

Mar Biol (2007) 153:199–211
DOI 10.1007/s00227-007-0798-6

RESEARCH ARTICLE

Temporal variance of disturbance did not affect diversity and structure of a marine fouling community in north-eastern New Zealand

Javier Atalah · Saskia A. Otto · Marti J. Anderson ·
Mark J. Costello · Mark Lenz · Martin Wahl

Received: 14 May 2007 / Accepted: 17 August 2007 / Published online: 6 September 2007
© Springer-Verlag 2007

Abstract Natural heterogeneity in ecological parameters, like population abundance, is more widely recognized and investigated than variability in the processes that control these parameters. Experimental ecologists have focused mainly on the mean intensity of predictor variables and have largely ignored the potential to manipulate variances in processes, which can be considered explicitly in experimental designs to explore variation in causal mechanisms. In the present study, the effect of the temporal variance of disturbance on the diversity of marine assemblages was tested in a field experiment replicated at two sites on the northeast coast of New Zealand. Fouling communities

grown on artificial settlement substrata experienced disturbance regimes that differed in their inherent levels of temporal variability and timing of disturbance events, while disturbance intensity was identical across all levels. Additionally, undisturbed assemblages were used as controls. After 150 days of experimental duration, the assemblages were then compared with regard to their species richness, abundance and structure. The disturbance effectively reduced the average total cover of the assemblages, but no consistent effect of variability in the disturbance regime on the assemblages was detected. The results of this study were corroborated by the outcomes from simultaneous replicate experiments carried out in each of eight different biogeographical regions around the world.

Communicated by A. Atkinson.

J. Atalah · M. J. Costello
Leigh Marine Laboratory, The University of Auckland,
P.O. Box 349, Warkworth, New Zealand

S. A. Otto
Department of Biology, Humboldt University of Berlin,
Unter den Linden 6, 10099 Berlin, Germany

M. J. Anderson
Department of Statistics, Tamaki Campus,
University of Auckland, Private Bag 92019,
Auckland, New Zealand

M. Lenz · M. Wahl
IFM-Geomar Leibniz-Institut für
Meereswissenschaften an der Universität Kiel,
Duesternbrooker Weg 20, 24105 Kiel, Germany

J. Atalah (✉)
School of Biology and Environmental Science,
Science Centre West, University College Dublin,
Belfield, Dublin 4, Ireland
e-mail: javier.atalah@ucd.ie

Introduction

In most habitats and ecosystems, large variation in population abundances, species diversity and community composition are observed at a wide range of temporal and spatial scales. Besides variability in population abundances and species composition, there is also heterogeneity in the processes which cause these variations, such as physical factors, resource availability and biological interactions (Underwood and Chapman 2000). This variability may be viewed as a nuisance that obscures simpler phenomena, e.g. stochastic events that destabilize communities or instability that interrupts deterministic biological interactions. However, in recent years environmental variance per se has been studied as a potentially important factor in determining the relative abundance of species in communities (Underwood 1996; Benedetti-Cecchi 2000).

The role of biological disturbances, such as predation or grazing, in determining species distribution and abundance in marine systems has long been recognized (Dayton 1971; Menge and Sutherland 1976; Ayling 1981). Additionally, physical disturbance is regarded as one of the major factors influencing species diversity in both terrestrial and aquatic natural communities (Dayton 1971; Grime 1977; White and Pickett 1985). In the present study, disturbance was defined as a physical force which results in loss of biomass (Grime 1977). In the marine environment, physical disturbance may be either natural such as storm damage, movement of boulders, burial under sand or impact by drifting logs; or anthropogenic such as trampling or collecting (White and Pickett 1985).

A disturbance regime is a combination of disturbance intensity, frequency and the area affected (Sousa 1979). While the term ‘intensity’ refers to the strength of the disturbing force, ‘frequency’ refers to the mean number of events per period of time (White and Pickett 1985; Sousa 2001). Additionally, disturbance is a process that, itself, fluctuates in space and time. Variation in the frequency, or in the length of intervals between disturbances, is an additional factor that might affect diversity (Robinson and Sandgren 1983; Butler 1989; Navarrete 1996; Benedetti-Cecchi 2003). This can be considered as the variance in the length of time periods between disturbances (around the mean interval length), which will be expressed as ‘temporal variability’ in this study.

The majority of studies on factors affecting the diversity of systems have focused on manipulating only the mean intensity of driving processes, whereas the relevance of the variance around the mean effect has been largely overlooked (Benedetti-Cecchi 2003). Although some previous investigation of variability in environmental processes has been considered (Caswell and Cohen 1995), there have been very few attempts to experimentally unravel variance from mean effects. Some experimental studies have attempted to include variability of disturbance by manipulating the frequency of events over a given period (Navarrete 1996; McCabe and Gotelli 2000). Unfortunately, it is not possible from these designs to disentangle the separate potential effects of frequency, intensity and temporal variability. To overcome this problem and to create experiments that unambiguously separate the mean (of either frequency or intensity) from the temporal variability of a predictor variable, Benedetti-Cecchi (2003) proposed an experimental design in which intensity and variability are treated as fixed, orthogonal factors. Previous work that has manipulated temporal variation in disturbance has used a single patterned sequence of disturbance events through time as a representative for a given level of variation in disturbance (Robinson and Sandgren 1983; Bertocci et al. 2005; Benedetti-Cecchi et al. 2006).

However, there are many different possible sequences of events that would lead to the same overall level of variance for a given treatment (Bertocci et al. 2005). Thus, to attribute differences among treatments to differences in levels of variance, per se, several different sequences need to be used to represent a given variance-in-disturbance regime. In this way, this study improves on the design used by Robinson and Sandgren (1983) and the one proposed by Benedetti-Cecchi (2003).

The aim of this study was to test the effects of the temporal variability of a physical disturbance regime of constant intensity on the richness, structure and relative abundances of organisms in a marine fouling assemblage. Several concepts, which are based on non-selective disturbance, exist that predict an enhanced diversity under disturbed conditions by interrupting competitive exclusion and thus supporting coexistence (Chesson and Huntly 1997; Sousa 2001). Diversity can also increase if the time intervals between single disturbance events become longer since more time is given for a large number of species to colonize (Connell 1978). This can be relevant especially for species with specific growth rates or short periods of recruitment. In a highly variable disturbance regime the single disturbance events are temporally more clustered, hence more space for colonization opened up during a short time span, and followed by larger time intervals without any disturbance. Under this regime, we expected an enhanced diversity by promoting the colonization of species that otherwise would not be able to recruit under constant disturbance regimes. Additionally, we used three different temporal sequences of disturbance events to provide a representative sample of each level of temporal variance. If the specific timing of a given disturbance interacts with seasonal patterns of reproduction and the arrival of recruits, then we expected to find significant variation in response to the specific sequences nested within a given disturbance regime.

For the experiments, a marine fouling community in the north-east coast of New Zealand was used as a model system. Because of the sessile nature of fouling organisms and their relatively fast colonization rates, they are especially suited for experimental manipulation aimed at elucidating the mechanisms underlying responses to disturbance regimes (Costello and Thrush 1991). Artificial substrata (rigid PVC panels) were used to standardize for physical habitat structure.

Methods

Study sites

The experiment was conducted in 2004/2005 at two sites in the north-east coast of New Zealand: Leigh Harbour

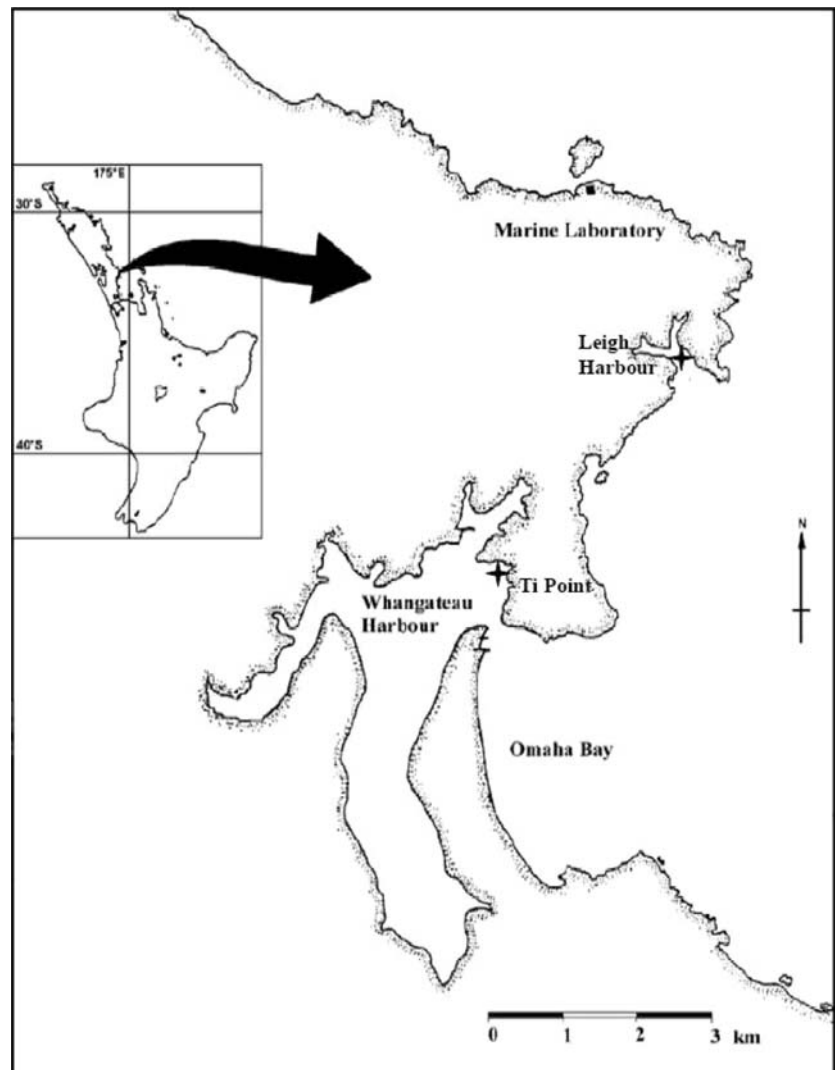
(36°17.23'S, 174°48.65'E) and Ti Point (36°19.02'S, 174°47.08'E), which is located at the mouth of Whangateau Harbour, a shallow tidal estuary (Fig. 1). Both sites were sheltered from wave exposure, safe from boating traffic and near Leigh Marine Laboratory. The local climate is maritime and warm temperate with distinctive seasons. Annual sea surface temperature between July 2004 and April 2005 ranged from 13 to 21°C (J. H. Evans, personal communication), and salinity generally ranges from 34.9‰ in early spring to 35.5‰ in late autumn (Evans and Ballantine 1985). Both study sites have a semidiurnal tide with a vertical range of ≈ 3.5 m. In terms of wave exposure, Leigh Harbour can be considered as sheltered and Ti Point as extremely sheltered. While Leigh Harbour can be described as a rocky shore with a sub-littoral fringe dominated by the brown algae *Carpophyllum maschalocarpum* and *Ecklonia radiata*, Ti Point exhibits a boulder beach with a *Carpophyllum flexuosum* stand.

Experimental set-up and sampling

Five experimental rings were placed at each site; each consisted of a 4 mm thick, 25 cm \times 210 cm PVC strip, whose ends were glued together to form a ring. To each ring ten PVC panels (15 cm \times 15 cm) roughened with sandpaper (grading no. 60) were attached as the artificial substrata. Panels were affixed to the inside of the rings facing into the centre using cable ties. Each ring was suspended from a buoy at a water depth of ~ 50 cm and anchored to the sea bottom (see experimental set-up in Valdivia et al. 2005). This set-up allowed the rings to move with changes in tidal height and water currents, so panels remained at a constant depth. Distances between rings were at least 1.5 times the rings' diameter, as required for a randomized block design (Hurlbert 1984).

Fouling assemblages were allowed to establish on the panels for 75 days (maturing phase) before the beginning

Fig. 1 Map showing the location of the two study sites: Leigh Harbour and Ti Point, and the location of the Leigh Marine Laboratory in relation to the North Island of New Zealand



of the 150-day-long experimental phase. Related studies have found that dominant species colonize within 14–28 days and a species equilibrium is established within 60 days (K. Hillock and M. J. Costello, unpublished data). During the experimental phase ten disturbance events were applied to two randomly positioned patches on a panel by pressing a given area with a solid PVC cylinder. The cylinder had a diameter of 4.6 cm and was applied twice per disturbance event, affecting 20% of the panel area. Additionally, the disturbed area was scraped to remove particles and all organisms that had not been removed by the PVC-cylinder, like encrusting algae and biofilm. The disturbance events therefore resulted in complete removal of biomass within this area at each disturbance event. The locations of the two disturbed patches per event were chosen at random using a 36 dot grid, with the additional caveat that the two patches were not allowed to overlap. For all disturbed panels, the mean time interval between disturbance events (frequency) was fixed at 15 days, the area of the panel disturbed was fixed at 20% of the panel, and the severity was fixed at complete removal of the biomass. Potential extraneous disturbances were minimized by removing large mobile invertebrates from experimental structures every 5 days during the course of the 150-day experiment. The presence of spatial autocorrelation between communities within experimental blocks was tested using multivariate Mantel correlograms (Oden and Sokal 1986) that are a modification of the Mantel test. No significant correlations were found at both study sites (results not shown), confirming the spatial independence of replicate assemblages.

There were three levels of temporal variability in disturbance, quantified by the standard deviation from the mean interval length: constant (SD = 0), low (SD = 5.77) and high (SD = 16.33) (Fig. 2). Undisturbed communities served as a reference. The constant level was achieved by a regular (uniform) spacing of disturbances at equal 15-day intervals, and consequently had only one possible temporal sequence. The low and high levels of temporal variability in disturbance were each achieved using three different temporal sequences (Fig. 2). Note that the average time between disturbance events is 15 days for all sequences. It is the variability in this time between events that was manipulated here. Treatment levels [undisturbed (*U*), constant disturbance (*C*), low variability in disturbance (*L*) and high variability in disturbance (*H*)] were randomly allocated to individual units in each of the experimental rings.

Sampling took place at the end of the experiment. Panels were removed from the rings and taken back to the laboratory in plastic tanks filled with seawater. A margin of 1 cm within the edge of the panel was ignored to avoid the sampling of edge effects. Thus, the total area per panel

analysed was 13 cm × 13 cm. A uniform grid of 100 points was used to facilitate estimation of percentage cover of each species, and communities were carefully examined with the naked eye and a dissecting microscope. In the case of multi-strata growth, total percentage cover exceeded 100%. All sessile taxa >1 mm in size were identified to the lowest possible taxonomic level. Taxa that could not be identified at the level of species or genus were grouped by morphological criteria. One category, hereinafter referred to simply as 'biofilm', consisted of a mixture of benthic diatoms and brown filamentous algae that could not be distinguished from one another quantitatively without microscopic examination.

The experiment was replicated at two sites and had three factors: treatment (fixed with four levels: undisturbed, constant, low and high variance-in-disturbance regimes); sequence (random with three levels, nested only in each of the low and the high treatments); and ring (random with five levels, crossed with Treatments and Sequences). The three degrees of freedom associated with treatment effects were examined by testing three specific a priori orthogonal contrasts of interest: (1) undisturbed versus disturbed (*U* vs. {*C*, *L*, *H*}), (2) constant versus variable (*C* vs. {*L*, *H*}) and (3) low versus high (*L* vs. *H*).

To investigate the effects on community structure, we used distance-based permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001a; McArdle and Anderson 2001) based on Bray–Curtis dissimilarities of untransformed percentage cover data. The use of a beta version of the new computer package PERMANOVA+ (Anderson and Gorley 2007), an add-on to Version 6 of the PRIMER program (Clarke and Gorley 2001) allowed partitioning of the multivariate variability according to the full experimental design (including fixed and random factors, interactions and dealing appropriately with contrasts, asymmetry and imbalance). Each term in the analysis was therefore tested using 4,999 permutations of the correct relevant permutable units (Anderson and ter Braak 2003). Significant terms were then investigated using a posteriori pair-wise comparisons with the PERMANOVA *t* statistic and 999 permutations. Differences in community structure among treatment levels were visualized with non-metric multidimensional scaling (nMDS) on the basis of Bray–Curtis dissimilarities of the untransformed percentage cover data. Similarity Percentage Analysis (SIMPER, Clarke 1993) was used to identify the percentage contribution of each species (or taxon) to any observed differences between communities of the different treatment levels and between the disturbed and undisturbed communities. Taxa were considered important if their contribution to percentage dissimilarity was ≥3%.

Univariate permutational analysis of variance (Anderson 2001b) was done on each of several variables: number of

Variability	Sequence	Disturbance events																														Sampling					
Constant	1	D			D				D				D				D				D				D				D					D			
	2	D	D				D	D				D				D				D				D				D					D				
	3	D					D				D				D				D				D				D				D						
High	1	D							D	D	D																										
	2	D	D	D	D																																
	3	D	D																																		
Month		Nov					Dec					Jan					Feb					Mar					Apr										
Time (No. of days)		0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	105	110	115	120	125	130	135	140	145		150				

Fig. 2 Schematic illustration of the timing of the disturbance events during the course of the experiment for each of the treatments, including the three sequences of disturbance within each of the low

and high levels of temporal variation in disturbance. *D* indicates a disturbance event performed on that day

taxa; total percentage cover; and cover of several dominant taxa. The distribution of each individual variable was first examined for departures from normality and homogeneity. Data were transformed, if necessary, to achieve approximate unimodal symmetry, to avoid right skewness and to eliminate intrinsic mean–variance relationships. Univariate analyses were achieved using a distance-based approach as described above for the multivariate analysis by choosing to use Euclidean distances for a single response variable when running PERMANOVA. This is preferable to traditional ANOVA, because PERMANOVA calculates *P*-values using permutations, rather than relying on tabled *P*-values, which assume normality. Significant terms were investigated further, as required, using a posteriori pairwise comparisons with 999 permutations. At Ti Point, one panel was lost during the experimental phase, so analyses for this site were consequently unbalanced. Type III SS (and its direct multivariate analogue) were used to analyse the unbalanced designs.

Results

Community structure

A total of 23 taxa were recorded on experimental panels at Leigh Harbour and 31 at Ti Point (Table 1). At neither site did the assemblages differ significantly between constant and variable disturbance regimes or among levels of temporal variability of disturbance, nor was there significant variability in assemblage structure due to different temporal sequences of disturbance (Table 2). However, disturbed assemblages differed significantly from undisturbed assemblages at both sites (*U* vs. *D*: $P < 0.001$). Also, at Ti Point assemblages differed significantly among rings (ring: $P < 0.001$). The nMDS plots (Fig. 3) illustrate that the undisturbed communities were distinguishable from disturbed communities, with no separation of assemblages experiencing different levels of temporal variation in disturbance.

At Leigh Harbour and Ti Point, 6 and 7 taxa, respectively, contributed the most to differences between

disturbed and undisturbed assemblages and were more abundant in the latter (Table 3). Crustose brown algae, the biofilm, *Ulvella* sp., crustose coralline algae and *Balanus trigonus* each contributed more than 3% to the observed dissimilarities between these two groups at each site. Additionally, at Leigh Harbour, *Obelia* sp. cover was higher in the undisturbed communities contributing 5% to the observed dissimilarities, while at Ti Point *Polysiphonia* sp. and *Smittina torques* made considerable contributions (5.6 and 5.7% respectively).

Mean number of taxa

At Leigh Harbour analyses showed that assemblages under temporally constant disturbance regimes had a significantly lower mean number of taxa compared to those subject to variable regimes (*C* vs. *V*: $P < 0.05$, Table 2), but this effect was small in size (Fig. 4). Additionally, at this site there was a significant ring effect on the mean number of taxa (ring: $P < 0.05$, Table 2a). In contrast, at Ti Point, no effect of disturbance, temporal variability of disturbance, ring or sequence was detected on the mean number of taxa (Table 2b).

Percentage cover

No effect of the temporal variability of disturbance or sequences on total cover was detected, although disturbances had a significant effect (*U* vs. *D*, Table 2). At Leigh Harbour, on average, total cover decreased from $162\% \pm 9.02$ SE to $91\% \pm 2.52$ SE ($P < 0.001$, Fig. 4), while at Ti Point it decreased from 160 ± 6.86 SE to $111\% \pm 2.91$ SE ($P < 0.001$, Fig. 4). Additionally, at both sites there was significant variation in total cover due to rings ($P < 0.001$, Table 2).

The analyses of the abundances of individual taxa revealed no consistent effects of temporal variability of disturbance (Fig. 5, Table 4). At Leigh Harbour, the percentage of the biofilm was significantly reduced by the disturbances ($P < 0.001$) and varied among rings

Table 1 List of taxa recorded on experimental panels at Leigh Harbour and at Ti Point by levels of treatment: *C* constant, *L* low, *H* high and *U* undisturbed. Relative cover of organisms at the end of the experiment is shown by: *open circle* not present, *filled circle* <1% cover, *double filled circle* 1–10% cover and *triple filled circle* >10% cover

Algae	Leigh Harbour				Ti Point				
	C	L	H	U	C	L	H	U	
Chlorophyta									
<i>Ulva</i> sp.	●●●	●●●	●●●	●●●	●●●	●●●	●●●	●●●	
<i>Enteromorpha</i> sp.	●●	●●	●●	●●	●●	●●	●●	●●	
<i>Cladophora</i> sp.	○	○	●	○	●	○	●	●	
<i>Codium</i> sp.	○	○	○	○	○	●	○	○	
Chromophyta									
Biofilm									
<i>Colpomenia sinuosa</i>	○	○	○	○	●	●	○	●	
<i>Scytosiphon lomentaria</i>	●	●	●	●	●●	●	●	●	
Crustose brown algae	●●●	●●●	●●●	●●●	●●●	●●●	●●●	●●●	
<i>Carpophyllum</i> sp.	○	○	○	○	○	●	○	○	
Rhodophyta									
Crustose coralline	●●	●●	●●	●●	●●	●●	●●	●●●	
<i>Hildenbrandia</i> sp.	○	○	○	○	○	○	●	○	
<i>Polysiphonia</i> sp.	●	●	●	●●	●●	●●	●●	●●	
Rhodomelaceae	○	●	●	●	○	●	●	●●	
<i>Acrochaetium</i> sp.	●	●	●●	●●	○	○	●	●	
Invertebrates									
Porifera									
Unidentified sponge 1	○	○	○	○	○	○	●	○	
Unidentified sponge 2	○	○	○	○	○	●	○	○	
Cnidaria									
<i>Obelia</i> sp.	●	●●	●●	●●	○	○	●	○	
<i>Bunodeopsis</i> sp.	○	○	●	●	●	●	●	●	
Annelida									
<i>Pomatocerus</i> sp.	○	○	●	○	○	○	●	○	
<i>Galeolaria mystrix</i>	○	●	○	●	●	○	○	○	
<i>Spirorbis</i> sp.	●	●	●	●	●	●	●	●	
Arthropoda									
Unidentified tube-amphipods	●	●	●	●●	●	○	●	●	
<i>Balanus decorus</i>	○	●●	●	●	●	●	○	○	
<i>Elminius modestus</i>	●	●●	●●	●●	●	●●	●●	●●	
<i>Balanus trigonus</i>	●●	●●	●●	●●●	●	●	●●	●●	
Bryozoa									
<i>Smittina torques</i>	○	●	●	○	●	●●	●	●●	
Lichenoporidae	○	●	○	○	○	○	●	○	
Unidentified bryozoan	○	○	●	○	○	●	○	●	
<i>Bugula neritina</i>	○	○	○	○	●	○	○	○	
Chordata									
<i>Corella eumyota</i>	○	○	○	○	○	○	○	●	
Didemnidae	○	○	●	○	●	○	●	○	
Treatment total no. spp.	13	18	21	17	19	19	22	19	
Site total no. spp.		23				31			

($P < 0.01$). The response of *Ulva* sp. to levels of temporal variability of disturbance varied among rings (L vs. $H \times$ ring, $P < 0.05$), but pair-wise comparisons did not detect any statistically significant effects ($P > 0.05$). Crustose brown algae showed significantly higher percentage cover in the undisturbed assemblages (U vs. D : $P < 0.001$). The cover of *B. trigonus* was significantly greater under variable than under constant disturbance regimes (C vs. V : $P < 0.01$). Additionally, the effects of disturbance on this barnacle varied among rings (U vs. $D \times$ ring: $P < 0.05$), but pair-wise comparisons did not detect any statistically significant effects ($P > 0.05$).

Levels of temporal variability of disturbance had a significant effect on the cover of crustose coralline algae (L vs. H : $P < 0.05$), but this effect was small in size (Fig. 5). Additionally, cover of this rhodophyte was significantly greater in undisturbed assemblages (U vs. D : $P < 0.05$, Fig. 5).

At Ti Point the biofilm had greater cover in the undisturbed than in the disturbed assemblages (U vs. D : $P < 0.001$). There was significant variability among sequences in the percentage cover of *Ulva* sp. [Sequence (L vs. H): $P < 0.05$], but there were no consistent effects of any of the fixed treatments. At Ti Point, the average

Table 2 PERMANOVA of Bray–Curtis dissimilarities among panels based on percentage cover (multivariate data) and permutational ANOVAs for the number of taxa and total percentage cover at each of Leigh Harbour and Ti Point

Source of variation	df	Multivariate		No. of taxa		Total cover	
		MS	F	MS	F	MS	F
(a) Leigh Harbour							
Treatment	3	1,457.5	3.52***	7.15	2.84*	9,234.8	19.40***
Undisturbed vs. disturbed (<i>U</i> vs. <i>D</i>)	1	3,569.10	6.06***	8.92	1.38	26,822.00	40.99***
Constant vs. variable (<i>C</i> vs. <i>V</i>)	1	305.72	1.26	7.37	4.61*	31.59	0.52
Low vs. high (<i>L</i> vs. <i>H</i>)	1	499.04	1.56	4.90	2.45	816.75	2.48
Ring	4	890.46	3.55**	9.54	3.83*	1,119.90	4.30*
Sequence (low vs. high)	4	264.63	1.12	0.36	0.15	274.94	1.12
Treatment × ring	12	204.26	0.8727	3.0539	1.2765	196.68	0.81967
(<i>U</i> vs. <i>D</i>) × ring	4	304.17	1.46	5.82	2.73	332.15	1.69
(<i>C</i> vs. <i>V</i>) × ring	4	97.74	0.49	0.80	0.42	91.24	0.51
(<i>L</i> vs. <i>H</i>) × ring	4	206.50	0.87	2.60	1.10	155.19	0.63
Sequence (low vs. high) × ring	16	236.94	1.01	2.35	0.98	245.16	0.99
Residual	10	234.83		2.40		248.65	
Total	49						
Transformation		None		None		None	
(b) Ti Point							
Treatment	3	901.44	2.52**	3.56	1.30	4,889.6	9.76***
Undisturbed vs. disturbed (<i>U</i> vs. <i>D</i>)	1	2,195.60	5.48***	3.80	0.93	13,756.00	24.04***
Constant vs. variable (<i>C</i> vs. <i>V</i>)	1	217.23	0.69	2.90	1.37	724.17	1.55
Low vs. high (<i>L</i> vs. <i>H</i>)	1	306.92	1.41	4.95	1.46	179.05	1.03
Ring	4	584.60	3.43**	4.71	2.30	1,117.60	4.32*
Sequence (low vs. high)	4	220.69	1.39	1.16	0.57	312.93	1.32
Treatment × ring	12	186.52	1.14	3.20	1.61	185.98	0.75
(<i>U</i> vs. <i>D</i>) × ring	4	169.81	0.94	4.44	1.81	171.86	0.72
(<i>C</i> vs. <i>V</i>) × ring	4	287.14	1.79	1.64	0.74	285.58	1.27
(<i>L</i> vs. <i>H</i>) × ring	4	108.30	0.68	3.64	1.80	92.95	0.39
Sequence (low vs. high) × ring	15	159.44	1.27	2.01	0.54	239.73	2.30
Residual	10	125.37		3.75		104.25	
Total	48						
Transformation		None		None		None	

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

Fig. 3 Non-metric multidimensional scaling ordinations of assemblages in each treatment on the basis of Bray–Curtis dissimilarities of untransformed percentage cover data for experimental panels at each of **a** Leigh Harbour and **b** Ti Point, for constant disturbed (open circle), undisturbed (cross symbol), and low (triangle) and high variability (solid square) of disturbance

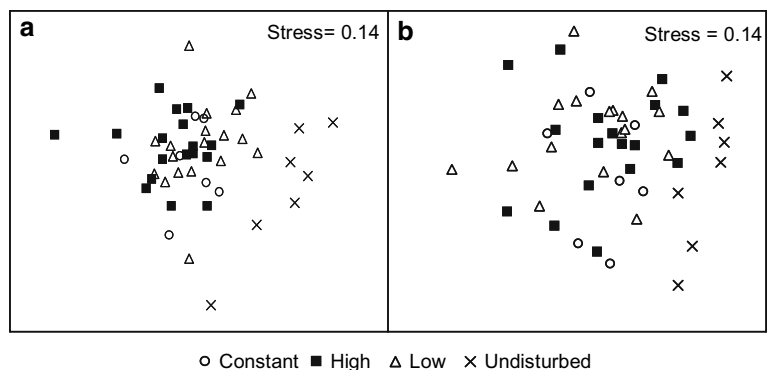
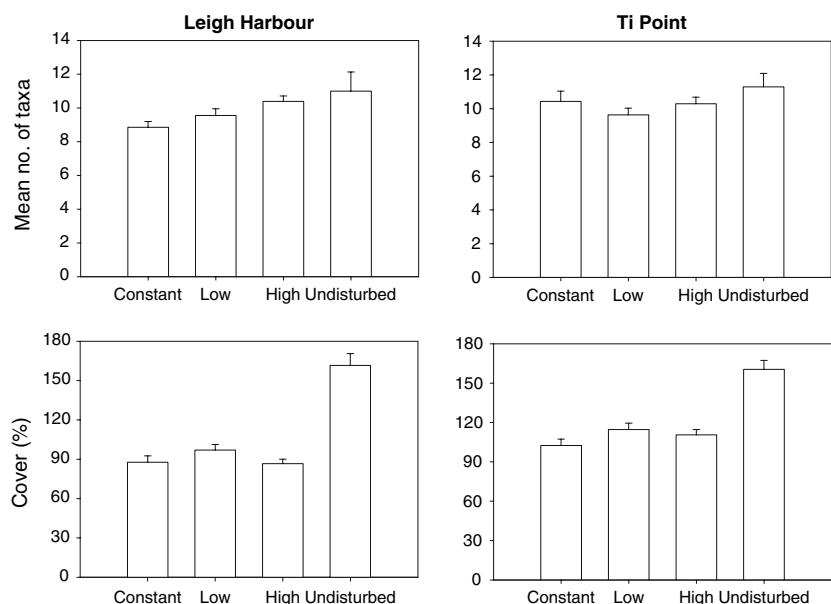


Table 3 Average percentage cover of several prominent taxa in disturbed and undisturbed assemblages at Leigh Harbour and Ti Point, including SIMPER results for contributions from the most important taxa towards the Bray–Curtis dissimilarity distinguishing these two groups ($\bar{\delta}_i$)

Taxa	Average percentage cover		$\bar{\delta}_i$	$\bar{\delta}_i\%$	$\frac{\bar{\delta}_i}{SD(\delta_i)}$
	Disturbed	Undisturbed			
(a) Leigh Harbour					
Crustose brown alga	20.1	44.3	10.4	29.6	1.4*
Biofilm	39.4	59.3	8.6	24.5	1.5*
<i>Balanus trigonus</i>	4.5	13.3	4.0	11.5	1.2*
<i>Ulrella</i> sp.	14.3	18.4	3.3	9.5	1.2*
<i>Obelia</i> sp.	1.9	4.4	1.7	5.0	1.7*
Crustose coralline algae	2.9	5.7	1.2	3.4	1.6*
(b) Ti Point					
Biofilm	63.2	82.0	8.3	33.5	1.5*
<i>Ulrella</i> sp.	17.1	17.6	3.3	13.3	1.4*
Crustose coralline algae	7.0	14.0	3.1	12.5	1.2*
Crustose brown alga	13.4	15.0	2.9	11.7	1.3*
<i>Smittina torques</i>	1.1	2.9	1.4	5.7	0.6
<i>Polysiphonia</i> sp.	4.4	3.0	1.4	5.6	1.0*
<i>Balanus trigonus</i>	1.5	3.7	1.0	4.2	1.3*

High values of the ratio $\bar{\delta}_i/SD(\delta_i)$ (indicated by an asterisk) denote that the contribution of that species or taxon to the dissimilarity is reasonably consistent across all pairs of samples in both groups

Fig. 4 Mean (± 1 SE) number of taxa and total percentage cover on experimental panels at Leigh Harbour and Ti Point within each of the treatments. Sample sizes varied from $n = 7$ to $n = 18$ as data were pooled across rings and sequences



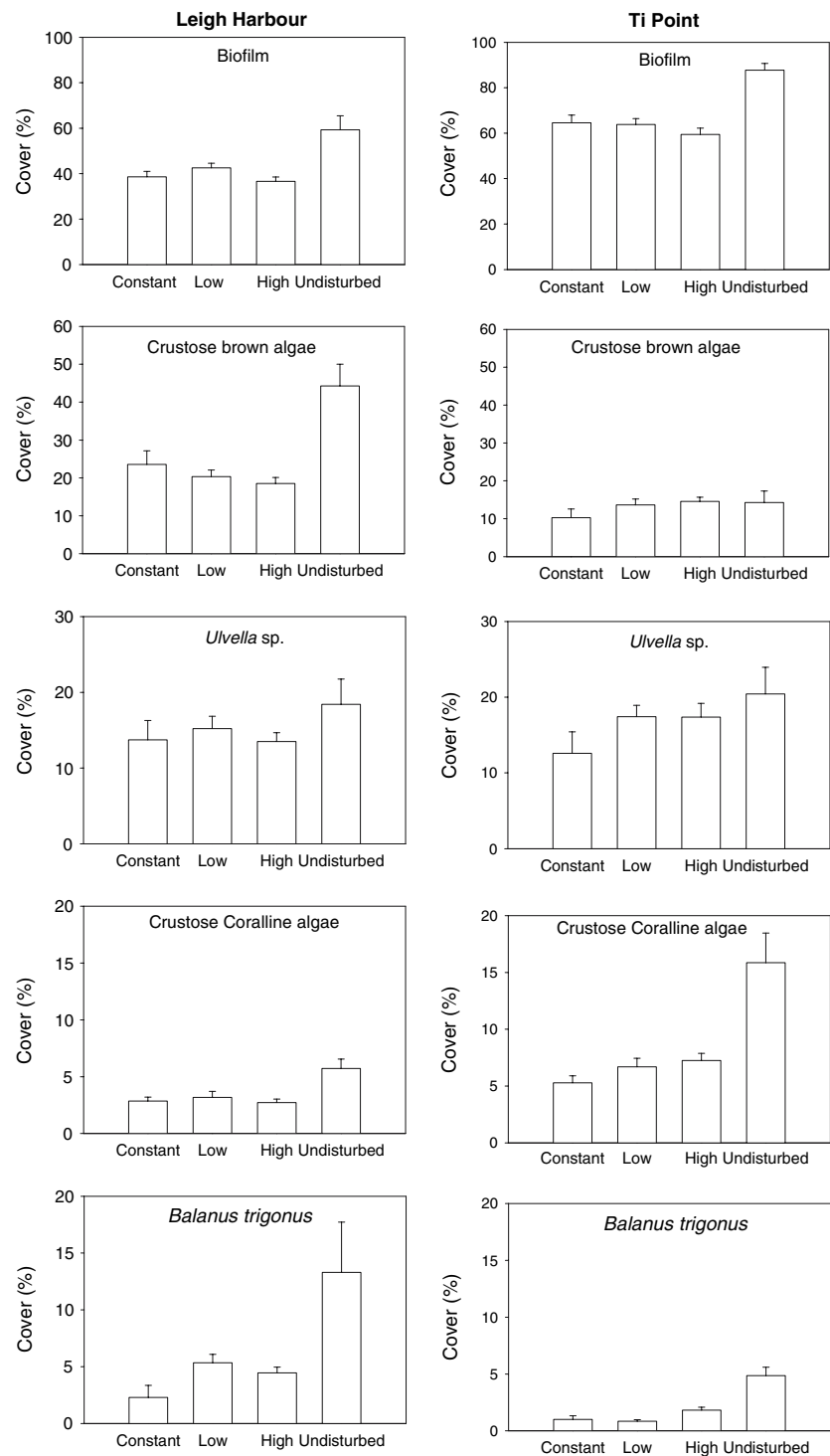
percentage cover of crustose brown algae was significantly greater in variable than in constant treatments (C vs. V : $P < 0.05$, Fig. 5). The cover of *B. trigonus* was greater under high variability regimes, but this effect was only significant in one ring (L vs. $H \times$ ring, $P < 0.05$). Average percentage cover of this barnacle was reduced in the disturbed communities (U vs. D : $P < 0.001$). Similarly, the cover of crustose coralline algae was significantly greater in undisturbed than in disturbed communities (U vs. D : $P < 0.05$). In general, at Ti Point there was significant variation among

rings in the percentage cover of all taxa analysed, except for *B. trigonus* ($P > 0.05$) and the biofilm ($P = 0.051$).

Discussion

The prediction that the temporal variability in disturbance regimes and the sequence of disturbance events in time have an effect on the richness, structure or cover of fouling assemblages was not supported by the results of this study.

Fig. 5 Mean (± 1 SE) percentage cover of several prominent taxa on experimental panels for each treatment at each of Leigh Harbour and Ti Point. Sample sizes varied from $n = 7$ to $n = 18$ as data were pooled across rings and sequences



None of the response variables measured in this experiment were consistently affected by the two different levels of temporal variability or by the different temporal sequences of disturbance events nested within them. The weak effects observed, that were also inconsistent across the two study sites, do not allow generalizations about the effects of temporal variability in disturbance regimes on fouling

assemblages. At Leigh Harbour, there was weak evidence for a slight increase in the mean number of taxa from constant to variable disturbance regimes. Similarly, at this site, a higher mean cover of *B. trigonus* was recorded when intervals between disturbance events were variable. Also, at Ti Point cover of the crustose brown algae was greater in assemblages under variable disturbance regimes.

Table 4 Results of permutational ANOVAs for percentage cover of the most prominent taxa at each of Leigh Harbour and Ti Point

Source of variation	df	Biofilm		<i>Ulvelia</i> sp.		Crustose brown algae		<i>Balanus trigonus</i>		Crustose coralline algae	
		MS	F	MS	F	MS	F	MS	F	MS	F
(a) Leigh Harbour											
Treatment	3	960.80	6.21**	36.62	1.08	8.26	5.85**	2.34	5.32**	14.26	5.54**
Undisturbed vs. disturbed (<i>U</i> vs. <i>D</i>)	1	2,639.10	9.87***	80.29	2.16	23.70	16.16***	3.82	2.80	37.69	8.10**
Constant vs. variable (<i>C</i> vs. <i>V</i>)	1	1.07	0.44	4.11	0.92	1.21	1.82	3.02	9.61**	0.47	1.15
Low vs. high (<i>L</i> vs. <i>H</i>)	1	240.01	2.55	26.01	0.60	0.01	0.84	0.08	1.59	4.48	4.05*
Ring	4	479.35	6.78**	235.05	15.24***	1.31	0.83	1.52	7.22**	2.68	0.61
Sequence (low vs. high)	4	91.75	1.41	17.01	1.17	0.71	0.47	0.04	0.19	1.09	0.25
Treatment × ring	12	69.07	1.01	30.41	2.08	0.95	0.61	0.43	2.32	2.27	0.52
(<i>U</i> vs. <i>D</i>) × ring	4	172.94	3.45	30.85	1.51	0.86	0.67	0.90	4.28*	3.66	1.05
(<i>C</i> vs. <i>V</i>) × ring	4	4.27	0.12	9.54	0.46	0.87	0.61	0.29	1.81	2.02	0.56
(<i>L</i> vs. <i>H</i>) × ring	4	28.14	0.43	50.63	3.52*	1.07	0.72	0.15	0.68	1.10	0.25
Sequence (low vs. high) × ring	16	65.67	1.72	14.36	0.61	1.51	2.35	0.20	0.23	4.42	1.55
Residual	10	38.20		23.70		0.64		0.88		2.85	
Total	49										
Transformation		None		None		Sqrt		ln(x + 1)		None	
(b) Ti Point											
Treatment	3	1,258.20	8.09***	65.87	0.71	0.84	1.88	2.11	7.40***	201.79	7.88***
Undisturbed vs. disturbed (<i>U</i> vs. <i>D</i>)	1	3,634.40	27.48***	85.27	0.89	0.16	0.40	4.27	10.61***	567.19	10.75**
Constant vs. variable (<i>C</i> vs. <i>V</i>)	1	11.64	0.27	105.14	1.02	2.02	8.45**	0.04	0.34	16.35	2.29
Low vs. high (<i>L</i> vs. <i>H</i>)	1	195.48	3.33	5.21	0.29	0.25	0.79	1.89	4.28*	8.45	0.96
Ring	4	286.94	3.15	278.13	10.48***	3.40	10.87***	0.17	1.68	41.73	4.93*
Sequence (low vs. high)	4	70.49	0.83	89.87	3.69*	0.06	0.20	0.07	0.68	5.93	0.75
Treatment × ring	12	90.74	1.04	31.38	1.23	0.55	1.92	0.23	2.17	20.61	2.47
(<i>U</i> vs. <i>D</i>) × ring	4	35.25	0.37	41.42	1.51	0.84	2.48	0.08	0.54	46.90	5.42
(<i>C</i> vs. <i>V</i>) × ring	4	228.63	2.95	45.19	1.88	0.16	0.62	0.20	1.31	4.07	0.53
(<i>L</i> vs. <i>H</i>) × ring	4	13.44	0.16	10.80	0.44	0.63	2.13	0.40	3.90*	11.16	1.41
Sequence (low vs. high) × ring	15	85.16	1.35	24.50	1.48	0.29	0.43	0.10	0.74	7.92	0.90
Residual	10	63.20		16.55		0.67		0.14		8.75	
Total	48										
Transformation		None		None		Sqrt		ln(x + 1)		None	

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

Not surprisingly, there was a strong effect of the disturbances themselves on total percentage cover and on the cover of the most common taxa, which was also reflected in changes to the overall structure of the community (Fig. 3). This indicated that the disturbance treatment was effective, though recruitment from the water column and vegetative growth from the margins of the disturbed patches led to a fast recovery of the affected areas. Subsequent studies on the panels in these locations during the same months the following year found that biofilm and brown crustose algae colonize panels within 2 weeks (K. Hillock and M. J. Costello, unpublished data). However, disturbance per se had no impact on taxon richness in this study, and a temporally variable spacing of the disturbances also did not influence the mean number of taxa in the way that we had predicted. Recruitment of new species and increased diversity due to greater availability of space from cleared patches caused by the temporal clustering of disturbance events (McCabe and Gotelli 2000; Sousa 2001) can only occur if space is a limiting resource and a large pool of potential colonizers are present in the water column.

One possible reason that no clear effects of temporal variability in disturbance were detected in our study could have been because the intensity of the disturbance was relatively large. Recent studies have shown that interactive effects of variability of ecological process are likely to occur at low levels of intensity. Benedetti-Cecchi et al. (2005) found that spatial variability of grazing interacted with low intensity levels of grazing to enhance the spatial variance of algal cover in rock pools. Atalah et al. (2007) found that temporally variable grazing regimes reduced algal cover more efficiently when combined with a relatively low overall intensity of grazing. Clearly, much more research is needed to determine, for any given system, the threshold mean level of disturbance at which *variability* in its occurrence will have any important additional effects.

The effects of variable disturbance regimes on quickly recovering organisms (e.g. the biofilm) will more likely be reflected in the temporal variance in the abundance of the organism rather than in the mean. For example, under a temporally constant disturbance regime, we observed that biofilm cover decreased moderately directly after each disturbance event but recovered quickly to the initial level thereafter. This led to a small measured temporal variance in its percentage cover. However, under temporally variable disturbance regimes, there was a larger increase in biofilm cover during prolonged gaps between disturbances. This was then followed by a dramatic decrease in its cover after a successive series of disturbance events. So there was greater temporal variability in the percentage cover of biofilm in the temporally variable disturbance regimes. This type of response has also been observed in studies

focused on predation, where enhanced temporal variability of species abundance and fluctuations in community structure occurred in response to variable regimes (Butler 1989; Navarrete 1996). In contrast, Bertocci et al. (2005), studying rocky shore assemblages, found the temporal variance of community structure was reduced by increased temporal variability in disturbance regimes.

An effect of the temporal sequences of disturbance would be expected if there were temporal variation in the availability of propagules or larvae, or in periods of vegetative growth. Crawley's (2004) results supported this mechanism in a study of a terrestrial plant community, where a large effect on community structure was detected when the timing of disturbance was correlated with the germination period of the plant. On the other hand, if the availability of larvae and propagules is fairly constant, e.g. due to the absence of seasonal variability in supply, then the particular temporal sequence within a disturbance regime is unlikely to have an effect. This experiment was conducted during spring and summer, and we did not observe any strong significant variation due to temporal sequences of disturbance. Seasonal patterns in recruitment do exist, however, for some of the taxa in this study. For instance, the brown alga *Scytosiphon lomentaria* and the crustose brown alga, both from the family Scytosiphonaceae, are known to disperse from winter to late spring (Adams 1994). However, recruitment of crustose brown algae was also observed in March and April (autumn). Colonization of amphipod crustaceans on subtidal artificial substrata is also known to vary seasonally in a cold-temperate environment (Costello and Myers 1996). Irrespective of temporal patterns in the availability of propagules, if disturbance and its temporal variability have no effect on the response variables (such as percentage cover), the order of time intervals between successive disturbance events is unlikely to have any influence. Significant variation in the slow-growing green alga *Ulvelva* sp. among sequences was more likely due to the different number of disturbance events that happened just before sampling, rather than by the mechanism described above.

One advantage of the experimental design was the disentanglement of the mean intensity from the variability of a physical disturbance regime. Furthermore, we considered the sequence of disturbance events in time, which is a novel approach in studies addressing effects of temporal variability of processes. An additional strength of our experimental design is that the time since the last disturbance event was constant for all the treatments. This avoided potential confounding effects of the disturbance timing in the interpretation of the results.

This study was done in eight other biogeographical regions (Wollongong, Australia; Coquimbo, Chile; New Castle, England; Rio de Janeiro, Brazil; Madeira, Portugal;

Egypt; Malaysia and Poland) using the same experimental design. Even considering the vast differences in the physical and biological nature of these different regions, the results obtained were very similar across all of them: no effect of the variability or the sequence of disturbance was detected, while a marked overall effect of disturbance on assemblages was observed in all cases (Sugden et al. 2007; C. Rich, M. Cifuentes and T. Porto, personal communication).

The results of this study suggest that the temporal variability of disturbance has little effect on the community structure of fouling assemblages. Although the disturbance itself had a noticeable impact on the structure of these communities, temporal variability in disturbance did not. It is likely that this is because: (1) fouling assemblages tend to have relatively fast colonization times, (2) propagules of many of the most abundant taxa in the fouling communities are apparently available to recolonize during much of the year and (3) open space is not apparently a strongly limiting factor for these communities.

Acknowledgments We thank L. Benedetti-Cecchi (University of Pisa) for helping with the experimental design and data analysis; W. Nelson (National Institute of Water and Atmospheric Research), D. G. Fautin (University of Kansas), V. Pearse (American Microscopical Society) and J. Buchanan (Victoria University of Wellington) for helping with the taxonomic identification. Thanks to Chloe Rich (University of Wollongong), Carmen Kamlah (University of Rostock), Tiago Porto (Universidade Federal Fluminense) and Mauricio Cifuentes (Universidad Católica del Norte) for helpful discussions. This study was part of the international research project GAME (Global Approach by Modular Experiments), funded by Stiftung Mercator.

References

- Adams NM (1994) Seaweeds of New Zealand: an illustrated guide. Canterbury University Press, Christchurch
- Anderson MJ (2001a) A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26:32–46
- Anderson MJ (2001b) Permutational test for univariate or multivariate analysis of variance and regression. *Can J Fish Aquat Sci* 58:626–639
- Anderson MJ, Gorley RN (2007) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth
- Anderson MJ, ter Braak CJF (2003) Permutation tests for multifactorial analysis of variance. *J Stat Comput Simul* 73:85–113
- Atalah J, Anderson MJ, Costello MJ (2007) Temporal variability and intensity of grazing: a mesocosm experiment. *Mar Ecol Prog Ser* 341:15–24
- Ayling AM (1981) The role of biological disturbance in temperate subtidal encrusting communities. *Ecology* 62:830–847
- Benedetti-Cecchi L (2000) Variance in ecological consumer-resource interactions. *Nature* 407:370–374
- Benedetti-Cecchi L (2003) The importance of the variance around the mean effect size of ecological processes. *Ecology* 84:2335–2346
- Benedetti-Cecchi L, Bertocci I, Vaselli S, Maggi E (2006) Temporal variance reverses the impact of high mean intensity of stress in climate change experiments. *Ecology* 87:2489–2499
- Benedetti-Cecchi L, Vaselli S, Maggi E, Bertocci I (2005) Interactive effects of spatial variance and mean intensity of grazing on algal cover in rock pools. *Ecology* 86:2212–2222
- Bertocci I, Maggi E, Vaselli S, Benedetti-Cecchi L (2005) Contrasting effects of mean intensity and temporal variation of disturbance on assemblages of rocky shores. *Ecology* 86:2061–2067
- Butler MJ (1989) Community response to variable predation: field studies with sunfish and freshwater invertebrates. *Ecol Monogr* 59:311–328
- Caswell H, Cohen JE (1995) Red, white and blue environmental variance spectra and coexistence in metapopulations. *J Theor Biol* 176:301–316
- Chesson P, Huntly N (1997) The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *Am Nat* 150:519–553
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Aust J Ecol* 18:117–143
- Clarke KR, Gorley RN (2001) PRIMER v5: user manual/tutorial, Plymouth
- Connell JH (1978) Diversity in tropical rain forest and coral reefs. *Science* 199:1302–1309
- Costello MJ, Myers AA (1996) Turnover of transient species as a contributor to the richness of a stable amphipod (Crustacea) fauna in a sea inlet. *J Exp Mar Biol Ecol* 202:49–62
- Costello MJ, Thrush SF (1991) Colonization of artificial substrata as an multispecies bioassay of marine environmental quality. In: Jeffrey DW, Madden B (eds) Bioindicators and environmental management. Academic, London, pp 401–418
- Crawley MJ (2004) Timing of disturbance and coexistence in a species-rich ruderal plant community. *Ecology* 85:3277–3288
- Dayton PK (1971) Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol Monogr* 41:351
- Evans JH, Ballantine WJ (1985) Leigh climate report—the climate in 1985. Leigh, Marine Laboratory, University of Auckland 111
- Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am Nat* 111:1169–1194
- Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. *Ecol Monogr* 54:187–211
- McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82:290–297
- McCabe DJ, Gotelli NJ (2000) Effects of disturbance frequency, intensity, and area on assemblages of stream macroinvertebrates. *Oecologia* 124:270–279
- Menge BA, Sutherland JP (1976) Species diversity gradients: synthesis of the roles of predation, competition and temporal heterogeneity. *Am Nat* 110:351–369
- Navarrete SA (1996) Variable predation: effects of whelks on a mid-intertidal successional community. *Ecol Monogr* 66:301–321
- Oden NL, Sokal RR (1986) Directional autocorrelation: an extension of spatial correlograms to two dimensions. *Syst Zool* 35:604–617
- Robinson JV, Sandgren CD (1983) The effect of temporal environmental heterogeneity on community structure: a replicated experimental study. *Oecologia* 57:98–102
- Sousa WP (1979) Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecol Monogr* 49:227–254
- Sousa WP (2001) Natural disturbance and dynamics of marine benthic communities. In: Bertness MD, Gaines SD, Hay ME (eds) Marine community ecology. Sinauer, Sunderland, pp 85–130

- Sugden H, Panusch R, Lenz M, Wahl M, Thomason JC (2007) Temporal variability of disturbances: is this important for the diversity of benthic subtidal assemblages? *Mar Ecol* (in press)
- Underwood AJ (1996) Spatial patterns of variance in density of intertidal populations. In: Floyd AW, Sheppard AW, De barro PJ (eds) *Frontiers of population ecology*. CSIRO, Melbourne, pp 369–389
- Underwood AJ, Chapman MG (2000) Variation in abundances of intertidal populations: consequences of extremities of environment. *Hydrobiologia* 426:25–36
- Valdivia N, Heidemann A, Thiel M, Molis M, Wahl M (2005) Effects of disturbance on the diversity of hard-bottom macrobenthic communities on the coast of Chile. *Mar Ecol Prog Ser* 299:45–54
- White PS, Pickett STA (1985) Natural disturbance and patch dynamics: an introduction. In: Pickett STA, White PS (eds) *The ecology of natural disturbance and patch dynamics*. Academic, Orlando, pp 3–13