RELATIVE ROLES OF HERBIVORY AND NUTRIENTS IN THE RECRUITMENT OF CORAL-REEF SEAWEEDS

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Abstract. The relative effects of and interactions between, bottom-up and top-down processes are fundamental to population and community structure in both terrestrial and marine systems. These issues are especially critical for seaweed populations on coral reefs, since both bottom-up and top-down factors are suggested as causes of algal invasions during reef degradation. Although algal invasions require the establishment of new recruits, most previous studies of tropical marine algae have focused on mature stages. We simultaneously manipulated nutrient supply to and herbivory on recruits of two ecologically different species of seaweed on the Great Barrier Reef. We found that herbivory strongly reduced both density and growth of recruits for both species, whereas nutrient supply had minor effects on growth of *Lobophora variegata* recruits and no detectable effects on *Sargassum fissifolium* recruits. Notwithstanding the dominance of herbivory over nutrient effects, herbivory was not uniform, but varied both between species and among response variables (density and size), and was apparently stronger for nutrient-enriched plants. Our data demonstrate that the relative importance of bottom-up and top-down processes may depend on the species, circumstances, and life-history processes under consideration. These results also emphasize the importance of herbivores to the protection of coral reefs against algal overgrowth.

Key words: algal recruitment; coral-reef algae; coral-reef degradation; coral reefs; Great Barrier Reef, Australia; herbivory; Lobophora variegata; *nutrient enhancement; nutrient supply and herbivory;* Sargassum fissifolium; *seaweeds; top down vs. bottom-up effects.*

INTRODUCTION

Coral-reef degradation often involves "blooms" of benthic algae, often at the expense of reef-building corals (Hughes 1994, Lapointe 1997, McCook 1999). There has been considerable controversy over the relative importance of nutrient limitation and herbivory in preventing overgrowth of corals by benthic algae on coral reefs (e.g., Lapointe 1997, Hughes et al. 1999). However, there have been few studies that simultaneously consider more than one process, especially using factorial experiments, and very few addressing the recruitment dynamics that are critical to the ability of algae to invade and colonize new areas during reef degradation (Diaz-Pulido and McCook 2002). Factorial experiments not only provide direct comparisons of the relative importance of each process, but clarify the interactions between them and hence the mechanisms involved (e.g., Miller and Hay 1996, Miller et al. 1999, McCook et al. 2001, Smith et al. 2001, Thacker et al. 2001, Jompa and McCook 2002). Such studies indicate

that the effects of nutrient supply on coral-reef algae are often small relative to those of herbivory, and often depend strongly on levels of herbivory (but not vice versa). Importantly, the nutrient supply–herbivory dichotomy ignores the potential roles of several other key processes, including coral–algal competition and disturbance–recruitment–recovery processes in regulating the relative abundances of corals and algae (Hughes 1994, Diaz-Pulido and McCook 2002, Jompa and McCook 2002).

The relative importance of and interactions between bottom-up and top-down processes in structuring populations and communities is also an important issue in ecology generally. "Bottom-up" refers to factors, such as resource limitation (e.g., by nutrient supply), that act on basal trophic levels, the effects of which propagate upward through a food web. "Top-down" refers to factors, such as herbivory and predation, that typically act on higher trophic levels, the effects of which move down the food web. There is now considerable evidence demonstrating critical roles for and interactions between both types of process in both terrestrial and marine ecosystems (Hunter and Price 1992, Menge et al. 1999, Menge 2000, Worm et al. 2001). However, there is very little information available on the relative roles of nutrient supply vs. herbivory processes in the ecology of early post-settlement stages of tropical marine plants (Belliveau and Paul 2002).

In terrestrial ecosystems, it has been suggested that bottom-up processes generally outweigh top-down processes, but that the relative contributions of both can covary in space and time and with the species or ecosystems involved (Hunter and Price 1992, Dyer and Letourneau 1999, Forkner and Hunter 2000). Experimental work in both freshwater and marine ecosystems indicates that bottom-up and top-down processes can act independently, simultaneously, or interactively in controlling the abundance of primary producers (Rosemond et al. 1993, Hillebrand et al. 2000, Hillebrand and Kahlert 2001, Lotze et al. 2001). There is also evidence that processes that affect propagule supply may overwhelm both nutrient limitation and herbivory effects (Underwood and Fairweather 1989, Worm et al. 2001).

Most evidence regarding the roles of resources or herbivores in controlling aquatic-plant populations comes from studies of adult plants. For example, it has been suggested that differences in herbivores, rather than nutrient supply, explain *Sargassum* distributions within and between reefs on the Great Barrier Reef, based on experiments using adult plants (McCook 1996, 1997). However, effects on adult stages could be countered by bottom-up effects on recruitment, especially during algal invasions (using ''recruitment'' in its broadest sense, to include both settlement and the post-settlement survival and growth of early life stages). Nutrients have been shown to enhance growth of *Sargassum* recruits in physiological experiments (Schaffelke and Klumpp 1997), but the relative importance of nutrients and herbivores to the early stages of coral-reef algae has not been tested in an ecological context.

Benthic algae have several life-history stages that may respond differently to environmental pressures. Algal propagules are released into the water column, dispersed via a pelagic phase, then settle, attach, and enter microscopic benthic communities, where they may spend some time in propagule banks before recruitment to the macroscopic communities (Santelices 1990). Nutrient limitation and herbivory have been shown to have critical effects on the development of early life stages of seaweeds within temperate systems (Lotze et al. 2001, Worm et al. 2001), but these processes and interactions may act very differently in the highly diverse ecosystems of tropical coral reefs.

We investigated the relative and interactive effects of nutrient supply and herbivory on the survival and growth of early, post-settlement stages of two algae, using factorial manipulations of both factors on a mid-shelf coral reef on the Great Barrier Reef, Australia. The study examined two species of brown seaweeds, *Sargassum fissifolium* and *Lobophora variegata*, both of which are common and often abundant on coral reefs, and have been suggested to be involved in macroalgal blooms and reef degradation (Hughes 1994, McCook 1996, Diaz-Pulido and Diaz 1997, Lapointe 1997, Jompa and McCook 2002, and references therein). Previous studies have demonstrated both herbivore and nutrient effects on adults of both taxa, and nutrient effects on early stages of *Sargassum* (McCook 1996,

Schaffelke and Klumpp 1997, 1998, Jompa and McCook 2002). Further, the biology of both species is relatively well documented, they provide marked contrasts in morphology, life cycle, and ecology (Steneck and Dethier 1994), and both are suggested to affect coral populations (Hughes 1994, McCook et al. 2001, Jompa and McCook 2002).

METHODS

Experimental site

The experimental site was on the reef slope of Rib Reef (18°28.422′ S, 146°52.783′ E; see Appendix A), between 6- and 9-m depth. We chose an offshore reef with relatively low nutrient concentrations and high abundance of herbivorous fishes (cf. inshore reefs), in order to maximize the potential effects of nutrient and herbivore manipulations. In this region, direct effects of terrestrial runoff of nutrients is minimal on mid-shelf and offshore reefs, whereas inshore reefs are frequently exposed to intense nutrient pulses from flood plumes during the austral summer (concentrations in the flood plumes reach 12.8 μmol/L NH_4 and 2.5 μmol/L PO_4). Nutrient concentrations offshore are generally low and often at the detection limit (0.17 μmol/L NH_4 and 0.14 μmol/L PO_4; Devlin et al. 2001; see Appendix B). Herbivorous fish, predominantly acanthurids (surgeonfishes) and scarids (parrotfishes), are abundant at Rib Reef ($\sim$100–440 and 80–140 individuals/census, respectively; census area $\sim$4000 m²) compared to inshore reefs (where the density of both groups is generally <30 individuals/census; data from, and species composition data in, Russ [1984] and references therein, see also McCook 1996). Larger invertebrate herbivores, such as *Diadema* spp. or other sea urchins were never observed at the experimental site.

Collection and seeding of recruits

Eggs of *Sargassum fissifolium* (Mertens) Agardh and spores of *Lobophora variegata* (Lamouroux) Womersley ex Oliveira were seeded together onto settlement plates in aquaria, (see Appendix C) and then transplanted to an offshore reef for factorial experimental manipulations of herbivory and nutrients for a period of 40 d. Algal recruits were seeded by placing reproductive adults of both *S. fissifolium* and *L. variegata* together in 10³-L outdoor aquarium tanks with terra-cotta settlement plates (11 × 11 cm side with rough texture). Adult algae were collected from 3–6 m depth on the fringing reef on a nearby inshore island (Goold Island: 18°10.85′ S, 146°10.05′ E). Algal propagules were released into the tank water and settled onto the plates (Appendix C). Egg release of *S. fissifolium* was enhanced by short periods (30 min) of desiccation followed by shaking the plants in the tank. Adult seaweeds were removed from the tanks after 10 d, and the plates maintained for another 40 d to allow attachment of new recruits. Tank seawater was replaced every 5 d to avoid excess growth of diatoms. Plates, with attached re-

cruits, were then transplanted to the experimental site and bolted to steel frames (40 × 40 cm) previously anchored to the substratum (Appendix D). Seven replicate plates were randomly allocated to each treatment combination and distributed over an area of ~2500 m². Plates were censused prior to placement to ensure similar ranges in initial densities across herbivore and nutrient treatments.

Herbivore treatments

We examined the effects of three herbivore treatments: (1) uncaged plots that allowed free access to large herbivores, (2) caged plots that excluded large herbivores, and (3) partial-cage plots intended to control for cage artifacts (Appendix D). Uncaged plots simply consisted of a steel frame and recruitment plate. Herbivore exclusions consisted of steel frames covered by a cage (40 × 40 × 25 cm high) made of 12-mm polyethylene mesh. Partial cages were identical to full cages except that two sides of the cage were removed to allow access for large herbivores. Full cages successfully excluded herbivorous fish such as acanthurids, scarids, pomacentrids (damselfishes), and siganids (rabbitfishes). Exclusion effects were assumed to be predominantly due to preventing grazing by larger herbivorous fishes. We did not observe changes in invertebrate mesoherbivore populations (e.g., gastropods, polychaetes, amphipods, isopods, or hermit crabs), or smaller herbivorous fish (e.g., blenniids) inside the cages. Moreover, few herbivorous gammarid amphipods (<5 individuals) were observed on plates at the end of the experiment, with no obvious pattern among treatments. In retrospect, the partial cages may have been limited as procedural controls, as they were too small to allow full access to larger herbivores. Data for partial cages were consistently intermediate between those of uncaged and caged plots, although consistently more similar to uncaged plots than full cages; in this sense partial cages may be retrospectively considered as an intermediate herbivory level rather than full procedural controls. Although these patterns may indicate some cage artifacts, most such secondary effects (e.g., reduced light and water flow) would be expected to reduce algal growth relative to uncaged plots, not enhance it. Importantly, any differences between partial and full cages could nonetheless be unambiguously attributed to the difference between partial and complete exclusion of large herbivores.

Nutrient treatments

Nutrient manipulations were carried out following a pulse protocol involving addition of nutrients for a 24-h period every 10 d for 40 d (during June–July 2000), using reagent-grade ammonium chloride and sodium dihydrogenphosphate added to ambient seawater. We used nutrient pulses rather than continuous supply predominantly because they more realistically simulated events such as flood plumes or resuspension events, which represent major nutrient inputs to reefs in this

region (Furnas and Brodie 1996, Russ and McCook 1999, Schaffelke 1999, Devlin et al. 2001), and because this approach allowed direct comparison with previous studies in this area and with these algae (Schaffelke and Klumpp 1998, Jompa and McCook 2002). Moreover, continuous nutrient applications are logistically difficult to sustain in an open reef field experiment (Miller et al. 1999). We applied three nutrient-concentration treatments: (1) ambient, untreated controls, using seawater from the lagoon of Rib Reef (average levels ranged between 0.07–0.13 μmol/L NH$_4$, 0.08–0.24 μmol/L NO$_3$, and 0.10–0.21 μmol/L PO$_4$); (2) medium, with ~5 μmol/L of NH$_4$ and 0.5 μmol/L PO$_4$; and (3) high, with ~10 μmol/L NH$_4$ and 1 μmol/L PO$_4$. Nutrient concentrations were confirmed using three replicate samples of filtered seawater in each treatment (as per Jompa and McCook [2002]). During each nutrient pulse, all settlement plates were retrieved from the experimental site, nutrient treatments were applied for 24 h in individual 10-L plastic buckets on board the research vessel, and then plates were returned to the field. Seawater (ambient and enriched) was replaced every 4–6 h during the 24-h pulse. The concentrations, ratios, and duration of these nutrient pulses are within the ranges recorded on inshore reefs in this area, and the duration and frequency of pulses were based on previous physiological studies (see Appendix B, also Schaffelke and Klumpp 1997, 1998).

To test the effectiveness of the nutrient manipulations, we measured tissue nutrient concentrations in *S. fissifolium* recruits at the end of the experiment. Algal tissue was removed from 12 supplementary caged settlement plates (4 plates per nutrient treatment) and the concentrations of C, N, and P determined (as in Jompa and McCook [2002]). Tissue N:C and P:C ratios of *S. fissifolium* in the high nutrient-enrichment treatments were significantly higher than that of the unenriched, ambient control treatments (one-way ANOVA, $P \ll 0.001$), and medium nutrient treatments were intermediate (Fig. 1). Although there was insufficient biomass of *L. variegata* for nutrient analyses in this experiment, Jompa and McCook (2002) found significant enhancement of tissue nutrients in *L. variegata* using the same nutrient-enhancement protocol.

Response variables and data analyses

The response variables included the number of individuals per plate as a measure of survival, and the length (from base to apex), width (longest dimension perpendicular to the length), and number of branches (for *S. fissifolium* only) as measures of growth. The number of injured recruits of *S. fissifolium* (i.e., with no primary or secondary branches or fronds, and with damaged thalli consistently showing bite marks or scars with varying degrees of healing), was also recorded as a proportion of total final density. This parameter provided a measure of grazing intensity, as distinct from total density of recruits (a measure of survival). Recruit length, width, and branch number were measured for
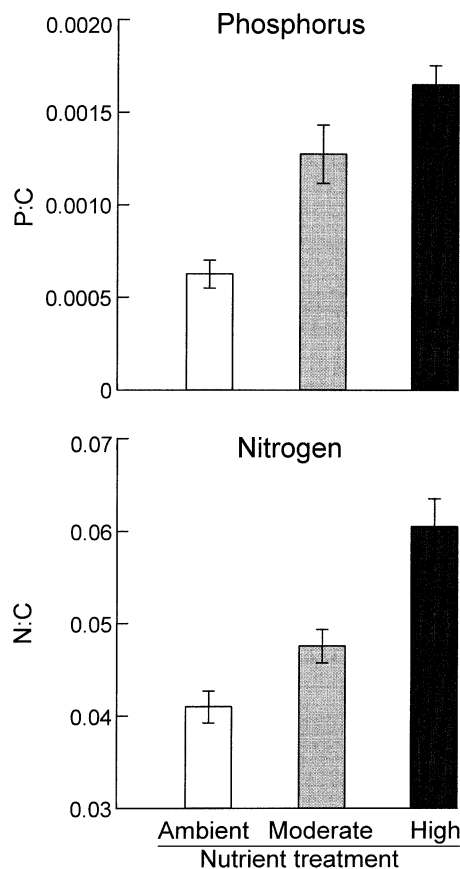
FIG. 1. Effects of nutrient-manipulation treatments on tissue P and N levels (expressed as ratios, P:C and N:C) of recruits of the brown seaweed *Sargassum fissifolium* across three nutrient-treatment levels. Data are means ± 1 SE; $n = 4$ settlement plates per nutrient treatment.

25 randomly selected individuals per plate for each species. All measurements were taken at the end of the experiment using a stereomicroscope.

Density data were analyzed using a factorial ANOVA with levels of nutrients and herbivores as fixed factors and plates as replicates. Length, width, and number of branches were analyzed using a factorial, nested ANOVA, with nutrients and herbivores as fixed factors and 25 recruits nested within plates. Post-hoc comparisons were made using Tukey's tests. Data were transformed ($\log_{10}$) for homogeneity of variance, and homogeneity of variance and normality of residuals confirmed (using Cochran's test and probability plots, respectively).

RESULTS

Effects of herbivores and nutrients on recruits of Sargassum fissifolium

Herbivore exclusion strongly enhanced the survival (density) and growth (length, width, and number of branches) of *Sargassum fissifolium* recruits, whereas nutrient enhancement had no significant effects on these variables (Fig. 2A–C, Appendices E–G). The density of recruits was seven-fold higher and the height and width of recruits were four-fold larger when protected from herbivores in full cages than when they were exposed to herbivores in the uncaged, open plots, and these results were consistent among nutrient treatments. The number of branches per plant was also higher in recruits protected from herbivores (5.1 ± 0.09 branches/plant [mean ± 1 SE]) than in partial cages and uncaged plots (2.4 ± 0.25 and 1.6 ± 0.14 branches/plant, respectively). Although density and number of branches of recruits in partial cages were higher than in uncaged plots (and not significantly so for height and width), they were consistently intermediate between uncaged and caged plots, and much more similar to uncaged plots than cages (Fig. 2). This pattern among treatments suggests that the major effect of the cages was indeed on herbivory (rather than artifact). The only possible nutrient effect on *S. fissifolium* growth involved a small, nonsignificant enhancement of width (but not length) in the high nutrient treatment within full cages (Fig. 1C).

There was a significant interaction between herbivore and nutrient effects on the proportion of remaining recruits that were injured. This proportion was negligible in herbivore-exclusion cages for all nutrient treatments (Fig. 2D, Appendix F), consistent with the interpretation of injury as a herbivore effect. In contrast, in uncaged plots with uninhibited herbivore access, the proportion of injured recruits was significantly increased by nutrient enhancement. Although this pattern did not occur within partial cages, it may indicate that recruits were more intensively grazed in nutrient-enriched treatments than were the unenriched recruits.

Effects of herbivores and nutrients on recruits of Lobophora variegata

Herbivores also strongly reduced the survival (density) and significantly decreased the size (length and width) of *Lobophora variegata* recruits. The density was six-fold higher and the size 1.3 times higher in recruits that were protected from herbivores than those exposed to herbivores in uncaged plots (Fig. 2E–G). Nutrient enhancement did not significantly affect the survival (density) of *L. variegata* (Fig. 2E), although growth (length and width) of *L. variegata* recruits were consistently and significantly higher in nutrient-enhancement treatments than ambient controls (in contrast to *S. fissifolium*; Fig. 2F and G, Appendix F). The effects of nutrients were, however, small compared to the effects of herbivores: recruits grew <10% more in the high nutrient treatment than in the unenriched treatment, but were 30% larger when protected from herbivores (Fig. 2F and G). As with *S. fissifolium*, the density and size of recruits within partial cages were significantly higher than in the uncaged plots, but were generally significantly lower than in the full cages (Appendix F).
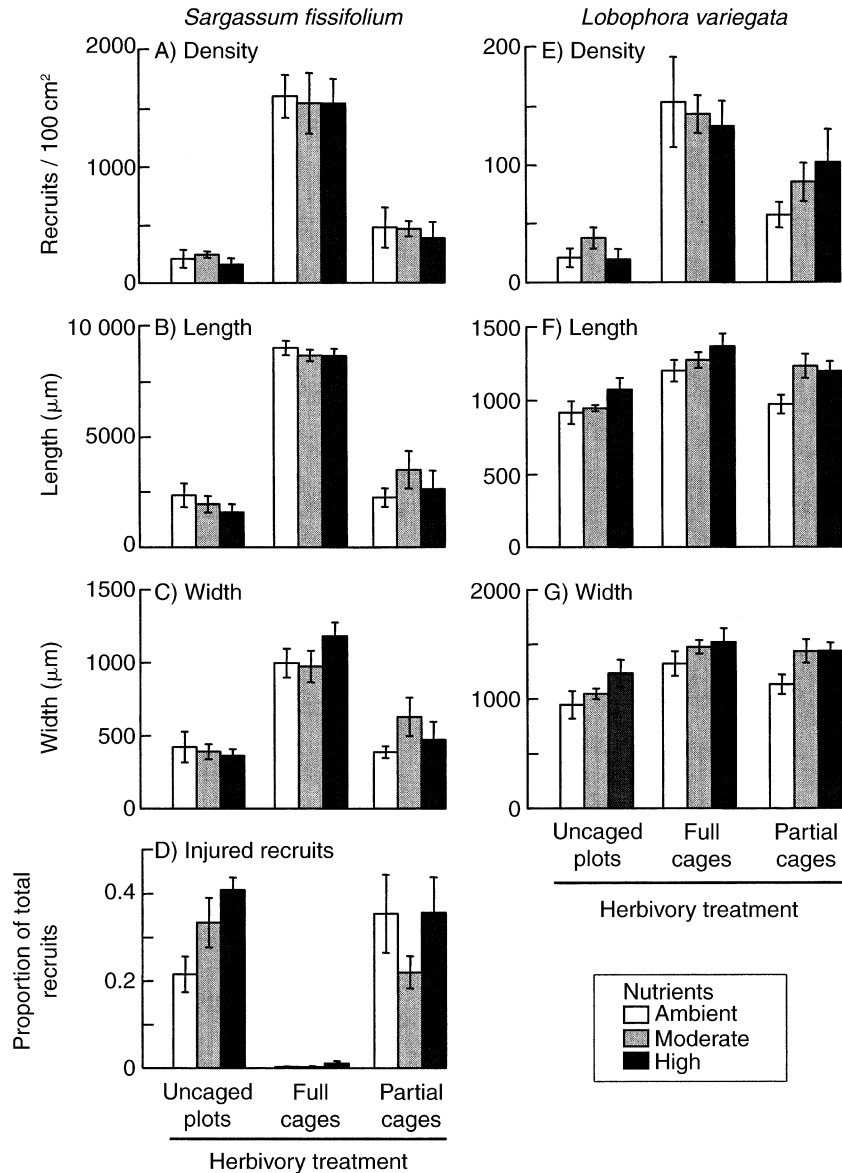
REPORTS

FIG. 2. Density and growth measures for two seaweeds, by herbivory and nutrient treatments. For *Sargassum fissifolium*, (A) density, (B) length, (C) width, and (D) proportion of injured recruits are shown; for Lobophora variegatz, (E) density, (F) length, and (G) width are shown. Data are means ± 1 SE; *n* = 7 settlement plates per herbivore–nutrient treatment combination.

DISCUSSION

Overall, our results suggest that, at our study site at least, top-down effects of herbivory dominated the survival and growth of early stages of two coral-reef seaweeds, and that bottom-up effects of nutrients were weak. However, the results also suggest that the magnitudes of the effects of herbivory and nutrients were variable and depended on the species and type of response measured.

Variability in response between species and between survival and growth

The different variables considered here are measures of three different processes: survival, growth, and in-

jury. Density through time, a measure of survival, responded strongly and consistently to herbivore exclusion, but had no detectable response to nutrient manipulations for both species. In contrast, the size or growth response to nutrients was species specific, with no significant response in *Sargassum fissifolium* and an increase in *Lobophora variegata*. The (net) growth response of both species to herbivory was similar in direction but not magnitude: both were reduced by herbivore grazing but growth was more strongly reduced in *S. fissifolium* than in *L. variegata*. Finally, the proportion of injured *S. fissifolium* recruits, primarily a measure of grazing intensity, responded differently to nutrients, depending on the level of herbivory.

These differences in response between species may reflect the different growth forms of the two species. For example, the *S. fissifolium* recruits were relatively large, erect, and formed a canopy, whereas *L. variegata* recruits were generally prostrate, smaller, and essentially understory. Apparently herbivore grazing frequently damaged *S. fissifolium*, thereby reducing growth as well as density. However, few of the remaining *L. variegata* plants showed any signs of grazing damage, so that herbivore grazing may have more often involved consumption of entire plants, affecting density but having less effect on growth of remaining plants. It is also possible that herbivore reduction of the *S. fissifolium* canopy increased light, and thereby ameliorated any herbivore-induced reduction in size of *L. variegata*. The contrast in nutrient effects between species may also reflect differences in physiology and function between thin-layered, simple, prostrate plants (*L. variegata* recruits) and larger, upright, leathery macrophytes with more complex tissue organization and a range of nutrient-uptake mechanisms (*S. fissifolium*; e.g., Steneck and Dethier 1994, Schaffelke 1999). Thus the impacts of bottom-up and top-down processes cannot be assumed to be uniform, but will vary among species and life-history stages or demographic factors.

Relative magnitude of effects of herbivore and nutrient treatments

Notwithstanding this variability, our results indicate that the negative effects of herbivores on the survival and growth of *S. fissifolium* and *L. variegata* overwhelmed any enhancement by nutrients. Effects of nutrients on growth were very small and found only in *L. variegata*, despite significant enhancement of tissue nutrient ratios. The relative strength of herbivore effects on macroalgal recruits in this study is consistent with previous work on adult *Sargassum* (McCook 1996, 1997). To some extent our results are specific to species, site, and other circumstances, such as distance from land, and to the nutrient-treatment protocol used. For example, lower herbivore abundances on inshore reefs (Russ 1984) may mean that herbivore effects are less strong in those habitats. However, it is unlikely that nutrient effects will be stronger in other areas, since effects of nutrient additions are likely to be strongest in areas with the least background inputs, such as our study site (Appendix B).

There has been little previous work specifically comparing the effects of nutrient supply and herbivory on early stages of macroalgae using factorial experiments, although evidence from temperate systems suggests that their relative importance varies (Lotze et al. 2001), and, unlike our results, may differ between early and adult stages. There is, however, considerable evidence for strong effects of top-down factors on early stages of seaweeds (Lubchenco 1983, Vadas et al. 1992, Hixon and Brostoff 1996, Wright and Steinberg 2001). More generally, previous factorial comparisons in aquatic

ecosystems have generally found reductions in herbivory cause much larger increases in algal populations than does nutrient enrichment, including studies of mature benthic algae on coral reefs (Miller et al. 1999, Thacker et al. 2001, Jompa and McCook 2002), in seagrass beds (Heck et al. 2000), and in freshwater periphyton communities (Hillebrand and Kahlert 2001). However, this pattern is not universal, since some factorial experimental studies have found both herbivores and nutrients to have significant effects on algal populations, and that neither effect dominated the other (e.g., Rosemond et al. 1993, Smith et al. 2001).

Addition of nutrients did not significantly increase growth of *S. fissifolium* recruits, even in the absence of herbivores. This outcome contrasts with results from laboratory experiments, in which nutrient enrichment increased growth of early stages of seaweeds, including species of *Sargassum* from this area (Schaffelke and Klumpp 1997, Van Alstyne and Pelletreau 2000). This contrast probably reflects the differing physiological and ecological contexts of the studies, rather than ineffective nutrient treatments, given that *S. fissifolium* tissue nutrients were enriched (Fig. 1), that *L. variegata* showed a growth response to nutrients, and that there may have been a response of herbivores to fertilization. Thus, it appears that *S. fissifolium* recruits in ambient water conditions on Rib Reef were nutrient sufficient, perhaps because water flow rates ensured sufficient nutrient supply, despite low concentrations (Miller et al. 1999, see discussion in McCook [1999]). McCook (1996) showed that adult plants of *Sargassum* transplanted to a similar, nearby reef, were nutrient sufficient. Further, physiological studies usually use isolated specimens in control conditions, whereas in our study (as in nature) recruits grew within a relatively dense algal mat. Under such conditions, nutrient demand may be less important than intra- or inter-specific competition for other resources, such as light.

Our results for the proportion of injured *S. fissifolium* recruits suggest that the strength of top-down effects increased with the bottom-up availability of nutrient resources to the algae. Nutrient-enriched recruits were apparently more intensively grazed than the unenriched recruits. Although this pattern was not consistent among partial cages, the results from uncaged plots are likely to more accurately represent natural processes, since herbivory appears to have been restricted within partial cages (see *Methods: Herbivore treatments*, above). This interaction between herbivory and nutrient availability may indicate preferential feeding by herbivores on nutrient-enriched plants, perhaps due to higher food quality. Miller et al. (1999) found that macroalgae grown under nutrient-rich conditions on a coral reef in Florida were preferred by herbivores and removed at a faster rate than unenriched macroalgae. Such interactions have been suggested in a variety of systems, including invertebrate grazers in temperate marine habitats (Hillebrand et al. 2000) and freshwater

REPORTS

lakes (Hillebrand and Kahlert 2001), as well as arthropods in terrestrial forests (Forkner and Hunter 2000).

Overall, our results demonstrate that interpretations of the importance and interactions between bottom-up and top-down factors will to some extent depend on the specific ecological or life-history processes being addressed. Enhanced growth of individuals, in particular, should not be assumed to lead necessarily to responses at the level of the population.

Relative importance of nutrient supply and herbivory during coral-reef degradation

The results of this study have important implications in terms of the mechanisms of coral-reef degradation, which typically involves overgrowth or replacement of corals by seaweeds. The debate over the relative contributions of overfishing and eutrophication to algal overgrowth and reef decline (Lapointe 1997, Hughes et al. 1999) has largely focused on established, mature algae, and ignored processes that affect recruits. For example, it is possible that herbivory and nutrient supply act differently on recruits and adults, and that eutrophication could lead to increased recruitment of algae. This situation could have profound implications for the size of adult populations within a site, and for the ability of seaweeds to colonize and invade new areas, especially after disturbances. However, the present results suggest that, for the two species studied, the relative effects of herbivory and nutrients are similar for recruits and adults (for data on adults see McCook [1996, 1997], Jompa and McCook [2002]). This result provides further support for the argument that, where herbivore populations are abundant, increased nutrients alone are unlikely to lead directly to increases in algal abundance, with consequent overgrowth of reefs, because herbivore consumption will increase and absorb any excess algal growth (McCook 1999). As herbivory has consistently strong effects on both adult and early stages of these algae, protection of herbivorous fish populations from overfishing is vital to preventing algal overgrowth of coral reefs (Hughes 1994, McCook 1999, Jompa and McCook 2002).

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REPORTS

APPENDIX A

A map showing the location of the experimental study site (Rib Reef) and of Goold Island, the source of reproductive adult plants, is available in ESA's Electronic Data Archive: *Ecological Archives* E084-046-A1.

APPENDIX B

Concentrations of water-dissolved, inorganic nutrients in ambient (untreated control) nutrient treatment during nutrient pulses (sampling) and in the water column at the experimental site in Rib Reef, together with published values for offshore and inshore reefs, are available in ESA's Electronic Data Archive: *Ecological Archives* E084-046-A2.

APPENDIX C

A diagram showing the method of seeding *Sargassum fissifolium* recruits onto ceramic settlement plates in aquarium tanks prior to transplantation to the study site for nutrient and herbivore manipulations is available in ESA's Electronic Data Archive: *Ecological Archives* E084-046-A3.

APPENDIX D

Photographs showing the three herbivore treatments are available in ESA's Electronic Data Archive: *Ecological Archives* E084-046-A4.

APPENDIX E

Photographs of plates showing *Sargassum fissifolium* recruits after 1 wk in uncaged plots, exposed to herbivores, and in full cages protected from herbivores, are available in ESA's Electronic Data Archive: *Ecological Archives* E084-046-A5.

APPENDIX F

Photographs showing settlement plates and close-up views of plates from uncaged plots and herbivore-exclusion cages after 40 days on the study reef are available in ESA's Electronic Data Archive: *Ecological Archives* E084-046-A6.

APPENDIX G

Results of factorial ANOVAs for effects of herbivore exclusion and nutrient enhancement on early stages of two coral-reef seaweeds are available in ESA's Electronic Data Archive: *Ecological Archive* E084-046-A7.