L. J. McCook

Effects of herbivory on zonation of *Sargassum* spp. within fringing reefs of the central Great Barrier Reef

Abstract A combination of small-scale transplants and herbivore exclusion was used to test the importance of herbivory, physiological tolerance limits, and recruitment and dispersal in regulating the distribution and abundance of the genus *Sargassum* on two nearshore fringing reefs of the central Great Barrier Reef, during 1992/1993. *Sargassum* (predominantly *S. oligocystum* and *S. tenerrimum*) were transplanted from reef-flat zones where they normally grow, to a seaward coral zone where they are not normally found. At Great Palm Island, coral-zone transplants only survived if protected from herbivores. At Brook Island, survival of uncaged coral-zone transplants was more variable but not significantly lower than plants returned to the *Sargassum* zone. Thus herbivory may be a major cause of the zonation patterns of adult *Sargassum* on these fringing reefs, but the importance of this factor varies between and within reefs. Since protected *Sargassum* survived and grew for up to 6 mo in the coral zone, the adult algae are not physiologically limited by any physical or chemical differences between zones. However, *Sargassum* recruitment to the coral zone was very low (mean 2.7 recruits m^{-2} over 13 mo), and was not significantly affected by herbivores. Since rates of herbivory were relatively slow, effective exclusion of *Sargassum* from the coral zone by herbivores may depend on low recruitment of the algae. In a broader context, the distribution of *Sargassum* may depend on the combined spatial patterns of herbivory and recruitment.

L.J. McCook
Australian Institute of Marine Science and
CRC Reef Research Centre, PMB No. 3,
Townsville MC, Townsville, Queensland 4810,
Australia

Introduction

The abundance of algae, particularly macroalgae, is an important aspect of coral reef status (e.g. Lapointe 1989; Done 1992; Hughes 1994), yet very little is known about patterns or causes of macroalgal distributions on the Great Barrier Reef (McCook and Price 1997a, b). Nearshore fringing reefs of the central Great Barrier Reef, GBR (Fig. 1) generally have abundant macroalgae, particularly of the genus *Sargassum*. In contrast, *Sargassum* is virtually absent from mid-shelf and outer-shelf reefs in the same area (McCook and Price 1997a; McCook et al. 1997). There is concern that these differences in macroalgal abundance indicate degradation of the highly accessible nearshore fringing reefs. Anthropogenic changes in water quality or fish stocks may be causing shifts from coral to algal dominance, and mid-shelf reefs may also be at risk (reviews in Yellowlees 1991; Baldwin 1992; Bell 1992). The present paper examines the causes of small-scale (100 m) zonation in *Sargassum* abundance within fringing reefs, in order to better understand any algal role as a cause, indicator, or symptom of reef degradation.

Nearshore fringing reefs of the central GBR often have distinct zones of macroalgal and coral abundance, including reef-flat areas dominated by macroalgae such as *Sargassum*, and reef-slope areas containing abundant corals (Done 1982; McCook and Price 1997a). The experiments described here examine the causes of zonation of *Sargassum* on these fringing reefs, and test three of the factors which elsewhere cause such zonation: differences in recruitment; physical-chemical environment including water quality (physiological tolerance limits); and herbivory. The paper focuses on why *Sargassum* does not occur in, or invade, the "coral zone" of these fringing reefs. The specific hypotheses ask whether adult *Sargassum* can survive and grow in the coral zone; whether *Sargassum* can recruit to the coral zone; and whether herbivores affect either recruitment or adult survival.

Fig. 1 Townsville area and central Great Barrier Reef (*arrows* mark Great Palm Island and Brook Island field sites). Inshore, fringing reefs which occur on islands of geological origin (*grey shading*) are exposed to anthropogenic and natural terrestrial runoff from mainland and islands themselves; in contrast, carbonate-based mid-shelf and outer-shelf reefs (*black shading*) are more removed from these influences. Inshore reefs generally have abundant *Sargassum* spp. and other macroalgae, which are rare on mid-shelf and outer-shelf reefs
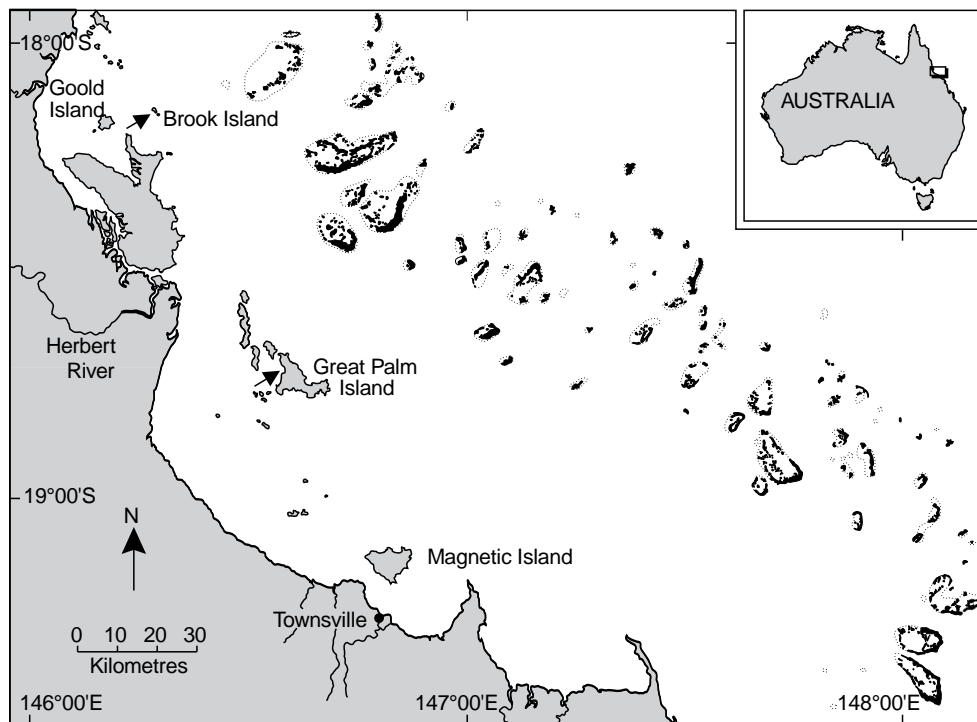
Materials and methods

Reef descriptions and study sites

High islands in this area (Fig. 1) often have extensive fringing reefs with distinct ecological zonation. In general, intertidal reef flats have a landward zone of sand and mud flats, merging into rubble and then hard carbonate substrate, which support large stands of fucalean macroalgae, predominantly *Cystoseira* and then *Sargassum* species. Between mean low-water spring-tide level and lowest astronomical tide, this zone merges into an area of abundant live coral, with filamentous algal turfs, often with an intermediary zone of soft corals. Substrate complexity increases markedly with coral abundance. Corals continue to a distinct reef edge, which slopes down to soft sediments at between 6 m (Great Palm Island) and 15 m (Brook Island) depth (Morrissey 1980; McCook and Price 1997a; McCook and Done unpublished data). Spring tidal ranges in this area reach 4 m. The presence of a sharp reef edge means that currents, wave action and turbidity can often vary dramatically with a few metres (McCook personal observations). In this paper, I refer to the "*Sargassum* zone" and "coral zone" for simplicity, but it should be realised that these zones are subjective, highly variable, and diverse in species composition. Herbivore abundances vary considerably between these zones (McCook personal observations; see also Russ 1984b for offshore reefs). Herbivorous fish, predominantly scarids, acanthurids, siganids and territorial pomacentrids are scarce compared to offshore reefs, but are more common in and near the coral zone than closer to shore (Williams 1982; Williams and Hatcher 1983; Russ 1984a). The sea-urchins *Diadema setosum* and *D. savignyi* are locally common in coral-zone areas with high substrate complexity, but are rare on the open reef flat, even at night (McCook personal observations).

Macroalgal abundance is highly seasonal on these fringing reefs, with a pronounced seasonal dieback (senescence) and regrowth of *Sargassum* species and *Cystoseira trinodis*, as well as blooms of various ephemeral and turfing species (McCook unpublished data; see also Price 1989; Vuki and Price 1994). Of the 8 or 9 distinct taxonomic entities of *Sargassum* found on these reefs (K. Edyvane personal communication), most grow rapidly during October to December, and length and biomass are greatest in summer (January

to March). Plants are most fertile in late summer (March to May). There is a severe dieback in April to June, whereby most longer fronds and stipes become necrotic and are lost (Price 1989; Martin-Smith 1993; Vuki and Price 1994; McCook unpublished data). Whilst the cues and causes for the annual dieback and regrowth of *Sargassum* are uncertain, these two phases may respond differently to ecological factors such as herbivory or abiotic conditions.

The study sites at Great Palm Island were near the reef edge in the middle of the extensive fringing reef at Coolgaree (Challenger) Bay (18°42.6′S; 146°34.5′E: Fig. 1). The reef here is about 1.5 km wide. The transplant and recruitment sites (Experiments 1, 2 and 4) were on the landward edge of the coral dominated zone ("coral zone"), amongst live corals and within range of grazing fishes (personal observations). Corals in this area are predominantly massive forms, with flat tops covered by turf algae. Sites with rubble/sand substrate were chosen to allow stakes to be driven in to anchor cages. Adult plants were collected from, and "return-transplants" returned to, an area 60 m east (landward), in the macroalgal-dominated "*Sargassum* zone" (Experiments 1 and 2). Both *Sargassum* and coral sites were in the extreme low intertidal ($\simeq 0.5$ m above tidal datum), only emerging very briefly most months and only during daylight in the winter (April to August). The difference in depth between the two sites was < 0.3 m.

The Brook Island study site (Experiment 3) was on the northern end of the fringing reef, at the northernmost island of the Brooks group (18°08.7′S; 146°16.5′E: Fig. 1). The reef here is much narrower than at Great Palm Island, and the zones are less distinct, with a wide area of interspersed patches of algal or coral dominance. There is a wider coral zone that gently shelves to ~5 m and then drops abruptly to ~15 m. The transplant distance was ~20 to 30 m.

Experiments 1 and 2: Great Palm Island transplant and caging experiments

Design

The design of Experiments 1 and 2 involved a one-factor ANOVA with four levels: open (uncaged) transplant; transplant with cage; transplant with partial-cage control; and a "return-transplant" returned to the *Sargassum* zone. Three replicate groups of plants

were randomly assigned to each treatment. Comparison of transplanted and returned plants tests for effects of environmental differences between the two zones. Comparison of caged and uncaged plants tests for effects of herbivores. Partial cages were identical to cages except that they had large holes cut in all four sides. By allowing fish access, these partially control for caging artifacts such as shading. It was not possible to use a complete factorial design, testing for herbivory in the *Sargassum*-dominated zone, since placement of cage structures in that landward zone would have been a considerable hazard to small boat traffic. Although transplantation only took a few minutes, "return-transplants" were qualitatively compared to surrounding untransplanted *Sargassum*, to ensure that "return-transplants" represented natural growth and survival.

Two experiments were run to compare treatment effects during different seasons. Experiment 1 used adult plants during the period of maximum size ("mature" phase); Experiment 2 used plants that were initially dormant and compared their regrowth ("regrowth" phase; dormant plants have basal holdfasts and short stipes only).

Methods

Naturally occurring mixtures of *Sargassum* species, predominantly *S. oligocystum* and *S. tenerrimum*, were collected as groups of plants attached to coral rubble rocks. These were counted, sorted into roughly even groups by frond numbers, and then randomly allocated to treatments and plots within the two zones.

Open (uncaged) plots were marked with four pegs (0.3 m long, 10 mm steel rod). Cages were 0.75 m high by 0.75 m × 0.75 m, and were made of 12 mm plastic mesh (Nylex, "Trical" high density polyethylene), anchored with steel-fence stakes and plastic cable ties. In the second "regrowth" experiment, 8 mm steel-rod frames were used to attach the mesh. Partial cages were identical to cages, except that 1 to 2 large holes (40 cm × 40 cm) were cut in each side to allow access for swimming herbivores. Both partial and complete cages were scrubbed every 1 to 2 mo, as required, to remove fouling filamentous algae.

The first "mature" experiment ran from December 1992 until March 1993, during the period of maximum abundance of the plants. These plants were initially relatively large, each group including fronds in the 15 to 50 cm size class. Frond densities were counted before allocation, and at 1 and 3 mo afterwards, as numbers of primary laterals (fronds/plot) in four size classes (0 to 5 cm; 5 to 15 cm; 15 to 50 cm; >50 cm). After 3 mo, the plants were retrieved, dried, and weighed.

The second "regrowth" experiment was set up in July 1993, and used dormant plants with few fronds longer than 5 cm (none >15 cm). These were retrieved then counted, dried and weighed in January 1994. Qualitative data included regular observations of plant condition, and observations of sites and mobile species composition at night and at different tide levels.

Experiment 3: Brook Island within-reef transplant experiment

This experiment contrasted plants transplanted from *Sargassum*-dominated patches to coral-dominated patches and plants returned to the *Sargassum*-dominated patches. Five replicate groups of plants were randomly assigned to each patch type. Coral rocks, with mixtures of *S. oligocystum* and *S. tenerrimum* plants attached, were collected, counted and relocated randomly to *Sargassum* or coral patches in mid-November 1992. Plants were recounted, collected, dried and weighed after only 1 mo. Again, qualitative observations included plant condition and mobile species composition, the latter observed at night and at different tide levels.

Experiment 4: Great Palm Island recruitment and caging experiment

Experiment 4 used a one-factor ANOVA with three replicate plots randomly assigned to each of three levels: open (uncaged) plots;

caged plots; and partial cages. Plot markers and cages were identical to those in Experiments 1 and 2. Each plot was chosen to include a large, flat block of carboniferous substrate ($\simeq$0.5 m^2), with no *Sargassum* or other fucalean macroalgae, and little or no live coral. Blocks were scraped and wire-brushed at the beginning of the experiment (December 1992) to remove most of the turf algae and sediments covering them. Quantitative descriptions were made of algae on each block every 2 to 3 mo until January 1994, when any *Sargassum* recruits were counted, dried and weighed. Cages were scrubbed every 1 to 3 mo, as necessary.

Data analyses

Data in Experiments 1, 2 and 3 were analysed at each date for treatment effects on biomass (dry weight), total frond numbers per block (density), and size distribution. Since patterns were consistent between biomass and density, analyses are only presented in detail for one variable. Initial densities were comparable (results not shown), except for density data at Brook Island (Experiment 3), where data were analysed for changes between initial and final density. Graphical interpretations of treatment effects on size distributions were confirmed by statistical comparisons of estimated mean frond length (details not shown). The data in Experiment 4 were analysed for differences in total frond number.

Analyses of means involved one-way ANOVA and Ryan's Q-test (Day and Quinn 1989) for post-hoc comparisons of means, using Systat^{TM}. Magnitudes of effects were estimated by the percentage of total variability (sum of squares) attributed to treatments (%SST). All data were tested for homogeneity of variances (Cochran's C-test), outliers, and independence and normality of residuals (graphically), and transformed as indicated by relationships between residuals and estimates. In general, dry weight was square-root-transformed and density data were log-transformed (except Experiments 3 and 4). Minor violations of assumptions were accepted where this clearly would not lead to false conclusions (Type I errors). However, data for Experiment 3 contained a strong outlier. Since outliers can increase the chances of Type II errors, these data were also analysed for effects on variances using an F-test. Note also that since sites were not randomly chosen from the entire zone, effects of zone cannot strictly be separated from effects of sites.

Results

Experiments 1 and 2: Great Palm Island transplant and caging experiments

There was a significant, pronounced and consistent effect of transplantation, but only in the presence of herbivores. The results for both times of year, and both biomass (dry weight) and density, show that *Sargassum* thrived in the coral-dominated zones, but only if protected from herbivores. Specifically, for mature plants at Great Palm Island (Experiment 1), the dry weight of *Sargassum* tissue remaining after 3 mo was significantly reduced in open and partially caged transplants, compared to plants protected from herbivores or returned to the *Sargassum* zone (Fig. 2, Table 1). Similarly, these plants had fewer (density; $P = 0.0001$, %SST = 92) and shorter (Fig. 3) fronds, although the differences in density were not significant at 1 mo ($P = 0.01$, %SST = 74, but multiple comparisons not significant). Regrowing *Sargassum* showed similar patterns (Experiment 2). Dry weight (Fig. 4, Table 2) and density ($P < 0.0001$, %SST = 94) were lower in unprotected
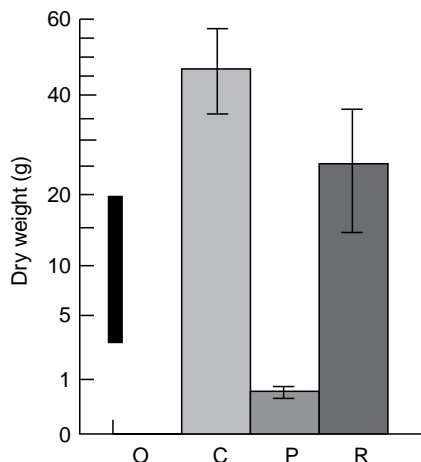
716

Fig. 2 *Sargassum* spp. (Experiment 1). Effects of transplantation and herbivory on biomass of mature plants at Great Palm Island, shown as dry weight of tissue after 2 mo. Data scaled to √dry weight, mean (±SE) of three replicates [*O* Open plots, plants transplanted to coral zone; *C* caged plants transplanted to coral zone; *P* partial cages, plants in coral zone; *R* return, i.e. open, uncaged plants returned to original, *Sargassum*-dominated zone; *black bar on extreme left* indicates critical minimum difference between two adjacent means using Ryan's *Q*-test (Table 1)]

transplants than in caged plants or those returned to the *Sargassum* zone. Importantly, protected plants were able to regrow from basal tissues in the coral zone, as well or better than in the *Sargassum* zone (Fig. 5), but only if protected in cages. Qualitative comparisons of untransplanted *Sargassum* and return-transplants showed that transplant artifacts were negligible compared to treatment effects.

Thus, overall growth and survival of unprotected transplants were poor, compared to plants either protected from herbivores or returned to their natural zone. Growth and survival of caged plants were in fact consistently, but insignificantly, higher than plants returned to the *Sargassum* zone. Thus, in the absence of herbivores, *Sargassum* growth in the coral zone was at least as good, and possibly slightly better (Type II error), than in the *Sargassum* zone. Partially caged plants, that were exposed to herbivores, consistently did much worse than fully caged plants, and insignificantly (but consistently) better than uncaged plants. This suggests that herbivory is important and that caging artifacts, the effect of the physical structure, are minor. Transplantation and/or
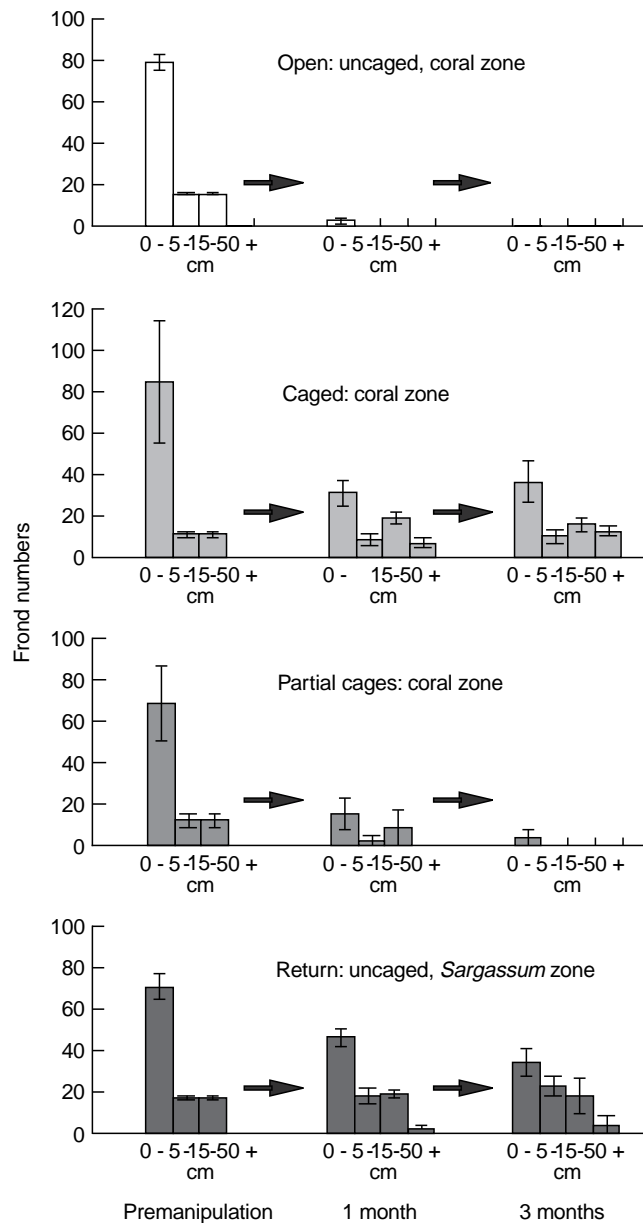

Fig. 3 *Sargassum* spp. (Experiment 1). Effects of transplantation and herbivory on size distributions of mature plants at Great Palm Island for each treatment, before manipulation, after 1 mo and after 3 mo of treatment. Data are numbers of primary lateral fronds per substrate plot, counted in four size classes: 0 to 5, 5 to 15, 15 to 50, and > 50 cm, and are untransformed, mean (±SE) of three replicate plots

Table 1 *Sargassum* spp. (Experiment 1). Analyses of transplant and herbivore effects on biomass of mature plants at Great Palm Island. Data are transformed to √dry weight [*%SST* percent of total variation (sum of squares) explained by each factor; *MS* mean square]. Homogeneity of variance tests are shown as Cochran's *C*-statistic; in this analysis, critical value for *C* = 0.77. Ryan's *Q*-test is used for stepwise comparisons of means: for adjacent means, rank = 2, and critical value for differences between means is 2.61 (transformed; Day and Quinn 1989)

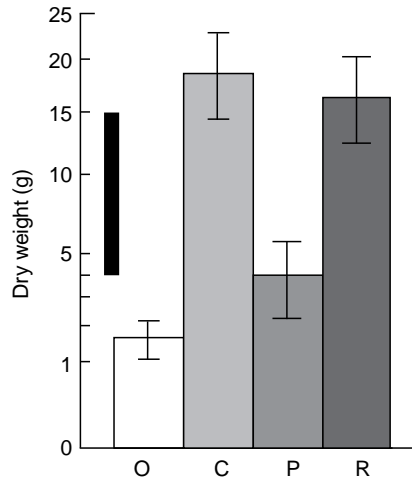| Comparison or factor	(*df*)	MS	*F*	*P*	%SST	Conclusions
ANOVA						
Treatment	(3)	31.38	23.21	0.0003	95%	Significant
Residual (*n* = 3)	(8)	1.35			5%	treatment effect
Cochran's *C*	0.72					
Ryan's *Q* multiple comparisons		cage ≃ return > partial ≃ open				

Fig. 4 *Sargassum* spp. (Experiment 2). Effects of transplantation and herbivory on biomass of regrowing plants at Great Palm Island, shown as dry weight of tissue after 6 mo. Data scaled to $\sqrt{\text{dry weight}}$, mean ($\pm$SE) of three replicates [*Black bar on extreme left* indicates critical minimum difference between two adjacent means using Ryan's *Q*-test (Table 2; *abbreviations O, C, P, R as in Fig. 2*)]

herbivory contributed much more variability ($\simeq 90\%$) than found within treatments. The consistent magnitude and direction of treatment effects between the two experiments is strong evidence for the validity of these effects.

Qualitative observations showed that plants exposed to herbivores lost their softer distal tissues ("leaves", vesicles and smaller stipes) before their basal stipes and holdfasts. These plants were generally less healthy: they were often very heavily fouled and necrotic, the stipes were bare and stringy, and often all that remained were basal holdfasts. Plants either returned to the *Sargassum* zone or never transplanted also appeared marginally less healthy than caged plants in the coral zone. These patterns were quantified by comparisons of size distributions (Fig. 3 and 5) and of mean stipe length. Stipes were significantly smaller in open and partial treatments ($P < 0.001$ and 0.03, %SST $= 87$ and 66 for mean stipe length for Experiments 1 and 2, respectively). Thus longer size classes decreased more than smaller size classes in these treatments: i.e. larger fronds suffered most damage, presumably because they were grazed first.

These effects appear to take ~ 3 mo, since at 1 mo the differences in density were smaller, and although treatment effects were significant, the differences could not be resolved in multiple comparisons. Analyses of initial
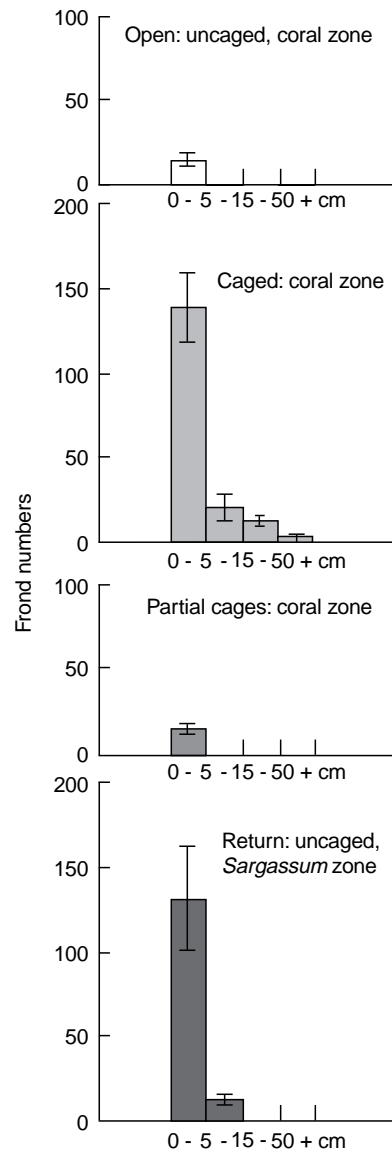

Fig. 5 *Sargassum* spp. (Experiment 2). Effects of transplantation and herbivory on size distributions of regrowing plants at Great Palm Island (further details as in Fig. 3 legend). All plants were initially <15 cm long; note that caged plants in coral zone had more long fronds than plants returned to *Sargassum* zone [Ryan's test of estimated mean frond length gave C > R $\simeq$ P $\simeq$ O (see legends of Figs. 2 and 4 for O, C, P, R explanations)]

densities preclude possible confounding premanipulation differences (for Experiment 1, $P > 0.84$, %SST $= 1$; see also Fig. 3).

Table 2 *Sargassum* spp. (Experiment 2). Analyses of transplant and herbivore effects on biomass of regrowth at Great Palm Island. Data transformation, abbreviations and procedures as for Table 1, except that critical value for difference between adjacent means in Ryan's *Q*-test is 1.68

Comparison or factor	(*df*)	MS	*F*	*P*	%SST	Conclusions
ANOVA						
Treatment	(3)	6.829	12.16	0.002	82%	Significant
Residual (*n* = 3)	(8)	0.562			18%	treatment effect
Cochran's *C*	0.38					
Ryan's *Q* multiple comparisons		cage $\simeq$ return > partial $\simeq$ open				

The time series (Fig. 3 and corresponding density data not shown) suggest that caging artifacts were real, although statistically insignificant and relatively minor (i.e. Type II error). Decreases in density in partial cages were not only consistently smaller, but took longer than in open plots. Thus, partial cages may only provide a limited control for cage artifacts, presumably because herbivore access is different from that in open plots.

Experiment 3: Brook Island
within-reef transplant experiment

There was no clear effect of herbivory in the coral zone at Brook Island, but there were some differences between zones, differences which may have been due to herbivory. Mean *Sargassum* biomass (Fig. 6, $P = 0.179$,
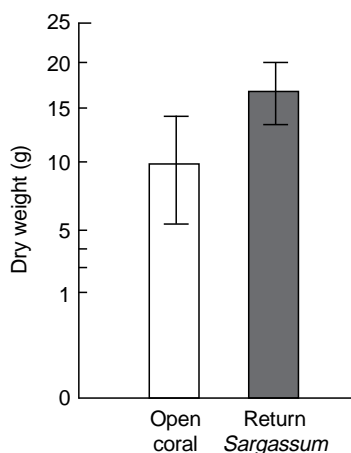

Fig. 6 *Sargassum* spp. (Experiment 3). Effects of transplantation on biomass at Brook Island, shown as dry weight of tissue after 1 mo transplantation. Data are scaled to $\sqrt{\text{dry weight}}$ and are mean ($\pm$ SE) of five replicates (*Open coral* open plots, plants transplanted to coral zone; *Return Sargassum* open, uncaged plants returned to original, *Sargassum*-dominated zone)

%SST = 11) and density (Table 3, Comparison A), although lower in the coral zone, were not significantly so. Plants in the coral zone were significantly more variable than those in the *Sargassum* zone (Table 3 Comparison C). Size distributions showed that coral-zone transplants had fewer long fronds, and most transplants were in poorer condition, with fewer leaves, vesicles and fine branches, than plants returned to the *Sargassum* zone.

Comparisons of means and variances were strongly dependent on a single, outlying transplant (see Table 3). Although most coral-zone transplants decreased in frond density, this transplant increased markedly. Density of plants in the *Sargassum* zone changed little. The outlying transplant appears to be the only transplant not to have been grazed during this first month. Excluding this transplant gives a highly significant treatment effect on mean density change (Table 3, Comparison B). Thus, the data suggest that variable initial success of coral-zone transplants outweighed a possible effect on mean survival.

Experiment 4: Great Palm Island recruitment
and caging experiment

Sargassum recruitment in the coral zone was low in all treatments, so that herbivore effects were undetectable (Fig. 7, Table 4). After a year, biomass and percent cover were negligible (<1% and <0.15 g) in all plots, all fronds were <2 cm long and most were <1 cm. Successful recruitment of *Sargassum* was unusual, with between 0 and 4 plants per plot [mean $\pm$ SD = 1.33 $\pm$ 1.4 or $\simeq$2.7 m^{-2}, whole thalli (frond numbers are higher)]. The blocks were rapidly colonised by abundant filamentous turf algae as well several common large macroalgae including *Lobophora* sp., *Padina* sp., *Colpomenia* sp., *Turbinaria* sp., *Dictyosphaeria* sp., *Chlorodesmis* sp., *Galaxaura* sp., *Amphiroa* sp. and crustose coralline algae. However, there were no discernible differences amongst cage treatments.

Table 3 *Sargassum* spp. (Experiment 3). Analyses of transplant effects at Brook Island. Data are (untransformed) difference between initial and final density. Changes in density were used since comparisons of initial densities showed initially higher numbers in coral transplants. Otherwise abbreviations and procedures as for Table 1, except that critical value of Cochran's test here is 0.906. A single strong outlier (Studentized residual = −3.915), a transplant which increased when all others decreased, led to significant differences in variances between treatments (fails Cochran's test, significant F-test). ANOVA is also shown (Comparison B) with this outlier omitted, resulting in very different conclusions (see data for Experiment 3 in "Results" and "Discussion")
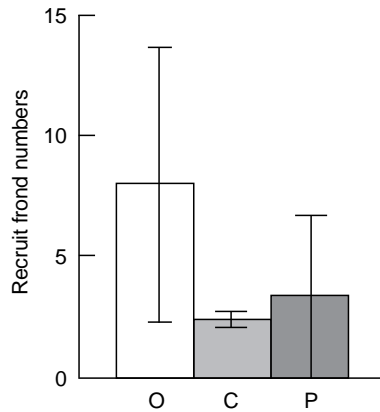
Comparison or factor	(df)	MS	F	P	%SST	Conclusions
ANOVA including outlier (A)						
Treatment	(1)	774.4	2.12	0.183	20%	No significant
Residual (n = 5)	(8)	364.2			80%	difference
Cochran's C	0.94					between means
ANOVA excluding outlier (B)						
Treatment	(1)	1693	12.98	0.009	63%	Highly significant
Residual (n = 5, 4)	(7)	130			37%	difference
Cochran's C	0.85					between means
F-test (C)						
Treatment (n = 5)	(4,4)		0.066	0.011		Significant difference between variances

Fig. 7 *Sargassum* spp. (Experiment 4). Effects of herbivore exclusion on recruitment at Great Palm Island, showing frond numbers after 1 yr. Data are mean (±SE) of three replicates (*abbreviations* as in Fig. 2 legend). Note that most plants (thalli) had several fronds

Discussion

The results of this study show that *Sargassum* are physiologically competent in the coral zone if protected from herbivores, but that recruitment to that zone may be rare. Without herbivore protection most adult plants decline within 3 mo. The results at Brook Island show that the importance of herbivores varies.

Physical or chemical differences between zones appear to have very little direct effects on survival of adult *Sargassum*. In the absence of herbivores, *Sargassum* survived at least as well and possibly better in the coral zone than in the adjacent *Sargassum* zone. This is a significant result in the context of GBR algal distributions, as it indicates that, under these conditions, *Sargassum* can not invade the coral zone, despite the abiotic environmental conditions being suitable for their growth and survival. In particular, this shows that *Sargassum* are not restricted between zones by any differences in water quality such as nutrient or sediment levels. This conclusion is consistent with several other studies, suggesting that *Sargassum* is not physiologically dependent on elevated nutrient or sediment conditions. Transplants across the continental shelf show that water quality does not directly explain patterns of algal abundance even at this, much larger, scale (McCook 1996). Although *Sargassum* is often more abundant on inshore reefs with high inputs of terrestrial sediments, sediment manipulations indicate that the algae is directly inhibited by sediments (J. Umar et al. unpublished

data). Field and aquarium experiments have indicated that *Sargassum* sp. growth is not limited by nutrient supply on either inshore or offshore reefs (McCook 1996; McCook et al. 1997), although in the laboratory, *S. baccularia* does show rapid uptake and increased production in response to short-term increases in nutrient supply (Schaffelke and Klumpp 1997). It remains possible that abiotic differences affect recruitment or dispersal or affect adult *Sargassum* indirectly (see following subsection).

Sargassum dispersal to and recruitment in the coral zone appear moderately low (Experiment 4; also Scott and Russ 1987 who did not record any *Sargassum* recruitment on nearby reefs with abundant adult *Sargassum*). The colonisation rates found in Experiment 4 would be sufficient for long-term invasion of the coral zone, but only at very low levels of subsequent mortality. However, at even moderate levels of subsequent mortality, such low recruitment is likely to strongly limit the algae's ability to colonise this zone.

Herbivory has an important influence on *Sargassum* distribution on these reefs. Although herbivorous fish were not demonstrated to be the critical factor excluded by the cages, they are the most reasonable explanation, especially given the greater loss of longer fronds in open and partially caged plots (Figs. 3 and 5; see also McCook 1996). Neither turtles or sea urchins are common at these sites, and neither is likely to be able to graze in partial cages.

The results from Brook Island are a useful test of the generality of these herbivore effects, suggesting that the importance of herbivory varies considerably both between and within reefs. Overall rates of herbivory were lower and apparently more variable at Brook Island than at Great Palm Island. Within Brook Island, the survival of transplants to the coral zone also varied considerably, in contrast to plants in their own zone. Over one month, most coral-zone transplants declined, but one grew. This variation is interpreted as real variability in the ability of plants to survive in the coral zone. Given the short duration of this experiment relative to Experiments 1 and 2, and the decline of all but one coral-zone transplant, it seems likely that there was a developing effect of herbivory that was masked by the variability within transplants. The outlying coral-zone transplant, that had not declined, may indicate spatial variation or stochasticity in grazing intensity. Possibly this transplant had simply not been found (yet) by the haphazardly roving schools of grazing fish, and given longer exposure it may have been reduced similarly to

Table 4 *Sargassum* spp. (Experiment 4). Analyses of herbivore effects on recruitment at Great Palm Island. Data are numbers of primary lateral fronds (untransformed), critical value of Cochran's test here is 0.871, otherwise abbreviations and procedures as for Table 1

Comparison or factor (ANOVA)	(*df*)	MS	*F*	*P*	%SST	Conclusions
Treatment	(2)	27.44	0.630	0.56	17%	No significant treatment effect
Residual (*n* = 3)	(6)	43.56			83%	
Cochran's *C*	0.74					

other transplants. This variation clearly overlies a distinct pattern in which (unprotected) transplants did generally decline. Thus, although the transplant effects were variable, the general pattern indicates that *Sargassum* is physiologically competent in the coral zone of these reefs, but usually declines unless protected from herbivores.

Zonation of herbivores and hence *Sargassum* on these fringing reefs is correlated with the availability of refuges from the herbivores' own predators. Such refuges are abundant in the topographically complex coral zone and rare in the *Sargassum* zone. Several previous studies also found that herbivore restrictions on algal abundance were linked to the substrate complexity or other factors that affect the vulnerability of herbivorous fish to their own predators (e.g. Hay 1981a; Hay and Taylor 1985; Lewis and Wainwright 1985). There is some evidence that fish abundances are higher on structurally complex substrates (Randall 1965; Talbot et al. 1978).

Previous studies of herbivore effects on algal "between habitat" distributions (Hay 1985) have all found herbivory to be critical, as in the current study. Herbivory has been shown to determine macroalgal distributions on reef slopes, reef flats and back-reef zones in Haiti, the Bahamas, Jamaica, the US Virgin Islands, Belize, Honduras and Panamá (e.g. Hay 1984 a, b; Lewis and Wainwright 1985; Lewis 1986; Morrison 1988). The significance of the herbivore effects in the current experiments is threefold: they are the first demonstration of the importance of herbivory to zonation of macroalgae on the GBR, and in particular to the prolific *Sargassum* beds on these reefs; they suggest that the causes of larger scale (cross-shelf) differences in *Sargassum* abundance (McCook 1996) are very similar to those found over a distance of 60 m in this study; and they demonstrate a strong herbivore effect in a zone with relatively low rates of herbivory and low algal recruitment.

Compared to the present results, most previous studies of herbivore effects on coral reefs have found higher rates of herbivory and more abundant algal recruitment in herbivore exclusions. In the Caribbean, Hay (1984a) found transplanted species of *Sargassum* and *Turbinaria* to be significantly reduced within days (see also Hay 1981a, b; Lewis 1985). Upon removing herbivore exclosures, Lewis (1986) found that most macroalgae were removed within days. On mid-shelf reef slopes in the same region as the present study, using *Sargassum* from nearby reefs, herbivores reduced tissue weight within one day (Steinberg et al. 1991). In contrast, herbivores in the coral zone at Great Palm Island and on mid-shelf reef flats (McCook 1996) took months to significantly reduce transplants. Presumably these low rates reflect the relatively low herbivore abundance on inshore reef slopes and mid-shelf reef flats (Williams 1982; Williams and Hatcher 1983; Russ 1984a, b); procedural differences and temporal or spatial variation may also contribute. Similarly, when herbivores were excluded from natural substrate in the Caribbean, macroalgal blooms occurred within months (Lewis 1986; Morrison 1988). Although these studies did not use cleared substrates, they contrast with my results, which showed no effect of herbivore exclusion on algal recruitment after one year (Experiment 4). The implication is that relatively low rates of herbivory can still serve as limits on algal abundance if algal colonisation is also relatively low.

Causes of *Sargassum* zonation and distribution

The apparent interaction between herbivory and recruitment in this study supports the suggestion (McCook 1996) that *Sargassum* distribution is dictated by a scale-dependent interaction between recruitment/dispersal, and herbivory. The large-scale distribution of *Sargassum* also appears to reflect interactions between algal recruitment rates and dispersal distances, and herbivore numbers and foraging distances: although herbivores apparently exclude *Sargassum* from mid-shelf reefs in general, plants occasionally occur on extensive mid-shelf reef flats which are closer to inshore *Sargassum* beds (McCook 1996; McCook et al. 1997). The presence of these plants may be due to the combination of large foraging distance for herbivores and more frequent *Sargassum* dispersal. Between the cross-shelf and within-reef scales, there is also an apparent gradient among fringing reefs in zonation and relative abundance of corals and algae: reefs further inshore apparently have fewer herbivores and *Sargassum* zonation extends further down the reef slope (implying successful recruitment to reef slope; e.g. Magnetic and Goold Islands-cf. Great Palm and Brook Islands: McCook personal observations).

Although the transplants showed that adult *Sargassum* are physiologically competent in the coral zone, differences in abiotic conditions may still indirectly affect the algae's distribution. For example, higher sediment levels on the reef flat may increase coral mortality (e.g. Stafford-Smith 1993) and hence increase substrate availability for *Sargassum*. There is also potential for feed-forward interactions involving abiotic factors. For instance, sediment-induced coral mortality may decrease substrate complexity and hence herbivore abundance, or the establishment of algal beds may increase sediment accumulation and hence coral mortality. Interestingly, my results do not conform to the model of Littler and Littler (1984), which suggests that in a high nutrient area, higher herbivore abundance should lead to increased dominance by coralline algae rather than corals, as here.

These ideas have implications for reef management in this area (McCook and Price 1997b). If *Sargassum* recruitment is in fact generally low, then the algae are unlikely to invade areas of coral dominance without prior disturbance to corals or reductions in herbivore abundances. This in turn implies that large beds of

Sargassum are likely to be a response to, rather than an initial cause of, coral mortality during reef degradation. Nonetheless, feed-forward interactions between coral mortality, substrate topography, herbivore abundance and macroalgal abundance could magnify and stabilize these changes. While speculative, these ideas are useful, as they highlight the need for information in several specific areas: temporal and spatial patterns of algal recruitment; the ability of established corals and algae to exclude each other; and the effects of abiotic factors on herbivore and coral abundances.

In summary, relatively low levels of herbivory appear able to prevent *Sargassum* invasion of coral-dominated zones, due in part to the rarity of *Sargassum* colonisation. In the absence of herbivores, the algae are physiologically competent outside their normal zone on inshore, fringing reefs.

References

Baldwin CL (1992) Impact of elevated nutrients in the Great Barrier Reef. Great Barrier Reef Marine Park Authority, Townsville (Res Publ No. 20)

Bell PRF (1992) Eutrophication and coral reefs – some examples in the Great Barrier Reef lagoon. Wat Res 26: 553–568

Day RW, Quinn GP (1989) Comparisons of treatments after an analysis of variance in ecology. Ecol Monogr 59: 433–463

Done TJ (1982) Patterns in the distribution of coral communities across the central Great Barrier Reef. Coral Reefs 1: 95–107

Done TJ (1992) Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247: 121–132

Hay ME (1981a) Spatial patterns of grazing intensity on a Caribbean barrier reef: herbivory and algal distribution. Aquat Bot 11: 97–109

Hay ME (1981b) Herbivory, algal distribution, and the maintenance of between-habitat diversity on a tropical fringing reef. Am Nat 118: 520–540

Hay ME (1984a) Predictable spatial escapes from herbivory: how do these affect the evolution of herbivore resistance in tropical marine communities? Oecologia 64: 396–407

Hay ME (1984b) Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? Ecology 65: 446–454

Hay ME (1985) Spatial patterns of herbivore impact and their importance in maintaining algal species richness. Proc 5th int coral Reef Symp 4: 29–34 [Gabrié C et al. (eds) Antenne Museum–EPHE, Moorea, French Polynesia]

Hay ME, Taylor PR (1985) Competition between herbivorous fishes and urchins on Caribbean reefs. Oecologia 65: 591–598

Hughes TP (1994) Catastrophes, phase-shifts and large scale degradation of a Caribbean coral reef. Science, NY 265: 1547–1551

Lapointe BE (1989) Caribbean coral reefs: are they becoming algal reefs? Sea Front 35: 84–91

Lewis SM (1985) Herbivory on coral reefs: algal susceptibility to herbivorous fishes. Oecologia 65: 370–375

Lewis SM (1986) The role of herbivorous fishes in the organization of a Caribbean reef community. Ecol Monogr 56: 183–200

Lewis SM, Wainwright PC (1985) Herbivore abundance and grazing intensity on a Caribbean coral reef. J exp mar Biol Ecol 87: 215–228

Littler MM, Littler DS (1984) Models of tropical reef biogenesis: the contribution of algae. Prog phycol Res 3: 323–363

Martin-Smith KM (1993) The phenology of four species of *Sargassum* at Magnetic Island, Australia. Botanica mar 36: 327–334

McCook LJ (1996) Effects of herbivores and water quality on the distribution of *Sargassum* on the central Great Barrier Reef: cross-shelf transplants. Mar Ecol Prog Ser 139: 179–192

McCook LJ, Price IR (1997a) The state of the algae of the Great Barrier Reef: what do we know? In: Wachenfeld D, Oliver J, Davis K (eds) State of the GBR World Heritage Area Report, Great Barrier Reef Marine Park, Authority, Townsville, pp 194–204

McCook LJ, Price IR (1997b) Macroalgal distributions on the Great Barrier Reef: a review of patterns and causes. In: Proceedings of the Great Barrier Reef; science, use and management. A national conference held at James Cook University of North Queensland, 25–29 November 1996. Vol. 2. Great Barrier Reef Marine Park Authority, Townsville, pp 37–46

McCook LJ Price IR Klumpp DW (1997) Macroalgae on the GBR: causes or consequences, indicators or models of reef degradation? Proc 8th int coral Reef Symp (1997) (in press) [Lessios HA, Macintyre I (eds) Smithsonian Tropical Research Institute, Panamá]

Morrison D (1988) Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. Ecology 69: 1367–1382

Morrissey J (1980) Community structure and zonation of macroalgae and hermatypic corals on a fringing reef flat of Magnetic Island (Queensland, Australia). Aquat Bot 8: 91–139

Price IR (1989) Seaweed phenology in a tropical Australian locality (Townsville, North Queensland). Botanica mar 32: 399–406

Randall JE (1965) Grazing effect on seagrasses by herbivorous reef fishes in the West Indies. Ecology 46: 255–260

Russ GR (1984a) Distribution and abundance of herbivorous fishes in the central Great Barrier Reef. I. Levels of variability across the entire continental shelf. Mar Ecol Prog Ser 20: 23–34

Russ GR (1984b) Distribution and abundance of herbivorous fishes in the central Great Barrier Reef. II. Patterns of zonation of mid-shelf and outershelf reefs. Mar Ecol Prog Ser 20: 35–55

Schaffelke B, Klumpp DW (1997) Growth of germlings of the macroalga *Sargassum baccularia* (Phaeophyta) is stimulated by enhanced nutrients. Proc 8th int coral Reef Symp [Lessions HA, Macintyre I (eds) Smithsonian Tropical Research Institute, Panamá]

Scott FJ, Russ GR (1987) Effects of grazing on species composition of the epilithic algal community on coral reefs of the central Great Barrier Reef. Mar Ecol Prog Ser 39: 293–304

Stafford-Smith MG (1993) Mortality of the hard coral *Leptoria phygia* under persistent sediment influx. Proc 7th int coral Reef Symp 1: 289–299 [Richmond RH(ed) University of Guam, Mangilao, Guam]

Steinberg PD, Edyvane K, de Nys R, Birdsey R, van Altena IA (1991) Lack of avoidance of phenolic-rich brown algae by tropical herbivorous fishes. Mar Biol 109: 335–343

Talbot FH, Russel BC, Anderson GRV (1978) Coral reef fish communities: unstable high-diversity systems? Ecol Monogr 48: 425–440

Vuki VC, Price IR (1994) Seasonal changes in the *Sargassum* populations on a fringing coral reef, Magnetic Island, Great Barrier Reef region, Australia. Aquat Bot 48: 153–166

Williams DMcB (1982) Patterns in the distribution of fish communities across the central Great Barrier Reef. Coral Reefs 1: 35–43

Williams DMcB, Hatcher AI (1983) Structure of fish communities on outer slopes of inshore, mid-shelf and outer shelf reefs of the Great Barrier Reef. Mar Ecol Prog Ser 10: 239–250

Yellowlees D (ed) (1991) Land use patterns and nutrient loading of the Great Barrier Reef region. Sir George Fisher Centre for Tropical Marine Studies, James Cook University of North Queensland, Townsville, Australia