

TEMPORAL VARIANCE REVERSES THE IMPACT OF HIGH MEAN INTENSITY OF STRESS IN CLIMATE CHANGE EXPERIMENTS

LISANDRO BENEDETTI-CECCHI,¹ IACOPO BERTOCCI, STEFANO VASELLI, AND ELENA MAGGI

Dipartimento di Biologia, Via A. Volta, 6, I-56126 Pisa, Italy

Abstract. Extreme climate events produce simultaneous changes to the mean and to the variance of climatic variables over ecological time scales. While several studies have investigated how ecological systems respond to changes in mean values of climate variables, the combined effects of mean and variance are poorly understood. We examined the response of low-shore assemblages of algae and invertebrates of rocky seashores in the northwest Mediterranean to factorial manipulations of mean intensity and temporal variance of aerial exposure, a type of disturbance whose intensity and temporal patterning of occurrence are predicted to change with changing climate conditions. Effects of variance were often in the opposite direction of those elicited by changes in the mean. Increasing aerial exposure at regular intervals had negative effects both on diversity of assemblages and on percent cover of filamentous and coarsely branched algae, but greater temporal variance drastically reduced these effects. The opposite was observed for the abundance of barnacles and encrusting coralline algae, where high temporal variance of aerial exposure either reversed a positive effect of mean intensity (barnacles) or caused a negative effect that did not occur under low temporal variance (encrusting algae). These results provide the first experimental evidence that changes in mean intensity and temporal variance of climatic variables affect natural assemblages of species interactively, suggesting that high temporal variance may mitigate the ecological impacts of ongoing and predicted climate changes.

Key words: aerial exposure; climate change; disturbance; diversity; mean intensity; rocky shore; temporal variance.

INTRODUCTION

There is increasing concern among scientists, policy-makers, and the general public about the societal and ecological consequences of climate change. Climate events can affect society directly by causing catastrophes and by threatening human health and indirectly by altering the functioning of ecological systems (Easterling et al. 2000b). Models of climate change generally agree that extreme events such as droughts, storms, and floods are becoming more frequent (Michener et al. 1997, Allen et al. 2000, Benestad 2003). Changes in the occurrence of extreme weather conditions produce concomitant changes to the mean and to the variance of the frequency distributions of corresponding climatic variables (Easterling et al. 2000a, b). For example, the incidence of extremely high temperatures results in long-term trends in mean values as well as in more or less pronounced increases in temporal variance, depending on the time scale considered (Hughes 2000, Muller and Stone 2001, Luterbacher et al. 2004).

Shifts in climate conditions can have profound ecological impacts, including changes in patterns of distribution, abundance, and diversity of species

(Hughes 2000, Zavaleta et al. 2003, Post and Forchhammer 2004), in the ability of assemblages to resist or to recover from other disturbances and in productivity (Grime et al. 2000). Most of these studies have, however, related average values of ecological variables to trends in average values of climate variables, offering little insights into the relative roles of climate means as compared with climate variances and into their interactions. Although some important studies have investigated the effects of changing the spatial or the temporal variability of processes such as competition (Hutchings et al. 2003), predation (Butler 1989, Navarrete 1996), and disturbance (Collins 2000, McCabe and Gotelli 2000), there seems to be little effort to understand effects of variance in the context of climate change.

Recent attention to these issues has led to the formulation of a framework for investigating the separate and combined effects of changes in mean intensity and spatial or temporal variance of ecological processes (Benedetti-Cecchi 2000a, 2003, Bertocci et al. 2005). The experimental designs proposed for these analyses can provide a useful starting point to investigate the effects of climate change on natural assemblages. High temporal variance implies that several climatic events occur over short intervals of time and that these alternate with long periods in which no event occurs (Benedetti-Cecchi 2003). Populations of long-

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¹ E-mail: lbenedetti@biologia.unipi.it

lived species may face more extreme physical conditions when climatic events such as droughts, floods and storms operate with high compared to low temporal variance over ecological time scales. This may be particularly true for less resilient species that recruit episodically and/or that have low dispersal capabilities (Gaines and Roughgarden 1985, Caley et al. 1996). In contrast, fugitive species may benefit from high temporal variance by taking advantage of newly released resources (Dayton 1971). These effects are, however, not independent of the average intensity of events. It is reasonable to expect that temporally variable events that operate with high intensity on average, have much larger effects on natural populations than events that operate with the same level of temporal variance, but with lower mean intensity. The idea that interactions between intensity and temporal variance of climate events may be responsible for major changes in populations and assemblages has never been investigated formally.

Assemblages of algae and invertebrates inhabiting intertidal habitats of rocky shores are exposed to variable physical conditions that can easily become detrimental to their life (Schonbeck and Norton 1978, Bertness and Leonard 1997, Dethier et al. 2005). Thermal stress due to aerial exposure and disturbance by waves are recurrent events that contribute to maintain spatial and temporal variability in the structure of these assemblages (Stephenson and Stephenson 1949, Dayton 1971, Sousa 1979). These effects can, however, be magnified by global warming and by the increasing frequency and intensity of storms, leading to quantifiable changes in patterns of abundance, distribution and diversity of species (Davison et al. 1993, Navarrete et al. 1993, Barry et al. 1995, Bertness et al. 1999, Sanford 1999).

While aerial exposure is a predictable event in systems characterised by large tides, it is less so where tides have low amplitude. In the northwest Mediterranean, for example, where tides rarely exceed 30 cm in amplitude, weather conditions can impose variable temporal patterns of aerial exposure and desiccation to sessile organisms offsetting any effect of the tide. Prolonged periods of calm sea and high barometric pressure can push the sea level below the mean low water level (MLWL) so that organisms remain exposed to air long enough to dry. Rough conditions, in contrast, maintain organisms constantly wet even at low tide. Therefore, changes in the timing of occurrence and duration of contrasting climatic conditions can have profound effects on the biota of these shores. Indeed, some climatic models predict changes in the intensity and temporal variance of storms, with strong events concentrating in short periods of time separated by longer periods of good weather (Muller and Stone 2001). These features make Mediterranean rocky seashores a valuable system to explore the ecological consequences of changes in mean intensity and temporal variance of climatic events.

We used a factorial experiment to test the hypothesis that temporal variance and mean intensity of aerial exposure would affect assemblages of rocky shores interactively, with temporal variance being more important under high than low mean intensity of exposure. Intensity of aerial exposure was defined as the time assemblages remained emersed over the study period. This was manipulated indirectly by transplanting organisms higher on the shore for defined periods of time. Temporal variance was defined with reference to the interval of time between successive manipulations. Organisms were moved up and down the shore either at regular or at variable intervals of time, while ensuring that the overall time spent in the high-shore position did not differ between levels of temporal variance over the duration of the study. Although this study was conducted under peculiar tidal conditions and focused on a specific aspect of climate change, it addressed the more general problem of whether the definition of extreme climate conditions in an ecological context should take into consideration both effects of mean intensity and temporal variance of events.

MATERIALS AND METHODS

Study sites and experimental design

This study was replicated at three sites (stretches of coast of 30–40 m long and hundreds to thousands of meters apart) chosen randomly to represent the exposed rocky shores south of Livorno, in the northwest Mediterranean. A first site was established in July 2001 and two additional sites were established in May 2002; experiments lasted two years at all sites. Assemblages on these shores are described in Benedetti-Cecchi (2000b, 2001). Briefly, low-shore assemblages were dominated by encrusting and filamentous algae (including several species in the genus *Ceramium*, *Polysiphonia*, and *Cladophora*) and by coarsely branched algae like *Laurencia obtusa* (Hudson) Lamouroux and *Chondria boryana* (J. Agardh) De Toni. In contrast, the barnacle *Chthamalus stellatus* (Poli) and cyanobacteria (*Rivularia* spp.) dominated higher on the shore. Although assemblages differed among habitats, most of the differences were due to changes in relative abundance of taxa rather than in species composition. A notable exception was the red alga *Rissoella verruculosa* (Bertoloni) J. Agardh, which was characteristic of the mid-shore habitat (Benedetti-Cecchi 2000b).

At each site, 32 cores 10 cm in diameter were drilled out of the rock from the low-shore habitat (0–5 cm above MLWL) using a diamond-tipped corer mounted on a petrol driller (Tanaka America, Auburn, Washington, USA). The cores, with intact assemblages on top, were then assigned randomly to the following treatments (defined according to the terminology commonly used in transplant experiments [Chapman 1986]), with eight cores per treatment: (1) disturbed cores (i.e., cores that were placed back to their original position immediately after drilling), (2) translocated

cores (i.e., cores moved to another place within the low-shore habitat), (3) cores transplanted to the mid-shore habitat (15–20 cm above MLWL), and (4) cores transplanted to the high-shore habitat (25–30 cm above MLWL). Within each treatment, four of the eight cores chosen at random were manipulated at almost regular intervals during the study period, whilst the remaining four cores were manipulated at variable intervals. This created a factorial experiment with two levels of temporal variance crossed with each treatment. Four replicate unmanipulated plots were also established in the low-shore habitat as controls. Thus, the experiment consisted of the following experimental conditions: unmanipulated controls (C), disturbed cores (low temporal variance, DL; high temporal variance, DH), translocated cores (low temporal variance, TL; high temporal variance, TH), cores transplanted to the mid-shore habitat (low temporal variance, ML; high temporal variance, MH) and cores transplanted to the high-shore habitat (low temporal variance, HL; high temporal variance, HH).

Intensity of aerial exposure was manipulated indirectly by transplanting the cores to different heights of the shore with respect to MLWL. Positions were chosen to represent distinct environmental conditions on the basis of our previous knowledge of the system (Menconi et al. 1999, Benedetti-Cecchi 2000b, 2001). With calm sea, the low-shore habitat was exposed to air only at low tide concomitant with high barometric pressure, the mid-shore habitat was always emersed at low tide and the high-shore habitat was emersed both at high and low tide. Small waves, like those produced by boats, washed both the low-shore and mid-shore habitats, but not the high-shore habitat. All habitats were almost continuously submersed when the sea was rough.

To obtain the condition of low temporal variance of aerial exposure, cores were transplanted into new holes either at mid-shore or high-shore heights for a month and then returned back to their original position in the low-shore habitat. This manipulation was applied approximately every three months, so that the overall length of time low-shore assemblages remained in the high-shore position was about four months in a year. Bad weather prevented a perfectly regular distribution of events in time. The condition of high temporal variance of aerial exposure was obtained by transplanting the cores at irregular intervals, but ensuring that the overall time cores were in the high-shore position was still four months per year. This enabled the independent manipulation of intensity and temporal variance of aerial exposure over the time scale of the study (Fig. 1).

Disturbed and translocated treatments were used to assess several potential artefacts associated with these manipulations (Chapman 1986, Kelaher et al. 2003). Disturbed cores controlled for the effects of drilling, manipulating and attaching the cores to the substratum. The translocation treatment controlled for possible

artefacts associated with moving the organisms to another place, irrespective of changes in vertical position. This was done by swapping positions between cores in the low-shore habitat.

Cores were attached to the substratum with epoxy putty (Subcoat S, Veneziani S.p.A, Lodi, Italy) at Site 1. This procedure ensured a firm attachment, but it was logistically demanding because it required new drills each time the cores had to be moved up or down the shore. A different technique was used at sites 2 and 3. Two stainless steel bars were anchored in opposite positions along each core with screws inserted into the rock. Each bar had an outward lip in correspondence to the top of the core that was used to screw the whole structure to the substratum. Regardless of type of manipulation, all cores were positioned into holes in such a way that their top was approximately at the same level of the natural substratum.

How well realized treatment conditions matched intended experimental effects depended on local climate. For example, rough weather could prevent aerial exposure of assemblages transplanted both to mid-shore and high-shore habitats. Similarly, calm sea and high barometric pressure might expose all habitats to aerial conditions. Thus, both good and bad weather could, in principle, eliminate intended differences among treatments. We addressed this issue in two ways. First, we collated daily data on the direction and speed of winds and on barometric pressure for the entire duration of the study (courtesy of the Istituto Idrografico e Mareografico di Pisa). These data served to determine the proportion of days intended experimental conditions were offset by adverse weather. Conditions in which rough sea might have prevented aerial exposure of both mid-shore and high-shore habitats at low tide were defined as those in which the daily average speed of winds was equal to or larger than 2.5 kn (1.286 m/s), in directions ranging from southeast to north. In contrast, conditions in which all habitats might have been exposed to air due to low sea levels were defined as those in which barometric pressure was equal to or larger than 570 and 574 hPa in winter and summer, respectively (to correct for seasonal changes in average aerial temperature) and in which the wind was either absent or blew seawards (eastern quadrant) at any speed.

Second, we deployed two replicate digital thermometers (FT-800 system, Econorma Sas, Treviso, Italy) at each tidal height in each site, in the proximity of transplanted cores. The thermometers were housed in PVC pipes that were screwed into the rock and measured either water or aerial temperature (depending on whether or not they were submersed) every hour for two months. At the end of the recording period the data were downloaded to a computer and the thermometers were deployed again in the field. These measurements were used as indicators of the status (emersed or submersed) of each habitat through time.

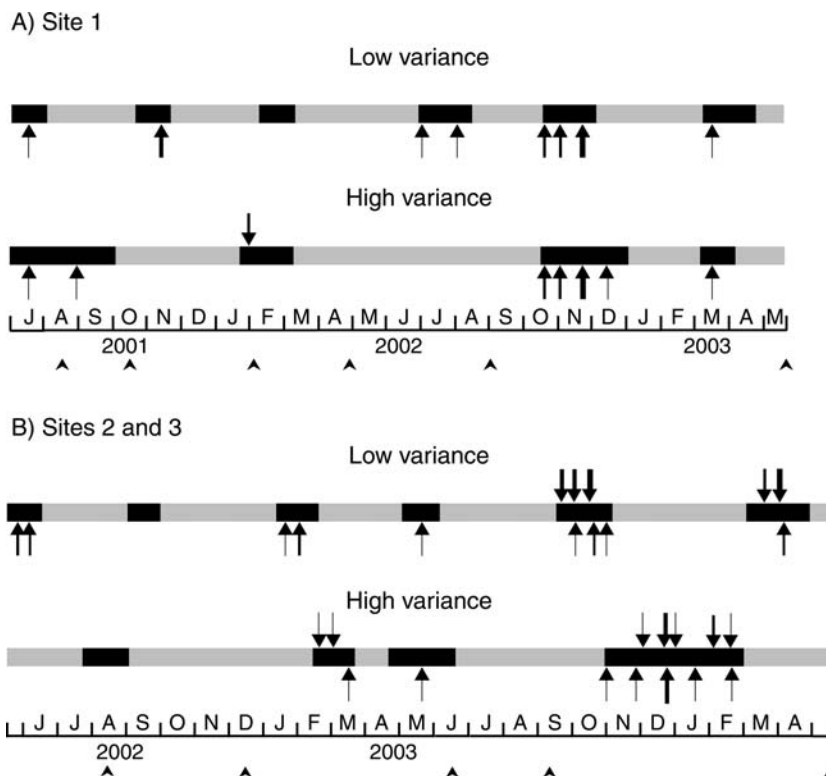


FIG. 1. Schematic representation of the experimental design. Black and gray blocks indicate periods in which cores were in high-shore and low-shore positions, respectively. Down-facing arrows indicate periods in which high barometric pressure and calm sea conditions exposed the low-shore habitat to air, while up-facing arrows indicate periods in which all habitats were submersed due to rough sea conditions. The temporal extent of these periods in which intended experimental conditions could not be maintained is indicated by the thickness of the arrows (with thinnest and thickest arrows corresponding to one and five days, respectively). Only events that coincided with the periods of transplantation are shown. Time of sampling is indicated by the arrowheads at the bottom of each panel.

Sampling and statistical analyses

Cores were sampled six times at site 1 and five times at sites 2 and 3. At each date of sampling, transplanted cores assigned to the two levels of temporal variance were in different phases with respect to the actual position on the shore and in relation to the interval of time since the last manipulation. To avoid the problem of confounding these contingencies with effects of variance, dates of sampling were chosen in such a way that the mean interval of time since the last manipulation was maintained as much as possible comparable across treatments (Fig. 1).

The number and percentage cover of dominant taxa on experimental cores and in unmanipulated quadrats were sampled nondestructively with a 7×7 cm plastic frame divided into 25 1.4×1.4 cm² sub-quadrats. Size of quadrats was dictated by the area available for sampling on each core and was appropriate to sample small organisms like those targeted in the study. Quantitative data were obtained by recording the number of sub-quadrats that contained a particular taxon and expressing final values as percentages. Organisms were identified to the most detailed level of taxonomic resolution

achievable in the field. Taxa that could not be identified at the level of species or genus were lumped into morphological groups (Littler and Littler 1980, Steneck and Dethier 1994).

Data were analysed using population-averaged generalized estimating equations (PA-GEEs), an extension of generalized linear models (GLMs) (Liang and Zeger 1986, Quinn and Keough 2002). PA-GEEs proved useful in the present context for two reasons. First, because the hypothesis investigated in this study applied to the entire duration of the experiment and not to single dates of sampling, an analysis that focused on population averages was desirable. Second, because experimental units were repeatedly sampled through time, a technique that could account for temporal autocorrelation was necessary. PA-GEEs enable the specification of a link function and an error structure for the residuals as in GLMs, and also take into account the correlation between observations on the same experimental unit. This results in robust estimates of variances and standard errors that can be used in hypothesis testing. Several patterns of correlation can be specified, although the procedure is robust to misspecification of the correlation structure (Hardin and Hilbe 2003). We used

TABLE 1. Summary of results from population-averaged generalized estimating equations (PA-GEEs).

Contrasts	Diversity		Encrusting corallines		Filamentous algae		<i>Chthamalus stellatus</i>		Coarsely branched algae	
	S1	S3	S1	S3	S1	S3	S1	S3	S1	S3
Control vs. others	NS	NS	NS	NS	NS	***	**	**	NS	NS
T	NS	NS	NS	*	**	**	**	NS	NS	NS
M	NS	*	***					NS	NS	**
H	NS	***	**					NS	NS	***
V	*	*	***	NS	**	NS	NS	NS	NS	NS
T × V	NS	NS	**	*	***	NS	**	NS	NS	NS
M × V	NS	*				NS		NS	NS	NS
H × V	NS	***				NS	*	NS	NS	*
M vs. T				*	**	**	**			
H vs. T				***	***	***	NS			
M × V vs. T × V			NS	NS	**		**			
H × V vs. T × V			NS	***	***		NS			

Notes: If disturbed and translocated cores did not differ significantly (translocated effect), then mid-shore and high-shore effects were examined by contrasting these treatments with the disturbed cores. If translocated and disturbed cores differed significantly, then mid-shore and high-shore terms were contrasted with the translocated cores. Similarly, if the effect of variance differed between translocated and disturbed cores (translocated × variance interaction), then the mid-shore × variance and high-shore × variance interactions were examined by contrasting these terms with the translocated × variance interaction. Full results of analyses are reported in Appendix A. Abbreviations: S1, site 1; S3, site 3; T, translocated; M, mid-shore; H, high-shore; V, variance; NS, not significant. Blank cells indicate that the test was not applicable.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

a first order autoregressive model AR(1) in all the analyses; this choice was motivated by the absence of clear seasonal patterns in the raw data, so that correlation of residuals was expected to decrease as the time lag between observations increased.

Two types of response variables were analyzed: number of taxa (used as a surrogate of diversity) and percentage covers of species or morphological groups. In the first case, a log-link function was used to relate the expected value of the response variable to the predictor variables, assuming a Poisson distribution of the error terms. In the second case, a Gaussian distribution was assumed for the errors and the identity link was used to relate the linear predictor with expected values of response variables. Tests of hypotheses were based on “treatment” contrasts and compared the unmanipulated condition vs. all other treatments in first place. Translocated cores were then compared to disturbed cores to detect possible artefacts associated with moving assemblages from one place to another within the same habitat. If this test was not significant, the effects of transplanting cores to the mid-shore and high-shore habitats were examined by contrasting these treatments with the disturbed cores. If translocated and disturbed cores differed significantly, the mid-shore and high-shore treatments were contrasted with the translocated cores. Similarly, if the effect of variance differed between translocated and disturbed cores (translocated × variance interaction), then the mid-shore × variance and high-shore × variance interactions were examined by contrasting these terms with the translocated × variance interaction (these are the mid-shore × variance vs. translocated × variance and high-shore × variance vs. translocated × variance contrasts in Table 1). Plots of residuals vs. predicted effects were examined after each

analysis to check for strong deviations from the distributional assumptions and homogeneity of variances.

RESULTS

Meteorological data indicated that rough sea conditions might have prevented aerial exposure of cores transplanted to mid-shore and high-shore habitats in 19 out of 235 days of experimental manipulation (8.1% of the time) for the condition of low temporal variance and in 15 out of 240 days (6.2% of the time) for the condition of high temporal variance (up-facing arrows in Fig. 1) at site 1. Similar values were obtained at sites 2 and 3, with cores transplanted to the mid-shore and low-shore habitats been submersed by waves in 17 out of 238 days of manipulation for the condition of low temporal variance (7.1% of the time) and in 10 out of 241 days for the condition high temporal variance (4.1% of the time). The number of days in which all habitats might have been exposed to air during the periods in which the transplanted cores were upshore were 0 at Site 1 and 10 out of 482 (2.1% of the time) and 24 out of 479 (5% of the time) for treatments exposed to low and high levels of temporal variance, respectively (down-facing arrows in Fig. 1) at sites 2 and 3. Collectively, these data indicated that the match between intended and realized experimental conditions was always above 90%.

Similar conclusions can be drawn from the temperature data, presented as daily average temperatures recorded between 10:00 and 18:00 (Fig. 2). Unfortunately, these data were not available for all habitats over the entire study period due to the malfunctioning or loss of some thermometers. Nevertheless, measurements indicated that the high-shore habitat was a distinct thermal environment experiencing more extreme tem-

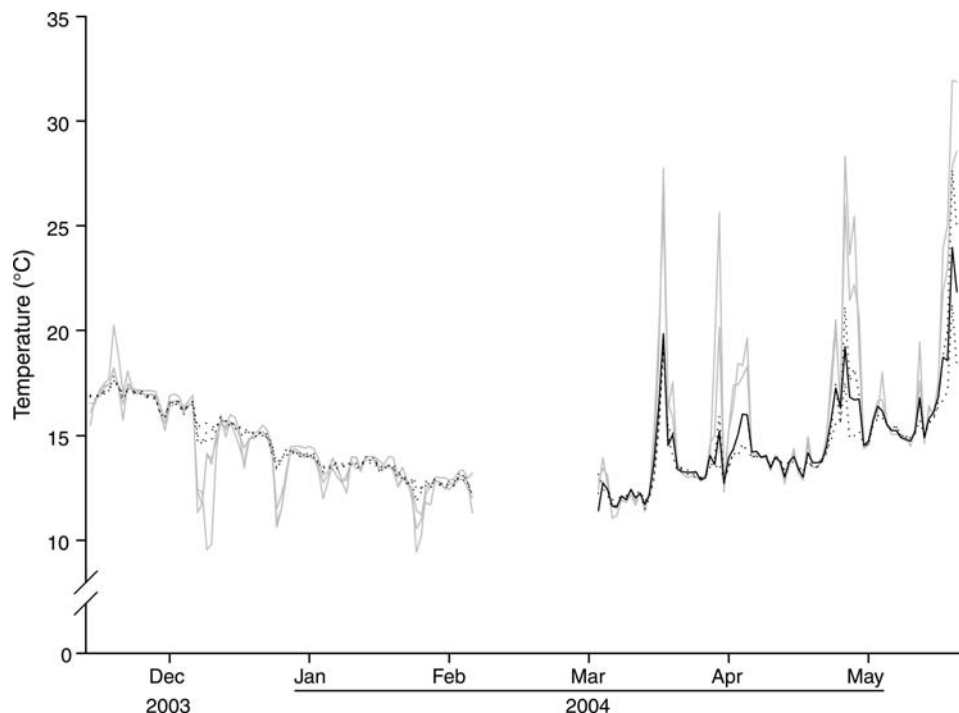


FIG. 2. Temporal trends in daily average temperatures (between 10:00 and 18:00 hours) in low-shore (dotted line, $n = 3$), mid-shore (black line, $n = 1$), and high-shore (gray line, $n = 3$) habitats. Originally there were two replicate thermometers in each habitat on each shore. Missing data are due to the malfunctioning or loss of thermometers.

perature values and larger temporal fluctuations than the low-shore habitat. These differences reflected the patterns of aerial exposure of the high-shore habitat, with emersion indicated by lower temperatures in winter (December–February) and by higher temperatures in spring (March–May) (Fig. 2). Analysis of data for the period December–February 2003 revealed significantly lower mean temperature values ($t = -2.5$, $P < 0.05$) and significantly larger mean temporal variances ($t = 9.8$, $P < 0.0004$) in the high shore compared to the low-shore habitat (these are one-tailed tests because of the directional nature of the hypotheses; both tests have 4 df and variances are homogenous when checked with Cochran's C test). Differences between the low-shore and mid-shore habitats were less clear. The single reading available for the mid-shore habitat in the period between March and May 2004 prevented general conclusions about this environment.

Assemblages transplanted to mid-shore and high-shore habitats changed both in terms of number and percentage cover of taxa from low-shore assemblages and in several cases effects differed in relation to the temporal variance of the manipulation (Fig. 3). Temporal variance significantly increased the mean number of taxa at site 1, although this effect was not unique to transplanted cores, but was also evident on disturbed and translocated cores (Fig. 3, Table 1). A similar result was observed at site 2 (Fig. 3), although no statistical analysis was undertaken in this case because many cores

went lost between time 2 and time 4, probably as a consequence of strong wave action. At site 3, in contrast, there were clear negative effects of transplantation on mean number of taxa, but only when cores were moved on a regular basis (Fig. 3). While treatment HL suffered a reduction of 32.4% in mean number of taxa compared to controls, this effects was only 16% in treatment HH. These patterns resulted in significant mid-shore \times variance and high-shore \times variance interactions in the analysis (Table 1).

Similar buffering effects of variance were observed for filamentous and coarsely branched algae (Fig. 3). At sites 1 and 2, effects of variance on filamentous algae differed between disturbed and translocated treatments, suggesting the occurrence of artefacts (Fig. 3). An effect of variance was, however, still evident at site 1 when cores transplanted to mid-shore and high-shore habitats were compared to translocated cores. **Percentage cover of filamentous algae was larger in treatments MH and HH compared to treatments ML and HL**, respectively, while no such difference occurred between TL and TH. These patterns resulted in significant mid-shore \times variance vs. translocated \times variance and high-shore \times variance vs. translocated \times variance contrasts in the analysis (Table 1). A similar effect of variance was observed at site 3 in the high-shore habitat (Fig. 3), although the test was not significant ($0.05 < P < 0.06$). **Also the percentage cover of coarsely branched algae was drastically reduced on cores transplanted to mid-**

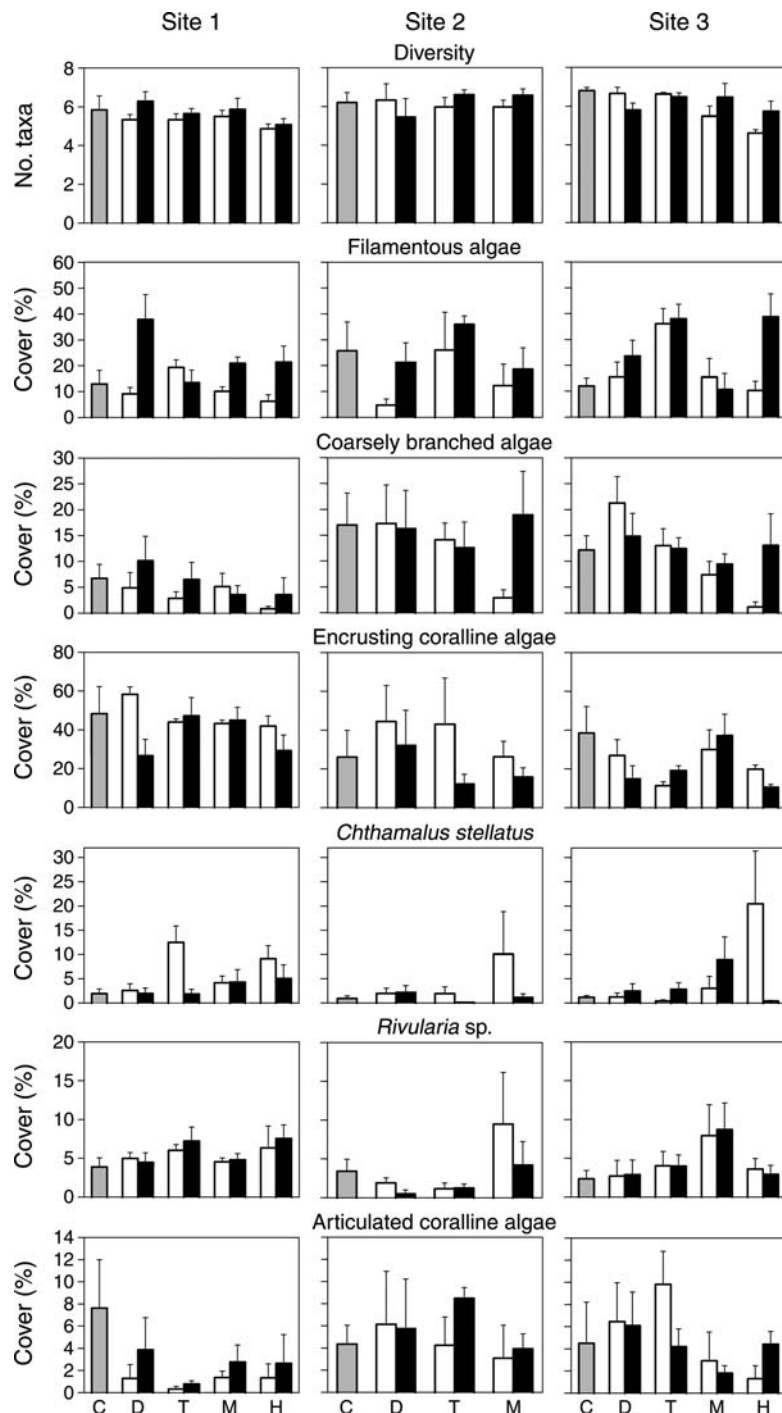


FIG. 3. Values of response variables (top row, no. taxa; other rows, percent cover by taxa) for the different treatments (mean \pm SE). Means were calculated by first averaging data from each core over time; $n = 4$ replicate cores except at site 2, where replication was sparse due to the loss of a large number of cores between the second sampling date and the fourth sampling date; cores that were lost contributed data only for the first part of the experiment). Abbreviations: C, controls (gray bars); D, disturbed; T, translocated; M, transplanted to the mid-shore habitat; H, transplanted to the high-shore habitat. Open bars show low variance; black bars show high variance.

shore (site 2) and high-shore (site 3) habitats at low, but not at high variance. The latter effect was statistically significant (Table 1).

In contrast to filamentous and coarsely branched algae, the percentage cover of encrusting coralline algae and *Chthamalus stellatus* were adversely affected by temporal variance (Fig. 3). Although disturbed and translocated treatments responded differently to a change in variance, as highlighted by significant translocated \times variance interactions (Table 1), there were differences between treatments HL and HH that emerged over and above any possible effect of the experimental procedure. A nonsignificant trend was evident for encrusting coralline algae at site 1 and a significant effect was observed at site 3 (contrast $H \times V$ vs. $T \times V$ in Table 1). At this site, the effect of variance in the high-shore habitat was in opposite direction of that observed for the translocated treatment in the low-shore habitat (Fig. 3). *C. stellatus* was similarly impacted by variance when transplanted to the mid-shore (Site 2) and to the high-shore (sites 1 and 3) habitats. The most dramatic effect occurred at site 3 in the absence of artefacts, as highlighted by the significant high-shore \times variance interaction in Table 1. At site 1, percentage cover of barnacles was lower on cores translocated at high variance than on cores translocated on a regular basis, but this effect of variance disappeared in the mid-shore habitat resulting in a significant $M \times V$ vs. $T \times V$ interaction (Table 1). Finally, no clear effects of treatments were observed for *Rivularia* sp. and articulated coralline algae (Fig. 3, Table 1).

DISCUSSION

Our results revealed interactive effects of mean intensity and temporal variance of aerial exposure on assemblages. Effects of variance were often in opposite direction of those elicited by changes in the mean. Increasing aerial exposure had negative effects both on diversity of assemblages and on percentage cover of filamentous and coarsely branched algae, but these effects were buffered by high temporal variance. The opposite was observed for barnacles (*Chthamalus stellatus*) and encrusting coralline algae, where high temporal variance of aerial exposure either reversed a positive effect of mean intensity (barnacles) or determined an impact that did not occur under low temporal variance (encrusting algae). The original hypothesis that temporal variance of aerial exposure was more important at high than low levels of mean intensity was supported for some response variables (e.g., encrusting coralline and filamentous algae at sites 1 and 3 and *C. stellatus* and coarsely branched algae at site 3; see also the regression coefficients in Appendix), but not others (e.g., barnacles and coarsely branched algae at site 1 and number of taxa at sites 1 and 3). In some cases (e.g., filamentous algae), effects of variance were also observed in disturbed and translocated treatments. When this occurred, comparison of transplanted and trans-

located treatments usually revealed the existence of intended effects of treatments over and above any effect of the experimental procedure. Effects of treatments could vary in magnitude and/or direction among sites, indicating that the sequence with which experimental manipulations were applied (sequences differed between site 1 and sites 2 and 3, see Fig. 1), intrinsic differences among sites or a combination of these factors, contributed to some of the variability observed in the data.

Much of our current understanding of ecological responses to environmental change comes from studies that have contrasted experimental conditions differing in mean values of predictor variables, e.g., CO_2 (Zavaleta et al. 2003), or in which effects of mean and variance are varied simultaneously through changes in the frequency of events, e.g., disturbance (Collins 2000). Recent studies have shown that changes in spatial or temporal variance of physical and biological processes can have significant effects on species and assemblages under constant mean conditions (Cardinale et al. 2002, Day et al. 2003, Hutchings et al. 2003). Our results add the almost unique evidence that effects of variance may not be independent of the mean. Therefore, further conceptual and methodological steps are required in order to improve our understanding of ecologically variable phenomena, including interactions between the mean and the variance of predictor variables (Benedetti-Cecchi 2003).

We predicted that high temporal variance of aerial exposure would have produced the largest effects when assemblages were transplanted to the high-shore habitat, under the most extreme conditions of aerial exposure (treatment HH). In principle, aerial exposure was expected to produce a variety of ecological responses, including both negative and positive effects on abundance, depending on the ability of organisms to withstand desiccation and on their capacity to colonize in emerged compared to submersed conditions. Indeed, both types of effects were observed in treatment HH and patterns appeared related to the life-history traits of taxa considered. Encrusting corallines were the most abundant taxa in the low-shore habitat, where they resisted colonization by other organisms. Sloughing of epithelial cells and grazing (by limpets) probably combined to maintain these algae free of epiphytes, as also reported in other studies (Steneck 1986). Encrusting corallines are, however, sensitive to desiccation so that extreme conditions of aerial exposure might have reduced their cover creating favourable conditions for the colonization of filamentous and coarsely branched algae. These latter groups included fast-growing species that were capable of recovering quickly from disturbance (Benedetti-Cecchi and Cinelli 1994, Benedetti-Cecchi 2000b) and a turf-like habit probably enabled them to withstand periodic aerial exposure by maintaining moist conditions.

Barnacles were numerically dominant high on the shore at the study sites, as a result of a combination of

low recruitment and greater mortality (possibly due to algal overgrowth) in the low-shore habitat (Benedetti-Cecchi et al. 2000). Therefore, it was not surprising that the abundance of these organisms increased when cores were transplanted upshore. The interesting result was that such an increase occurred under low, but not under high temporal variance of aerial exposure. This suggested that the long intervals between consecutive transplantations imposed by treatment HH in which cores were in the low-shore habitat, were detrimental to young barnacles which, in contrast, could withstand the shorter intervals of submersion determined by treatment HL.

Replacement of encrusting corallines and barnacles by the more diversified groups of filamentous and coarsely branched algae produced an increase in diversity in treatments exposed to high temporal variance of aerial exposure. Although this effect was more pronounced at site 3, it showed that temporal variance alone, i.e., with no concomitant changes in mean intensity, could affect diversity. This result has broad theoretical and empirical implications because patterns of diversity are commonly explained in relation to changes in either mean intensity of disturbance (Connell 1978, Mackey and Currie 2001) or as a function of frequency of disturbance (Miller 1982, Collins 2000, McCabe and Gotelli 2000), which combines both intensity and temporal variance (Benedetti-Cecchi 2003). The possibility that temporal variance alone can affect patterns of diversity opens new avenues of research. In particular, understanding the time scales over which variance of disturbance might be relevant in relation to the life histories, patterns of dispersal and colonizing capabilities of species, seems pressing in order to enable more accurate predictions of the consequences of climate change on global diversity (Fields et al. 1993, Barry et al. 1995, Hughes 2000).

Our temperature data indicated that the high-shore habitat was more variable than the mid-shore and low-shore habitats. Thus, in addition to the level of temporal variance imposed experimentally, organisms transplanted to the high-shore habitat were also exposed to larger natural fluctuations of the thermal environment. Future experiments might be designed to quantify the increase in environmental variance that an organism would face in the high-shore compared to the low-shore habitat, using the procedures described by Denny and co-workers (Denny et al. 2004).

Future studies should also clarify the specific mechanisms whereby variance affects assemblages. Although identifying such mechanisms was beyond the scope of the present study, a few possibilities deserve particular attention. First, variance may increase the chance that fluctuations in environmental variables exceed some physiological threshold for any given organism. This is analogous to the mechanism proposed to relate the risk of extinction of natural populations to the variability of the environment (Inchausti and Halley 2003). Alternative, but not mutually exclusive explanations, include

cumulative effects of variance on populations and the possibility that large temporal fluctuations in environmental variables may affect (increase or decrease) the likelihood with which events coincide with important periods of reproduction and recruitment of organisms (Bertocci et al. 2005).

A potential caveat must, however, be considered when interpreting the results of the present study. By transplanting the cores upshore, we did not only increase exposure of low-shore organisms to aerial conditions, but also changed the biological features of the surrounding habitat. Climate events would obviously affect only aerial exposure and not the surrounding habitat, at least on the short term. Thus, for climate conditions to explain our results, it is necessary to rule out possible effects due to changes in the strength of biological interactions such as grazing and competition across the vertical gradient of the shore. We believe our results were largely driven by physical processes because a companion experiment (data not shown) indicated that most effects of variance associated with treatment HH disappeared when the cores transplanted to the high-shore habitat were masked with plastic screens that reduced incident radiation and temperature. In addition, neither changes in biological interactions nor variation in intensity of recruitment across the vertical gradient of the shore would explain the observed differences between treatments HL and HH, as these treatments were placed in the same habitat.

A large number of ecological effects have been ascribed to recent shifts in climate conditions, including changes in physiology (Helmuth et al. 2002), distribution (Hughes 2000, Walther et al. 2002), and diversity (Kappelle et al. 1999) of native and invading species. These effects have been largely interpreted in terms of changes in mean values of climatic variables such as temperature, although some studies have explicitly acknowledged that changes in the incidence of extreme events and in their temporal variability can have profound effects on ecological systems (Gaines and Denny 1993, Easterling et al. 2000a). These studies also recognized the difficulties inherent in interpreting and predicting the effects of variable processes due to lack of empirical data. Here we have provided the first unequivocal evidence that mean intensity and temporal variance of climatic events interactively affected natural assemblages of rocky seashores, suggesting that large temporal variance may mitigate the ecological impacts of ongoing and predicted climate changes in these systems. Because shifts in the mean as well as in the variance of climatic variables occur at global scales, understanding these effects will be key to predict the ecological and societal consequences of climate variability.

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APPENDIX

Detailed results of statistical analyses using population-averaged generalized estimating equations (*Ecological Archives* E087-151-A1).