

Temporal variability and intensity of grazing: a mesocosm experiment

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ABSTRACT: Grazing has long been recognised as a structuring force for plant assemblages. Most of this knowledge comes from experiments in which grazers have been excluded or their densities manipulated. However, the intensity of grazing can vary, in space and time. Recently, an increasing number of studies have stressed the importance of the variance around the mean of ecological processes, but the potential effects of temporal variability in grazing in marine systems have not yet been explored. We examined the separate effects of intensity and temporal variability of grazing by the gastropod *Cantharidus purpureus* (Gemelin, 1971) on algal assemblages in a mesocosm experiment. In replicated experiments, algal assemblages grown on artificial substrata were subject to grazing regimes with mean intensity and temporal variance as crossed factors. In the first experiment, the more variable regimes led to greater reductions in algal cover, regardless of the level of grazing intensity. In the second experiment, variability elicited a similar effect, but this effect was larger for the low- than for the high-intensity treatments. These results indicate that temporally variable grazing regimes may have greater effects on algal assemblages than those anticipated from changes in the mean intensity of grazing alone. Thus, we suggest that temporal variability is a potentially important aspect of grazing processes that should be examined and incorporated into predictive models.

KEY WORDS: *Cantharidus purpureus* · Grazing frequency · Percentage cover · Macroalgal assemblages

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INTRODUCTION

Trophic interactions, such as grazing, are a critical source of variability in many marine ecosystems, producing dramatic changes in resource abundance, size distribution, composition, succession and species diversity (Ayling 1981, Lubchenco & Gaines 1981, Navarrete 1996). Most of our knowledge about the effects of grazing on algal communities comes from the exclusion of consumers from a system (see reviews by Lubchenco & Gaines 1981, Hawkins & Hartnoll 1983). Such experiments usually result in the growth of filamentous or foliose algae in areas from which they would normally be absent, suggesting that

grazing prevents the establishment of these macroalgae (Lubchenco 1982). Crustose algae are usually less affected, and some may be grazer resistant (Dethier & Steneck 2001). However, grazing varies not only spatially, but also over time within a given area, as a consequence of seasonality, fluctuation in physical factors, recruitment or predation and diurnal migrations into the algal canopy (Freeman 1998). For example, at any given spatial and temporal scale, the same average number of grazers per unit area per day (i.e. the same grazing intensity) might be constant or, in contrast, discrete grazing events might be interspersed with periods of little or no grazing (here called variable grazing).

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The importance of the variance around the mean effect of ecological processes has been stressed in theoretical reflections (Benedetti-Cecchi 2003). Some empirical studies have examined explicitly the effects of temporal variance in ecological processes, such as disturbance or predation, in both marine (Bertocci et al. 2005) and freshwater (Robinson & Sandgren 1983) systems. Nevertheless, studies focused on the variability in grazing have been largely restricted to terrestrial systems (McKenzie 1997). The only exceptions have focused on spatial rather than temporal variability (Benedetti-Cecchi et al. 2005). Thus, the present study examined the effects of temporal variability in grazing, and its potential interaction with different levels of grazing intensity, in a marine ecosystem.

Our study explicitly examined the relative importance of the intensity and temporal variability in grazing by the gastropod *Cantharidus purpureus* (Gemelin, 1971) on algal assemblages in a mesocosm caging experiment. Mesocosms and artificial substrata usefully standardise habitat conditions and help control for environmental variables. In the present study, assemblages were naturally colonised from the local environment. Other studies in the mesocosms have found assemblages on panels in these mesocosms to be highly similar to those on identical panels placed in a nearby harbour (K. Hillock & M. J. Costello unpubl. data).

The shallow subtidal areas of the rocky reefs of the NE coast of New Zealand support a diverse mosaic of encrusting, turfing and foliose algae. These areas are often dominated by grazing molluscs, such as the large turbinid gastropod *Cookia sulcata*, the patellid limpet *Cellana stellifera*, and the 2 trochids *Trochus viridis* and *Cantharidus purpureus*. Most subtidal grazing gastropods are apparently generalist herbivores (Creese 1988). Herbivorous gastropods are of potentially great importance in the ecology of subtidal communities, primarily through the high density (up to 133 ind. m⁻², Ayling 1981) and biomass they achieve. *C. purpureus* was used as a model grazer in the present study. It actively grazes on benthic algae (e.g. green filamentous algae) and on kelp epiphytes (Freeman 1998), and inhabits algal patches with average densities ranging from 4 to 42 ind. m⁻² (Ayling 1981). The experimental design used here tested the potential interaction between temporal variability in grazing and mean intensity of grazing, including the hypotheses that (1) exclusion of *C. purpureus* will lead to changes in algal abundance and community structure, (2) high intensities of grazing will result in different relative algal cover compared to that resulting from low-intensity grazing regimes, and (3) temporally variable grazing will create algal assemblages different from those created under a constant grazing regime.

MATERIALS AND METHODS

Experimental set-up. A 6 wk mesocosm caging experiment was carried out at the Leigh Marine Laboratory in NE New Zealand. The mesocosm consisted of a 1500 l tank (90 cm in height, 195 cm in diameter), having an approximate flow of 8 l min⁻¹ of unfiltered seawater, sourced from the adjacent rocky reef. Water temperature ranged from 15 to 17°C. The mesocosm was outdoors, under a light shade cloth, and so experienced natural light levels comparable to nearby shallow subtidal areas. Prior to the beginning of the experiment, organisms were allowed to settle and establish on substrata consisting of polyvinyl chloride (PVC) panels (15 cm × 15 cm × 4 mm thick). Panels were placed horizontally within the mesocosm at a depth of 0.65 m over a period of 4 mo. A cage (measuring 15 cm × 15 cm × 5 cm high) covered each of the panels. Cages were made of stainless-steel wire 2 mm mesh and had 2.5 cm wide outward flanges extending from each side of the bottom edge. The flanges were affixed to a plastic mesh with cable ties so that cages could be opened, allowing manipulation of grazer density and temporal frequency of occurrence inside each cage. Medium-sized gastropods (17 to 21 mm shell length) were collected from nearby subtidal rocky reefs for use in the experiment. At the beginning of the experiment (time = 0), grazers were introduced to panels belonging to a given treatment (see next subsection). Every 2 wk, all gastropods were replaced by new individuals to standardise, among treatments, the inter-individual variability in grazing behaviour. The cages were scrubbed with a plastic brush every week to remove detritus and organisms that could change water flow and/or light levels inside the cages.

Experimental design. Panels were allocated randomly to treatment combinations in a 2-way factorial ANOVA design, with intensity and temporal variability in grazing as fixed factors (Table 1). The experi-

Table 1. *Cantharidus purpureus*. Temporal structure in occurrence and density of grazers per panel each week during course of experiment for each treatment combination (1G = 1 grazer, 2G = 2 grazers, 4G = 4 grazers)

Treatment		Week					
		1	2	3	4	5	6
Low:	constant	1G	1G	1G	1G	1G	1G
	variable	2G		2G		2G	
High:	constant	2G	2G	2G	2G	2G	2G
	variable	4G		4G		4G	
Ungrazed							

mental design was derived from that used to investigate the effects of spatial variability, as described by Benedetti-Cecchi et al. (2005). Two levels of mean intensity were chosen: low (1 grazer per cage) and high (2 grazers per cage). These levels were chosen to correspond to 44 and ~ 89 ind. m^{-2} , and are within the range of natural average densities of the guild of gastropod grazers found in the field (Ayling 1981). Different levels of temporal variability were achieved by changing the temporal occurrence of grazers inside cages while keeping the average number of gastropods $panel^{-1} d^{-1}$ over the whole period (i.e. the average intensity) constant. Two levels of variability were chosen: a constant grazing regime, which was obtained by including the same density of grazers on panels during the whole experimental phase (1 grazer per cage for the low-intensity level and 2 grazers per cage for the high-intensity level); and a variable grazing regime, which was achieved by including grazers only every second week (2 grazers per cage every second week for the low-intensity level and 4 grazers per cage every second week for the high-intensity level). Selection of levels of variability was rather arbitrary, since the pattern of natural variability of grazers was not known in detail before the experiment. The design chosen resulted in 4 different combinations of grazing treatments (Table 1), and each was replicated 5 times. In addition, 5 replicated ungrazed caged panels were used as references or controls. All panels were separated by 15 cm from each other and positioned randomly in a 5×5 array across the mesocosm. The entire experiment was repeated independently, using different panels, on each of 2 occasions: in September and in November 2005. Each experiment ran for 6 wk.

Sampling. The upper side of the panels was sampled non-destructively at the beginning of each experiment (time = 0) and every subsequent week (i.e. 7 times in total), by examining communities carefully with the naked eye and estimating and recording the percentage cover of each identifiable taxon of algae. A regular grid with 100 intersecting points was used to facilitate estimation. In the case of multi-strata growth, total percentage cover exceeded 100%. A margin of 1 cm around each panel was ignored to avoid edge effects. Thus, the total area sampled per panel was 13×13 cm. All algae >1 mm present were recorded and identified to the lowest possible taxonomic level. Taxa that could not be identified to the level of species or genus were grouped by morphological criteria. One category, hereafter referred to simply as 'biofilm', consisted of a mixture of benthic diatoms and brown filamentous algae of the family Ectocarpaceae that could not be distinguished from each other quantitatively without microscopic examination. The other taxonomic cate-

gories could be grouped as either filamentous or crustose. The former were green algae (mainly from the family Ulvaceae) and red algae (mainly of the genera *Polysiphonia*, *Acrochaetium*, *Ceramium* and from the family Rhodomelaceae), and less common turfing coralline algae and the brown alga *Scytosiphon lomentaria* Link. The crustose algae were the brown *Ralfsia* sp., green *Ulvea* sp., and coralline algae.

Statistical analyses. A 2-way repeated-measures analysis of variance (RM-ANOVA) was used to analyse the total percentage cover of the 4 most prominent taxa (biofilm, green filamentous algae, *Ralfsia* sp., and *Ulvea* sp.) in response to the treatments. The Mauchly test was used to check the assumption of sphericity and Greenhouse-Geisser adjusted p-values were used for the within-subject terms when the assumption of sphericity was violated. Levene's test was used to check the assumption of homogeneity of variances, and the assumption of normality was checked by visual inspection of residual plots. In addition, planned comparisons of the percentage cover of prominent taxa on ungrazed control panels versus the grazed communities (across all grazing regimes) were done using the RM-ANOVA test, as described above. SNK tests were used to compare appropriate means for factors that were found to be statistically significant in the RM-ANOVA analyses. Although pair-wise SNK tests do control experiment-wise Type I error for the analysis of any single variable, no additional formal corrections for multiple tests were made across the 5 univariate variables analysed separately in each of the 2 experiments, so results should be interpreted with some caution in this regard.

Effects of intensity and variability in grazing at the community level were examined using principal response curves (PRC, Van den Brink & ter Braak 1999). PRC is a special case of redundancy analysis for multivariate responses to treatments versus controls in a repeated-measures design. It provides a simple means of visualising and testing overall community response by determining the sizes of treatment effects relative to a control, here the ungrazed community, through time. PRC also generates taxon weights that indicate which taxa are driving observed treatment differences from the control. The statistical significance of the deviations of treatments from the control through time, as displayed by PRC ordination diagrams, was tested using 999 random permutations. The software CANOCO (ter Braak & Šmilauer 2002) was used to perform the PRC and associated permutation test; 7 and 8 algal taxa were included in the analysis of the first and second experiments, respectively. Cover data were transformed to $x' = \ln(x + 1)$ before proceeding with the PRC, as in ter Braak & Šmilauer (2002).

RESULTS

At the beginning of the first and second experiments, panels had a mean total algal cover of 86.08% (SE = 1.03) and 144.40% (SE = 2.19), respectively (Fig. 1). Most algal groups had greater cover at the beginning of the second experiment than at the beginning of the first, the only exception being the biofilm, which had a mean cover of 66.40% (SE = 1.21) and 64.80% (SE = 2.85) prior to the first and second experiments, respectively. The largest difference in algal cover prior to the experiments was that of *Ralfsia* sp. (first experiment mean = 7.88%, SE = 0.97; second experiment mean = 57.80%, SE = 4.43).

Effect of grazing on algal assemblages

Changes in the total cover and cover of the most prominent taxa were observed in response to grazing during both experiments. Total cover and cover of biofilm were greater in the ungrazed than in the grazed assemblages (Fig. 1, Table 2, ungrazed (U) vs. grazed (G): $p < 0.001$). Green filamentous algae had greater cover in ungrazed than in grazed assemblages during the first experiment (Fig. 1, Table 2, U vs. G: $p < 0.001$), although the size of this effect was variable over time (Table 2, Time \times U vs. G: $p < 0.05$). During the second experiment, cover of this alga was as low in ungrazed as in grazed treatment regimes (Fig. 1, Table 2). Overall average percentage cover of *Ralfsia* sp. did not differ statistically significantly in the ungrazed vs. the

grazed assemblages during the first experiment (Fig. 1, Table 2, U vs. G: $p > 0.05$). The green crustose alga *Ulvellla* sp. had greater cover in ungrazed than in grazed assemblages during the first experiment (Fig. 1, Table 2, U vs. G: $p < 0.001$) although, once again, the size of this effect was variable over time (Table 2, Time \times U vs. G: $p < 0.05$). During the second experiment, both *Ralfsia* sp. and *Ulvellla* sp. had greater cover in grazed than in ungrazed treatments (Fig. 1, Table 2, U vs. G: $p < 0.001$ and $p < 0.05$, respectively). Thus, biofilm and filamentous algae had less, and crustose algae greater, cover when grazed.

Effect of grazing intensity and variability on algal assemblages

Total cover of all algae was greater, on average, under constant than under variable grazing regimes, and the size of this main effect was greater in the first experiment than in the second (Figs. 2 & 3, Tables 3 & 4). Also, the size of this effect in both experiments was greater for the low-intensity than for the high-intensity grazing regimes. Generally there was greater average cover of biofilm in constant compared to variable grazing regimes (Tables 3 & 4, Fig. 3), and this effect was especially large in the second experiment for low-intensity situations (Tables 3 & 4, Intensity \times Variability: $p < 0.001$). For green filamentous algae, similar results were obtained in the 2 experiments. There was greater average cover in the constant than in the variable grazing regimes (Table 3, Variability:

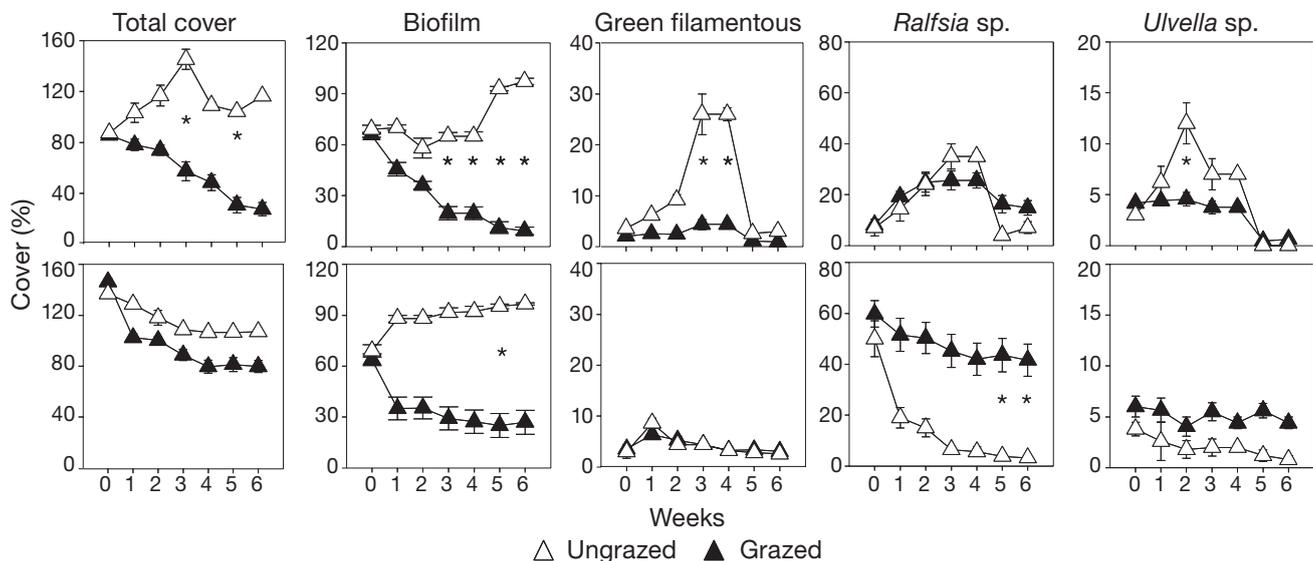


Fig. 1. Effect of *Catharidus purpureus* grazing on algal community. Mean (± 1 SE) percentage total cover, and cover of biofilm, green filamentous algae, *Ralfsia* sp. and *Ulvellla* sp. in each grazing treatment ($n = 5$) for Expt 1 (top panels) and Expt 2 (bottom panels). (Δ) Ungrazed treatments, (\blacktriangle) all grazed treatments pooled. Note differences in scales of y-axes for different taxa.

*Statistically significant differences between treatments at $p < 0.05$ for given sampling week (SNK test)

Table 2. Effect of *Catharidus purpureus* grazing on algal community. RM-ANOVA table examining ungrazed vs. grazed (U vs. G) percentage cover for each of the most prominent taxa in Expts 1 and 2. Greenhouse-Geisser adjusted p-values were computed for within-subject terms: * $p < 0.05$, ** $p < 0.1$, *** $p < 0.001$

	df	Total cover		Biofilm		Green filamentous		<i>Ralfsia</i> sp.		<i>Ulvella</i> sp.	
		MS	F	MS	F	MS	F	MS	F	MS	F
Expt 1											
Between subjects											
U vs. G	1	82 709.8	40.18***	55091.6	98.05***	1975.7	61.95***	36.1	0.051	104.9	9.22***
Residual	23	2058.3		561.9		31.9		713.6		11.4	
Within subjects											
Time	6	2452.7	10.81***	1289.1	11.65***	561.8	80.35***	1501.1	18.09***	138.2	28.96***
Time \times U vs. G	6	4322.2	19.05***	3936.4	35.56***	340.9	48.76***	270.6	3.26*	37.0	7.75***
Residual	138	226.8		110.7		7.0		83.0		4.8	
Expt 2											
Between subjects											
U vs. G	1	10 261	9.39**	81734.4	19.71***	0.02	0.001	30 426.0	7.79**	261.7	4.73*
Residual	23	1093		4146.3		22.4		3907.8		55.3	
Within subjects											
Time	6	5046	31.91***	80.0	0.71	42.9	9.23***	2127.1	19.25***	9.7	1.55
Time \times U vs. G	6	693	4.38***	2051.1	18.27***	4.4	0.94	443.4	4.01*	2.7	0.44
Residual	138	158		112.2		4.7		110.5		6.3	

$p < 0.05$), but no obvious effect of intensity. There were no strong effects of variability on *Ralfsia* sp., except in low-intensity treatments in Expt 2, where it apparently had greater average cover under variable than under constant grazing regimes (Table 3, Intensity: $p < 0.05$, Variability: $p = 0.05$, Intensity \times Variability = 0.07). *Ulvella* sp. showed no consistent patterns of response across the 2 experiments. It had greater average cover in the constant grazing than in the variable grazing regimes in Expt 1 (Variability $p < 0.05$), but the opposite pattern occurred in Expt 2 (Table 3).

The first PRC axis explained 68% of the variation in treatment effects for the Expt 1 and 82% for the Expt 2. In both experiments, grazed assemblages deviated increasingly and statistically significantly from assemblages on ungrazed control panels over time (Fig. 4, Expt 1: $F = 72.94$, $p = 0.001$; Expt 2: $F = 123.75$, $p = 0.001$). For the first experiment, assemblages under variable grazing regimes showed larger deviations from the controls than did constantly grazed assemblages. Although no consistent pattern was observed regarding different levels of grazing intensity over the first few weeks, by Week 6, high-intensity grazing had caused greater changes to assemblages than low-intensity grazing (for either the variable or constant regimes, Fig. 4). All taxa had a positive weight for the PRC coefficient, indicating decreases in their average percentage cover in grazed communities relative to the controls. Taxa with weights below 0.5 (i.e. crustose algae) had either a weak or an unclear response to treatments. Filamentous algae all had weights higher than 0.5, showing a strong general response. The biofilm had the highest weight, suggesting the strongest negative effects of grazing on this taxon.

During the second experiment, assemblages under variable grazing regimes showed larger deviations from the control than those under constant regimes of the same intensity (Fig. 4). This difference was much larger for the low than for the high level of grazing intensity (Fig. 4). As in the first experiment, the biofilm had the highest positive weight. Crustose algae (*Ulvella* sp. and *Ralfsia* sp.) had negative weights and showed increasing cover with grazing, particularly *Ralfsia* sp., which had a large negative weight.

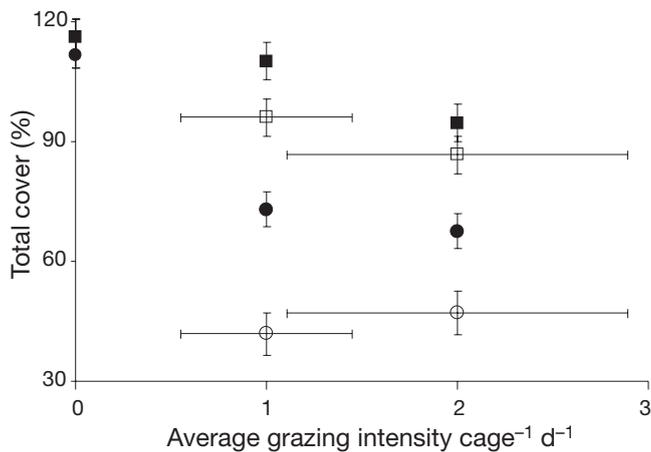


Fig. 2. Effect of *Catharidus purpureus* grazing on algal community. Mean (± 1 SE) total algal cover as a function of mean (± 1 SE) grazing intensity in constant (●, ■) and variable (○, □) regimes during Expt 1 (○, ●) and Expt 2 (□, ■). Data pooled across all sampling dates

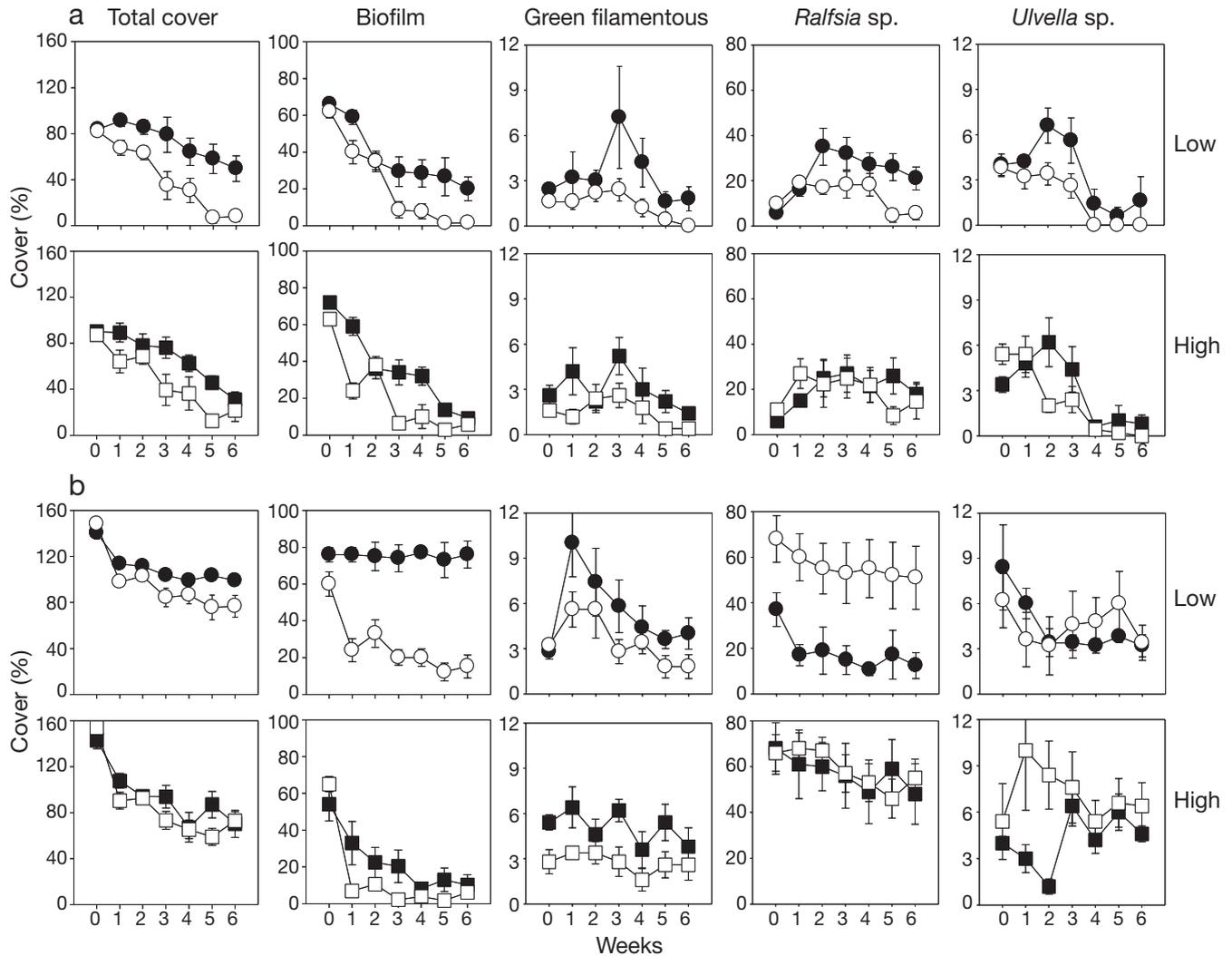


Fig. 3. Effect of *Catharidus purpureus* grazing on algal community. Mean (± 1 SE) percentage total cover and cover of biofilm, green filamentous algae, *Ralfsia* sp. and *Ulvella* sp. in each grazing treatment ($n = 5$) for (a) Expt 1 and (b) Expt 2. Low-intensity (O,●), high-intensity (□,■), variable (O,□), constant treatments (●,■). Note differences in scales of y-axes for different taxa.

*Statistically significant differences between treatments at $p < 0.05$ for given sampling week (SNK test)

DISCUSSION

The effects of temporal variability in grazing on total cover, individual taxa and on overall assemblage structure were broadly similar in both experiments. As expected, grazing reduced the cover of biofilm and filamentous algae, while crustose algae increased. However, the finding that variable grazing regimes removed algal cover more effectively than constant regimes was not anticipated. This indicates that temporal variation in grazing can be important in structuring algal assemblages.

Total cover and the cover of filamentous algae (biofilm and green filamentous) were lower, on average, under variable than under constant grazing regimes. In the first experiment, the effect of variabil-

ity in grazing was independent of the intensity of the process, while in the second there was an interactive effect: the effect of increased temporal variability was much larger for the low-intensity treatment than for the high-intensity treatment. For green filamentous algae, the effect of temporal variability in grazing is relevant for the first experiment only, since these algae were not affected by grazing in the second experiment, probably due to the low percent cover observed. Nevertheless, in general, the effect of an ecological process (in this case, grazing) with low average intensity may have a stronger influence on a response variable if it occurs in intermittent pulses (i.e. with a large temporal variance) than if it occurs constantly and evenly over the same time period (Berlow 1999, Benedetti-Cecchi 2000).

Table 3. RM-ANOVA table of effects of intensity and variability in grazing by *Catharidus purpureus* on percentage cover of most prominent taxa in each experiment. Greenhouse-Geisser adjusted p-values were computed for within-subject terms: *p < 0.05, **p < 0.01, ***p < 0.001

	df	Total cover		Biofilm		Green filamentous		<i>Ralfsia</i> sp.		<i>Ulvella</i> sp.	
		MS	F	MS	F	MS	F	MS	F	MS	F
Expt 1											
Between subjects											
Intensity (I)	1	0.9	0.00	60.5	0.24	1.4	0.06	54.1	0.06	0.2	0.02
Variability (V)	1	23 271.6	16.50***	8611.5	34.05***	136.0	5.43*	1314.6	1.52	70.0	7.21*
I × V	1	1015.2	0.72	1.8	0.01	2.9	0.11	745.2	0.86	5.2	0.54
Residual	16	1410.4		252.9		25.1		866.4		9.7	
Within subjects											
Time (T)	6	10 621.9	49.78***	8536.7	87.00***	38.1	9.47**	879.5	12.33***	63.4	17.07***
T × I	6	57.4	0.27	96.3	0.98	1.4	0.34	18.0	0.25	3.5	0.95
T × V	6	957.7	4.49**	553.4	5.64**	8.8	2.19	428.3	6.01**	12.5	3.36*
T × I × V	6	175.2	0.82	168.4	1.72	2.4	0.59	33.2	0.47	1.4	0.39
Residual	96	213.3		98.1		4.0		71.3		3.7	
Expt 2											
Between subjects											
Intensity (I)	1	5282.9	5.60*	36 676.8	39.47***	10.31	0.56	15 121.6	4.94*	45.7	0.7
Variability (V)	1	4213.0	4.45*	29 609.3	31.87***	160.71	8.76*	13 701.6	4.48	77.3	1.2
I × V	1	333.3	0.35	13 800.7	14.85**	1.03	0.06	11 611.6	3.79	71.4	1.1
Residual	16	943.6		929.2		18.35		3061.1		64.3	
Within subjects											
Time (T)	6	11 308.2	82.34***	3613.2	63.04***	30.43	6.47***	868.2	6.78**	12.01	2.20
T × I	6	444.5	3.24*	621.4	10.84***	14.43	3.07*	98.9	0.77	16.00	2.93*
T × V	6	716.4	5.22**	767.4	13.39***	4.73	1.01	138.0	1.08	7.17	1.31
T × I × V	6	114.8	0.84	210.3	3.67*	2.85	0.60	49.2	0.38	21.71	3.97*
Residual	96	137.3		57.3		4.70		128.1		5.47	

Table 4. Summary of post-hoc SNK tests among levels for effects of intensity and variability in grazing by *Catharidus purpureus* on percentage cover of most prominent taxa in each experiment (L = low, H = high, C = constant, V = variable). <, >: statistically significant differences between means at p < 0.05; =: no statistically significant difference at p > 0.05. Because of a statistically significant Intensity × Variability interaction for the biofilm in the second experiment (see Table 3), separate tests were done within each level as appropriate

Cover	Expt 1		Expt 2	
	Intensity	Variability	Intensity	Variability
Total cover	L = H	C > V	L < H	C > V
Biofilm	L = H	C > V	For C: L > H For V: L = H	For L: C > V For H: C = V
Green filamentous	L = H	C > V	L = H	C > V
<i>Ralfsia</i> sp.	L = H	C = V	L < H	C = V
<i>Ulvella</i> sp.	L = H	C > V	L = H	C = V

It has been predicted that variability in ecological processes may affect the mean value of the response variable simply as a result of a mathematical property of nonlinear functions, known as Jensen's inequality (Ruel & Ayres 1999). If the relationship between grazer density and mean algal cover is a convex function (Lubchenco & Gaines 1981, Benedetti-Cecchi et al. 2005), Jensen's inequality predicts that variability in

grazing density will have a positive effect on the estimated mean algal cover. However, the results of this study showed the opposite effect: an increase in the temporal variance of grazing had a negative effect on algal cover. This indicates that other mechanisms may be operating here or that this mathematical property loses explanatory power in the context of this inherently stochastic and interactive ecological system.

The larger effects elicited by variable grazing regimes could reflect an asymmetry in the response of algae to temporal changes in the intensity of grazing. More specifically, the negative effect caused by intermittent increases in grazing intensity may be larger than the positive effects accrued in the absence of grazing over an equivalent period of time. Asymmetry may arise from synergistic, rather than additive effects. For example, the collective effects of several individuals grazing together may be more severe than the effect of individuals acting in isolation (Coolen 2002), because intraspecific competition for food may intensify effects (Marshall & Keough 1994).

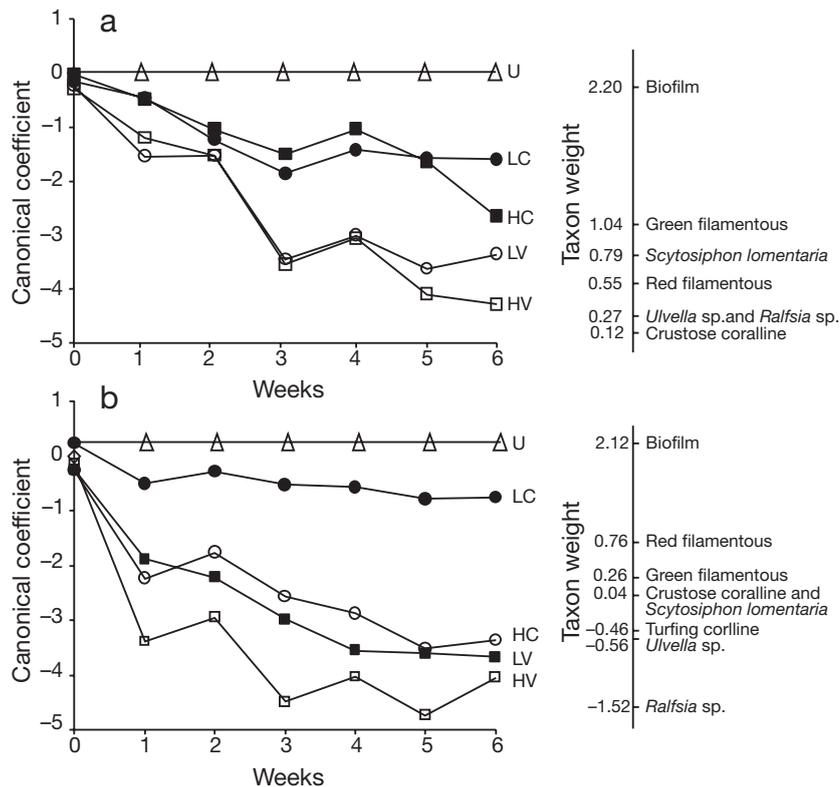


Fig. 4. Effect of *Catharidus purpureus* grazing on algal community. Principal response curves (PRC) comparing algal communities in each treatment combination with ungrazed control over time (U = ungrazed; LC = low, constant; HC = high, constant; LV = low, variable; HV = high, variable) for (a) Expt 1 and (b) Expt 2. Weights are shown for each taxon included in analysis. Taxa with positive weight values decreased in cover in grazed assemblages relative to control, those with negative weights showed opposite trend; taxa with weights between -0.5 and 0.5 had either a weak or unclear response to treatments

The differences in the initial algal cover between the first and second experiment can be explained by the time of year that the experiments were conducted. The first experiment started in September and the second in November, so that there was a 2 mo difference in the timing of the panel colonisation process. Towards the end of the year (as the southern hemisphere approaches summer) the water temperature and the light levels were higher, which may have favoured the colonisation and growth of algae during the second experiment. This was particularly true for *Ralfsia* sp., whose cover was ~7-fold higher during the second experiment. Greater cover also meant increased thickness of the algal crust, which improved its resistance to grazing, particularly under low-constant treatments. This was the primary cause of the interactive effect observed.

The overall results presented here concur with experimental studies of grazing in terrestrial systems (McKenzie 1997), where the temporal occurrence of grazing was more important than grazing intensity in determining rates of grass tiller reduction. On the other

hand, Benedetti-Cecchi et al. (2005), who studied the effects of spatial (rather than temporal) variance of grazing on intertidal (rather than subtidal) algal assemblages, found that increased spatial variability in grazing enhanced algal cover compared to more uniform regimes of equal grazing intensities. This may have been due to a 'size refuge' (an escape from grazing) attained by algae reaching a particular size (Lubchenco & Gaines 1981). Similarly, studies focused on temporal variability of predation in aquatic systems found that variable regimes led to different prey community structure because some species attained a size at which they were no longer vulnerable to predation (Navarrete 1996). This mechanism was not observed in the present study, probably due to the short duration of the periods that grazers were excluded (2 wk). Contrary to the effect of temporal variability in trophic interactions (grazing or predation), temporal variability of physical disturbance has shown no clear effects on the relative abundance, richness or structure of aquatic communities (Robinson & Sandgren 1983, Bertocci et al. 2005).

The simple prediction that a higher intensity of grazing would decrease the percentage cover of individual taxa and change the structure of the assemblages more than a lower intensity of grazing was also generally supported by these experiments. If algae are edible, they should be more abundant at low grazing intensity and less abundant or absent at high grazing intensity. Lubchenco & Gaines (1981) and Benedetti-Cecchi et al. (2005) suggest algal cover is a decreasing exponential function of grazing intensity. This function predicts unappreciable or very subtle effects of grazing over certain levels of intensity, once an asymptote in mean algal cover is reached. This might explain the absence of any clear differences in cover between assemblages exposed to different levels of intensity over the first few weeks in the first experiment; the high level of intensity chosen was close to the maximum natural densities observed for the molluscan grazer guild and approximately 2-fold higher than estimates of natural densities of *Cantharidus purpureus* (Ayling 1981). In the second experiment, increasing grazing intensity led to a clear decrease in total algal cover, and also interacted with the effects of variability in the process. The reduction in cover of biofilm and green filamentous algae for

temporally variable compared to constant grazing regimes was much greater for low than for high grazing intensities.

The drastic decrease in algal cover and the shift from filamentous to crustose algal forms in grazed compared to ungrazed assemblages supports the large body of studies describing the effects of grazers on algal assemblages (e.g. Lubchenco & Gaines 1981, e.g. Hawkins & Hartnoll 1983, Creese 1988) and on terrestrial plant assemblages (Lindroth 1989). Ungrazed assemblages tended to be dominated by the biofilm, leading to a considerable decrease in the cover of other taxa. In contrast, grazed assemblages were dominated by crustose forms (i.e. *Ralfsia* sp. and *Ulveella* sp.). There are many examples in which monocultures formed by competitively superior species develop on hard surfaces of shallow subtidal systems (Lubchenco 1982). In the present study, grazers were a strong interactor, preventing the dominance of biofilm, and thus indirectly affecting other taxa in the assemblage. During the second experiment, cover of the crustose alga *Ralfsia* sp. increased in grazed assemblages, indicating an indirect positive effect of grazing on this species. Grazing prevents overgrowth of crustose algae by other algae (here biofilm and green filamentous algae) and creates space for settlement. Crustose algae have relatively slow growth rates and tend to be easily overgrown (McQuaid & Froneman 1993). In addition, the photosynthetic rate of *Ralfsia* sp. can be enhanced by grazers through their mucus and nutrient generation (Branch et al. 1992) and by their clearing of space to create secondary growth sites (McQuaid & Froneman 1993).

The results of this study indicated that temporally variable grazing regimes can lead to larger reductions of algal cover, evident for individual taxa and for the algal assemblage as a whole, either independently of changes in the mean density of grazers (as in the first experiment), or interacting with levels of grazing intensity (as in the second experiment). Regardless of the mechanisms underlying these observed effects, this study showed that effects of grazing can depend not only on the intensity, but also on the temporal variability of the process. Clearly, further work is required to test and extend inferences from this small-scale mesocosm study more generally to field-based populations. However, temporal variation is undoubtedly a natural feature of temperate rocky reef systems, and therefore should be examined and incorporated into predictive models. Experiments that allow separation of the effects of the mean and the variance of ecological processes, and which can identify their potential interactive effects, may enable explanation of patterns of changes in populations and assemblages that cannot be deduced simply by manipulating the intensity of a process.

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