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Changes in temporal variance of rocky shore organism abundances in response to manipulation of mean intensity and temporal variability of aerial exposure

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ABSTRACT: We tested the hypothesis that mean intensity and temporal variability of aerial exposure exert interactive effects on temporal variance in abundances of algae and invertebrates on rocky shores of the NW Mediterranean Sea. Transplantations of assemblages to different heights on the shore were used to manipulate the aerial exposure indirectly. Different periods of residency of assemblages at each height were distributed over 2 yr to generate different levels of temporal variability of aerial exposure. Total durations of periods of emersion and submersion of organisms were kept comparable across all treatments to avoid confusion between intensity and temporal variability of aerial exposure. Interactive effects between these 2 factors were observed for some response variables (filamentous and encrusting coralline algae, *Chthamalus stellatus*, *Patella* spp. and number of taxa), with mean intensity of aerial exposure either magnifying or dampening effects of temporal variability. Specific responses were related to the life histories of the focal organisms, in particular the ability to resist and to recover from aerial exposure. The experimental design we used can help in separating effects of shifts in mean values and temporal variances of climate variables in studies of climate change.

KEY WORDS: Aerial exposure · Mean intensity · Temporal variance · Disturbance · Rocky shore · Mediterranean Sea · Climate change

INTRODUCTION

Modifications of climatic variables through human activities can cause drastic changes in natural assemblages (Kappelle et al. 1999, Hughes 2000, Walther et al. 2002). Models of climate change predict an increase in the frequency and shifts in the temporal patterns of extreme events such as storms (Michener et al. 1997), droughts and floods (Easterling et al. 2000a,b), exceptional air (Folland & Karl 2001) and sea temperatures (Gaines & Denny 1993), leading to changes in patterns of distribution, abundance and diversity of species (Hughes 2000, Zavaleta et al. 2003, Post & Forchammer 2004) and in productivity (Grime et al. 2000).

Intertidal assemblages on rocky shores are particularly vulnerable to changes in climate variables (Raffaelli & Hawkins 1996). Thermal fluctuations and desiccation due to aerial exposure can drastically affect spatial and temporal patterns in assemblages (Dayton 1971, Denny 1988). Underlying mechanisms include photoinhibition (Davison et al. 1993), and thermal (Schonbeck & Norton 1978) and osmotic stresses (Hawkins & Jones 1992). These effects can be exacerbated by climate events such as global warming and storminess (Navarrete et al. 1993, Barry et al. 1995, Sanford 1999), which in turn can affect biological interactions (Bertness & Leonard 1997, Bertness et al. 1999, Molina-Montenegro et al. 2005).

In the NW Mediterranean Sea, where the amplitude of tides is very small, the occurrence of aerial exposure can be difficult to predict. In this system, current weather conditions can buffer or magnify any tidal ef-

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fect. Prolonged periods of high barometric pressure and calm seas can push the sea level below the Mean Low Water Level (MLWL), exposing sessile organisms to air for long periods. Such conditions may affect the physiology (Silva et al. 2005) and growth of organisms (Davison et al. 1993, Tanaka & Nakaoka 2004, Dethier et al. 2005), their tolerance to the impact of waves (Haring et al. 2002) and grazing (Buschmann 1990, Harley 2003). In contrast, waves reduce drying out of intertidal organisms during low tides and can have positive effects on transport of nutrient particles to filter-feeders (Hawkins & Jones 1992). However, the prolonged submersion of organisms living high on the shore can result in enhanced mortality due to predation (Minchinton & Scheibling 1993) and overgrowth (Denley & Underwood 1979). Therefore, changes in temporal patterns in the occurrence of contrasting weather conditions can have drastic effects on these assemblages. Climate data indicate that such changes are already occurring, with temporal variance of disturbance increasing as strong storms become aggregated over brief periods of time and the duration of calm weather conditions between stormy periods increases (Muller & Stone 2001).

In the present study we used a factorial experiment to test the hypothesis that mean intensity and temporal variability of aerial exposure would affect temporal variance in the abundance of taxa interactively (hereafter we will refer to temporal variability as the effect of the predictor variable, while temporal variance will refer to fluctuations in response variables). Aerial exposure was manipulated indirectly by transplanting organisms to 2 different heights on the shore. Such transplantations were potentially associated with different periods of emersion, resulting in different intensities of aerial exposure. Levels of temporal variability were obtained by moving organisms up and down the shore either at regular or at variable intervals of time, while maintaining the overall duration of aerial exposure constant among treatments. Because assemblages were composed mainly of fast-growing organisms, we predicted that temporal variability of aerial exposure would enhance temporal fluctuations in abundances of target species (the response variables examined). Effects of variability were, however, expected to be larger under mild than under intense disturbances, the latter condition reducing the mean values of response variables to such low values that large fluctuations would not occur (Taylor 1961).

MATERIALS AND METHODS

Study site. The study was carried out at 2 sites (stretches of shore 30 to 40 m long, about 1000 m apart) on the rocky coast of Calafuria in the NW Mediterranean Sea (43° 30′ N, 10° 20′ E). Site 1 was set up in July 2001, Site 2 in May 2002 and the experiment lasted 2 yr at both sites. The portions of shore line examined extended from 0 to about 30 cm above MLWL. Sessile organisms were exposed to air during periods of calm weather and high barometric pressure. Highshore (20 to 30 cm above MLWL) assemblages were dominated by the barnacle *Chthamalus stellatus* (Poli) and cyanobacteria (*Rivularia* spp.). The fleshy red alga *Rissoella verruculosa* (Bertoloni) J. Agardh characterized the midshore habitat (10 to 20 cm above MLWL), while lowshore (0 to 10 cm above MLWL) assemblages were dominated by encrusting (mainly coralline algae and the brown alga *Ralfsia verrucosa* (Areshough) J. Agardh) and filamentous algae (including several species in the genera *Ceramium*, *Polysiphonia* and C*ladophora*). At this height of the shore, mussels (*Mytilus galloprovincialis* Lamarck), calcareous algae such as *Corallina elongata* Ellis *et* Solander and *Jania rubens* (L.) Lamouroux and coarsely branched algae such as *Laurencia obtusa* (Hudson) Lamouroux and *Gastroclonium clavatum* (Roth) Ardissone were present. The limpets *Patella aspera* Gmelin, *P. caerulea* L. and *P. rustica* L. were the most common herbivores. Further descriptions of these assemblages are provided by Benedetti-Cecchi (2000, 2001).

Experimental design. A total of 32 cores (10 cm in diameter) were drilled out of the rock from the lowshore habitat (0 to 5 cm above MLWL) at each site using a diamond-edged corer mounted on a petrol drill (TED-262L, Tanaka). Eight cores bearing intact assemblages were assigned at random to each of the following treatments: (1) disturbed cores (D: cores drilled out of the rock and then placed back in their original position), (2) translocated cores (T: cores exchanged horizontally within the same height on the shore), (3) cores transplanted to the midshore habitat (M: 15 to 20 cm above MLWL) and (4) cores transplanted to the highshore habitat (H: 25 to 30 cm above MLWL). Within each treatment, 4 cores were manipulated at almost regular intervals of time, while the remaining cores were manipulated at variable intervals (variability was calculated as the variance of the intervals of time between successive manipulations). Four unmanipulated plots were established in the lowshore habitat as controls.

Transplantation of cores to different heights on the shore was used to manipulate the intensity of aerial exposure indirectly. As suggested by previous studies conducted on the same shore, when seas were calm the lowshore habitat emerged only at low tide during periods of high barometric pressure, the midshore habitat always emerged at low tide and the highshore habitat was always exposed to air. When seas were rough, all habitats were almost continually submerged (Menconi et al. 1999, Benedetti-Cecchi 2000, 2001). Temperature measurements taken over time at each height on the shore indicated that the lowshore, midshore and highshore habitats corresponded to distinct thermal environments (Benedetti-Cecchi et al. 2006).

Low variability in aerial exposure was obtained by transplanting the cores into new holes at midshore or highshore levels for a month, then moving them back to their original positions, and repeating this manipulation approximately every 3 mo. In this way, assemblages remained in the upshore position for about 4 mo yr^{-1} in total. Rough seas prevented a perfectly regular distribution of transplantations during the experiment. High variability was obtained by transplanting the cores irregularly, with the caveat that the overall residency time of cores in upshore positions still totalled 4 mo yr^{-1}. This allowed separation of the effects of intensity and temporal variability of aerial exposure.

Transplantation may produce several procedural artefacts (Chapman 1986, Kelaher et al. 2003). Disturbed cores were established to control for potential effects of drilling, manipulating and reattaching the cores, while translocation controlled for artefacts associated with moving organisms to another place, irrespective of changes in height on the shore.

At Site 1, cores were attached to the substratum with epoxy putty (Subcoat S, Veneziani). At Site 2, 2 L-shaped stainless steel bars were screwed to each core so that they were diametrically opposite one another, and the projecting lugs were used to screw the whole structure to the substratum. This technique avoided the need for new drillings to remove the hardened epoxy putty each time the cores had to be moved. All cores were positioned into holes taking care that their upper surfaces were approximately flush with the adjacent substratum.

Both good and bad weather may offset intended differences among treatments. Waves may submerge assemblages transplanted to midshore and highshore habitats preventing aerial exposure, while calm seas and high barometric pressure might occasionally expose the lowshore habitat to air. Daily data on barometric pressure, the direction and speed of winds and hourly data on temperature in the proximity of cores were collected to address this issue. These data indicated a close match (>92%) between intended and realized experimental conditions and will not be discussed further here (Benedetti-Cecchi et al. 2006).

Sampling and statistical analyses. All cores and a new set of controls chosen randomly on each occasion were sampled 6 (at Site 1) and 5 (at Site 2) times over the course of the experiment. At each sampling date, transplanted cores assigned to the 2 levels of temporal variability 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 effects with variability in aerial exposure, sampling dates were chosen in such a way that the mean interval of time since the last manipulation was comparable across treatments. This corresponded to about 60 and 54 d for Sites 1 and 2, respectively.

Organisms were sampled visually with a 7 × 7 cm plastic frame divided into 25 sub-quadrats of 1.4 × 1.4 cm. The frame was centred within the area available on the top of each core. Given the small size of the organisms sampled and their spatial variability, mostly on scales of centimetres (Benedetti-Cecchi 2001), the size of quadrats was considered appropriate for obtaining unbiased estimates of abundances (Andrew & Mapstone 1987). Sessile organisms were quantified as number of sub-quadrats that contained a particular taxon, expressing final values as percentages, while motile animals were counted as number of individuals on each core or unmanipulated control. Organisms were identified to the most detailed level of taxonomic resolution achievable in the field, aggregating into morphological groups those taxa that could not be identified at the level of species or genus.

Analysis of variance (ANOVA) was used to examine effects of treatments on temporal variance in abundance of individual taxa during the course of the experiment. Variances were obtained from the repeated measures of abundance of each taxon on each core over the course of the study (i.e. calculating the variance of the abundance of taxa across all the dates of sampling for each core). Although these measures were not independent, a single measure of temporal variance was obtained from each core for a given taxon. These measures were considered independent for the purpose of the analysis. Taxa that were present only occasionally at a site or that had very low abundances throughout the study were excluded from the analysis. Thus, the taxa analysed at one site were not necessarily the same as those analysed at the other site. The analysis included the *a priori* contrast of unmanipulated controls versus all 'other' conditions (treatments), and partitioning of the mean square associated with 'other' conditions into the effects of the crossed factors Treatment (fixed, 4 levels) and Variability (fixed, 2 levels). At Site 2, one replicate core was lost for each of the treatments. Missing data were replaced with the means obtained from the remaining 3 replicate cores in each treatment and the degrees of freedom were adjusted accordingly in analyses, leading to 24 degrees of freedom in the residual term instead of 27 (Underwood 1997). When necessary, data were log-trans-

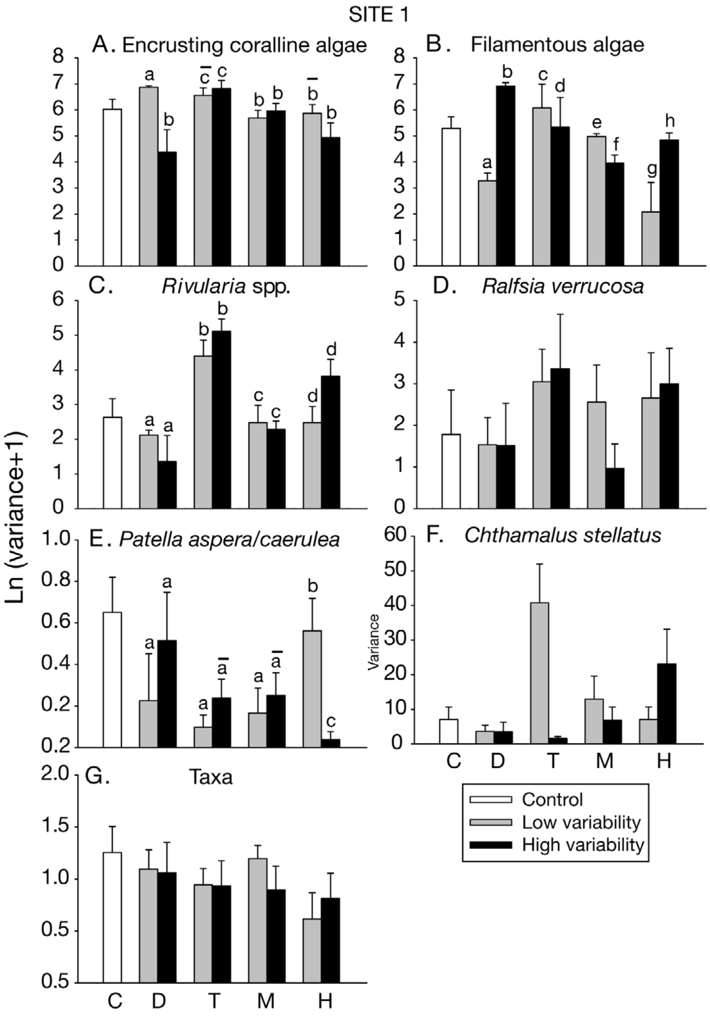

Fig. 1. Temporal variance (means + SE, n = 4) in abundance and numbers of taxa at Site 1 for unmanipulated controls (C) and for disturbed (D) and translocated (T) cores in the lowshore habitat and for cores transplanted to the midshore (M) and highshore (H) habitats. Treatments D–H were repeated with a regime of low and high temporal variability. Data were collected on 6 sampling dates over a period of 2 yr. Different letters indicate means that differed significantly (SNK test, p = 0.05). Bars above letters indicate treatments that could not be ranked unequivocally when compared to other treatments within the same level of variability. Thus, only comparisons between high and low levels of variability are appropriate in these cases. Note that different panels have different scales

formed to homogenize variances (after Cochran's *C* test). SNK tests were used for *a posteriori* comparisons of the means ($\alpha = 0.05$). When disturbed and translocated treatments differed, indicating artefacts associated with the experimental procedure, the latter treatment provided the reference condition against which to compare effects of mean intensity and temporal variability of aerial exposure (using SNK tests). Otherwise disturbed cores were used for reference.

RESULTS

Site 1

Increasing aerial exposure reduced temporal variance in abundance of encrusting coralline algae (Fig. 1A). This effect was influenced by temporal variability of exposure for disturbed cores, only resulting in a significant Treatment × Variability interaction (Table 1). Despite differences between disturbed cores and the other treatments, a comparison of cores transplanted to midshore and highshore habitats with translocated cores (moved laterally within shore levels) indicated a consistent effect of aerial exposure that was independent of temporal variability of disturbance.

A similar response was observed for filamentous algae, with differences between disturbed and translocated cores suggesting the occurrence of artefacts. However, when transplanted and translocated cores were compared, a significant negative effect of increasing aerial exposure became evident for treatments manipulated at low, but not at high variability (Fig. 1B). Collectively, these patterns produced a significant Treatment × Variability interaction in the analysis (Table 1).

Temporal variance in abundance of *Rivularia* spp. was significantly larger on translocated than on disturbed cores, suggesting a positive effect of moving these organisms from one place on the shore to another at the same tidal height (Fig. 1C). Despite this effect, temporal variance in abundance was significantly reduced on cores transplanted upshore compared to translocated cores, with the lowest values observed in the midshore habitat. These effects were independent of temporal variability of aerial exposure and resulted in a significant main effect of Treatment (Fig. 1C, Table 1).

Temporal variance in the density of *Patella aspera/caerulea* was significantly larger in control plots than in the other experimental conditions (which could not be distinguished statistically) (Fig. 1E, Table 1). Nevertheless, a trend was evident towards an increase in temporal variance on cores transplanted to the highshore habitat with low temporal variability, while cores transplanted to the same habitat with high temporal variability displayed the lowest level of temporal variance in density of grazers. These 2 treatments differed significantly when compared with the SNK test (Fig. 1E).

Experimental conditions had no significant effects on temporal fluctuation in abundance of *Ralfsia*

Table 1. ANOVA for variance in abundance and numbers of taxa across 6 sampling dates for cores and unmanipulated controls established at Site 1. *F*-ratio for each test was calculated using the Residual MS as denominator

Source of variation	df	Encrusting corallines			Filamentous algae			*Ralfsia verrucosa*			*Rivularia* spp.			*P. aspera*/ *caerulea*		
		MS	*F*	p	MS	*F*	p	MS	*F*	p	MS	*F*	p	MS	*F*	p
Condition	8	5.32			5.14			2.82			2.41			0.49		
Control vs. Others	1	1.90	2.52	>0.1	0.01	0.00	>0.9	1.09	0.31	>0.5	0.83	0.93	>0.3	0.88	10.0	<0.01
Among Others	7	3.17			5.88			3.06			2.63			0.14		
Treatment (Tr)	3	2.56	3.40	<0.05	2.19	1.25	>0.3	5.31	1.49	>0.2	4.14	4.66	<0.01	0.07	0.75	>0.5
Variability (V)	1	4.18	5.55	<0.05	17.03	9.73	<0.01	0.46	0.13	>0.7	0.52	0.58	>0.4	0.00	0.00	>0.9
Tr × V	3	3.45	4.58	<0.05	5.84	3.34	<0.05	1.69	0.48	>0.7	1.82	2.05	>0.1	0.26	2.90	>0.05
Residual	27	0.75			1.75			3.55			0.89			0.09		
Cochran's *C*-test		*C* = 0.450, p > 0.05			*C* = 0.336, p > 0.05			*C* = 0.214, p > 0.05			*C* = 0.287, p > 0.05			*C* = 0.275, p > 0.05		
Transformation		Ln(*x*+1)			Ln(*x*+1)			Ln(*x*+1)			Ln(*x*+1)			Ln(*x*+1)		

Source of variation	df	*Chthamalus stellatus*			No. of taxa		
		MS	*F*	p	MS	*F*	p
Condition	8	7.45			1.22		
Control vs. Others	1	1.30	0.02	>0.8	3.93	2.22	>0.1
Among Others	7	8.33			0.84		
Treatment (Tr)	3	7.87	0.14	>0.9	1.43	0.81	>0.4
Variability (V)	1	15.76	0.28	>0.5	0.00	0.00	>0.9
Tr × V	3	6.30	0.11	>0.9	0.52	0.29	>0.8
Residual	27	55.74			1.77		
Cochran's *C*-test		*C* = 0.446, p < 0.05			*C* = 0.144, p > 0.05		
Transformation		None			Ln(*x*+1)		

verrucosa, *Chthamalus stellatus* and number of taxa (Fig. 1D,F,G, Table 1).

Site 2

Temporal variance in abundance of encrusting coralline algae at this site was significantly larger in unmanipulated plots than the average in other conditions (Fig. 2A, Table 2). Although differences among experimental conditions were not significant (Table 2), a reverse in the effect of temporal variability of aerial exposure between cores transplanted to midshore and highshore habitats was evident (Treatment × Variability interaction in Table 2: $0.05 < p < 0.1$). Whilst variability of aerial exposure produced a slight increase in temporal variance in the midshore habitat, the reverse occurred in the highshore habitat. These patterns were supported by post hoc comparisons of treatment means with the SNK test (Fig. 2A).

A significant main effect of Treatment was detected for filamentous algae (Fig. 2B, Table 2). Although differences in temporal variance occurred between disturbed and translocated cores, transplanting these algae higher on the shore elicited significant changes in temporal variance with respect to the translocated treatment. In particular, the largest temporal fluctuations in abundance were observed in the highshore habitat and the lowest occurred in the midshore habitat (Fig. 2B).

A main effect of Treatment was observed also for articulated coralline algae, which were abundant enough at this site to be included in the analyses (Table 2). Increasing aerial exposure significantly reduced temporal variance in abundance of these algae, with effects emerging despite differences between translocated cores (Fig. 2C).

Treatments had no effects on temporal variance in abundance of *Ralfsia verrucosa* (Fig. 2D), coarsely branched algae (Fig. 2E) or *Rivularia* spp. (Fig. 2F). In contrast, *Chthamalus stellatus* was significantly more variable on cores maintained at high than low levels of temporal variability of aerial exposure in all but the highshore habitat where the reverse occurred (Fig. 2G). These patterns resulted in a significant Treatment × Variability interaction in the analysis (Table 2).

A significant Treatment × Variability interaction also resulted from the analysis of temporal variance in number of taxa (Fig. 2H, Table 2). While temporal variability of aerial exposure had no significant effect on disturbed and translocated cores, fluctuations in abundance were enhanced significantly under a regime of high temporal variability of aerial exposure on cores transplanted to the midshore and highshore habitats (Fig. 2H).

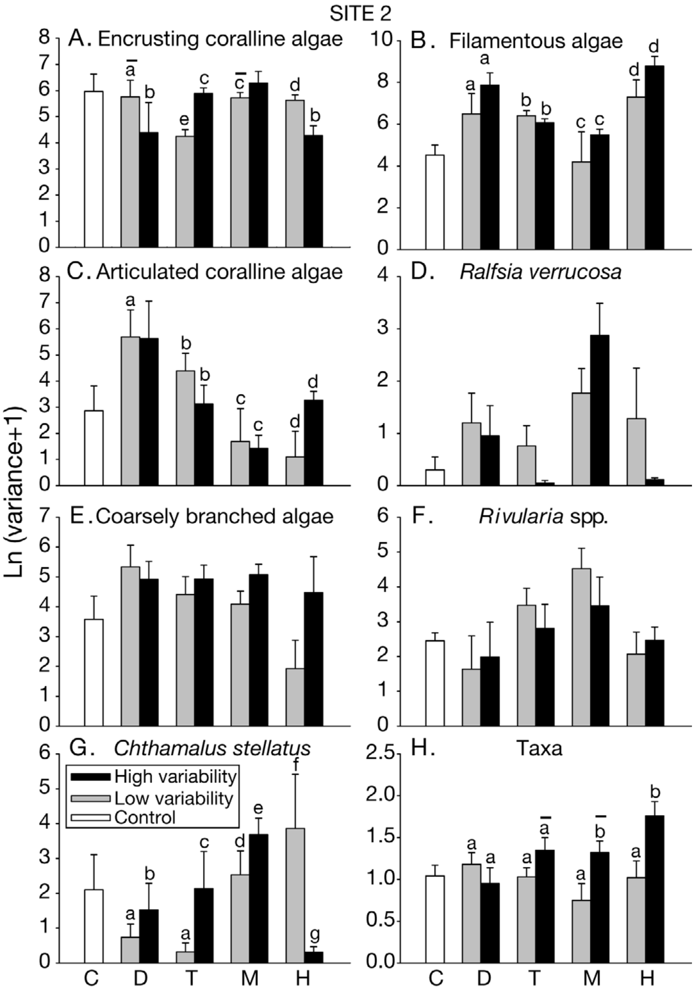

Fig. 2. Temporal variance in abundance and numbers of taxa at Site 2 for unmanipulated controls (C) and for disturbed (D) and translocated (T) cores in the lowshore habitat and for cores transplanted to the midshore (M) and highshore (H) habitats. Data are means (+SE), with n = 3 for treatment M at low and high variability and for treatment H at high variability, n = 4 in all other treatments. Data were collected on 5 sampling dates over a period of 2 yr. Notation as in Fig. 1. Note that different panels have different scales

DISCUSSION

This study demonstrated variable responses of organisms to changes in mean intensity and temporal variability of aerial exposure. While temporal fluctuations in abundance of organisms were influenced interactively by these factors in some cases (filamentous algae and *Patella aspera/caerulea* at Site 1 and encrusting coralline algae, *Chthamalus stellatus* and number of taxa at Site 2), intensity of aerial exposure operated independently of temporal variability in others (encrusting corallines and *Rivularia* spp. at Site 1 and filamentous and articulated coralline algae at Site 2). In the presence of interactions, increasing temporal variability of aerial exposure either reduced (*Patella aspera/caerulea* at Site 1 and *C. stellatus* and encrusting corallines at Site 2) or enhanced (filamentous algae at Site 1 and number of taxa at Site 2) temporal fluctuations of response variables compared to treatments manipulated on a regular basis, and this happened mostly in the highshore habitat. In the absence of a statistical interaction between intensity and temporal variability of aerial exposure, variance in response variables either increased (filamentous algae at Site 2) or decreased (*Rivularia* spp. at Site 1 and articulate coralline algae at Site 2) with increasing aerial exposure. These effects emerged above possible artefacts associated with the different experimental procedures used at the 2 sites that were, however, readily detected by the appropriate controls.

We predicted that a sequence of intense bouts of aerial exposure with high temporal variability would prevent large fluctuations in abundances of target species by driving organisms to local extinction or by reducing their abundances to such low values that large variances would be intrinsically impossible (Taylor 1961). This prediction was supported for some organisms, like barnacles, in which low levels of temporal variance corresponded to low levels of mean abundance, as reported by Benedetti-Cecchi et al. (2006).

The large fluctuations in abundance of *Chthamalus stellatus* observed on cores transplanted to the highshore habitat under a regime of low temporal variability of aerial exposure likely reflected the fact that barnacles benefited from living high on the shore, where they were numerically dominant (Benedetti-Cecchi et al. 2000). More difficult to explain was the coincidence between low values of mean abundance under a variable regime of aerial exposure (Benedetti-Cecchi et al. 2006) and the drastic reduction in temporal fluctuations we observed. A possible explanation would be that cores placed in an upshore position were exposed to elevated recruitment levels and that recruits suffered higher rates of mortality under the more variable regime of aerial exposure. This regime imposed both longer and shorter intervals of time between subsequent manipulations than the less variable treatments. In particular, under high temporal variability, recruits of barnacles might have been maintained in the lowshore habitat long enough to allow agents of mortality to depress barnacle recruit abundance to such low values that a relevant accumulation of individuals from one period of emersion to the next was made impossible. Among the agents of mor-

Table 2. ANOVA for variance in abundance and number of taxa across 5 sampling dates for cores and unmanipulated controls established at Site 2. Calculations of *F*-ratios as in Table 1

Source of variation	df	Encrusting corallines			Filamentous algae			Articulated corallines			*R. verrucosa*			Coarsely branched algae		
		MS	*F*	p	MS	*F*	p	MS	*F*	p	MS	*F*	p	MS	*F*	p
Condition	8	2.61			3.48				7.87			2.67			11.17	
Control vs Others	1	7.08	5.25	<0.05	0.07	0.05	>0.8	0.95	0.30	>0.5	0.09	0.02	>0.8	7.37	3.13	>0.05
Among Others	7	6.60			3.96			8.86			2.59			4.67		
Treatment (Tr)	3	1.93	1.43	>0.3	6.01	4.00	<0.05	16.19	5.12	<0.01	1.60	0.33	>0.8	5.52	2.34	>0.05
Variability (V)	1	0.14	0.11	>0.5	5.48	3.65	>0.05	1.15	0.36	>0.5	0.03	0.01	>0.9	6.89	2.92	>0.1
Tr × V	3	4.41	2.91	>0.05	1.41	0.94	>0.4	4.10	1.30	>0.2	0.96	0.20	>0.8	3.07	1.30	>0.2
Residual	24[a]	1.52			1.50				3.16			4.80			2.36	
Cochran's *C*-test		*C* = 0.357, p > 0.05			*C* = 0.283, p > 0.05			*C* = 0.322, p > 0.05			*C* = 0.293, p > 0.05			*C* = 0.310, p > 0.05		
Transformation		Ln(*x*+1)			Ln(*x*+1)			Ln(*x*+1)			Ln(*x*+1)			Ln(*x*+1)		

Source of variation	df	*Rivularia* spp.			*Chthamalus stellatus*			No. of taxa		
		MS	*F*	p	MS	*F*	p	MS	*F*	p
Condition	8	2.18			6.97				0.92	
Control vs. Others	1	0.02	0.00	>0.9	0.07	0.02	>0.8	0.37	3.14	>0.05
Among Others	7	2.15			7.95				0.62	
Treatment (Tr)	3	1.95	0.29	>0.8	4.41	1.40	>0.2	0.06	0.53	>0.6
Variability (V)	1	0.00	0.00	>0.9	0.83	0.26	>0.6	1.27	10.71	<0.01
Tr × V	3	0.21	0.03	>0.9	13.87	4.39	<0.05	0.97	8.11	<0.001
Residual	24[a]	6.78			3.16				0.12	
Cochran's *C*-test		*C* = 0.318, p > 0.05			*C* = 0.384, p > 0.05			*C* = 0.174, p > 0.05		
Transformation		Ln(*x*+1)			Ln(*x*+1)			Ln(*x*+1)		

[a] Degrees of freedom corrected for missing data

tality, algal overgrowth can strongly affect the survival of barnacles in the lowshore habitat in this system (Benedetti-Cecchi et al. 2000). This result was in agreement with theoretical modelling and empirical laboratory studies indicating that when fluctuations in environmental forcing variables are strongly autocorrelated in time or space, long-lasting negative conditions for species persistence become more likely and this can increase the risk of extinction of organisms (Heino 1998, Pike et al. 2004).

Alternatively, the large fluctuations in abundance of *Chthamalus stellatus* observed under reduced variability of aerial exposure might be determined by chance effects, like the coincidence of aerial exposure with the timing of recruitment of barnacles (between May and August on our shores, Benedetti-Cecchi et al. 2000). In this scenario, effects of the sequence of events rather than temporal variability per se would have driven temporal variance in the abundance of barnacles. This, however, was unlikely because cores assigned to the conditions of high and low levels of temporal variability of aerial exposure were both in the upshore position during the main periods of barnacle recruitment (Benedetti-Cecchi et al. 2006). Therefore, results can not be explained simply in terms of the timing or sequence of disturbance with respect to the period of barnacle recruitment. Instead, fluctuations in barnacle abundance appeared to be driven by cumulative effects of bouts of aerial exposure over the course of the study.

While observations on barnacles supported the original hypothesis of lower temporal fluctuations in the most stressful conditions at one site, data on other taxa did not conform to this prediction. We postulated that a combination of high mean intensity and high temporal variability of aerial exposure would reduce mean values of response variables to low levels, increasing local extinctions and preventing large temporal fluctuations in abundance. Indeed, none of the taxa examined in the present study were driven to complete extinction (see also mean abundance values reported in Benedetti-Cecchi et al. 2006), and response variables such as abundance of filamentous algae and number of taxa displayed increased, rather than decreased temporal fluctuations, under a regime of high temporal variability and high mean intensity of aerial exposure. Collectively, these results suggested that resistance to desiccation and/or quick recovery allowed assemblages to withstand the most severe environmental conditions imposed experimentally.

Theoretical and empirical studies have shown that fluctuations in physical variables may allow the persistence of species by reducing the intensity of biotic interactions (Pickett & White 1985, Chesson & Huntly 1997, Crawley 2004). This might have been the case for filamentous algae, which displayed larger fluctuations in abundance in combination with low densities of grazers. In fact, the low temporal variance in density of *Patella* spp. at Site 1 under a variable regime of transplantation to the highshore habitat corresponded to a mean grazer abundance (no. individuals × 49 cm^{-2}) of 0.04 ± 0.04 (mean ± SE, n = 4). This value was much lower than the mean abundance observed under a constant regime of transplantation at the same height on the shore: 0.67 ± 0.19 (mean ± SE, n = 4). It was under this regime of low grazing pressure that filamentous algae displayed large fluctuations in abundance when transplanted to the highshore habitat (compare Fig. 1B with Fig. 1D).

Similar arguments can explain the increase in temporal variance of number of taxa on cores transplanted with high temporal variability. Experimental sequences of emersion and submersion may have produced qualitative and quantitative changes of resources during the course of the experiment, providing only temporarily suitable conditions for colonization and persistence of organisms with contrasting life-history attributes (Littler & Littler 1980, Steneck & Dethier 1994). For example, while the abundance of barnacles decreased with increasing temporal variability of emersion in the highshore habitat, the reverse occurred for filamentous algae (Benedetti-Cecchi et al. 2006). Thus, increased fluctuations in aerial exposure generated opportunities for colonization and persistence to a wider range of taxa than more regular environmental conditions, thus promoting larger temporal variances in abundance.

Some considerations of the experimental procedures used are necessary for a correct interpretation of results. First, our experimental design could not separate the effect of temporal variability of aerial exposure per se from the specific sequences of transplantations chosen to generate the 2 levels of this factor. The need for such an implementation was suggested by differences in results between Site 1 and Site 2. Although these discrepancies may reflect spatially variable processes, different sequences were used to generate comparable levels of temporal variability at the 2 sites. Replication of random sequences of events within levels of variability (Gonzalez & Holt 2002) will be necessary to separate these 2 sources of variability in future studies on aerial exposure or other disturbances in natural assemblages.

A second caveat to be considered is that, in addition to exposing assemblages to air, transplantation exposed organisms to biological habitats that were different from the sites of origin. Effects of habitat were also revealed by the differences between translocated and disturbed cores low on the shore. Thus, observed effects of transplantation could be due to changes in the biotic habitat surrounding the experimental cores rather than to changes in physical conditions. Although this possibility cannot be ruled out in the present study, preliminary data from another experiment showed that effects of temporal variability of transplantation to the highshore habitat disappeared when cores were covered with plastic roofs to reduce solar radiation and temperature, suggesting that physical processes were more important than biotic habitat in these experiments. Furthermore, biotic habitat could not explain the different responses to high and low levels of temporal variability at the same height of the shore, as observed for some variables in the present study.

The results presented here add to increasing evidence that temporal variability of ecological processes can have considerable effects on temporal changes in assemblages (Collins 2000, Bertocci et al. 2005). Our data further indicate that effects of temporal variability may not be independent of the mean intensity of a given process. A similar conclusion was reached by Bertocci et al. (2005), who examined effects of mean intensity and temporal variability of mechanical disturbance in the assemblages investigated in the present work. Both analyses demonstrated that increasing the mean intensity of a process either magnified or dampened effects of temporal variance, depending on the organisms considered. Although general conclusions are premature, these results show that predicting the response of populations to changes in mean intensity and temporal variability of ecological processes will require considerations of the life histories of the focal organisms. In particular, the ability to resist and to recover from disturbances are key traits that determine the extent to which populations can track environmental change under various levels of mean intensity of perturbations.

These considerations have important implications for our ability to investigate ecological responses to climate change. Although most studies have focused on changes in mean levels of climatic factors (Kappelle et al. 1999, Hughes 2000, Walther et al. 2002), numerical models generally predict shifts in both the mean and in temporal variance of climate variables (Allen et al. 2000, Benestad 2003). Predicting the ecological consequences of these shifts should benefit from the widespread application of the experimental procedures used in the present investigation.

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