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Effects of mean intensity and temporal variance of sediment scouring events on assemblages of rocky shores

Stefano Vaselli[1, 2,*], Iacopo Bertocci[2], Elena Maggi[2], Lisandro Benedetti-Cecchi[2]

[1]Laboratory of Coastal Biodiversity, Centro Interdisciplinar de Investigação Marinha e Ambiental, Rua dos Bragas, 289-4050-123 Porto, Portugal
[2]Dipartimento di Biologia, Via Derna 1, 56126 Pisa, Italy

ABSTRACT: Climatic models predict an increase in temporal variance and intensity of extreme events such as storms and rainfall for the near future. These events are likely to modify current patterns of sediment delivery on rocky shores. We used a factorial experiment to test the hypothesis that changes in intensity and temporal variance of disturbance due to scouring of sediment affected the establishment of algae and invertebrates on a rocky shore in the northwest Mediterranean. The experimental design included replicated sequences of disturbance events within the high level of temporal variance, so that the effect of variance could be separated from effects associated with any particular sequence of events. Multivariate analyses showed a trend towards an interaction between intensity and temporal variance of disturbance, with assemblages exposed to a combination of low intensity and high temporal variance of disturbance being distinguished from the other assemblages. Similar patterns were displayed by filamentous and coarsely branched algae. Temporal variance enhanced their cover under low intensity of disturbance, whilst the opposite occurred under high intensity. Increasing intensity of disturbance reduced the mean number of taxa in experimental areas regardless of levels of temporal variance. Sequence of disturbance was also significant for all these response variables. These results support the proposition that changes in intensity and temporal variance of disturbance by sediment may have reverberating effects on the structure and diversity of rocky shores assemblages, contributing to explain regime shifts in marine coastal habitats such as the replacement of canopy algae by turf-forming species.

KEY WORDS: Climate change · Disturbance · Diversity · Scour · Sedimentation · Temporal variance

INTRODUCTION

Ecologists have long recognized the importance of physical and biological disturbances in influencing patterns of species abundance and distribution in space and time (Pickett & White 1985). Almost all natural systems are exposed to recurrent processes that remove organisms from assemblages, releasing resources such as nutrients, food and space. These chronic, usually localized disturbances have been the subject of considerable research into the mechanisms of species colonization and ecological succession (Connell & Slatyer 1977). There is now substantial theoretical and empirical information explaining how changes in intensity, frequency and spatial extent of disturbance affect species diversity and assemblage dynamics in terrestrial and aquatic systems (Collins 2000, McCabe & Gotelli 2000). There are, however, 2 important aspects of disturbance that have often eluded the attention of empirical ecologists and may account for abrupt changes in composition and abundance of species in natural habitats. First, assemblages are exposed to multiple sources of disturbance operating simultaneously over ecological time scales. These com-

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*Email: svaselli@biologia.unipi.it. Present address: Pisa

pounded perturbations may interact in complex ways jeopardizing predictions based on knowledge of ecological responses to individual perturbations (Paine et al. 1998). Second, how changes in temporal variance of disturbance (as opposed to changes in mean intensity) affect the structure of assemblages is rarely addressed. Indeed, most experimental studies examining the effects of temporally variable patterns of disturbance have focused on the frequency of events, i.e. the number of disturbances over an explicit temporal scale. Although this approach is appropriate to address specific ecological issues (e.g. fire management in forests, Collins 2000), frequency of disturbance confounds intensity and temporal variance of events over the time scale of the study (Benedetti-Cecchi 2003). Climate models predict an increase both in mean intensity and temporal variance of events such as storms and rainfall over ecological time scales (Easterling et al. 2000), but few studies have attempted to disentangle these disturbance traits or have examined their interactions (Bertocci et al. 2005, Benedetti-Cecchi et al. 2006). Rising variance in environmental variables can foretell impending regime shifts (Carpenter & Brock 2006), so empirical studies in which the variance of ecological processes is manipulated explicitly are urgently needed to assess the response of assemblages to increasing environmental fluctuations.

Changes in land use and alteration of the hydrological cycle at a global scale have increased coastal erosion and runoff at the sea–land interface over the past 5 decades (Vitousek et al. 1997). Propagation of these disturbances from land to marine habitats is strongly influenced by precipitation (French 1997). Coastal erosion is expected to increase under climate change with possible consequences for the temporal patterns of sediment delivery to marine coastal environments. Forecasted scenarios of soil loss and runoff include long periods of low sediment deposition, interrupted by short periods of heavy sediment loads in marine coastal habitats (Nearing et al. 2004).

Storms and sedimentation are major sources of disturbance on rocky shores. Strong waves remove organisms from the substratum, opening gaps (Benedetti-Cecchi 2000) in which patterns of recovery may be affected by interactive effects of sediment and wave action through different mechanisms including inhibition of settlement, smothering and abrasion of recently settled propagules and direct elimination of less tolerant species (Vadas et al. 1992). Sediment may also have positive effects on sessile organisms, by preventing the monopolisation of space by competitively dominant species (Airoldi 2003), increasing local levels of nutrients or providing protection from other sources of disturbance (Taylor & Littler 1982, Littler et al. 1983, McQuaid & Dower 1990, Gorgula & Connell 2004, Connell 2005).

We manipulated levels of intensity and temporal variance of disturbance (i.e. variance of time intervals between consecutive events) due to scouring of sediment in factorial combinations, focusing on the effects of these treatments during recovery of midshore assemblages of algae and invertebrates in patches of bare rock resembling those naturally created by heavy storms (Benedetti-Cecchi 2000), in the northwest Mediterranean. Thus, the study examined the compounded effects of varying regimes of sediment scouring that were superimposed on the natural disturbance regimes operating in the habitat (Paine et al. 1998). Effects of sediment scouring on rocky shore assemblages have often been inferred from observations, but experimental evidence is scant (but see Kendrick 1991, Airoldi 2003). The specific hypotheses tested in the present experiment were similar to those devised in similar studies (Bertocci et al. 2005, Benedetti-Cecchi et al. 2006). In particular, we predicted that the largest effect of disturbance on mean values of response variables would occur under a regime of high intensity and high temporal variance of events. Under these conditions, organisms experienced a fluctuating environment with strong disturbance events clustered in short periods of time, alternating with relatively long periods in which no experimental disturbance was applied. Ecological effects would range from the extirpation of species during the most extreme periods of disturbance, to the recovery of fast-colonizing organisms during mild periods. Thus, expected effects would range from positive to negative, depending on the capability of species to resist to and recover from disturbance. Effects of treatments were expected to prompt changes in assemblage structure detectable using multivariate statistical approaches. These hypotheses were tested with an implemented version of the basic experimental design (Benedetti-Cecchi 2003), in which the level of high temporal variance of disturbance was replicated in 3 randomly chosen sequences. This enabled us to tease apart the effect of variance from effects associated with any of the particular sequences chosen.

MATERIALS AND METHODS

Study site. The experiment was conducted at Calafuria, a sandstone rocky coast about 2 km long, located a few kilometres south of Livorno, Italy (43° 30′ N, 10° 20′ E), in the northwest Mediterranean. Midshore assemblages of this coast have been described elsewhere (Menconi et al. 1999). Dominant organisms were the barnacle *Chthamalus stellatus* (Poli), cyanobacteria *Rivularia* spp., herbivores (mainly *Patella* spp.) and a variety of filamentous, encrusting and fleshy algae. The coast was influenced mostly by terrigenous sediment discharged by rivers or transported from the land to the shore during heavy rains. Sand originating from subtidal habitats might also have influenced midshore assemblages when resuspended by wave action.

Experimental design. The experiment started in June 2003 and was designed to assess the effects of intensity and temporal variance of disturbance due to scouring of sediment on patterns of colonization of organisms in cleared quadrats. The experimental design consisted of the following factors: (1) Intensity of disturbance, 2 levels (low and high), fixed; (2) Temporal variance of disturbance, 2 levels (low and high), fixed and crossed with Intensity; (3) Sequence of disturbance, 3 levels (various distributions of disturbance events), random and repeated only within the highest level of Temporal variance; and (4) Area, 3 levels, random and nested within each combination of levels of the other factors, with 3 replicate quadrats in each area. A total of 27 areas (patches of substratum of about 1 × 1.5 m that extended between 0 and 0.3 m above the mean low water level) were used in the experiment. Three unmanipulated areas (no sediment added) served as controls. In all areas, three 10 × 10 cm quadrats were scraped clean with a chisel mounted on a battery drill and used as replicate units. Experimental areas were located randomly on the shore and both areas and quadrats were marked at their corners with epoxy putty (Subcoat S, Veneziani) for subsequent relocation. A sandblasting gun attached to a scuba tank was used to generate disturbance over each area where the quadrats were located. The sediment used in the experiment was a commercial building sand of size 0.25–0.5 mm that was chosen after preliminary analyses indicated about 80% of natural sediment in the area was in this range.

Assemblages were disturbed 9 times over 18 mo, each time adding either 1000 g (low intensity) or 2000 g (high intensity) of sediment to the appropriate experimental areas, using the sand blaster with the nozzle held about 30 cm from the substratum. Ideally, sediment traps should have been used to characterise the depositional environment and to choose levels of experimental factors. Unfortunately, strong wave action prevented the use of sediment traps in the midshore habitat. As an alternative, we quantified the amount of sediment present at the study location by collecting 3 replicate samples in each of 4 areas (located close to those used for experimental treatments) over 6 dates starting in the second year of the experiment (see 'Collection and analysis of data' for details).

Levels of temporal variance of disturbance were generated either by sandblasting the areas 9 times in 18 mo at regular intervals or by concentrating the events of disturbance over short time periods separated by longer periods in which no disturbance was applied (Fig. 1). Bad weather prevented a perfectly regular distribution of events of disturbance over the entire duration of the study. The resulting levels of low and high temporal variance in the time interval between disturbances were 0.1 and 2.85 mo, respectively (Fig. 1). The high level of temporal variance of disturbance was close to the variance in the time interval between natural events of heavy rain (defined as precipitation of ≥10 mm rain h^{-1}; World Meteorological Organization; www.wmo.ch), which was 2.73 mo. This value was calculated based on hourly rain data for the study area collected from January 2001 to December 2005 (courtesy of the Servizio Idrologico Regionale della Regione Toscana). Periods of heavy rainfall were associated with the transport of heavy loads of sedi-

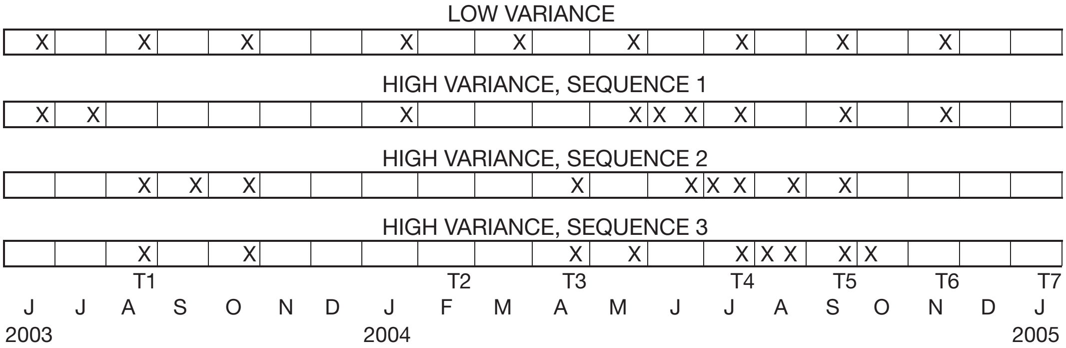

Fig. 1. Distribution of disturbance events (X) over the course of the experiment for each level of temporal variance and sequence of disturbance. T1–T7 are the times of sampling. The full experimental design included 2 levels of intensity crossed with each level of temporal variance and sequence of disturbance, with 3 replicate patches nested in each condition and 3 unmanipulated patches as controls. The variance of the time interval between successive disturbances was 0.10 and 2.85 mo for the low and the 3 sequences of high temporal variance of events, respectively

ment to the shore (authors' pers. obs.). It should be noted that we choose the variance in the time interval between disturbances as an easy way to differentiate between regular and variable regimes of disturbance. Other methods might have been used to model the temporal occurrence of events. In particular, statistical distributions such as the exponential and the negative binomial will provide useful alternative approaches to model the duration of intervals between disturbances in future analyses.

The time required to sandblast the areas assigned to the low and high intensity regimes of disturbance was approximately 2 and 4 min, respectively. To control for possible artifacts associated with the flow of compressed air, 15 additional experimental areas were established (3 replicate areas for each of the 3 sequences of high temporal variance of disturbance, 3 for the low level of temporal variance and 3 unmanipulated controls). Compressed air with no sediment was blown on each area at the same rate (sequence and duration) as that characterising the areas exposed to high intensity of disturbance. Lack of resources prevented controls for artifacts associated with a regime of low intensity of disturbance.

Collection and analysis of data. To quantify natural levels of sediment at the study sites, algal turfs and the associated sediment were collected by scraping the surface underneath a metal cylinder of 4.4 cm in diameter using a paint scraper. Three replicate samples were collected in each area at each of 6 dates; the distances among samples in each area were similar to those separating the cleared quadrats in experimental areas (10s of cm). Samples were stored in plastic bags and brought to the laboratory where they were treated with hydrogen peroxide (H_2O_2 130 vol) for 36 h to remove algae and organic matter (Golterman et al. 1983). Dissolved organic matter that accumulated at the surface was removed with a spoon. Pieces of coralline algae, resistant to the treatment, were removed using tweezers. H_2O_2 was then eliminated with a syringe and the sediment was washed with distilled water and then put in the oven for 24 h at 100°C. The sediment was then sieved (mesh size 250 µm) and the 2 fractions weighed with a precision balance (to the nearest 0.1 mg).

Biological assemblages were sampled in experimental quadrats 7 times between June 2003 and January 2005 using a non-destructive method (Fig. 1). At each date of sampling the time lag between that date and the last event of disturbance necessarily differed among levels of temporal variance or sequence of disturbance. The 7 dates were thus selected in such a way that the time between each event of disturbance and the next sampling date was, on average, the same among the different temporal regimes of disturbance used in the experiment. Thus, treatments could only be compared in terms of differences in overall means over the course of the study and not at single sampling dates.

Organisms in cleared quadrats were sampled using a plastic frame of 8 × 8 cm with sixteen 2 × 2 cm quadrats; estimates of algal abundance were obtained visually by assigning to each taxon a score ranging from 0 to 4 in each quadrat and adding up the 16 estimates (Dethier et al. 1993). Final values were expressed as percentage cover. Whenever possible, organisms were identified in the field to genus or species; when this was not possible, taxa were lumped into morphological groups (Steneck & Dethier 1994). Densities of limpets and other mobile animals were obtained by counting the number of individuals present in the quadrats.

Effects of experimental treatments were investigated on whole assemblages as well as on individual taxa. Multivariate responses were examined by comparing the centroids describing the average assemblage of each experimental area over the course of the study. To obtain the centroids, data from the 3 replicate quadrats in each area, at each time of sampling, were first averaged and a dissimilarity matrix based on the Bray-Curtis index was generated among the full set of 189 observations (27 areas × 7 sampling dates). Because Bray-Curtis is a semi-metric index (Legendre & Anderson 1999), centroids cannot be obtained simply as arithmetic averages of these dissimilarities (Anderson 2001). Thus, we first calculated principal coordinates (Gower 1966) from the Bray-Curtis dissimilarity matrix. This places the observations into a Euclidean space without altering the Bray-Curtis measure; i.e. the distance between any pair of observations based on the principal coordinates is equivalent to the dissimilarity between those observations obtained from the original variables. Centroids were then obtained as arithmetic averages of the principal coordinates over the 7 sampling dates (McArdle & Anderson 2001) using the computer program PCO.exe (Anderson 2003). Multivariate effects were assessed with permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) based on the matrix of Euclidean distances between each pair of centroids. Each term in the analysis was tested individually over the appropriate denominator (with 999 permutations of the relevant units). Multivariate patterns were visualized with a metric multidimensional scaling (MDS) plot.

Individual variables were analysed with population-averaged generalised estimating equations (PA-GEEs), an extension of generalised linear models (GLMs) for correlated data (Quinn & Keough 2002, Hardin & Hilbe 2003). This technique uses quasi-likelihood functions to model the marginal response of a variable over a subpopulation of correlated observations (e.g. the abundance of a particular taxon measured repeatedly in the same quadrat over time), accounting for the correlation structure present in the data (see also Benedetti-Cecchi et al. 2006 for an ecological application of GEEs in a similar context). We fitted GEE models assuming a Gaussian distribution of the error terms and using an identity link for percentage cover data, whereas a Poisson distribution and a log-link were used for count data. A first order autoregressive model AR(1) was used in all the analyses to model temporal autocorrelation in response variables. It is worth noting that this technique is robust to misspecification of the correlation structure, so that robust estimates of variances and standard errors can be obtained for hypothesis testing even if the assumed form of correlation structure is incorrect (Hardin & Hilbe 2003). For simplicity, analyses were done on data averaged across the 3 quadrats in each area and areas were used as replicates. These analyses assumed independence among areas and homogenous variances across treatments. Plots of residuals against fitted values were inspected to check for strong deviations from these assumptions. Analyses were performed in R2.01 (R Development Core Team 2003).

RESULTS

The amount of sediment present on the shore at different times fluctuated in the range of 0–1600 g × 1.5 m^{-2}, with the exception of a peak of 4000 g × 1.5 m^{-2} observed in one area (Fig. 2). Although these data cannot be used to assess sediment dynamics, they offer a view of baseline levels of sediment present at the study location during the course of the experiment.

The multivariate analysis indicated no significant effects of treatments on assemblages (Table 1). A trend towards an interaction between intensity and temporal variance of disturbance was, however, present in the data (0.1 < p < 0.05) (Table 1). Despite considerable variability, assemblages exposed to different levels of intensity of disturbance separated in the MDS plot when disturbances were applied with high temporal variance (Fig. 3). The first 2 axes of the metric MDS plot explained 53.4 % of the total variation.

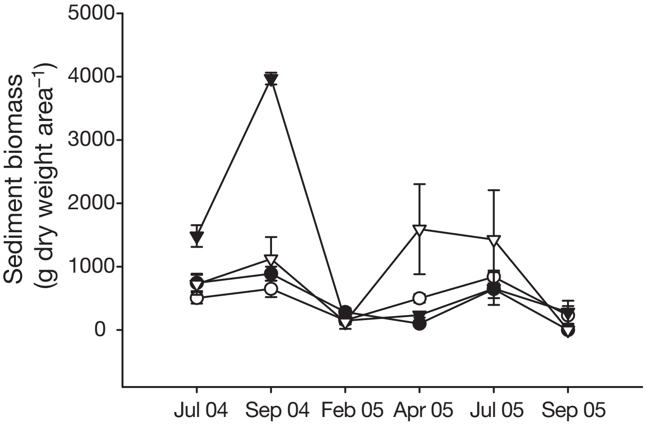

Fig. 2. Mean (±1 SE) dry weight of sediment collected (n = 3) in each of 4 areas (▼, ▽, ●, ○) over 6 dates

Experimental disturbance by sediment significantly affected the mean number of taxa (used as a surrogate measure of species diversity) establishing in the experimental clearings, with lower values occurring in treatments exposed to high than low levels of intensity of disturbance. Differences in mean number of taxa between high and low levels of temporal variance of disturbance also depended on the specific sequence of events (Table 2, Fig. 4a). Interactive effects between intensity and temporal variance of disturbance were observed for filamentous and coarsely branched algae (Table 2, Fig. 4b,c). High temporal variance of disturbance in-

Table 1. PERMANOVA examining effects of treatments on multivariate assemblages

Source of variation	df	MS	Pseudo *F*	p	Permutable units and denominator for *F*
Among experimental levels	8	772.23	0.91	0.460	27 Replicate Areas
Control vs. Treatments	1	548.27	0.64	0.715	27 Replicate Areas
Among Treatments	7	804.22	0.94	0.555	27 Replicate Areas
Temporal Variability	3	1108.29	1.30	0.194	27 Replicate Areas
Low vs. High Variance	1	679.83	0.43	1.000	4 Among Sequence cells[a]
Among Sequences	2	1366.90	1.60	0.095	27 Replicate Areas
Intensity	1	664.31	0.78	0.577	27 Replicate Areas
Intensity × Temporal Variability	3	546.79	0.64	0.902	27 Replicate Areas
Intensity × Low vs. High Variance	1	819.75	2.08	0.090	8 Intensity × Sequence cells[b]
Intensity × Sequences	2	399.64	0.47	0.979	27 Replicate Areas
Residual	18	852.79			

[a] One low variance and 3 high variance sequences used as permutable units, but only high variance sequences used for calculating denominator mean square

[b] Two low variance and 6 high intensity × sequence cells used as permutable units, but only intensity × sequence cells used for calculating denominator mean square

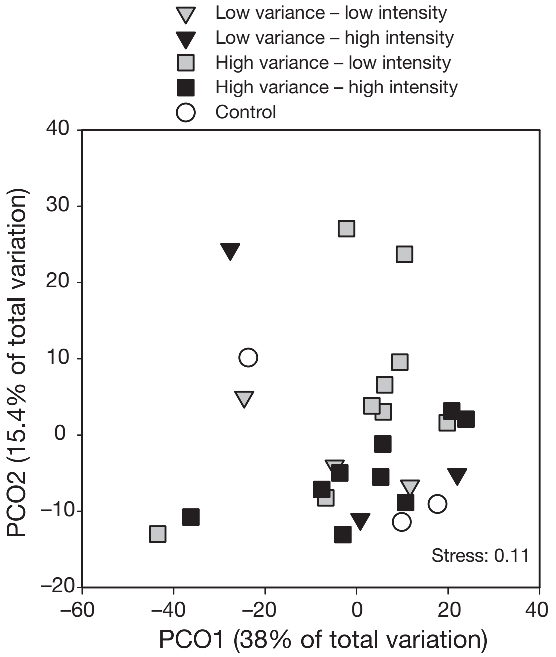

Fig. 3. Metric MDS plot of centroids of experimental areas over the 7 dates of sampling. Centroids were calculated using principal coordinates (see 'Materials and methods')

creased the percentage cover of filamentous algae under low intensity of disturbance, whilst the reverse occurred when disturbance was high (Fig. 4b). The same pattern was observed for coarsely branched algae although the abundance of these algae in disturbed plots never exceeded that of the controls (Fig. 4c). The magnitude and significance of these effects differed among sequences of disturbance, as shown by the I × S interactions in Table 2 (see also Fig. 4b,c). Effects of experimental disturbance by sediment were overall negative on the recruitment of the barnacle *Chthamalus stellatus* that was less abundant in treatment than in control plots (Fig. 4f). Although not statistically significant, there was a trend towards a larger recruitment of barnacles to clearings maintained under a regime of low temporal variance of disturbance when intensity of disturbance was also low, whereas the opposite pattern occurred when disturbance was intense (Table 2, Fig. 4f). No significant effects of experimental treatments were observed on encrusting organisms such as coralline algae and cyanobacteria, nor on herbivores of the genus *Patella* (Table 2, Fig. 4d,e,g).

Procedural controls for artefacts detected a significant increase in percentage cover of barnacles in areas exposed to high temporal variance of flow of compressed air (estimated coefficient = 2.34; $p < 0.001$) and

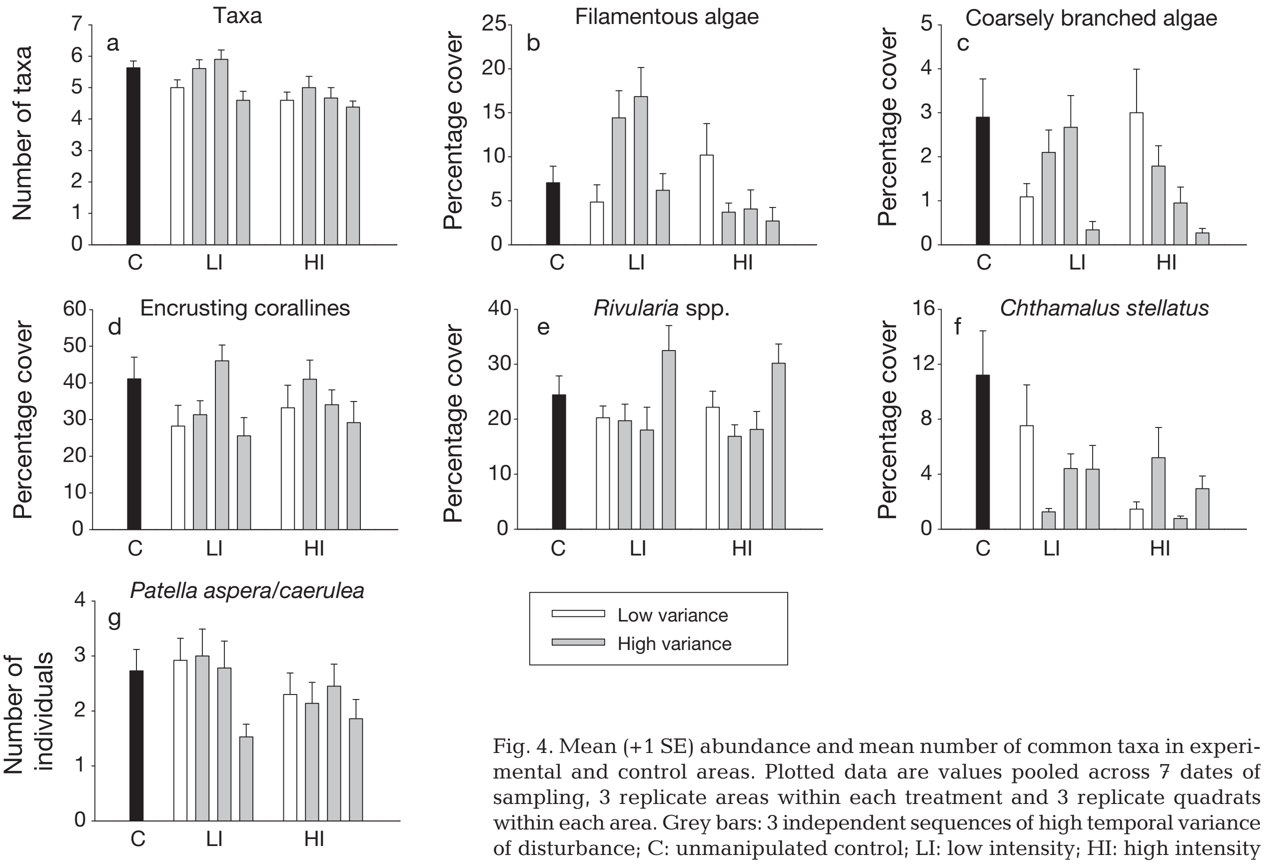

Fig. 4. Mean (+1 SE) abundance and mean number of common taxa in experimental and control areas. Plotted data are values pooled across 7 dates of sampling, 3 replicate areas within each treatment and 3 replicate quadrats within each area. Grey bars: 3 independent sequences of high temporal variance of disturbance; C: unmanipulated control; LI: low intensity; HI: high intensity

Table 2. Analysis of data using population-averaged generalized estimating equations (PA-GEEs). E: estimated coefficient; SE: standard error; *p < 0.05; **p < 0.01; ***p < 0.001

Contrasts	Number of taxa		Filamentous algae		Coarsely branched algae		Encrusting corallines	
	E	SE	E	SE	E	SE	E	SE
Control vs. Treatments = C vs. Tr								
Intercept	5.01***	0.12	7.78***	1.07	0.83***	0.13	35.25***	2.48
C vs. Tr	0.07***	0.02	–0.14	0.43	0.04	0.03	0.77	1.14
Among Treatments								
Intercept	4.63***	0.14	7.92***	1.13	0.79***	0.15	34.38***	2.51
Intensity = I	–0.36*	0.14	–2.66	1.13	–0.21	0.15	0.63	2.51
High vs. Low Variance = V	0.04	0.06	0.09	0.75	–0.12	0.07	1.19	1.84
Sequence 1 = S_1	0.19	0.18	0.62	1.80	–0.01	0.17	2.37	3.69
Sequence 2 = S_2	0.10	0.13	0.81	0.90	–0.03	0.14	2.86	1.55
Sequence 3 = S_3	–0.16*	0.08	–1.16*	0.57	–0.31***	0.09	–1.64	1.69
I × V	–0.03	0.06	–1.70*	0.75	–0.19**	0.07	–0.31	1.84
$I \times S_1$	–0.10	0.18	–3.75*	1.80	–0.12	0.17	0.58	3.69
$I \times S_2$	–0.09	0.13	–1.67	0.90	–0.38**	0.14	–2.11	1.55
$I \times S_3$	0.08	0.08	0.30	0.57	–0.06	0.09	0.57	1.69
Correlation coefficient	0.48***	0.09	0.40**	0.13	0.09	0.08	0.53***	0.10
Scale parameter	1.65	125.20	7.46	517.42				

Contrasts	*Rivularia* spp.		*Chthamalus stellatus*		*Patella aspera/caerulea*	
	E	SE	E	SE	E	SE
Control vs. Treatments = C vs. Tr						
Intercept	22.64***	1.56	4.10***	0.84	0.82***	0.07
C vs. Tr	0.18	0.59	0.89	0.50	0.01	0.01
Among Treatments						
Intercept	22.46***	1.63	3.18***	0.76	0.80***	0.08
Intensity = I	–0.99	1.63	–0.90	0.76	–0.05	0.08
High vs. Low Variance = V	0.26	0.84	–0.28	0.58	–0.04	0.03
Sequence 1 = S_1	–1.39	1.50	–0.70	1.36	–0.04	0.09
Sequence 2 = S_2	–0.47	1.26	–0.23	0.49	0.02	0.06
Sequence 3 = S_3	2.67	1.22	0.07	0.38	–0.10	0.05
I × V	–0.48	0.84	0.61	0.58	0.01	0.03
$I \times S_1$	–1.33	1.50	2.12	1.36	–0.03	0.09
$I \times S_2$	–0.02	1.26	–0.41	0.49	0.04	0.06
$I \times S_3$	–0.10	1.22	0.14	0.38	0.04	0.05
Correlation coefficient	0.41***	0.12	0.57***	0.14	0.35	0.11
Scale parameter	221.62		47.14		1.44	

a reduction in number of limpets in treated compared to control areas (estimated coefficient = –0.10; $p < 0.01$). No significant results were obtained for the other taxa analysed (Fig. 5).

DISCUSSION

The initial hypothesis that the largest effects of disturbance on mean values of response variables would occur under a regime of high intensity and high temporal variance of events must be rejected on the basis of the experimental evidence. Increasing intensity of disturbance led to a decrease in mean number of taxa, but this effect was independent of changes in temporal variance of disturbance. Intensity and temporal variance of disturbance interactively influenced the establishment of filamentous and coarsely branched algae, with temporal variance increasing algal abundance under low intensity of disturbance and the opposite occurring under high intensity of disturbance. As a result, for both taxa, percentage cover values in the high intensity–high temporal variance treatment were similar to those observed in the low intensity–low temporal variance treatment. A similar pattern was observed in the multivariate analysis, where assemblages in the high intensity–high temporal variance treatment tended to separate from those in the low intensity–high variance treatment, but were indistinguishable from those in the low variance–low intensity treatment. Intensity of disturbance had an adverse effect on the abundance of barnacles under low, but not high, temporal variance of events, in contrast to what was observed for filamentous and coarsely

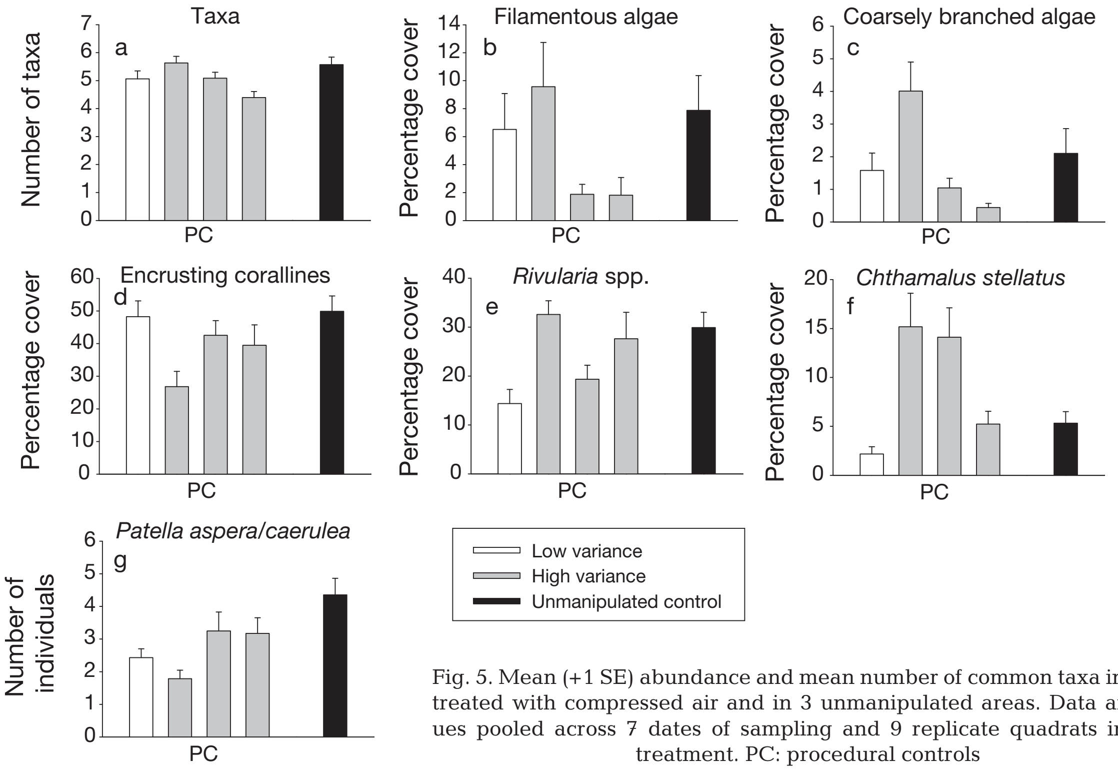

Fig. 5. Mean (+1 SE) abundance and mean number of common taxa in areas treated with compressed air and in 3 unmanipulated areas. Data are values pooled across 7 dates of sampling and 9 replicate quadrats in each treatment. PC: procedural controls

branched algae. However, this effect was not significant and should be interpreted with caution due to the possible occurrence of artifacts.

Other studies examining the effects of disturbance by sediment on turf-forming algae have reported contrasting results. Whilst some investigations have documented positive effects of sediment on turf-forming species (Littler et al. 1983, Irving & Connell 2002), others have reported negative effects due to an excess of sediment on settlement and recruitment of algae (Renaud et al. 1997, Eriksson & Johansson 2005, Thomsen & McGlathery 2006). Although a majority of these studies dealt with effects of accumulation and not scouring of sediment, our data agree with these findings, indicating that both positive and negative effects of sediment are possible depending on levels of intensity and temporal variance of disturbance.

The capability of turf-forming algae to persist in the presence of sediment may be a consequence of the modes of reproduction and dispersal of these organisms, which are characterised mostly by vegetative propagation and fragmentation, respectively. Both traits can increase the probability of algae finding suitable places for colonization when sedimentation makes most of the substratum unsuitable for the establishment of propagules (Airoldi 1998, Eriksson & Johansson 2005). For instance, Airoldi (1998) found that turf was able to resist sediment scouring by vegetative propagation and regrowth of survival axes. Jenkins et al. (1999) described a situation in which sediment entrapped in turf-forming algae actually benefited these algae in the presence of grazing limpets. In our experiment, high temporal variance of events of disturbance may have influenced recruitment in 2 ways: (1) at low intensity of disturbance by allowing higher colonization only to those species resistant to scour by sediment such as algal turfs; and (2) at high intensity of disturbance by exceeding critical levels, overcoming the threshold of physiological tolerance of algae and then inhibiting colonization and/or subsequent growth.

Pulse events of disturbance by sediment scouring negatively affected the mean number of taxa (a surrogate measure of diversity) in assemblages in experimental clearings compared to clearings where sediment was not added. Furthermore, clearings exposed to high levels of intensity of disturbance had reduced diversity compared to clearings maintained at low intensity of disturbance, regardless of the temporal variance of events. These results are in agreement with those of Kendrick (1991) who found a lower number of species on boulders subjected to treatments of erosion and scouring by sediment than on unmanipulated ones. The mechanisms proposed to explain negative effects on diversity include inhibition of recruitment (Devinny & Volse 1978), direct scour of species (Kendrick 1991, Airoldi 1998) and interactions with other environmental variables (e.g. light) with consequent switches in dominance of species (Connell 2005).

Intensity and temporal variance of disturbance were not the only processes driving the observed patterns in the data. Sequence of disturbance, either as a main effect or in interaction with intensity, was also significant for filamentous and coarsely branched algae and for mean number of taxa. This likely reflected the coincidence of disturbance with events of recruitment in experimental clearings, as discussed in Bertocci et al. (2005). These effects could be detected unambiguously in the present experiment because 3 sequences of events were replicated within the level of high temporal variance of disturbance. This illustrated the importance of replicating sequences of events within levels of temporal variance to unconfound the effects associated with different sources of variability and ultimately to examine effects of variance over and above any effect of sequence.

Encrusting organisms were resistant to the different regimes of disturbance used in the experiment. Treatments had no significant effects on encrusting coralline algae and cyanobacteria *Rivularia* spp. These results are in agreement with findings of a number of studies documenting little to no effect of sediment on encrusting coralline algae (e.g. Kendrick 1991), but contrasted with the results of other investigations in which negative effects of sediment were detected on these taxa (Ayling 1981, Melville & Connell 2001). Airoldi (2003) discussed possible reasons accounting for differences among studies, including species-specific responses to disturbance and characteristics of the regime of sedimentation. Our results showed that phylogenetically distant but morphologically similar taxa such as encrusting coralline algae and cyanobacteria could resist various combinations of intensity and temporal variance of disturbance, suggesting that morphology was the key trait enabling these organisms to thrive under variable regimes of sedimentation.

The response of barnacles to the experimental treatments was idiosyncratic. Although a trend towards a negative effect of intensity of disturbance was evident in a regime of low temporal variance of events and not under high temporal variance, effects were not significant (Fig. 4f). In addition, procedural control for artifacts indicated that colonization of barnacles might be enhanced by a flow of compressed air applied with high temporal variance that could get rid of natural sediment present in experimental areas. Both results likely reflected negative effects of sediment on larval settlement and recruitment as a consequence of severe sand scour and burial during storms (e.g. Underwood 1998).

One of the most abrupt changes in assemblages of rocky shores reminiscent of a regime shift at the global scale is the replacement of canopy algae by turf-forming algae (Airoldi 2003, Gorgula & Connell 2004). This modification likely reflects the direct and indirect effects of various anthropogenic disturbances in marine coastal environments, including pollution, sedimentation and nutrient input (Gorgula & Connell 2004, Connell 2005, Schiel et al. 2006). Our results indicate that an increase in temporal variance of disturbance by sediment scouring, concomitant with a moderate increase of sediment loads above current ambient levels (the low intensity treatment), can contribute to this regime shift by enhancing the cover of turf-forming algae (filamentous species) or preventing their loss under increased sedimentation (coarsely branched algae). The tendency of assemblages in the high variance–low intensity treatment to separate from the other assemblages in the multivariate analysis also suggests that important ecological changes may occur under these conditions. The environmental scenario defined by this particular combination of experimental treatments is not unrealistic given current and expected climate modifications (Easterling et al. 2000, Alley et al. 2003). These results suggest that extremities in environmental conditions should be defined in terms of specific combinations of mean intensity and temporal variance of events, rather than on the basis of each of these traits separately or by confounding them into synthetic metrics such as frequency of disturbance. This offers a new perspective for interpreting and predicting the consequences of climate change at local and global scales on natural assemblages.

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