Temporal stability of European rocky shore assemblages: variation across a latitudinal gradient and the role of habitat-formers


Compensatory dynamics, overyielding and statistical averaging are mechanisms promoting the temporal stability of natural communities. Using the model of European intertidal rocky shore assemblages and collating 17 datasets, we investigated how the strength of these stability-enhancing mechanisms varies with latitude and how it can be altered by the loss of habitat-formers (e.g. canopy-forming macroalgae). Community stability decreased with increasing latitude, mostly as a consequence of a greater synchronization of species fluctuations. Statistical averaging and overyielding (i.e. richness effect) promoted stability, but their strength did not vary with latitude. An experimental removal of macroalgal canopies caused a strengthening of the statistical averaging effect that was consistent across the latitudinal gradient investigated. Nonetheless, the loss of canopies depressed stability by enhancing the synchronization of species fluctuations on southernmost shores, while it had weak effects on shores at higher latitudes. Variation in life-history traits among canopy-forming species and/or in prevailing environmental conditions across a gradient of latitude could underlie variable effects of habitat-formers on species fluctuations. Our study showed 1) that the stability of intertidal assemblages and strength of compensatory dynamics varies with latitude, 2) that canopy-forming macroalgae, exerting a strong control on understory species, can influence the strength of compensatory dynamics and 3) that biological forcing (i.e. facilitation) can be as important as environmental forcing in enhancing the synchronization of species fluctuations.

Concerns over the consequences of biodiversity loss for the ability of ecosystems to supply goods and services to mankind have fuelled research on the diversity-stability hypothesis (Tilman 1996, Chapin et al. 1998, McCann 2000). This has ultimately led to the recognition that community stability can be promoted by different mechanisms (Lehman and Tilman 2000, Cottingham et al. 2001, Loreau and de Mazancourt 2008, Isbell et al. 2009).

Asynchronous species dynamics, fostered by interspecific competition and/or differential response to disturbances or environmental stress, can sustain stability by generating negative species covariances (Tilman 1999, Yachi and Loreau 1999, Ives et al. 1999, McCann 2000). In addition, when most species perform better in multi- than monospecific assemblages, temporal stability is enhanced via a greater increase in the average of the aggregate property in respect to its variance. This mechanism, generally referred to as overyielding, occurs whenever the average of a community property increases with species diversity (Lehman and Tilman 2000). Finally, the statistical averaging of fluctuations in the
abundances of individual species within a community can lead to greater temporal stability in communities at increasing levels of species richness (statistical averaging or portfolio effect; Doak et al. 1998).

The role of these mechanisms and, in particular, of species fluctuations, on stability has been investigated in a variety of terrestrial and aquatic systems, including lacustrine plankton, vascular plant communities, invertebrate and vertebrate assemblages (Klug et al. 2000, Fischer et al. 2001, Romanuk and Kolasa 2002, Romanuk et al. 2006, Houlanhan et al. 2007, Vasseur and Gaedke 2007, Valone and Barber 2008). These studies have revealed that a variety of factors, such as species traits and trophic-level, environmental conditions, resource availability and spatial and temporal scale investigated, can generate large context-dependency in the strength of the mechanisms underlying community stability.

Little effort has, however, been made to assess how the importance of mechanisms generating stability can vary in space, within a given ecosystem. For instance, there is a trend for increased strength in biological interactions, such as interspecific competition (Connolly et al. 2001, Bertness and Ewanchuk 2002), herbivory (Pennings and Silliman 2005, Coleman et al. 2006) or predation (Vermeij 1978, Sanford et al. 2003), from high to low latitudes. The significance of asynchronous species fluctuations can, therefore, be expected to vary with latitude, as a consequence of variation in the strength of biological interactions and environmental forcing (Campbell et al. 2011). Predicting the direction of this change is, however, difficult, since the relative importance of weak versus strong interactions (Klug et al. 2000, McCann 2000, Griffin et al. 2009), as well as that of differential response among species to environmental fluctuations (Ives et al. 1999, 2000, Yachi and Loreau 1999, Klug et al. 2000), in generating compensatory dynamics is yet to be fully elucidated.

Another aspect that has been poorly explored is the role that habitat-formers or ecosystem engineers (species that create or modify habitats) can play in determining stability levels. The presence of habitat-formers is a major driver of the structure and functioning of species assemblages (Bruno and Bertness 2001). By setting prevailing environmental conditions and, in particular, dampening their oscillations, habitat-formers can modulate the direction and strength of inter-specific interactions (Bruno and Bertness 2001, Kraufvelin et al. 2006, Callaway 2007, Brooker et al. 2008). Thus, they can be hypothesized to have a large influence on the mechanisms that promote stability. For instance, by modifying species interactions and/or their response to disturbances or environmental stress, habitat-formers could directly govern the synchronization of species fluctuations. In addition, through their pervasive effects on species identity and relative abundances, they might alter the contribution of statistical averaging and overyielding to stability by modulating evenness (Doak et al. 1998, Cottingham et al. 2001, Li and Stevens 2010; but see Isbell et al. 2009). Alteration to species evenness in the presence of habitat-formers, such as canopy-forming macroalgae, seems likely when they are perennial and their abundance/biomass is disproportionately greater than that of associated species. Some studies have reported greater stability for dominant than subordinate species (Lepš 2004, Steiner et al. 2005, Polley et al. 2007). Thus, as argued by Grman et al. (2010), a large abundance of particularly stable species might enhance community stability by a mechanism similar to the sampling effect (Huston 1997).

We investigated patterns of variation in the stability of intertidal rocky shore assemblages and underlying mechanisms along a latitudinal gradient in Europe. Furthermore, we assessed how the mechanisms promoting stability could be altered by the loss of canopy-forming macroalgae. We focused on these habitat-formers since their role in maintaining intertidal biodiversity has been well-documented, and they are reported to be declining on many temperate rocky shores worldwide (North Atlantic: Jenkins et al. 1999; Mediterranean: Benedetti-Cecchi et al. 2001, Airoldi and Beck 2007; New Zealand: Lilley and Schiel 2006; California: Thom and Widdowson 1978; Baltic Sea: Vogt and Schramm 1991). Specifically, we tested the hypothesis that the stability in the cover of sessile rocky intertidal species would vary along a gradient of latitude as a consequence of variation in the synchrony of species fluctuations, statistical averaging and overyielding (i.e. richness effect sensu Cardinale et al. 2006). In addition, we tested the hypothesis that the effect of macroalgal canopy removal on stability and underlying mechanisms would vary between southern and northern European rocky shores. In line with the above mentioned trend for the strength of biological interactions to decrease towards higher latitudes (Vermeij 1978, Connolly et al. 2001, Bertness and Ewanchuk 2002, Sanford et al. 2003, Pennings and Silliman 2005, Coleman et al. 2006), Campbell et al. (2011) have suggested that a weakening of the relationship between diversity and stability towards higher latitudes might be generated by the prevalence of physical forcing over biological forcing. In accordance, we predicted that the removal of canopies would have little effect on the stability of rocky intertidal communities at higher latitudes, where physical forcing prevails. In contrast, at lower latitudes, where biological interactions (either negative or positive) play an important role in regulating the relationship between diversity and stability, the removal of canopies should generate a large effect on stability.

**Material and methods**

Estimates of temporal variance in total cover and in cover of individual taxa are required for analysing temporal stability of communities and underlying mechanisms. A total of 17 datasets were used to investigate latitudinal patterns in the mechanisms promoting stability (Table 1). Species fluctuations can be synchronous at some timescales, but not at others, so that long time-series enabling partitioning at varying scales are of paramount importance to identify discontinuities (Vasseur and Gaedke 2007, Downing et al. 2008, Keitt 2008). The overall duration (about two years) and sampling intervals (i.e. 2–6 months) of the studies included in our analyses enable encompassing major environmental fluctuations (i.e. seasonal). Thus, although we cannot provide any insight into longer term trajectories, the data used in this study are adequate to describe short- to mid-term oscillations in rocky benthic assemblages characterized by relatively fast species turn-over.
Table 1. Details of datasets used in the correlative and experimental analyses, ordered from low to high latitudes.

<table>
<thead>
<tr>
<th>Dataset</th>
<th>Country</th>
<th>Region</th>
<th>Sampling period</th>
<th>Sampling interval</th>
<th>Canopy-forming species/dominant taxa</th>
<th>Plot size</th>
<th>Canopy cover (%)</th>
<th>Canopy/understorey</th>
</tr>
</thead>
<tbody>
<tr>
<td>1(1)</td>
<td>Italy</td>
<td>Ionian Sea (Med.)</td>
<td>2006–2007</td>
<td>3–6 month (5)</td>
<td>Cystoseira amentacea</td>
<td>0.09 m²</td>
<td>93</td>
<td>2.14 ± 0.44</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Chondrus crispus, Mastocarpus stellatus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2(2)</td>
<td>Portugal‡</td>
<td>Atlantic</td>
<td>2006–2007</td>
<td>2–5 month (5)</td>
<td>Chondrus crispus, Mastocarpus stellatus</td>
<td>0.09 m²</td>
<td>43</td>
<td>1.27 ± 0.28</td>
</tr>
<tr>
<td></td>
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<tr>
<td>3</td>
<td>Italy††</td>
<td>Ligurian Sea (Med.)</td>
<td>2003–2005</td>
<td>2–6 month (7)</td>
<td>None/EC–AT</td>
<td>0.06 m²</td>
<td>98</td>
<td>7.6 ± 1.39</td>
</tr>
<tr>
<td></td>
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</tr>
<tr>
<td>4</td>
<td>Italy</td>
<td>Ligurian Sea (Med.)</td>
<td>2006–2007</td>
<td>3–6 month (6)</td>
<td>Cystoseira compressa</td>
<td>0.09 m²</td>
<td>98</td>
<td>7.6 ± 1.39</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Chondrus crispus, Mastocarpus stellatus</td>
<td>0.67 m²</td>
<td>80</td>
<td>5.61 ± 0.30</td>
</tr>
<tr>
<td>5(3)</td>
<td>Spain</td>
<td>Atlantica</td>
<td>2002–2004</td>
<td>4–6 month (4)</td>
<td>Sargassum muticum</td>
<td>0.09 m²</td>
<td>80</td>
<td>5.61 ± 0.30</td>
</tr>
<tr>
<td>6</td>
<td>France</td>
<td>North Atlantic</td>
<td>2006–2008</td>
<td>4–6 month (4)</td>
<td>Fucus serratus</td>
<td>0.09 m²</td>
<td>84</td>
<td>0.78 ± 0.02</td>
</tr>
<tr>
<td>7</td>
<td>UK</td>
<td>North Atlantic</td>
<td>2002–2004</td>
<td>4–6 month (4)</td>
<td>Fucus serratus</td>
<td>0.09 m²</td>
<td>71</td>
<td>0.78 ± 0.02</td>
</tr>
<tr>
<td>8(4)</td>
<td>Ireland</td>
<td>North Atlantic</td>
<td>2006–2008</td>
<td>4–6 month (4)</td>
<td>Fucus serratus</td>
<td>0.09 m²</td>
<td>71</td>
<td>0.78 ± 0.02</td>
</tr>
<tr>
<td>9</td>
<td>Germany</td>
<td>North Sea</td>
<td>2006–2008</td>
<td>4–6 month (4)</td>
<td>Fucus serratus</td>
<td>0.09 m²</td>
<td>71</td>
<td>0.78 ± 0.02</td>
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<tr>
<td>10</td>
<td>France</td>
<td>North Atlantic</td>
<td>2006–2008</td>
<td>4–6 month (4)</td>
<td>Fucus serratus</td>
<td>0.09 m²</td>
<td>71</td>
<td>0.78 ± 0.02</td>
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<td>11</td>
<td>Germany</td>
<td>North Sea</td>
<td>2006–2008</td>
<td>4–6 month (4)</td>
<td>Fucus serratus</td>
<td>0.09 m²</td>
<td>71</td>
<td>0.78 ± 0.02</td>
</tr>
<tr>
<td>12</td>
<td>UK</td>
<td>North Atlantic</td>
<td>2006–2008</td>
<td>4–6 month (4)</td>
<td>Fucus serratus</td>
<td>0.09 m²</td>
<td>71</td>
<td>0.78 ± 0.02</td>
</tr>
<tr>
<td>13</td>
<td>UK</td>
<td>North Atlantic</td>
<td>2006–2008</td>
<td>4–6 month (4)</td>
<td>Fucus serratus</td>
<td>0.09 m²</td>
<td>71</td>
<td>0.78 ± 0.02</td>
</tr>
</tbody>
</table>

Experimental datasets used to assess the effects of canopy removal on stability and underlying mechanisms are reported in brackets under the Dataset column; this numbering order is followed in Fig. 2; the total number of sampling events is reported in brackets in the Sampling interval column. athese datasets had a spatial structure (replicated sites) and generated 3 subsets of data. Dominant taxa are reported for the cases in which canopy-formers were absent (dataset 3, 4) or not dominant (dataset 6, 8). Canopy cover (%) refers to the time at which the experiment was shortly started. The ratio between the cover of the canopy and that of the understorey sessile assemblage is reported under the column Canopy/understorey. ‡Bertocci et al. 2010, Mar. Ecol. Prog. Ser. 414: 107–116; †Bertocci et al. 2010, Ecology 86: 2061–2067; ††Vaselli et al. 2008, Mar. Ecol. Prog. Ser. 364: 57–66. EC = Algal turfs.

A subset of nine datasets including the experimental removal of canopy-forming macroalgae were further used to test our hypothesis on the effects of the loss of this morphological group on stability and underlying mechanisms (Table 1). Canopy-forming species varied among sites (Table 1). Except for Site 4, where canopies were made of Ascophyllum nodosum, Fucus serratus and F. vesiculosus were the main canopy-formers on northern shores. In contrast, species forming canopies were more variable at lower latitudes; Chondrus crispus and Mastocarpus stellatus on the coast of Portugal, Cystoseira compressa in the Ligurian Sea and Cystoseira amentacea var. stricta in the Ionian Sea.

In all cases, canopies were removed at the beginning of the experiment, recruits were selectively removed thereafter with no further disturbance to other species and sampling started about three months after the initial treatment. Canopy-forming species were removed by hand to minimize disturbance to understorey assemblages. At the beginning of the experiment, the cover of the canopy and that of understorey assemblages showed a marked trend to decrease when moving from southern to northern shores (Table 1), although this correlation was not significant (Spearman $r_s = -0.62, p = 0.07$).

The percentage cover of all macroscopic sessile taxa ($> 1$ mm) was quantified visually in each study by means of grids divided into sub-quadrats, except for datasets 6 and 8 where it was estimated with the point-intercept method. Across datasets, the size of plots varied between 0.01 and 0.67 m² (Table 1), but it was not correlated with latitude (Spearman $r_s = -0.05, p = 0.86$). Thus, although larger plots were more effective in sampling rare species (significant positive correlation between plot size and number of singletons: Spearman $r_s = 0.79, p = 0.0001$) that are likely to exhibit large temporal variability in cover, latitudinal patterns in stability and underlying mechanisms were independent of plot size.

In marine environments, where competition for primary space among sessile organisms is generally strong, cover is an important property of communities (Connolly and Muko 2003). In addition, since rocky benthic assemblages can be multi-layered, the total percentage cover of organisms is not constrained to 100% and can be reasonably taken as a proxy for biomass (Cavanaugh et al. 2010).

For each plot, temporal stability of cover at the community level was estimated as the ratio between the mean (across the time series) and the standard deviation of percentage cover ($\mu/\sigma$, the inverse of the coefficient of variation; Lehman and Tilman 2000). Since variations in temporal stability can be generated by changes in either the numerator, the denominator or both, we formally analysed variations in $\mu$ and $\sigma$, across a latitudinal gradient and following the experimental removal of algal canopies.

The degree of synchrony of species fluctuations has often been examined by calculating the sum of all pair-wise species covariances in a plot and interpreting negative plot covariances as evidence of the prevalence of asynchronous fluctuations and, hence, of a positive contribution of the covariance effect to community stability (Lehman and Tilman 2000).
The validity of this metric has been recently challenged by Loreau and de Mazancourt (2008), who have argued that it does not allow comparisons between communities differing in species richness and that the underlying assumption of species fluctuating independently is highly unrealistic. Here, community-wide synchrony in species cover ($\varphi$) was calculated for each plot by means of a measure of synchrony recently proposed by the same authors (Loreau and de Mazancourt 2008). This is calculated as $\varphi = \sigma^2_{ct} \sum_{i=1}^{S} \sigma^2_{ci}$, where $\sigma^2_{ct}$ is the variance in total community cover and $\sigma^2_{ci}$ is the standard deviation in cover of species $i$, in a community with $S$ species. This statistic varies between 0 (perfect asynchrony) and 1 (perfect synchrony) and makes no specific assumption about the magnitude and distribution of species abundances and variances.

The strength of the statistical averaging effect is dependent upon the scaling relationship between the mean and the variance (mean-variance scaling, Tilman 1999). This relationship follows Taylor’s power law: $S^2 = cm^z$, where $S^2$ is the variance, $c$ is a constant, $m$ is the mean and $z$ is the scaling coefficient. Larger values of $z$ indicate a more rapid increment in the variance with the mean and, assuming that species in a community are independent, have equal abundances and mean-variance rescaling coefficients, statistical averaging is supposed to promote stability whenever $z > 1$. Thus, $z$ was calculated for each taxon in each plot as the slope of the regression of log(variance) versus log(mean).

In order to assess how variations in the value of $z$ could be related to variations in species dominance (Doak et al. 2002), in order to take into account the autocorrelation of data in species cover ($\varphi$) and standard deviation ($\sigma$) between communities differing in species richness and that in which evidence of variation in the effects of the removal of macroalgal canopies along a latitudinal gradient using a regression approach. Thus, data were analyzed by means of a two-way factorial ANOVA, including the factors Site (random) and Canopy (fixed, control versus removal). The shores investigated were subsequently separated into northern and southern according to prevalent climatic conditions. In particular, shores investigated along the coasts of Italy and Portugal (<45°N of latitude) are characterized by a Mediterranean climate (Lusitanian-Mediterranean bioregion, with hot, dry summers and warm, wet winters), while those investigated at higher latitudes (>45°N of latitude), except for those in the North Sea experiencing cold winters, are under the influence of an oceanic climate (Eastern Atlantic Boreal bioregion, with mild winters and cool summers). Evidence of variation in the effects of the canopy removal with latitude was, however, not conclusive. Data for 8 out of the 9 sites analyzed had 5 replicates (n = 5) for each of the control and the canopy removal treatment. In order to maintain a balanced design and enable a straightforward analysis, the same number of plots was randomly selected from the greater number available for both control and canopy-removal plots at the remainder site (i.e. n = 8 experimental dataset 4, in Table 1). Homogeneity of variances was checked by means of Cochran’s test (Underwood 1997). In some cases, it could not be achieved by transformation, but data were analyzed nonetheless, since analysis of variance is robust to departure from this assumption when there are many independent replicates and sizes of samples are equal (Underwood 1997). Results were, however, interpreted with caution, by judging significance more conservatively ($\alpha = 0.01$). SNK tests were used for a posteriori comparisons of the means.

**Results**

The stability of rocky shore assemblages decreased significantly from southern to northern shores ($y = 1.339 - 0.013x; F_{1,94} = 8.31, p < 0.01, R^2_{adj} = 0.07, CI = -0.023, -0.005$; Fig. 1A). Both total assemblage cover ($y = 1.655 + 0.008x; F_{1,94} = 10.22, p < 0.01, R^2_{adj} = 0.09, CI = -0.008, 0.017$) and standard deviation ($y = 0.348 + 0.021x; F_{1,94} = 17.25, p < 0.001, R^2_{adj} = 0.15, CI = 0.004, 0.030$) significantly increased with latitude.

Species synchrony also increased with latitude ($y = -2.608 + 0.034x; F_{1,94} = 24.24, p < 0.001, R^2_{adj} = 0.20, CI = 0.005, 0.049$; Fig. 1B), indicating a weakening of the covariance effect when moving from southern to northern rocky shores. In contrast, there was no significant relationship between latitude and richness effect ($F_{1,94} = 3.25, p > 0.05$), mean-variance scaling coefficient $z$ ($F_{1,94} = 1.94, p > 0.05$) or evenness ($F_{1,94} = 0.01, p > 0.05$). Importantly, $z$, ranging between 1.19 and 1.79 across sites, was always among them. Assumptions of linearity and homogeneity of variances were checked by visual inspection of residual plots. Log transformation was effective in removing non-linearity and variance heterogeneity in response variables. BCa (bias-corrected accelerated percentile) bootstrap confidence intervals set at 95% were calculated using 999 iterations.

Unfortunately, the geographical positioning of sites for which experimental data were available (Table 1) did not allow assessment of variation in the effects of the removal of macroalgae along a latitudinal gradient using a regression approach. Thus, data were analyzed by means of a two-way factorial ANOVA, including the factors Site (random) and Canopy (fixed, control versus removal). The shores investigated were subsequently separated into northern and southern according to prevalent climatic conditions. In particular, shores investigated along the coasts of Italy and Portugal (<45°N of latitude) are characterized by a Mediterranean climate (Lusitanian-Mediterranean bioregion, with hot, dry summers and warm, wet winters), while those investigated at higher latitudes (>45°N of latitude), except for those in the North Sea experiencing cold winters, are under the influence of an oceanic climate (Eastern Atlantic Boreal bioregion, with mild winters and cool summers). Evidence of variation in the effects of the canopy removal with latitude was, however, not conclusive. Data for 8 out of the 9 sites analyzed had 5 replicates (n = 5) for each of the control and the canopy removal treatment. In order to maintain a balanced design and enable a straightforward analysis, the same number of plots was randomly selected from the greater number available for both control and canopy-removal plots at the remainder site (i.e. n = 8 experimental dataset 4, in Table 1). Homogeneity of variances was checked by means of Cochran’s test (Underwood 1997). In some cases, it could not be achieved by transformation, but data were analyzed nonetheless, since analysis of variance is robust to departure from this assumption when there are many independent replicates and sizes of samples are equal (Underwood 1997). Results were, however, interpreted with caution, by judging significance more conservatively ($\alpha = 0.01$). SNK tests were used for a posteriori comparisons of the means.
In general, the effects of the experimental removal of canopy-forming macroalgae on stability and underlying mechanisms varied among sites (Table 2). Removing the canopy resulted in a significant decrease in temporal stability only at the four southernmost sites (Table 2, Fig. 2A). Except for one site, it also caused a decline in mean total cover (Table 2, Fig. 2B). Worth noting is that the magnitude of this effect was particularly large at some of the northern sites (Fig. 2B). In contrast, the standard deviation of cover was significantly altered by the removal of the canopy only at a few sites (Table 2); however, it tended to increase with canopy loss at southern sites and decrease at northern sites (Fig. 2C). Like standard deviation, significant effects of the treatment on the synchronization of species fluctuations emerged throughout the latitudinal range investigated (Table 2, Fig. 2D). However, species fluctuations tended to become more synchronous at southern sites when algal canopies were removed, while an opposite trend emerged for sites at higher latitudes (Fig. 2D).

The removal of the canopy caused an increase in the mean-variance scaling coefficient, \( z \), suggesting a generalized enhancement of the statistical averaging; this effect was, however, significant at some sites, but not at others (Table 2, Fig. 2E). Likewise, removing canopies fostered evenness, but only at some sites (Table 2, Fig. 2F). Finally, the richness effect did not vary between control and canopy removal plots (Table 2).

**Discussion**

The temporal stability \( (\mu/\sigma) \) in the cover of rocky benthic communities tended to decrease with increasing latitude. This pattern can result from a decrease in the mean or an increase in the standard deviation of the aggregate property or both (Lehman and Tilman 2000). Both mean total cover \( (\mu) \), and the standard deviation of cover \( (\sigma) \), increased with latitude, but the negative relationship between stability \( (\mu/\sigma) \) and latitude suggests that the proportional increment in total assemblage cover was smaller than that of standard deviations. Statistical averaging contributed to enhance stability (i.e. \( z > 1 \)), but effects were invariant across the latitudinal gradient. Although the relationship between cover and species richness (i.e. richness effect) was positive (overyielding) in some plots (~78%) and negative (underyielding) in others (~22%), no general pattern emerged across the latitudinal range investigated. Therefore, the reduction in stability towards higher latitudes was mainly driven by greater synchronization of species fluctuations, ultimately resulting in positive or less negative summed species covariances (Lehman and Tilman 2000). These patterns indicate that compensatory dynamics (i.e. the covariance effect) are neither ubiquitous nor rare, but they are likely to vary in space, being influenced by a complex mix of biological and physical processes (Valdivia and Molis 2009).

The prevalence of positive or less negative species covariances (i.e. synchronous species fluctuations) has often been explained by inferring a greater signature of environmental forcing relative to that of biological processes, such as competition or predation (Houlahan et al. 2007, Valone...
Table 2. ANOVA of the effects of Treatment (canopy present vs canopy removal) and Site on temporal stability ($\mu/\sigma$), mean cover ($\mu$), standard deviation ($\sigma$), species fluctuations ($\phi$), statistical averaging ($z$), richness effect and evenness ($a$). Degrees of freedom for each term and interaction included in the analysis are reported in brackets. **$p<0.01$; ***$p<0.001$.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Treatment = $T_r$ (1)</th>
<th>Site = $S_i$ (8)</th>
<th>$T_r \times S_i$ (8)</th>
<th>Residual (72)</th>
<th>Cochran's test</th>
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<tr>
<td>Response variable</td>
<td>MS</td>
<td>F</td>
<td>MS</td>
<td>F</td>
<td>MS</td>
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<tr>
<td>Temporal stability ($\mu/\sigma$)</td>
<td>130.265</td>
<td>5.03</td>
<td>30.37</td>
<td>4.95***</td>
<td>25.922</td>
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<tr>
<td>Mean ($\mu$)</td>
<td>57470.630</td>
<td>24.73**</td>
<td>9964.892</td>
<td>35.48***</td>
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<tr>
<td>Std dev. ($\sigma$)</td>
<td>567.449</td>
<td>0.73</td>
<td>1051.194</td>
<td>9.20***</td>
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<td>0.176</td>
<td>3.07</td>
<td>0.083</td>
<td>10.21***</td>
<td>0.058</td>
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<tr>
<td>Statistical averaging ($z$)</td>
<td>1.115</td>
<td>20.67**</td>
<td>0.291</td>
<td>13.25***</td>
<td>0.054</td>
</tr>
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<td>Richness effect</td>
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<td>0.09</td>
<td>0.067</td>
<td>18.20***</td>
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<tr>
<td>Evenness ($a$)</td>
<td>0.450</td>
<td>1.95</td>
<td>0.355</td>
<td>13.76***</td>
<td>0.231</td>
</tr>
</tbody>
</table>

and Barber 2008). A recent meta-analysis, including both aquatic and terrestrial environments, has reported a weakening of the stabilizing effect of richness as latitude increased (Campbell et al. 2011). Speculating on this pattern, the same authors (Campbell et al. 2011) have inferred that, at high latitudes, environmental forcing would prevail on biological drivers (i.e. negative species interactions, such as competition and predation) in shaping the relationship between diversity

Figure 2. Effects of canopy removal at different European sites on (A) stability in community cover ($\mu/\sigma$), (B) mean community cover ($\mu$), (C) standard deviation in community cover ($\sigma$), (D) species synchrony ($\phi$), (E) mean-variance scaling coefficient ($z$) and (F) evenness ($a$). Sites on the $x$-axis are ordered following an increasing latitudinal gradient according to the numbering presented in Table 1 and divided in the groups Southern Europe (below 45°N) and Northern Europe (above 45°N). Data are means $\pm$ SE ($n = 5$). Asterisks indicate significant differences between the control and the canopy removal treatment for each site.
and stability. The same mechanism could be invoked as an explanation for the greater synchrony of species fluctuations on rocky shores at higher latitudes, where fluctuations in physical variables (e.g., light, temperature) are wider than on shores at lower latitudes.

Stress due to desiccation and heat is an important determinant of the structure and dynamics of rocky intertidal assemblages (Connell 1972). As shown by Helmuth et al. (2002), thermal stress is regulated by the interplay between tidal amplitude and timing of low tides and, hence, it does not decrease linearly with increasing latitude. Indeed, on the west coast of the United States, some northern sites were more thermally stressful than some southern sites for intertidal invertebrates, suggesting that the interaction between climate and timing of low tides can create a complex mosaic of thermal environments along a gradient of latitude (Helmuth et al. 2002). Detailed information on tidal regimes, comparable to that produced by Helmuth et al. (2002) for the west coast of the United States, is, to the best of our knowledge, not available for the European coasts investigated. Nonetheless, if we assume the occurrence of a mosaic of thermal environments (Helmuth et al. 2002), the linearity in the variation of stability and species synchrony with latitude would suggest a greater influence of other environmental variables covarying with latitude (i.e., light, temperature) than that of tidal amplitude and timing of low tides. This does not, by any means, imply that the interaction between the tidal regime and local climate plays no role in generating latitudinal patterns in stability and species synchrony at the sites we investigated.

Alternatively, variation in temporal dynamics of populations might underlie the latitudinal pattern in species synchrony. The temporal turn-over of species composition slows down towards higher latitudes, as a consequence of lower mean temperatures (Shurin et al. 2007). The temporal scale necessary to observe strong diversity effects on stability might be longer at high latitudes, due to slower population dynamics of species (Campbell et al. 2011). Thus, when investigated over a two-year temporal scale, the stabilizing effect of compensatory dynamics could have emerged on shores at lower latitudes, where species turn-over is faster, but not on those at higher latitudes, where species turn-over is slower.

The removal of canopy-forming macroalgae had a strong negative impact on temporal stability only at four sites; interestingly, these were the southernmost investigated. Removing algal canopies caused a generalized decrease in mean covers, but this was smaller at the four most southern sites (ranging between 20.0 and 30.0%; mean ± SE: 21 ± 3.8) than at the five most northern sites (ranging between 40.0 and 97.0%; mean ± SE: 71.85 ± 10.6). The standard deviation of cover was significantly altered by the removal of the canopy only at a few sites, but it tended to increase with canopy loss at southern sites and decrease at northern sites (Fig. 2C).

Thus, at southern sites, changes in both $\mu$ (decreasing) and $\sigma$ (increasing) of cover after canopy removal were destabilizing in direction and caused a decline in temporal stability. At these sites, the drop in mean community cover caused by the canopy removal was not as large as it could be expected from the large ratio of canopy cover to that of understorey assemblages (Table 1). This suggests that understorey species compensated (i.e., increased in cover) for the decline in mean community cover caused by the elimination of the canopy-forming species. A trend for species fluctuations to become more synchronous following the removal of the canopy would confirm that most species responded positively to changed environmental conditions. Thus, at Sites 2 and 3, the enhanced strength of the statistical averaging effect caused by the removal of the canopy was not sufficient to counter destabilizing effects of smaller community cover and more positive species covariances.

At northern sites (except for Site 4), the large decrease in mean community cover ($\mu$), mainly generated by the loss of the canopy-forming species, was compensated for by a decrease in the standard deviation of community cover ($\sigma$). This ultimately resulted in little overall change in temporal stability ($\mu/\sigma$). Similar compensation between destabilizing effects arising from decreased abundance and stabilizing effects, due to decreased temporal variability, have been recently documented in a subtidal marine system (Long et al. 2011).

Which mechanisms sustained community stability at northern sites, in the face of destabilizing effects of decreased mean cover? The removal of the canopy, generating less synchronous species fluctuations, promoted the stabilizing effects of compensatory dynamics. This, along with a generalized strengthening of statistical averaging, was effective in countering destabilizing effects due to the decline in community cover (Fig. 2). Thus, although the loss of dominant canopy-forming species led to a decline of community cover, the strengthening of the mechanisms promoting stability in response to disturbance was able to provide an insurance against the collapse of this ecosystem function. This suggests that a large abundance of particularly stable species (i.e., canopy-forming species on rocky shores) does not always enhance overall community stability (Leš 2004, Polley et al. 2007, Grman et al. 2010).

The occurrence of different canopy-forming species across the European shores investigated prevents assessing to what extent the impact of their loss on stability and underlying mechanisms was driven by local environmental conditions or by species-specific life traits. On southern shores, manipulated canopy-forming species varied from Chondrus crispus and Mastocarpus stellatus on Atlantic coasts of Portugal (Site 2), to smaller sized Cystoseira compressa and C. amentacea var. strycta on shores located in SE (Site 1) and NW (Site 3) Italy, respectively. Although these species largely differ in both architecture and size, their removal caused a consistent increase in the synchronization of species fluctuations and a drop in stability on southern shores. In contrast, on northern shores, the effects of removing Fucus spp. were markedly different from those of removing the canopies formed by Ascophyllum nodosum (at Site 4) that were more similar to those recorded at southern sites.

The ratio between canopy and understorey assemblage covers might have played an important role in determining the response of species fluctuations and stability to the removal of canopies formed by different species. This ratio was generally small at sites where canopies where made by
Fucoids, while it was larger in the presence of other canopyforming species (i.e. at Sites 1 to 4). This suggests that species-specific traits of habitat-formers could generate variation in their effects on the synchronization of species fluctuation and stability of associated assemblages. More specifically, attributes of Fucoids, such as size, architecture and toughness of tissues, might modify environmental conditions in such a way to enhance the synchronization of species fluctuations.

On the other hand, effects of canopy-forming macroalgae on understorey organisms have been previously shown to vary with latitude (Leonard 2000). For instance, on the east coast of the USA, the effects of canopies formed by *Ascophyllum nodosum* on associated organisms (i.e. barnacles) were positive at southern sites, but negative at northern ones (Leonard 2000). In addition, even slight variations in climate (i.e. maximum daily temperatures) were sufficient to alter the sign of the interactions between the habitat-former and the associated species (Leonard 2000). More generally, the occurrence of positive species interactions is predicted to increase along an increasing gradient of stress (i.e. the stress-gradient hypothesis; Bertness and Callaway 1994). While predictions from this conceptual framework have been tested and refined in a variety of environments (Callaway 2007, Brooker et al. 2008, Bulleri 2009), the implications of shifts in the sign and strength of species interactions on stability and underlying mechanisms remain largely unexplored.

By dampening variations in physical conditions, the presence of macroalgal canopies would be predicted to reduce the signature of environmental forcing, resulting in the prevalence of biological interactions, such as competition and, hence, of less synchronous species fluctuations (Houlahan et al. 2007, Valone and Barber 2008). On shores at higher latitudes, species fluctuations showed, in contrast, a consistent tendency to become less synchronous following the experimental removal of the canopy-forming *Fucus* spp. This means that most species started fluctuating more asynchronously when fully exposed to variations in physical variables (e.g. light and temperature) that are particularly wide at high latitudes. Thus, on northern shores, the effects of biological forcing (i.e. the presence of canopy-forming macroalgae) in synchronising species fluctuations overwhelmed those of environmental forcing.

At the four most southern European sites, synchrony in species fluctuations tended to increase in canopy removal plots. Amelioration of harsh physical conditions (i.e. desiccation and heat) by the canopy could have enhanced negative species interactions among understorey species, in line with predictions from the stress-gradient hypothesis (Bertness and Callaway 1994). Once deprived of a canopy, most of the species could have tracked more closely variations in environmental conditions, resulting in a greater synchronization of their fluctuations (Houlahan et al. 2007, Valone and Barber 2008, Engelen and Santos 2009).

Our findings, together with those of Campbell et al. (2011), point towards the occurrence of a latitudinal trend in the stability of natural communities. This would be mostly produced by variations in the contribution of compensatory dynamics, at odds with the more consistent contribution of statistical averaging and richness effect. In addition, our results suggest that the potential of biological interactions to generate positive covariances (i.e. biological forcing) has been greatly overlooked (but see Wilby and Shachak 2004, Steiner et al. 2005). In some cases, habitat-formers would be able to synchronize species fluctuations over the levels generated by local physical conditions. Thus, greater synchronization of species fluctuations does not necessarily reflect a prevalence of environmental forcing over biological forcing, as often assumed (Houlahan et al. 2007, Valone and Barber 2008, Campbell et al. 2011). For these reasons, framing the biodiversity–stability relationship into facilitation theories, such as the stress-gradient hypothesis (Bertness and Callaway 1994), might contribute to reconcile contrasting effects of biodiversity reported in the literature (Cottingham et al. 2001) by enabling a more balanced account of abiotic and biotic forces at play.

Acknowledgements – We sincerely thank D. Vasseur and P. Perraitis for providing valuable comments on an earlier version of the ms. The final version has been greatly improved by insightful comments and constructive criticism from M. Bracken. The project has been carried out in the framework of the MarBEF Network of Excellence ‘Marine Biodiversity and Ecosystem Functioning’ which was funded by the Sustainable Development, Global Change and Ecosystems Programme of the European Community’s Sixth Framework Programme (contract no. GOCE-CT-2003-505446). While writing, FB was supported from an Assegno di Ricerca from the University of Sassari.

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