in brackets. Taxa cumulating up to 90% of the contribution to the within-site similarities are shown

Taxon	% coverage <sub><i>i</i></sub>	Contribution <sub><i>i</i></sub>	% <sub><i>i</i></sub>	Contribution <sub><i>i</i></sub> /SD
<b>BG, barren ground (30)</b>				
<i>Phymatolithon</i> spp.	70.78	49.31	78.90	2.95
<i>Littorina littorea</i>	6.67	3.96	6.33	1.92
<i>Hildenbrandia rubra</i>	7.92	2.62	4.19	0.56
<i>Haemescharia hennedyi</i>	12.32	2.56	4.09	0.31
<b>EFB, exposed <i>Fucus</i> bed (34)</b>				
<i>Phymatolithon</i> spp.	42.67	16.13	40.35	1.27
<i>Fucus serratus</i>	32.37	9.08	22.71	0.75
<i>Chondrus crispus</i>	17.89	5.27	13.19	0.81
<i>Corallina officinalis</i>	8.63	2.09	5.23	0.61
<i>Mastocarpus stellatus</i>	9.24	1.96	4.91	0.50
<i>Ulva</i> spp.	11.66	1.70	4.26	0.38
<b>EM, exposed mole (36)</b>				
<i>Cladophora rupestris</i>	86.68	49.02	73.15	3.10
<i>Phymatolithon</i> spp.	20.56	6.28	9.37	1.07
<i>Verruca stroemia</i>	22.75	5.88	8.78	0.94
<b>SFB, semi-sheltered <i>Fucus</i> bed (40)</b>				
<i>Fucus serratus</i>	76.27	29.30	40.33	2.43
<i>Phymatolithon</i> spp.	66.51	26.89	37.02	3.69
<i>Cladophora rupestris</i>	38.40	12.52	17.24	1.96
<b>SH, sheltered harbour (43)</b>				
<i>Ceramium virgatum</i>	31.79	7.63	23.60	0.67
<i>Fucus serratus</i>	30.69	6.24	19.28	0.59
<i>Electra pilosa</i>	22.29	4.85	15.00	0.73
<i>Bonnemaisonia hamifera</i>	23.57	4.03	12.47	0.39
<i>Phyllophora</i> spp.	12.14	2.34	7.24	0.62
<i>Chondrus crispus</i>	9.97	2.31	7.13	0.73
<i>Ulva</i> spp.	8.87	1.30	4.02	0.56
Ectocarpales	10.81	1.14	3.53	0.31

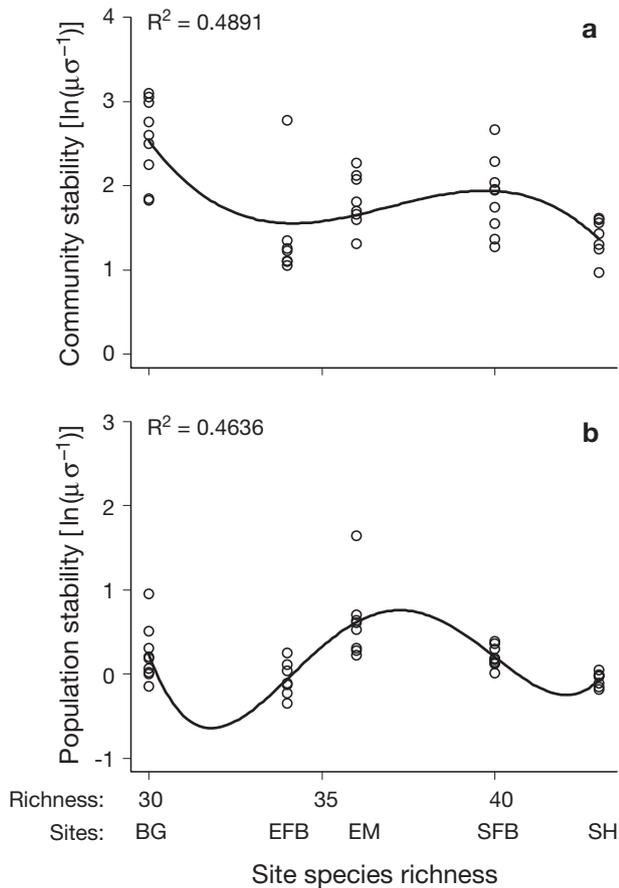


Fig. 1. Relationship between species richness and stability in percent coverage of epibenthic species. Stability was calculated as the quotient between the temporal mean in coverage,  $\mu$ , and its standard deviation,  $\sigma$ , over the same time period. (a) Stability of total community coverage. (b) Stability of coverage of single species averaged across 52 species. Each circle represents the stability of a 0.25 m<sup>2</sup> plot that was followed over time. BG: barren ground; EFB: exposed *Fucus* bed; EM: exposed mole; SFB: semi-sheltered *Fucus* bed; SH: sheltered harbour. Regression parameters of site-specific species richness ( $N$ ) are: community stability =  $227.25 - 18.53N + 0.50N^2 - 0.004N^3$ ; population stability =  $31450 - 346N + 14N^2 - 0.25N^3 + 0.0017N^4$

cant trend of increase (Fig. 2, Table 3). On the other hand, the summed covariances were independent of species richness (Fig. 2, Table 3). Summed covariances were on average ( $\pm$ SEM) less than zero ( $-766.2 \pm 188.5$ , 1-sample  $t$ -test,  $p \geq 0.001$ ). When analysing each site separately, however, we found that summed covariances were less than zero at BG, EM and SH (1-sample  $t$ -tests,  $p \leq 0.03$ ), but not at EFB and SFB (1-sample  $t$ -test,  $p \geq 0.09$ ). As a consequence of the insignificant relationship between the summed covariances and diversity, the net variance (i.e. summed variances plus summed covariances) followed a similar pattern to that of the summed variances, showing an irregular increase over the species richness gradient (Fig. 2, Table 3).

Table 2. Results of orthogonal polynomial regressions of species richness on community and population stability

Source	df	MS	$F$	$p$
<b>Community stability</b>				
Species richness, $N$	4	1.81	9.40	<0.0001
$N_{\text{linear}}$	1	3.44	17.82	0.0002
$N_{\text{quadratic}}$	1	0.79	4.08	0.0511
$N_{\text{cubic}}$	1	2.63	13.61	0.0008
$N_{\text{quartic}}$	1	0.40	2.09	0.1569
Residual	35	0.19		
<b>Population stability</b>				
Species richness, $N$	4	0.59	7.56	0.0002
$N_{\text{linear}}$	1	0.15	1.94	0.1725
$N_{\text{quadratic}}$	1	0.48	6.17	0.0179
$N_{\text{cubic}}$	1	0.30	3.89	0.0566
$N_{\text{quartic}}$	1	1.42	18.25	0.0001
Residual	35	0.08		

The fitted  $z$ -values ( $\pm$ SEM) for the 3 taxa with the highest contributions to the within-site similarities were  $1.26 \pm 0.14$  for *Phymatolithon* spp.,  $1.38 \pm 0.06$  for *Fucus serratus*, and  $1.12 \pm 0.1$  for *Cladophora rupestris*; the fitted  $z$ -value for the entire data set was  $1.34 \pm 0.01$ . According to their  $z$ -values, the stability of these taxa should have decreased with species richness, but the individual regressions showed differing patterns. The stability of *Phymatolithon* spp. tended to decrease with increasing species richness, while that of *F. serratus* and *C. rupestris* showed large departures from linearity that resulted in a significant quartic fit for both species (Fig. 3, Table 4).

## DISCUSSION

### Community stability

Our observations suggest that community stability decreased as the number of species increased, in contrast to what most theoretical and empirical work predicts (reviewed by Hooper et al. 2005, Stachowicz et al. 2007). In addition, the patterns of community and population stability were highly complex. In the present study, the average total community coverage significantly increased with species richness (i.e. overyielding) and the variance scaled with the mean coverage with  $1 < z < 2$ . Overyielding and  $z$ -values between 1 and 2 should have led to a positive diversity–stability relationship (Tilman et al. 2006, van Ruijven & Berendse 2007). Yet, increasing stability with increasing diversity also requires increasingly negative species covariances and an even distribution of species abundances.

On average, summed covariances were significantly less than zero. At both sites dominated by the canopy forming *Fucus serratus*, however, covariances were equal to or larger than zero. Positive covariances for

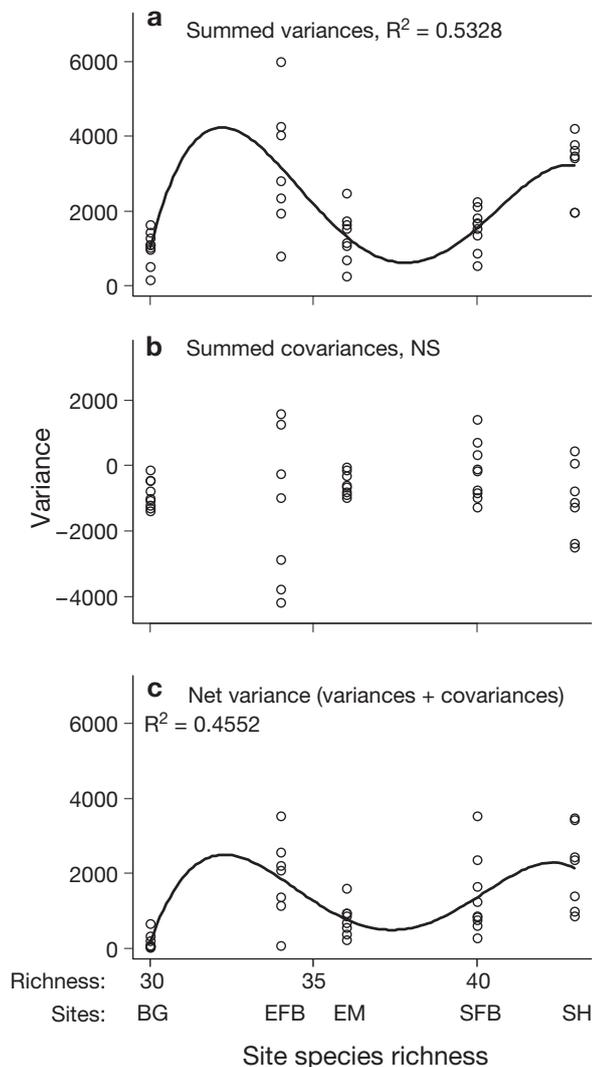


Fig. 2. Relationship between site-specific species richness and (a) summed variances, (b) summed covariances and (c) net variance (summed variances plus summed covariances). Site abbreviations as in Fig. 1. Regression parameters of site-specific species richness ( $N$ ) are: summed variances =  $-7465\,000 + 810\,900N - 32\,790N^2 + 585N^3 - 4N^4$ ; net variance =  $-5\,522\,000 + 602\,900N - 24\,530N^2 + 441N^3 - 3N^4$

these sites may have resulted from the positive effect of *F. serratus* on obligate understory species (N. Valdivia unpubl. data). Moreover, persistent removals of the *F. serratus* canopy caused compensatory dynamics of species with different environmental tolerances; the resulting negative covariances buffered the community stability but reduced the population stability (N. Valdivia unpubl. data). Therefore, the covariance in the species responses to environmental disturbances can strongly influence the stability of the shores studied here. In the present study, the insignificant relationship between species covariances and species richness probably prevented a positive effect of diversity on stability.

Table 3. Results of orthogonal polynomial regressions of species richness on summed variances, summed covariances and net variance (summed variances + summed covariances)

Source	df	MS	F	p
<b>Summed variances</b>				
Species richness, $N$	4	8 490 828	9.98	<0.0001
$N_{\text{linear}}$	1	7 589 923	8.92	0.0051
$N_{\text{quadratic}}$	1	142 765	0.17	0.6846
$N_{\text{cubic}}$	1	19 102 565	22.45	<0.0001
$N_{\text{quartic}}$	1	7 128 060	8.38	0.0065
Residual	35	850 863		
<b>Summed covariances</b>				
Species richness, $N$	4	1 564 017	1.11	0.3662
$N_{\text{linear}}$	1	426 974	0.30	0.5851
$N_{\text{quadratic}}$	1	555 457	0.40	0.5337
$N_{\text{cubic}}$	1	4 858 397	3.46	0.0715
$N_{\text{quartic}}$	1	415 240	0.30	0.5902
Residual	35	1 405 830		
<b>Net variance (summed variances + summed covariances)</b>				
Species richness, $N$	4	5 137 088	7.31	0.0002
$N_{\text{linear}}$	1	11 617 286	16.54	0.0003
$N_{\text{quadratic}}$	1	135 017	0.19	0.6638
$N_{\text{cubic}}$	1	4 693 597	6.68	0.0141
$N_{\text{quartic}}$	1	4 102 454	5.84	0.0210
Residual	35	702 542		

The relationship between species richness and stability was also influenced by the relative abundance of species. In this experiment, 3 taxa explained ca. 60% of the sum of all of the species coverage values. When few taxa numerically dominate the system, community stability can be driven by fluctuations of these components (Steiner et al. 2005, Polley et al. 2007). In addition, large differences among species abundances can result in negative and curvilinear richness–stability relationships when  $z = 1.2$  (Lhomme & Winkel 2002). In our case, the  $z$ -values were close to 1.2 (e.g.  $1.26 \pm 0.14$  for *Phymatolithon* spp., but  $1.35 \pm 0.01$  for all species), suggesting that large heterogeneity among species abundances may also explain the negative and complex pattern of community stability.

Overyielding probably resulted from the multilayered structure of macrobenthic assemblages, which allows single species to expand by differential use of the available space. Erect life forms use little space of primary substratum, but can expand above the substratum and thus increase in abundance. This leads, in some cases, to a total percent coverage of >100. For instance, seaweeds can develop and expand a canopy in an area where the primary substratum is monopolised by encrusting forms (Connell 2003). Such a spatial structure was apparent in the present study, as encrusting, turfing, and canopy-forming algae formed 3 layers of biota. This suggests that if we had focused on 1 layer of species (i.e. had not allowed total percent coverage values >100), we probably would not have found overyielding. On the other hand, large spatial

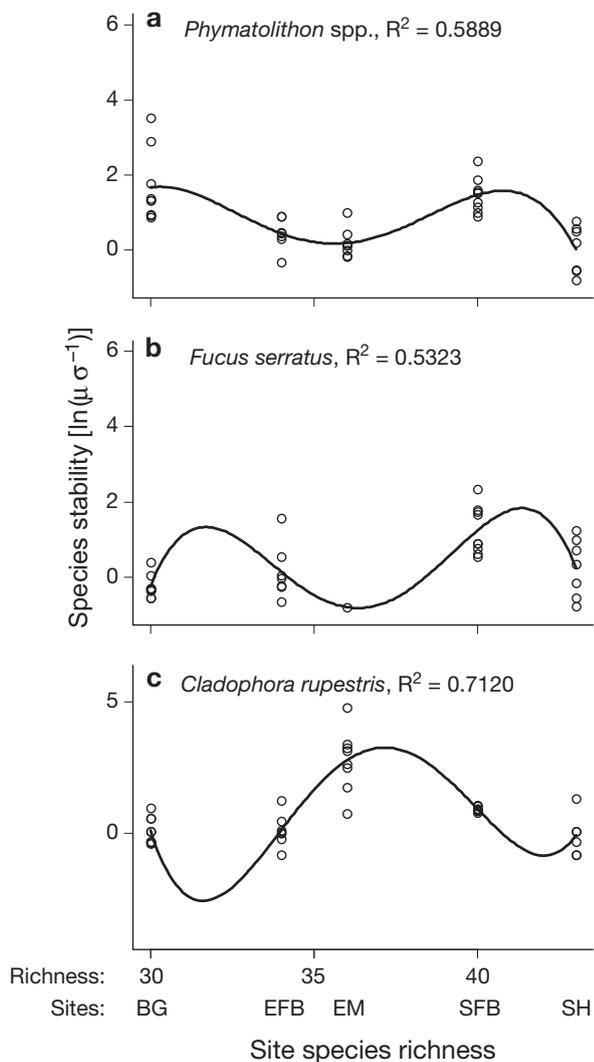


Fig. 3. Patterns of stability in percent coverage of the 3 taxa with the highest and most consistent contributions to the within-site similarities. Site abbreviations as in Fig. 1. Regression parameters of site-specific species richness ( $N$ ) on stability ( $S$ ) are as follows:  $S_{\text{Phymatolithon spp.}} = -3014 + 346.5N - 14.83N^2 + 0.27N^3 - 0.002N^4$ ;  $S_{\text{Fucus serratus}} = -7531 + 841N - 0.35N^2 + 0.6N^3 - 0.004N^4$ ;  $S_{\text{Cladophora rupestris}} = 1980 - 1324N + 54.51N^2 - 0.9N^3 + 0.007N^4$

structures may also have caused community stability to decrease with species richness, because such structures create refuges and increase the probability of survival in communities dominated by a few species (Dunstan & Johnson 2004, 2006).

### Population stability

We detected significant fluctuations in the pattern of population stability across the species richness gradient, but we did not find a clear trend of decreasing values. Population stability should decrease with increas-

Table 4. Results of orthogonal polynomial regressions of species richness on the stability of each of the 3 dominant taxa

Source	df	MS	F	p
<b><i>Phymatolithon</i> spp.</b>				
Species richness, $N$	4	4.70	12.54	<0.0001
$N_{\text{linear}}$	1	3.75	10.00	0.0032
$N_{\text{quadratic}}$	1	1.14	3.03	0.0904
$N_{\text{cubic}}$	1	12.09	32.25	<0.0001
$N_{\text{quartic}}$	1	1.82	4.86	0.0341
Residual	35	0.37		
<b><i>Fucus serratus</i></b>				
Species richness, $N$	4	3.05	7.97	0.0002
$N_{\text{linear}}$	1	4.88	12.72	0.0013
$N_{\text{quadratic}}$	1	1.83	4.79	0.0372
$N_{\text{cubic}}$	1	3.53	9.22	0.0051
$N_{\text{quartic}}$	1	1.97	5.15	0.0312
Residual	28	0.38		
<b><i>Cladophora rupestris</i></b>				
Species richness, $N$	4	10.88	21.02	<0.0001
$N_{\text{linear}}$	1	0.28	0.54	0.4659
$N_{\text{quadratic}}$	1	20.80	40.19	<0.0001
$N_{\text{cubic}}$	1	1.30	2.51	0.1225
$N_{\text{quartic}}$	1	21.14	40.84	<0.0001
Residual	34	0.52		

ing diversity if the latter is positively related to the number of potential competitive interactions or to the variety of adaptive responses to the environment (Ives et al. 2000). In the present study, the absence of a negative diversity-covariance relationship suggests that both the variety of environmental tolerances and the number of competitive interactions were independent of diversity. The differential use of space could have alleviated competition at high-diversity sites, reducing the probability of compensatory changes that cause individual populations to be more variable.

According to their  $z$ -values, the stability of single species should have decreased with species richness (Tilman 1999). However, individual species tended to be more stable at sites where they were more abundant. Similarly, a recent experiment in which species abundances varied across the diversity gradient showed that the stability of single species performed differently than expected based on variance-mean rescaling (van Ruijven & Berendse 2007). Because constancy in species abundance is an assumption of statistical averaging (Doak et al. 1998), this mechanism may be well supported by manipulative experiments, but probably not by observational studies.

Our observations agree with studies conducted in multitrophic systems, showing no clear diversity effect on population stability (McGrady-Steed & Morin 2000, Steiner et al. 2005), but they contradict studies conducted on single trophic levels that show negative relationships (Tilman et al. 2006, van Ruijven & Berendse 2007). In our case, primary producers domi-

nated the assemblages in terms of abundance, but 57% of the taxa were invertebrates. On the other hand, keystone consumers can strongly control the community structure (Paine 1966). Therefore, the high stability of *Phymatolithon* spp. at the species-poor BG site might be related to the large density of the periwinkle *Littorina littorea* observed at the study site. Epibenthic grazers like *L. littorea* control the recruitment of algae, thereby affecting the structure of macrobenthic assemblages (McQuaid 1996). The grazing activity of *L. littorea* at BG may be an important factor in depressing species richness and simultaneously promoting the persistence of encrusting algae like *Phymatolithon* spp. at high abundances. Manipulative experiments are necessary to address the role of trophic interactions on the relationship between diversity and stability.

In conclusion, we observed a negative and curvilinear pattern in community stability and a complex pattern in population stability. Probably, putative positive effects of overyielding and variance–mean rescaling on community stability were offset by strong heterogeneity among species abundances and invariant species covariances across the species richness gradient. The observational evidence presented here is not unequivocal, since we did not control for factors that might have covaried with species richness, such as wave exposure or nutrient levels. In addition, ecosystem properties such as fluxes of nutrients and carbon were not assessed. Because different ecosystem properties can have different responses to changes in diversity (Jiang et al. 2008), experiments that explore multiple ecosystem properties may provide a more comprehensive view of the functional role of diversity. Nevertheless, we still suggest that the relative abundance of species and ecological interactions influencing the covariances among species may play a pivotal role in the relationship between diversity and ecosystem stability.

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#### LITERATURE CITED

- Bartsch I, Tittley I (2004) The rocky intertidal biotopes of Helgoland: present and past. *Helgol Mar Res* 58:289–302
- Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation. PRIMER-E Ltd, Plymouth
- Connell SD (2003) The monopolization of understory habitat by subtidal encrusting coralline algae: a test of the combined effects of canopy-mediated light and sedimentation. *Mar Biol* 142:1065–1071
- Cottingham KL, Brown BL, Lennon JT (2001) Biodiversity may regulate the temporal variability of ecological systems. *Ecol Lett* 4:72–85
- Doak DF, Bigger D, Harding EK, Marvier MA, O'Malley RE, Thomson D (1998) The statistical inevitability of stability–diversity relationships in community ecology. *Am Nat* 151:264–276
- Dunstan PK, Johnson CR (2004) Invasion rates increase with species richness in a marine epibenthic community by two mechanisms. *Oecologia* 138:285–292
- Dunstan PK, Johnson CR (2006) Linking richness, community variability, and invasion resistance with patch size. *Ecology* 87:2842–2850
- Elton SC (1958) The ecology of invasions by animals and plants. The University of Chicago Press, Chicago, IL
- Gessner MO, Inchausti P, Persson L, Raffaelli DG, Giller PS (2004) Biodiversity effects on ecosystem functioning: insights from aquatic systems. *Oikos* 104:419–422
- Giller PS, Hillebrand H, Berninger UG, Gessner MO and others (2004) Biodiversity effects on ecosystem functioning: emerging issues and their experimental test in aquatic environments. *Oikos* 104:423–436
- Hector A, Schmid B, Beierkuhnlein C, Caldeira MC and others (1999) Plant diversity and productivity experiments in European grasslands. *Science* 286:1123–1127
- Hooper DU, Chapin III, FS, Ewel JJ, Hector A and others (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* 75:3–35
- Ives AR, Klug JL, Gross K (2000) Stability and species richness in complex communities. *Ecol Lett* 3:399–411
- Jiang L, Pu Z, Nemergut DR (2008) On the importance of the negative selection effect for the relationship between biodiversity and ecosystem functioning. *Oikos* 117:488–493
- Johnson KH, Vogt KA, Clark H, Schmitz O, Vogt D (1996) Biodiversity and the productivity and stability of ecosystems. *Trends Ecol Evol* 11:372–377
- Lehman CL, Tilman D (2000) Biodiversity, stability, and productivity in competitive communities. *Am Nat* 156:534–552
- Lhomme JP, Winkel T (2002) Diversity–stability relationships in community ecology: re-examination of the portfolio effect. *Theor Popul Biol* 62:271–279
- Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72–76
- MacArthur RH (1955) Fluctuations of animal populations and a measure of community stability. *Ecology* 36:533–536
- McGrady-Steed J, Morin PJ (2000) Biodiversity, density compensation, and the dynamics of populations and functional groups. *Ecology* 81:361–373
- McQuaid CD (1996) Biology of the gastropod family Littorinidae. II. Role in the ecology of intertidal and shallow marine ecosystems. *Oceanogr Mar Biol Annu Rev* 34:263–302
- Paine R (1966) Food web complexity and species diversity. *Am Nat* 100:65–75
- Polley HW, Wilsey BJ, Derner JD (2007) Dominant species constrain effects of species diversity on temporal variability in biomass production of tallgrass prairie. *Oikos* 116:2044–2052
- R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. *Trends Ecol Evol* 17:170–176

- Sokal RR, Rohlf RJ (1995) *Biometry*. Freeman and Company, New York
- Stachowicz JJ, Bruno JF, Duffy JE (2007) Understanding the effects of marine biodiversity on communities and ecosystems. *Annu Rev Ecol Evol Syst* 38:739–766
- Steiner CF, Long ZT, Krumins JA, Morin PJ (2005) Temporal stability of aquatic food webs: partitioning the effects of species diversity, species composition and enrichment. *Ecol Lett* 8:819–828
- Taylor LR (1961) Aggregation, variance and the mean. *Nature* 189:732–735
- Tilman D (1996) Biodiversity: population versus ecosystem stability. *Ecology* 77:350–363
- Tilman D (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80:1455–1474
- Tilman D, Lehman CL, Thomson KT (1997) Plant diversity and ecosystem productivity: theoretical considerations. *Proc Natl Acad Sci USA* 94:1857–1861
- Tilman D, Lehman CL, Bristow CE (1998) Diversity–stability relationships: Statistical inevitability or ecological consequence? *Am Nat* 151:277–282
- Tilman D, Reich PB, Knops JMH (2006) Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* 441:629–632
- van Ruijven J, Berendse F (2007) Contrasting effects of diversity on the temporal stability of plant populations. *Oikos* 116:1323–1330
- Vasseur DA, Gaedke U (2007) Spectral analysis unmask synchronous and compensatory dynamics in plankton communities. *Ecology* 88:2058–2071
- Walker BH (1992) Biodiversity and ecological redundancy. *Conserv Biol* 6:18–23
- Yachi S, Loreau M (1999) Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc Natl Acad Sci USA* 96:1463–1468

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