Response of grazers to sudden nutrient pulses in oligotrophic versus eutrophic conditions

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ABSTRACT: Herbivores can consume more nutrient rich algae than nutrient poor algae, and such foraging behaviour may counter the negative effects of elevated nutrients on algal habitats. Understanding this phenomenon may be useful in understanding why some localities have greater persistence and resilience than others in the face of sudden increases in nutrient loads (e.g. run-off from storm events). We used 3 successive field experiments to test, and subsequently accept, the hypotheses that under intense regimes of herbivory (1) molluscs reduce a greater percentage cover of opportunistic algae (turfs) exposed to elevated nutrients, and consequently these algae have less biomass than those exposed to ambient nutrients, (2) turfs exposed to elevated nutrients attract greater densities of herbivores, and (3) grazers exposed to sudden increases in nutrient rich algae reduce algal biomass more when background nutrient loads are normally low (ambient nutrient conditions) than when they are high (enriched nutrient conditions). Critically, these effects were greater under oligotrophic conditions, suggesting that the response of grazers to sudden nutrient events would be greater in systems where nutrient concentrations are usually low. However, grazers were not able to control increased algal growth when nutrient enrichment occurred over a longer period (i.e. eutrophic conditions). These observations support the idea that grazers may provide useful functions in systems susceptible to human activities that reduce water quality over short periods (i.e. short-term increase in nutrient availability), but that this mechanism may not be sufficient to reduce the long-term effects of eutrophication.

KEY WORDS: Elevated nutrients · Habitat shift · Grazing · Turf-forming algae

INTRODUCTION

Opportunistic algae can become competitive dominants in the presence of elevated nutrients (Lotze et al. 2000), but grazers may counter this effect in some systems (Neckles et al. 1993, Hillebrand et al. 2000, Hillebrand 2003, Roll et al. 2005) by consuming greater biomass of plants and algae that are higher in nitrogen content (Neckles et al. 1993, Williams & Ruckelshaus 1993, Karez et al. 2000, Silliman & Zieman 2001). Greater consumption of algae may occur as a population response (i.e. increased herbivory; Boyer et al. 2004, Karez et al. 2004, Roll et al. 2005) or through the greater per capita consumption of nutrient enriched biomass (e.g. Nicotri 1980, Arrontes 1990). As opportunistic algae are often fast growing and have physi-

ologies enabling the rapid uptake of available nutrients (Hein et al. 1995), grazers are likely to preferentially consume such algae soon after eutrophication events (e.g. runoff from storm events), possibly constraining outbreaks of fast growing algae (Lotze et al. 2000, Roll et al. 2005).

The way in which the nutrient status of a system (i.e. oligotrophic versus eutrophic) affects the food preference of herbivores is not well understood (Watson & Norton 1985). Studies of food preference demonstrate that the feeding history and nutritional status of herbivores can determine feeding behaviour and food preference (Watson & Norton 1985, Norton et al. 1990, Bamstedt et al. 1999). When given a choice between food of different nutritional values, herbivores are more likely to consume those with higher nutritional

value (Watson & Norton 1985, Arrontes 1990, Boyer et al. 2004, Goecker et al. 2005, Loney et al. 2006). In contrast, when only low nutrient food is available, herbivores often consume greater quantities to compensate for the low nutrient value (e.g. Berner et al. 2005, Fink & Von Elert 2006, Huberty & Denno 2006). It may be expected, therefore, that although individuals may consume smaller quantities of nutrient rich food, herbivore populations with historical access to low nutrient food (i.e. on oligotrophic coasts) would preferentially consume greater quantities of nutrient rich food than populations with historical access to food of high nutrient value (i.e. on eutrophic coasts).

Although individual herbivores may display a preference for nutrient rich algae, there is conflicting evidence as to whether populations of herbivores can (Neckles et al. 1993, Hillebrand et al. 2000, Hillebrand 2003, Roll et al. 2005) or cannot control increased algal growth associated with elevated nutrients (e.g. Lotze et al. 2001, Lotze & Worm 2002, Worm & Lotze 2006). It is possible that herbivores may not be able to counteract the effects of elevated nutrients if there is no population response (i.e. individual consumption does not increase; Worm & Lotze 2006) or if nutrients rise above threshold concentrations (e.g. Hauxwell et al. 1998, Lotze & Worm 2002). This would mean that whilst nutrients may have disproportionately greater effects on oligotrophic coasts (Russell et al. 2005), any compensatory response of grazers may only reduce the effects of elevated nutrients over short periods (Boyer et al. 2004), but not when there is long-term eutrophication.

In South Australia, turf-forming algae appear to form competitive dominants on subtidal rock adjacent to heavily urbanised coast (Gorgula & Connell 2004) and constitute a large part of the diet of many of the herbivorous molluscs (Clarkson & Shepherd 1985), which are the most abundant benthic macrograzers of this region (D. Gorman & S. D. Connell, unpubl. data). Under naturally intense regimes of herbivory, we tested the hypotheses that (1) molluscs reduce a greater percentage cover of turf-forming algae exposed to elevated nutrients, and consequently, these turf-forming algae have lower biomass than those exposed to ambient nutrients, (2) a greater density of herbivores graze algae exposed to elevated nutrients, and (3) grazers exposed to sudden increases in nutrient rich algae reduce algal biomass more when nutrient loads are normally low (ambient nutrient condition) than when they are high (enriched nutrient conditions).

MATERIALS AND METHODS

Natural patterns and experimental reefs. Experiments were done on experimental reefs in Abalone Cove, West Island, South Australia (35° 36' S, 138° 35' E). The study site consists of a sloping boulder reef that terminates in sand at ~5 m depth and supports diverse assemblages of algae (Shepherd & Womersley 1970) and dense populations of molluscan grazers (Clarkson & Shepherd 1985) which were 2 to 100 times greater than those observed at 6 sites on adjacent coastal areas (Fleurieu Peninsula; D. Gorman & S. D. Connell, unpubl. data, Table 1). Experiments focused on the most common and abundant species: *Clanculus* spp., *Turbo* spp., and *Astralium aureum*. Other benthic grazers (e.g. echinoids, *Heliocidaris erythrogramma*) are rarely observed on the adjacent coast of the mainland (Fleurieu Peninsula) and westward through to the Great Australian Bight (D. Gorman & S. D. Connell, unpubl. data). The turf-forming algae quantified in this study comprised annual, fine filamentous thalli that can form close-knit 'turfs' <2 cm in vertical height. The most abundant members of the turf were *Feldmannia* spp.

The experimental reefs used for all 3 experiments were set on sand (~5 m depth) at least 10 m from the natural reef. Each reef was constructed from 2 square 60×60 cm metal frames, each with a concrete base (60×60 cm). The lower base was set on the sand. The upper base, 20 cm above the lower base, created a platform for boulders (see Shepherd & Turner 1985 for a photograph of the experimental reefs). Each reef contained approximately 9 boulders, 7 of which were taken from natural reef and placed on the experimental reefs, leaving a gap in the middle of each reef for 2 'experimental' boulders (see next 2 subsections for treatments). This design has been successfully used to test for the effects of molluscan grazers because the 20 cm space between the concrete bases restricts movement of molluscs, making it possible to control

Table 1. Comparison of natural nutrient concentrations (DIN: dissolved inorganic nitrogen = ammonium + nitrate + nitrite; µmol l^{-1}) and mollusc abundances (ind. m^{-2}) at different sites within South Australia

	Nutrient concentration DIN	Mollusc abundance
West Island	0.29[a]	113[b]
Experimental reefs (high density)	0.15[c]	111[c]
Experimental reefs (low density)	No data	46[d]
Adjacent coast	No data	1 – 25[e]
Adelaide Metropolitan	6.00[a]	4 – 54[e]

[a]Gorgula & Connell 2004 (sampled in March); [b]Clarkson & Shepherd 1985; [c]Russell & Connell 2005 (sampled in February); [d]this study; [e]D. Gorman & S. D. Connell, unpubl. data

the number of molluscan grazers on each experimental reef (see Russell & Connell 2005). The density of grazers was manipulated at the start of each experiment by either adding (from the natural reef) or removing molluscs. At the beginning of each of the 3 successive experiments, boulders similar to those on experimental reefs, but devoid of obvious macroscopic marine life, were placed in the gap left between the other boulders at the centre of each reef.

Effects of nutrients on grazing. In February 2003, 10 experimental reefs with high densities of grazing molluscs (111 ± 9.6 SE m^{-2}) were used to test whether the percentage cover of grazing marks of molluscs was greater on reefs exposed to short-term elevated concentrations of nutrients (n = 5 reefs) than on reefs with ambient concentrations of nutrients (n = 5 reefs). Percentage covers were quantified approximately 4 wk after addition of nutrients by placing a 100 mm × 100 mm grid containing 25 points over the boulder and recording the presence of either turf-forming algae or grazing scars directly beneath each point (Drummond & Connell 2005). Molluscs consumed small filamentous algae down to the substratum (Clarkson & Shepherd 1985), leaving defined grazing scars, which were easily quantified. The effects of grazing were striking in their support of the hypothesis (see Results), but we were less confident about this effect at sparser densities of grazers (i.e. <50% of initial densities). To reduce this uncertainty, we re-tested this hypothesis at sparser densities of grazers (46.7 ± 5.4 SE m^{-2}; 0.8 to 43 times greater than 6 sites on the adjacent peninsula), using an extra replicate (n = 6 reefs per treatment) to detect a potentially smaller effect-size, whilst also quantifying the biomass of turf-forming algae in addition to their percentage cover. This second experiment was run for 4 wk in December 2003. Algal biomass was sampled by placing the opening of a plastic jar (surface area of 14.52 cm^2) over the experimental boulder and removing all visible algae off the rock and into the jar. Algae were oven dried (70°C) for 48 h to constant weight before being weighed. These experiments focused on the early and rapid phase of growth by turfs, the phase most likely to be affected by sudden increases in nutrient concentrations, and either overwhelmed by the effects of grazers or subject to their control.

Response of grazers to short-term nutrient pulses under long-term ambient and enriched conditions. The effects of long-term nutrient conditions (ambient versus enriched) and short-term nutrient pulses (ambient versus elevated) on grazing were tested together in a crossed design (n = 6 per treatment) (Fig. 1). In January 2004, grazers were isolated on reefs with either ambient (low) or enriched (high) conditions for 3 mo (long-term nutrient status) before being presented with algae with ambient (low) and elevated (high) con-
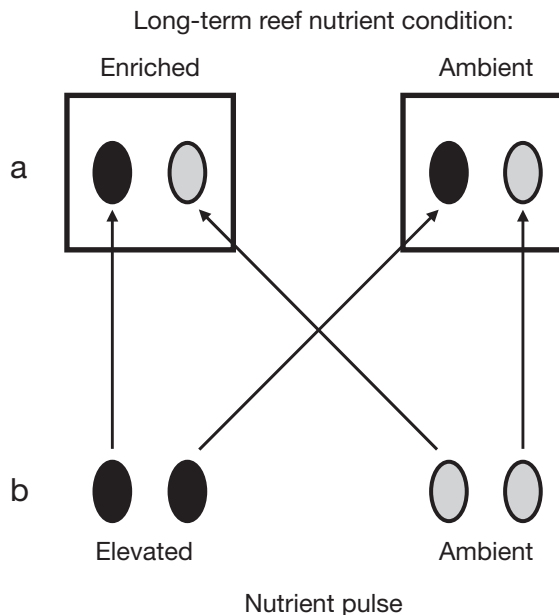

Fig. 1. Schematic diagram showing how we created the conditions needed to test for the effects of nutrient condition and sudden nutrient pulse on grazing. Initially, grazers were isolated with algae associated with (a) reefs of either ambient or enriched nutrient conditions before (b) being presented with algae associated with both elevated (black oval) and ambient (gray oval) concentrations of nutrients (i.e. sudden pulse of nutrients)

centrations of nutrients (i.e. short-term pulse in nutrient status). The translocated algae were cultured on boulders, devoid of obvious macroscopic marine life, that had been placed on experimental reefs without herbivorous molluscs. Algae were allowed to grow for 4 wk before these boulders were moved to experimental reefs that contained molluscs (46.7 ± 5.4 m^{-2}) associated with either long-term ambient or enriched conditions. Two boulders were placed at the centre of each experimental reef: one that had been exposed to ambient nutrients and one that had been exposed to elevated nutrients (i.e. sudden change in nutrients). Four weeks after the boulders were moved onto the experimental reefs, biomass of algae was sampled as above (see 'Effects of nutrients on grazing').

To test the hypothesis that greater densities of molluscs graze on turf-forming algae exposed in the short-term to elevated nutrients as compared to ambient nutrients, we counted the number of molluscs observed grazing each experimental boulder on 2 occasions, viz. 2 wk after commencement and the night before biomass samples were collected. Counts were done an hour after sunset because the molluscs at the field site were more active at night. As all boulders on experimental reefs were selected to be of similar size, the number of molluscs is expressed per boulder (i.e. number ~300 cm^{-2}).

The biomass of algae and number of grazers on the experimental boulders (short-term nutrient pulse: ambient versus elevated) were initially analysed using a randomised block ANOVA within each level of long-term reef nutrient condition (ambient or enriched); treatments were reef (random blocks) and nutrient pulse (fixed and orthogonal). A 2-factor ANOVA was then used to test for the effects of long-term reef nutrient condition (ambient versus enriched; fixed and orthogonal) and nutrient pulse (ambient versus elevated; fixed and orthogonal). Although in the strictest sense the 2 treatment boulders on each reef were not independent (violating the assumptions of ANOVA), there were 9 boulders on each reef, so grazers had the choice of grazing on more than the 2 experimental boulders (i.e. the total number of grazers on the treatment boulders was not the same as the total number of grazers on each reef), so we have interpreted the 2-factor ANOVA because the density of grazers on one boulder did not depend on the density on the other boulder.

Nutrient content of algae. To test the explicit assumption that nutrient content of algae exposed in the short-term to elevated nutrients was greater than in algae exposed to ambient nutrients, samples of turf-forming algae were collected from boulders in January 2004 (ambient versus elevated; n = 6). Samples were dried using the same method as for biomass samples from previous experiments (see above). Samples were ground using a sterile porcelain mortar and pestle, weighed to the nearest 0.1 mg and analysed for percentage nitrogen content using a GV Isoprime mass spectrometer.

Nutrient addition. Nutrients were supplied as 12 g of Osmocote Plus® slow release fertilizer per nutrient boulder (6 mo release: 15, 5, 10 N-P-K). At the beginning of the experiments, 4 nylon mesh bags (1 mm mesh size) were each filled with equal amounts of Osmocote® pellets and attached to the 4 sides of the experimental boulder using cable ties. Each bag was ~2 cm in diameter and was situated slightly below the top surface of the experimental boulder. This configuration of deployment does not modify water flow or increase habitable surface on the boulder, and explicit tests for artefacts associated with this experimental protocol have shown that treatments do not confound the interpretation of experiments by artefacts (Gorgula & Connell 2004). Moreover, this approach has been tested against other experimental protocols and suggested to be the most appropriate method of elevating nutrients in subtidal experiments (Worm et al. 2000). In this study, water samples were not collected for nutrient analysis because the same weight of fertilizer (12 g per boulder) has been used twice to successfully increase water nutrient concentrations at the same study site at the same time of year; nitrate concentrations were ele-

vated by approximately 87% above ambient (Russell & Connell 2005) and nitrate and phosphorus by approximately 90 and 38%, respectively (Gorgula & Connell 2004).

RESULTS

Effects of nutrients on grazing

Molluscs consumed more algae when nutrients were elevated over the short-term. In February 2003, the percentage cover of grazing scars of molluscs was greater on boulders that were exposed to elevated nutrients than those exposed to ambient nutrients (mean ± SE; 31 ± 5.6%; 14 ± 2.7%, respectively; ANOVA: $F_{1,8} = 7.35$, p = 0.027). We re-tested this hypothesis in January 2004 using lower densities of grazers and more replicates and detected a greater proportion of grazing marks on boulders exposed to elevated nutrients (Fig. 2a, ANOVA: $F_{1,10} = 31.62$, p < 0.001). Moreover, this pattern translated into lower biomass of turf-forming algae on boulders exposed to elevated nutrients (Fig. 2b, ANOVA: $F_{1,10} = 12.17$, p < 0.01). These biomass sample data were ln-transformed to meet assumptions of variance homogeneity (Cochran's C-test) (Underwood 1997).
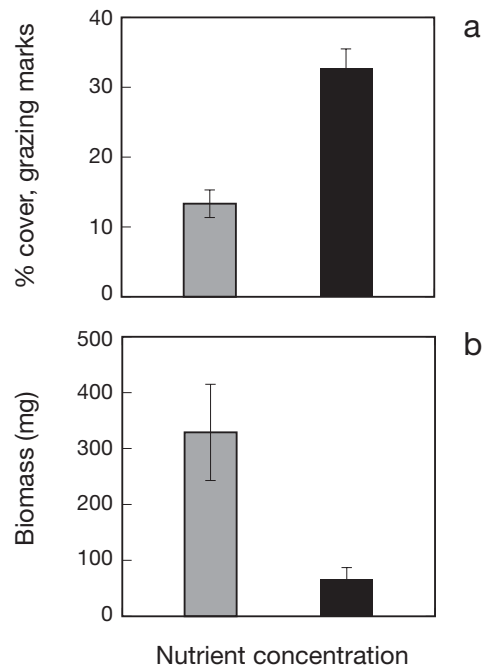

Fig. 2. (a) Percentage cover (mean +SE) of grazing marks of molluscs and (b) biomass (mg; mean ± SE) of turf-forming algae exposed in the short-term to ambient (gray bars) or elevated (black bars) nutrient concentrations

Response of grazers to short-term nutrient pulses under long-term ambient and enriched conditions

A short-term increase in nutrient concentration (elevated) had negative effects on the biomass of turf-forming algae in the presence of grazers under long-term ambient, but not enriched conditions (Fig. 3, Table 2a). On reefs with long-term ambient conditions, mean biomass of turf-forming algae was an order of magnitude less on boulders exposed to a short-term pulse of elevated nutrients (mean ± SE; 4.5 ± 0.9 mg, Fig. 3) than on boulders exposed to ambient nutrients (38.9 ± 13.4 mg, Fig. 3). On reefs with long-term enriched conditions, differences in the short-term pulse of nutrients (ambient versus elevated) had no detectable effect on biomass of algae (Fig. 3, Table 2b). In contrast to the short-term nutrient pulse, long-term
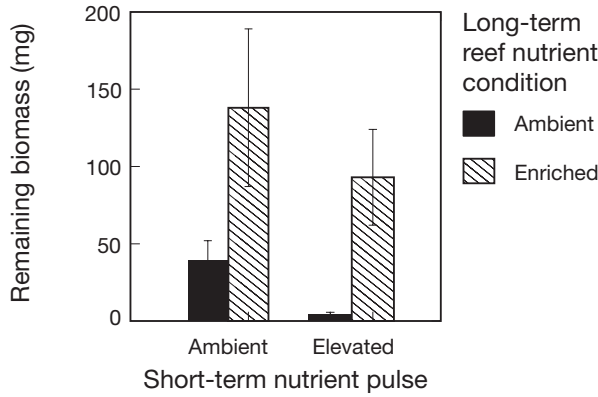
nutrient condition had a positive effect on biomass of algae, so that there was a greater biomass of algae under enriched conditions than under ambient conditions (Fig. 3, Table 3). On reefs with long-term ambient conditions, a greater number of molluscs was present on boulders exposed to short-term elevated nutrients rather than those exposed to ambient nutrients after 2 (Fig. 4a, block ANOVA: $F_{1,5} = 10.55$, p = 0.023) and 4 wk (Fig. 4b, $F_{1,5} = 9.40$, p = 0.028). In contrast, there was no difference in the number of grazers

Table 3. Two-factor ANOVA testing for the interactive effects of long-term nutrient condition (ambient versus enriched) and short-term nutrient pulse (ambient versus elevated) on the biomass of turf-forming algae on boulders after grazing by molluscs. **Bold**: significant. Ln(x) transformation was used to meet assumptions of homogeneity of variances (Cochran's C-test) (Underwood 1997)

Source of variation	df	MS	F	p
Nutrient condition	1	16.62	5.89	**0.025**
Nutrient pulse	1	13.12	4.65	**0.040**
Condition × Pulse	1	0.59	0.21	0.650
Residual	20	2.82		

Fig. 3. Biomass (mg; mean ± SE) of turf-forming algae exposed to a sudden nutrient pulse (ambient versus elevated) following long-term exposure to ambient or enriched nutrient conditions after grazing by molluscs

Table 2. Randomised block ANOVAs testing for effects of short-term nutrient pulse (ambient versus elevated) on the biomass of turf-forming algae on boulders after grazing by molluscs on reefs exposed to long-term (a) ambient and (b) enriched conditions. **Bold**: significant. Ln(x) transformation was used to meet assumptions of homogeneity of variances (Cochran's C-test) (Underwood 1997)

Source of variation	df	MS	F	p
(a) Ambient conditions				
Reef	5	0.11	0.45	0.800
Nutrient pulse	1	1.82	7.09	**0.045**
Residual	5	0.27		
(b) Enriched conditions				
Reef	5	1.20	2.12	0.214
Nutrient pulse	1	0.77	1.37	0.295
Residual	5	0.56		

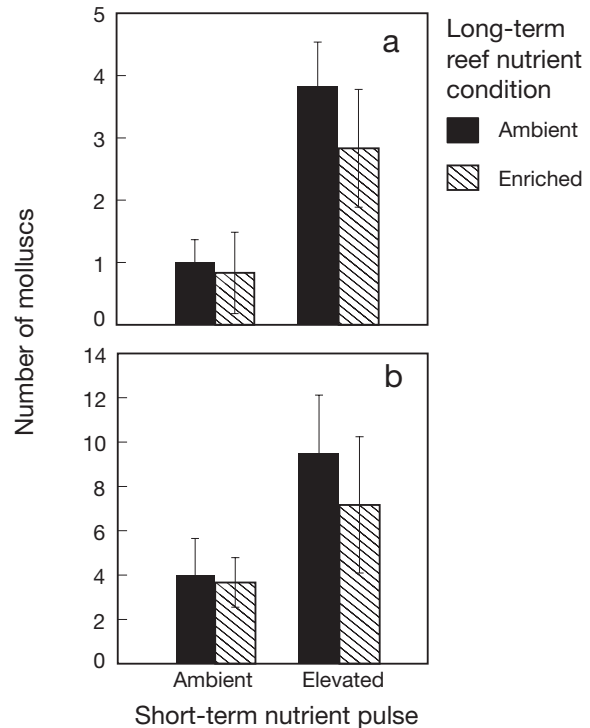Fig. 4. Number of molluscs (mean ± SE) grazing on algae exposed to a sudden nutrient pulse (ambient versus elevated) following long-term exposure to ambient nutrient conditions (a) after 2 wk and (b) after 4 wk

between boulder treatments on reefs with long-term enriched conditions after either 2 or 4 wk (Figs. 4a,b; all $F_{1,5} < 5.46$, p > 0.05).

Nutrient content of algae

The mean nitrogen content of turf-forming algae was greater in treatments with elevated nutrients (mean ± SE; 0.48 ± 0.04 %) than in those with ambient nutrients (0.37 ± 0.01 %), but the test for the difference between these means was marginally non-significant (ANOVA: $F_{1,10}$ = 4.32, p = 0.06). We re-tested for differences after removing an outlying sample (i.e. a low concentration from the treatment of elevated nutrients) and significant differences between the means were detected (elevated 0.51 ± 0.04 %, ambient 0.37 ± 0.01 %; ANOVA: $F_{1,9}$ = 7.89, p = 0.02). We report both analyses so that the reader can assess whether the 2 reported means are likely to represent real differences (using α = 0.05).

DISCUSSION

Our key finding was that herbivorous molluscs under long-term low nutrient conditions (i.e. ambient) reduced algal biomass at a greater rate when presented with a short-term pulse of algae with elevated rather than ambient nutrients. It is important to note, however, that grazers were unable to reduce algal biomass when nutrient concentrations were elevated over a longer period (i.e. enriched versus ambient nutrient condition). Grazers may indeed exert some control over the effects of increasing nutrients, but not over longer periods, as they may not increase consumption at some locations exposed to long-term eutrophication (Worm & Lotze 2006). Therefore, any compensatory response of grazers is likely to only reduce the effects of pulse elevation of nutrients (e.g. storm run-off) and not increase resilience of coasts in the face of long-term eutrophication (e.g. urbanisation), leading to the habitat switches observed on many human-impacted coasts (Jackson 2001, Eriksson et al. 2002).

Importantly, grazers exposed to a short-term pulse in nutrient rich algae responded more strongly when long-term nutrient condition was low (ambient) than high (enriched). It appears that molluscs in low nutrient conditions consumed more algae when exposed to sudden increases in nutrients. The feeding history of herbivores affects food choice (Watson & Norton 1985); hence, food with greater nutrient content is likely to be preferentially consumed by herbivores with previous access to low nutrient food. Grazers have been shown to consume more biomass of algae of greater nitrogen

content (Neckles et al. 1993, Williams & Ruckelshaus 1993, Karez et al. 2000). Greater consumption of fast growing, opportunistic algae on oligotrophic coasts could be an important check on the effects of sudden, but short-term elevation of nutrients (e.g. storm run-off), as it is possible that grazers in these areas are likely to consume the nutrient rich opportunistic algae at greater rates.

Increased consumption may occur due to either an increase in the attraction of consumers to prey or greater per capita consumption (Connell 2000). While consumers can increase in number through immigration, the experimental reefs used in this study prevented the immigration of molluscs (Russell & Connell 2005); hence, grazing pressure on reefs is most likely to have increased through greater per capita consumption. In salt marshes, molluscs remove greater biomass of plant matter that has been exposed to elevated nutrients (Silliman & Zieman 2001). Some herbivores, however, may consume greater quantities of poor quality food in order to meet nutritional requirements (Cruz-Rivera & Hay 2001, Berner et al. 2005, Fink & Von Elert 2006), while others do not change feeding rate across nutrient gradients (Worm & Lotze 2006). Further work is required in our system to distinguish between redistribution of foraging activity and increased per capita consumption. Regardless of the mechanism, our results suggest that changes in foraging effort are likely to be important for the consequences of nutrient driven changes to benthic habitats.

Although grazing in the presence of elevated nutrients can cause a switch in the relative dominance of algae (e.g. Lotze et al. 2001, Russell & Connell 2005), it still remains to be shown whether our small-scale results are relevant at broad scales. The influence of grazers can be variable over broad scales (Connell & Vanderklift 2007) and respond differently to nutrient levels across broad geographic areas (Hauxwell et al. 1998, Worm & Lotze 2006). Therefore, it would be useful to understand whether the relative abundance of algae on large expanses of coast subjected to elevated nutrients can be held in check by grazers, and whether the lack of grazers on some reefs can explain shifts from perennial to opportunistic algae (e.g. Gorgula & Connell 2004).

We emphasise 3 issues that indicate a need for careful interpretation of the ability of grazers to absorb the effects of enriched nutrient loads. First, tissue analysis and interpretation of nutrient status of turf-forming algae is not straightforward. In general, small filamentous algae with simple cellular structure (such as the turf-forming algae in this study) have high turnover of biomass, high growth rates, and are likely to store less nutrients in their tissues than longer-lived species

(Hein et al. 1995, Pedersen & Borum 1996, Copertino et al. 2005), so differences in tissue nutrient concentrations are often small and difficult to detect. Second, we did not quantify any shift in the species composition of the algal turfs, which could be an important consideration for future research, as some studies have shown shifts in algal dominance under varying nutrient regimes (e.g. Lotze et al. 2001). Third, the locations and spatial extent at which herbivores confer resilience to nutrient driven change are likely to vary with the feeding mode of herbivores. Large sections of coast can lack dense populations of grazers that are associated with strong control of benthic habitat (Connell & Vanderklift 2007). Furthermore, the response of grazers to different nutrient levels can vary among regions (Hauxwell et al. 1998, Worm & Lotze 2006). In order to increase generality in our understanding of the effects of eutrophication, marine ecologists may need to recognise such biogeographic differences so that the importance of grazing is recognised, but not overstated.

In conclusion, the concomitant increase in coastal nutrient loads (Vitousek et al. 1997) and loss of consumers (Hughes et al. 2005) are associated with an increase in the rate at which systems switch from larger and longer-lived habitats (e.g. kelps that form forests, corals that build reefs) to alternate habitats with less physical structure and shorter life (e.g. turf-forming algae) (Connell 2007). Increased grazing in the presence of elevated nutrients may resist blooms of fast growing macroalgae by reducing (Roll et al. 2005), if not counteracting, their effects. Herbivores can respond to elevated nutrient concentrations by removing greater amounts of turf-forming algae, possibly as a function of increased per capita consumption. Importantly, molluscs responded positively to sudden increases in nutrient rich algae, and this response was greater on reefs with oligotrophic conditions, suggesting that grazers may show greater responses to increased nutrient concentrations on oligotrophic coasts where small increases in nutrient loads can have disproportionately large effects on opportunistic algae (Lotze et al. 2001, Russell et al. 2005). By preferentially consuming the more opportunistic, fast growing algae, molluscs may resist the effects of elevated coastal nutrients by creating space for other, longer-lived species to colonise. This compensatory response of herbivores to the effects of nutrients deserves to be tested over broader scales to understand its potential relevance to coastal management, particularly because human harvesting of herbivores tends to be greater in locations of greater nutrient run-off (i.e. human-dominated coasts). The combined loss of grazers and increase in nutrients may make some coastal systems more vulnerable to change (Eriksson et al. 2007),

depending on both the nutrient condition (oligotrophic versus eutrophic) and loss of functional groups of grazers, and thereby account for observations that some localities have greater persistence and resilience.

LITERATURE CITED

Arrontes J (1990) Diet, food preference and digestive efficiency in intertidal isopods inhabiting macroalgae. J Exp Mar Biol Ecol 139:231–249

Bamstedt U, Nejstgaard JC, Solberg PT (1999) Utilisation of small-sized food algae by *Calanus finmarchicus* (Copepoda, Calanoida) and the significance of feeding history. Sarsia 84:19–38

Berner D, Blanckenhorn WU, Korner C (2005) Grasshoppers cope with low host plant quality by compensatory feeding and food selection: N limitation challenged. Oikos 111: 525–533

Boyer KE, Fong P, Armitage AR, Cohen RA (2004) Elevated nutrient content of tropical macroalgae increases rates of herbivory in coral, seagrass, and mangrove habitats. Coral Reefs 23:530–538

Clarkson PS, Shepherd SA (1985) Distribution and feeding of archaeogastropods in a boulder habitat at West Island, South Australia. J Malac Soc Aust 7:35–44

Connell SD (2000) Is there safety-in-numbers for prey? Oikos 88: 527–532

Connell SD (2007) Water quality and the loss of coral reefs and kelp forests: alternative states and the influence of fishing. In: Connell SD, Gillanders BM (eds) Marine ecology. Oxford University Press, Melbourne, p 556–568

Connell SD, Vanderklift MA (2007) Negative interactions: the influence of predators and herbivores on prey and ecological systems. In: Connell SD, Gillanders BM (eds) Marine ecology. Oxford University Press, Melbourne, p 72–100.

Copertino M, Connell SD, Cheshire A (2005) The prevalence and productivity of turf-forming algae on a temperate subtidal coast. Phycologia 44:241–248

Cruz-Rivera E, Hay ME (2001) Macroalgal traits and the feeding and fitness of an herbivorous amphipod: the roles of selectivity, mixing, and compensation. Mar Ecol Prog Ser 218:249–266

Drummond SP, Connell SD (2005) Quantifying percentage cover of subtidal organisms on rocky coasts: a comparison of the costs and benefits of standard methods. Mar Freshw Res 56:1–12

Eriksson BK, Johansson G, Snoeijs P (2002) Long-term changes in the macroalgal vegetation of the inner Gullmar Fjord, Swedish Skagerrak coast. J Phycol 38:284–296

Eriksson BK, Rubach A, Hillebrand H (2007) Dominance by a canopy forming seaweed modifies resource and consumer control of bloom-forming macroalgae. Oikos 116: 1211–1219, doi: 10.1111j.2007.0030–1299.15666

Fink P, Von Elert E (2006) Physiological responses to stoichiometric constraints: nutrient limitation and compensatory feeding in a freshwater snail. Oikos 115:484–494

Goecker ME, Heck KL Jr, Valentine JF (2005) Effects of nitrogen concentrations in turtlegrass *Thalassia testudinum* on

consumption by the bucktooth parrotfish *Sparisoma radians*. Mar Ecol Prog Ser 286:239–248

Gorgula SK, Connell SD (2004) Expansive covers of turf-forming algae on human-dominated coast: the relative effects of increasing nutrient and sediment loads. Mar Biol 145: 613–619

Hauxwell J, McClelland J, Behr PJ, Valiela I (1998) Relative importance of grazing and nutrient controls of macroalgal biomass in three temperate shallow estuaries. Estuaries 21: 347–360

Hein M, Pedersen MF, Sand-Jensen K (1995) Size-dependent nitrogen uptake in micro- and macroalgae. Mar Ecol Prog Ser 118:247–253

Hillebrand H (2003) Opposing effects of grazing and nutrients on diversity. Oikos 100:592–600

Hillebrand H, Worm B, Lotze HK (2000) Marine microbenthic community structure regulated by nitrogen loading and grazing pressure. Mar Ecol Prog Ser 204:27–38

Huberty AF, Denno RF (2006) Consequences of nitrogen and phosphorus limitation for the performance of two planthoppers with divergent life-history strategies. Oecologia 149:444–455

Hughes TP, Bellwood DR, Folke C, Steneck RS, Wilson J (2005) New paradigms for supporting the resilience of marine ecosystems. Trends Ecol Evol 20:380–386

Jackson JBC (2001) What was natural in the coastal oceans? Proc Natl Acad Sci USA 98:5411–5418

Karez R, Engelbert S, Kraufvelin P, Pedersen MF, Sommer U (2004) Biomass response and changes in composition of ephemeral macroalgal assemblages along an experimental gradient of nutrient enrichment. Aquat Bot 78: 103–117

Karez R, Engelbert S, Sommer U (2000) 'Co-consumption' and 'protective coating': two new proposed effects of epiphytes on their macroalgal hosts in mesograzer-epiphyte-host interactions. Mar Ecol Prog Ser 205:85–93

Loney PE, McArthur C, Sanson GD, Davies NW, Close DC, Jordan GJ (2006) How do soil nutrients affect within-plant patterns of herbivory in seedlings of *Eucalyptus nitens*? Oecologia 150:409–420

Lotze HK, Worm B (2002) Complex interactions of climatic and ecological controls on macroalgal recruitment. Limnol Oceanogr 47:1734–1741

Lotze HK, Worm B, Sommer U (2000) Propagule banks, herbivory and nutrient supply control population development and dominance patterns in macroalgal blooms. Oikos 89: 46–58

Lotze HK, Worm B, Sommer U (2001) Strong bottom-up and top-down control of early life stages of macroalgae. Limnol Oceanogr 46:749–757

Neckles HA, Wetzel RL, Orth RJ (1993) Relative effects of nutrient enrichment and grazing on epiphyte-macrophyte (*Zostera marina* L.) dynamics. Oecologia 93:285–295

Nicotri ME (1980) Factors involved in herbivore food preference. J Exp Mar Biol Ecol 42:13–26

Norton TA, Hawkins SJ, Manley NL, Williams GA, Watson DC (1990) Scraping a living: a review of littorinid grazing. Hydrobiologia 193:117–138

Pedersen MF, Borum J (1996) Nutrient control of algal growth in estuarine waters. Nutrient limitation and the importance of nitrogen requirements and nitrogen storage among phytoplankton and species of macroalgae. Mar Ecol Prog Ser 142:261–272

Roll SK, Diehl S, Cooper SD (2005) Effects of grazer immigration and nutrient enrichment on an open algae-grazer system. Oikos 108:386–400

Russell BD, Connell SD (2005) A novel interaction between nutrients and grazers alters relative dominance of marine habitats. Mar Ecol Prog Ser 289:5–11

Russell BD, Elsdon TE, Gillanders BM, Connell SD (2005) Nutrients increase epiphyte loads: broad scale observations and an experimental assessment. Mar Biol 147: 551–558

Shepherd SA, Turner JA (1985) Studies on southern Australian abalone (genus *Haliotis*). VI. Habitat preference, abundance and predators of juveniles. J Exp Mar Biol Ecol 93: 285–298

Shepherd SA, Womersley HBS (1970) The sublittoral ecology of West Island, South Australia. 1. Environmental features and algal ecology. Trans R Soc South Aust 94: 105–137

Silliman BR, Zieman JC (2001) Top-down control of *Spartina alterniflora* production by periwinkle grazing in a Virginia salt marsh. Ecology 82:2830–2845

Underwood AJ (1997) Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge

Vitousek PM, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG (1997) Human alteration of the global nitrogen cycle: sources and consequences. Ecol Appl 7:737–750

Watson DC, Norton TA (1985) Dietary preferences of the common periwinkle, *Littorina littorea* (L.). J Exp Mar Biol Ecol 88:193–211

Williams SL, Ruckelshaus MH (1993) Effects of nitrogen availability and herbivory on eelgrass (*Zostera marina*) and epiphytes. Ecology 74:904–918

Worm B, Lotze HK (2006) Effects of eutrophication, grazing, and algal blooms on rocky shores. Limnol Oceanogr 51: 569–579

Worm B, Reusch TBH, Lotze HK (2000) *In situ* nutrient enrichment: methods for marine benthic ecology. Int Rev Hydrobiol 85:359–357