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REPORT

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Effects of sediment deposition on the seaweed *Sargassum* on a fringing coral reef

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Abstract Coral reef degradation may involve shifts from coral to algal dominance and may be caused in part by increased sediment loads. Inshore fringing reef flats in the central Great Barrier Reef region are often subjected to periods of high sedimentation and are often dominated by macroalgae such as *Sargassum*. Experiments reported here examine the impacts of sediments on the recruitment, growth, survival, degeneration and vegetative regeneration of *Sargassum microphyllum* on a fringing coral reef flat in the central Great Barrier Reef. Comparison of three levels of sediment deposition (experimental addition, control (ambient condition) and experimental removal) showed that increased amounts of sediment significantly decreased rates of recruitment, growth, survival and vegetative regeneration, but not degeneration of *S. microphyllum*. In addition, the regenerative ability of *S. microphyllum* thalli with short, persistent erect branches (untreated) was compared with that of thalli experimentally cut back to the holdfast. This experimental damage significantly reduced regeneration.

Introduction

There is wide concern about coral reef degradation due to anthropogenic changes in water quality. In particular, human activities such as deforestation, agriculture, coastal development, construction, mining, drilling and dredging can result in an increased sediment load which in turn may cause severe degradation of coral reefs (e.g. Rogers 1990).

In the central Great Barrier Reef region there is concern that increases in nutrient and sediment levels from terrestrial runoff may be contributing to degradation of inshore coral reefs (review by McCook and Price 1997). In this region, the abundance and composition of macroalgae seems to be correlated with cross-shelf differences in sedimentation and turbidity. On many nearshore fringing reefs, particularly on the reef flats, macroalgae such as *Sargassum* are often extremely abundant (Morrissey 1980; Price 1989; Vuki and Price 1994; McCook et al. 1997). These large brown algae are generally absent from mid- to outer shelf reefs (Vuki and Price 1994; McCook et al. 1997). On inshore reefs, sedimentation rates and turbidity are generally high compared to mid- and outer shelf reefs. Even among inshore reefs, abundance and vertical distribution of *Sargassum* is often greater on reefs closer to terrestrial inputs (McCook 1997). The higher sediment load on the inshore coral reefs may lead to increased macroalgal abundance and decreased abundance of corals.

The effects of sediments on fringing reef biota on the Great Barrier Reef have been of particular concern on Magnetic Island, near Townsville, Queensland, where tourism developments and recurrent dredging of a deep-water shipping channel have led management authorities to establish extensive monitoring programs (e.g. Benson et al. 1994). An assessment of the impact of dredging found some significant changes in the abundance of *Sargassum* and other algae. However, the ecological significance of these changes was ambiguous, due to confounding effects of seasonality, a priori differences between sites, and limited taxonomic resolution (in contrast, effects on corals could be resolved in detail; Benson et al. 1994).

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If higher rates of sedimentation lead to increased macroalgal abundance, they may act directly, by enhancing macroalgal recruitment or survival; or indirectly, by inhibiting competitors (e.g. corals) or herbivores (e.g. fish). Both direct or indirect impacts could involve effects of either suspended sediment (turbidity) or sediment deposition on the substratum. Most tropical, experimental work on the effects of sedimentation has focussed on corals (reviews in Hodgson 1990a, b; Rogers 1990; Stafford-Smith 1993). In contrast, very little work has been done on the effects of sedimentation on macroalgae, and most studies have been correlative rather than experimental (e.g. Espinoza and Rodriquez 1987). There is evidence that sediments may inhibit attachment and recruitment of some temperate macroalgae (Devinny and Volse 1978) and that *Sargassum* is more abundant on hard substrata with little sand cover (e.g. McCourt 1984; Ang 1985a).

Studies on environmental influences on *Sargassum* abundance are also important in a broader context. Species of the macroalga *Sargassum* often dominate the benthic vegetation of fringing reefs in the Pacific, both in terms of thallus size and standing crop (Tsuda 1972; Ang 1986) and often form dense mono- or multi-specific stands on reef flats or reef slopes in the tropics (Morrissey 1980). The genus is often restricted in its distribution to inshore coral reefs (Tsuda 1972; Ang 1986). The abundance of *Sargassum* is important in terms of reef primary production, habitat structure and harvesting for human uses (e.g. Ang 1987; Martin-Smith 1993a; Schaffelke and Klumpp 1997a).

Populations of *Sargassum* species often show marked seasonal changes in abundance (e.g. McCourt 1984, Ang 1985b). Individual thalli (plants or genets) of *Sargassum* consist of a perennial holdfast and short main axis (stem), which produces varying numbers of annual, primary lateral fronds (main branches, ramets). On fringing reef flats in the central Great Barrier Reef region, most species of *Sargassum* have a strongly seasonal growth cycle, with spring-summer production of large, multi-branched fronds and autumnal degenerative loss of most frond tissue (Price 1989; Martin-Smith 1993b; Vuki and Price 1994). In winter, the thalli of *S. microphyllum* consist only of the perennial holdfast and main axis, with short (<15 cm and usually <10 cm), relatively simple lateral branches. While the cues for the annual degeneration and vegetative regeneration of *Sargassum* are still uncertain (Vuki and Price 1994), the two phases may respond differently to sedimentation.

The present studies aimed to investigate quantitatively the effects of sediment load on the macroalga *S. microphyllum* C. Agardh on a fringing coral reef in the Great Barrier Reef region. Six separate experiments distinguished between sediment effects on different life history variables (i.e., recruitment, growth and survival/mortality) and seasonal stages (i.e., thallus degeneration and vegetative regeneration) of this species, using both individual plants and populations.

Study sites, experimental design and methods

Study area and sediment characteristics

This study was conducted on the fringing coral reef in Geoffrey Bay (19°9′S, 146°51′E), on the southeast side of Magnetic Island (Fig. 1). Magnetic Island is a high continental, granite island located approximately eight kilometres north of Townsville. Vuki and Price (1994) described the physical environment of the area. The fringing reef in Geoffrey Bay is relatively well developed, with diverse hermatypic coral and benthic algal biota. The reef can be separated into three major zones, the inner sedimentary accumulation, the reef flat and the reef slope (Morrissey 1980). The southern part of the reef flat includes numerous shallow tidal pools and low, flat-topped microatolls. Study sites were established on these microatolls, where the predominant organism was *Sargassum microphyllum*. Most microatolls are above water for short periods (3–4 h) during spring low tides, but not during neap low tides.

Sediment conditions in the waters near Magnetic Island have been described in some detail (Smith 1978; Kelly 1982; Benson et al. 1994; Larcombe et al. 1995). Terrigenous sediments derive both from local runoff and from resuspended sediments (Larcombe et al. 1995), including dredged sediments (Benson et al. 1994). Within Geoffrey Bay, turbidity is higher, and sediment particle size and carbonate content are smaller on the

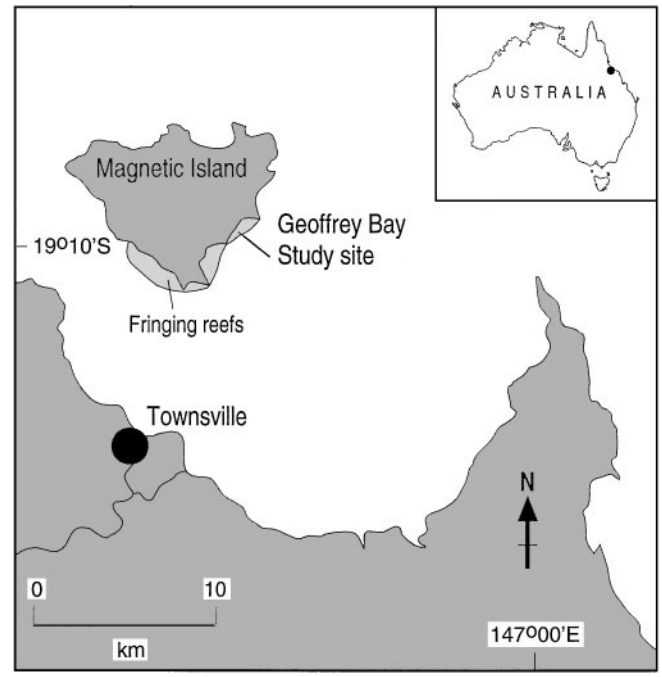

Fig. 1 Map of Magnetic Island area, northeastern Australia, showing location of study area on the fringing coral reef in Geoffrey Bay (after Vuki and Price 1994). *Lighter shading* indicates fringing reefs

inner reef than on the reef slope, apparently reflecting differences in water movement and resuspension of fine sediments (Smith 1978). Turbidity on the reef flat is high relative to the reef slope, indicating considerable resuspension of fine sediments on the shallower reef flat (reef flat extinction coefficient and max. secchi depth were 0.46–0.85 m^{-1} and 1.5 m, respectively, compared to. 0.28–0.31 m^{-1} and 5.0 m on the reef slope, Kelly 1982).

Sediment parameters were measured in August 1996. This was after the experimental period, but they probably represent typical conditions, since major dredging works had finished before the experimental periods (Benson et al. 1994), and since these sites appear intermediate to the range of reef flat sediment conditions in this area (*personal observation* for sediment depths; also e.g. Hansen et al. 1992 for particle sizes, nutrients and bacteria). Particle size distributions were measured by sieving and weighing randomly collected samples. pH and redox were measured using a hand-held meter. pH was measured with a Model PBFC standard electrode calibrated against pH 6, 7 and 8 standards. Redox was measured using a combination Calomel reference-platinum electrode. Carbon and nitrogen levels were analyzed on a Perkin Elmer CHNS 2400 elemental analyzer. Phosphate was analyzed on a Varian Liberty 220 plasma emission spectrometer, following perchloric or nitric acid digestion. Organic carbon was analyzed by acid dissolution and high temperature catalytic oxidation on a Beckman total organic carbon analyzer. Carbonate was estimated by the difference between total carbon and total organic carbon. Bacterial densities were determined on formalin preserved samples by direct counts of DAPI (Diamidino-phenylindole) stained cells using epifluorescence microscopy.

The microatoll study sites are usually covered in a thin deposit of fine sandy sediments, over hard carbonate substrata. Typical ambient sediment deposits ranged from 1–10 mm depth (mean $\pm$SD, 4.4 ± 2.6 mm, $n = 20$, dry weights 17.9 ± 9.9 g/100 cm^2, $n = 6$). No long-term net accumulation of sediment was apparent on the sites during or after the experiments. Mean particle size distributions were 6.6% fine gravel, 31.2% coarse sand (particle size, 200 μm -2 mm), 54.1% fine sand (62–200 μm) and 8.1% silt and clay ($n = 11$). Sieved sediments from adjacent pools, which were added during the experiments (see later), had no gravel but slightly more coarse sand (58.1%) and less fine sand (39.5%) and clay (2.4%; $n = 6$). Microatoll sediments were predominantly terrigenous ($8.9\% \pm 0.3\%$ carbonate, mean $\pm$SD of 6 samples), slightly basic (mean pH 7.68, range 7.13–7.95, $n = 6$) and not reducing (mean redox potential E_h 139 millivolts, range 83–157 millivolts, increasing with depth, $n = 12$). Sieved pool sediments were slightly higher in carbonates ($10.6\% \pm 0.4\%$ mean $\pm$ SD of 6 samples). Particulate nutrient levels were slightly higher in microatoll sediments than sieved pool sediments (mean $\pm$ SD of 6 samples for microatoll and pool sediments respectively were: total organic carbon TOC 7.5 ± 1.2 and 3.2 ± 0.6 mg/g dry weight; total N 700 ± 100 and 200 ± 50 μg/g dry weight; total P 277 ± 18 and 232 ± 9 μg/g dry weight). Mean bacterial densities for the microatoll sediments were 9.17×10^8 cells/g dry weight of sediment.

Experimental design

Sediment manipulations

In each experiment three levels of sediment load were used: experimental removal, control (natural or ambient condition), and experimental addition. Sediment removal was achieved by gently flushing the quadrats with seawater whilst submerged on a rising tide, to minimize stress to the algae. Flushing was never observed to dislodge macroscopic *Sargassum* thalli. Increased sediment load was achieved by adding sediment to approximately double the thickness of the ambient sediment layer (i.e. up to 20 mm) in individual quadrats. Sediments were collected from the microatolls and pools adjacent to the quadrats, sieved (<2 mm) and immediately added to the submerged quadrats as a fine "rain", again on a rising tide. Although some sediments settled on algal thalli, wave action and the rising tide ensured that algae were not buried. Sediments in control treatments were not manipulated, but left at background or ambient levels.

The sediment treatments were applied at the beginning of each experiment and re-applied at two week intervals throughout the experimental periods (up to 15 months). Sediment deposits generally took between one to two weeks to return to background levels. Differences in suspended sediments between treatments were probably negligible, given the size and interspersion of quadrats and the mixing caused by predominantly southeasterly winds on the shallow reef flat. Thus, the experiments primarily test for effects of sediment deposit thickness. Sediment was flushed from all treatments before data collection, to avoid bias in recording small thalli.

Experiment 1: the effects of sedimentation on recruitment of *S. microphyllum*

The first experiment tested for effects of sediments on recruitment, using quadrats cleared of all pre-existing *Sargassum*. The experimental design was a 1-factor anova, with five replicate, 50 cm × 50 cm permanent quadrats randomly assigned to each of the three treatments. These quadrats were placed on microatolls in areas dominated by *S. microphyllum*. The quadrat positions were marked by stainless steel screws inserted into the substratum. In each quadrat all macroscopic *S. microphyllum* thalli, including any holdfasts, were removed at the beginning of the study (July 1993) using

a paint scraper, and the holdfast areas (only) were then thoroughly burnt with a gas torch. Consequently, any *S. microphyllum* thalli subsequently appearing were assumed to be due to recruitment, either as new settlement or as growth of microscopic individuals which had already settled. After three months (October 1993), nine months (April 1994) and 15 months (October 1994), the density of primary laterals of *S. microphyllum* in each quadrat was recorded.

Experiment 2: the effects of sedimentation on recruitment, growth and survival of *S. microphyllum*

To test for effects of sediments on whole populations, the second experiment measured combined abundance of recruits and pre-existing plants. In this case, all *S. microphyllum* inside the quadrats was left undisturbed at the beginning of experiment. Therefore, the *S. microphyllum* recorded at later dates could have resulted both from the survival of pre-existing thalli and from recruitment. The experimental design was again a 1-factor anova with five replicate, 50 cm $\times$50 cm permanent quadrats randomly assigned to each treatment.

The abundance of *S. microphyllum* in this experiment was recorded in terms of both percent cover and density of primary laterals. A 100 point string grid was used for estimating percent cover, while density was recorded as the total number of primary laterals of *S. microphyllum* in a quadrat. The primary laterals were recorded in four length classes (0–3 cm, 3–10 cm, 10–25 cm and $>$ 25 cm) to provide size distributions. Percent cover and density were recorded immediately before sediment manipulation (at the beginning of the experiment, July 1993) and three months (October 1993), nine months (April 1994) and 15 months (October 1994) thereafter.

Experiment 3: the effects of sedimentation on growth and survival of *S. microphyllum*

To resolve sediment effects on adult plants, the third experiment used individual established plants. The experimental design was a 1-factor nested anova with five groups of *S. microphyllum* thalli nested within each sediment treatment. Each group included three individually tagged *S. microphyllum* thalli. These thalli were located adjacent to one of the permanent quadrats set up for experiment 2 and were labelled with small tags inserted in the substratum adjacent to the holdfast.

The density and size of *S. microphyllum* was recorded as the number of primary laterals present in each individual thallus, using four size classes of primary lateral length: 0–3 cm, 3–10 cm, 10–25 cm and $>$25 cm. The number of primary laterals was recorded before manipulation of sediment (at the beginning of the experiment in July 1993) and three months (October 1993), nine months (April 1994) and 15 months (October 1994) thereafter.

Experiments 4 and 5: the effect of sedimentation on degeneration of *S. microphyllum*

To test the effect of sedimentation on the seasonal degeneration of *S. microphyllum*, two experiments monitored the loss of tissues from mature plants during autumn. Experiment 4 tested the effect of sedimentation on changes in the length of the primary laterals of degenerating *S. microphyllum*, using individual plants. The experimental design was a 1-factor nested anova with five groups of *S. microphyllum* thalli randomly nested within sediment treatments. Each group included three individually tagged *S. microphyllum* thalli. Each thallus was labelled with a small tag inserted in the substratum adjacent to the holdfast. The length of all primary laterals of each *S. microphyllum* thallus was measured immediately before sediment manipulation (March 1994) and again after three months (June 1994). The mean length for each individual thallus was then used in the analysis.

Experiment 5 involved a 1-factor anova intended to test the effect of sedimentation on both percent cover and density of primary laterals of *S. microphyllum* populations. Quadrats were selected and assigned as for experiment 1. After three months (June 1994), cover and density of primary laterals of *S. microphyllum* were recorded, as in experiment 2.

Experiment 6: the effects of sedimentation and experimental damage to thalli on vegetative regeneration of *S. microphyllum*

The final experiment tested for effects of both sediments and tissue damage on regeneration success. The experimental design was a two-factor anova. The first factor was sediment load with the three levels described previously. The second factor was damage to thalli with 2 levels: normal (control) thalli and experimentally-excised thalli. Each treatment combination was replicated five times in 50 cm $\times$ 50 cm permanent quadrats. These quadrats were set up in June 1994 as described for experiments 2 and 5. In fifteen randomly chosen quadrats, the erect parts of all *S. microphyllum* thalli were experimentally cut off, leaving only the holdfasts. In the remaining 15 quadrats, the pre-existing *S. microphyllum* thalli were left unmanipulated as controls. These thalli had naturally degenerated to the persistent holdfast, axes and short primary laterals.

Regeneration success was estimated as the proportion of original thalli which showed regrowth after three months (September 1994). The position of each *S. microphyllum* thallus was recorded before initial sediment treatment and again at the end of the experiment, using quadrat maps and photographs. Comparing these photographs and maps ensured that no new recruits were included in the final data. The cover and density of *S. microphyllum* were also recorded after three months.

Data analysis

Data were analyzed using Statistix Version 4.0 software. Since the nested factor (group) in experiment 3 was not significant ($P > 0.25$), the data were then re-analyzed without the nested factor using a one-way anova. Multiple comparisons of means for all data sets were carried out using Ryan's Q test ($\alpha = 0.05$) to adjust for the number of comparisons. Homogeneity of variances of all data sets were confirmed using Cochran's test.

Results

Experiment 1

There was a statistically significant effect of sedimentation on the recruitment of *Sargassum microphyllum* (Fig. 2; ANOVA, $P < 0.001$). Addition of sediments significantly reduced recruitment of *S. microphyllum* at all three sampling dates (3, 9, 15 months). Although sediment removal significantly enhanced recruitment relative to the control population during the first three months, the differences at the later sampling dates were not statistically significant.

Experiment 2

The abundance of *S. microphyllum* in quadrats was significantly affected by sediment load (Fig. 3; ANOVA, $P < 0.001$ for both changes in percent cover and density at all three dates). Abundance varied seasonally over the sampling dates where sediments were unmanipulated or removed. Both percent cover and density increased during the first growing season (3 and 9 months) and then declined between 9 and 15 months, showing the annual "die-back" during the austral winter. Differences between sediment removal and unmanipulated (control) treatments were not statistically significant at any of the sampling dates. In contrast, where sediments were added, the average percent cover and density did not change significantly throughout the study, so that abundance was always significantly less than in either of the other treatments.

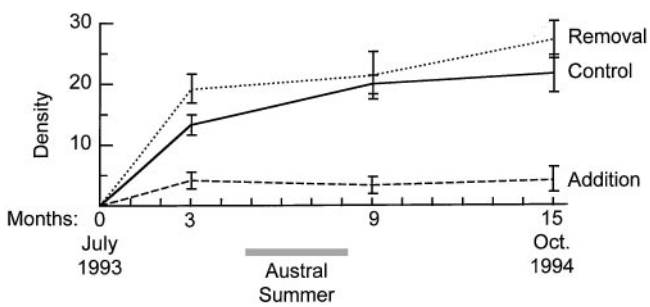

Fig. 2 The effect of sediment on recruitment of *S. microphyllum* (experiment 1). Data are density of primary laterals per 0.25 m^2 at 3, 9 and 15 months after commencement of the experiment (July 1993), expressed as means ($\pm$SE) of 5 replicates

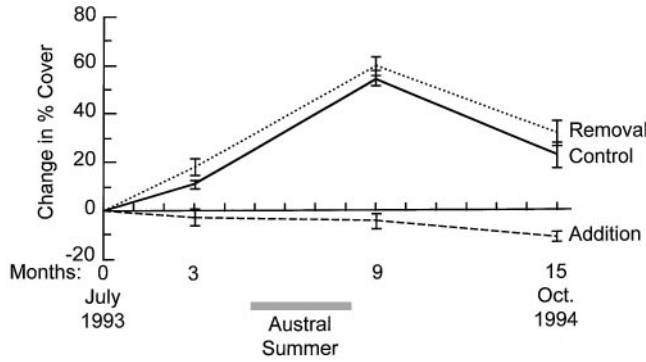

Fig. 3 The effect of sediment on changes in percent cover of *S. microphyllum* populations (experiment 2). Data include both pre-existing and recruited plants, and are the differences between percent cover before and 3, 9 and 15 months after commencement of the experiment (July 1993), expressed as means ($\pm$SE) of 5 replicates

The size distribution of the primary laterals of *S. microphyllum* also changed in response to sediment load (Fig. 4). Comparisons of primary lateral density by size class before and after 3 and 9 months of treatments show that where sediment was removed or unmanipulated (control), the density of the smallest size class decreased, while that of larger ones increased. This implies that short fronds were growing into larger size classes, as expected. In contrast, where sediment was added, the density of the smallest size classes also decreased greatly, but that of the larger classes increased only slightly, if at all. This suggests that increased sediment load reduced the survival and growth of shorter laterals into larger size classes.

Experiment 3

The growth and survival of mature *S. microphyllum* thalli were significantly affected by the amount of sedimentation (Fig. 5, ANOVA, $P \leq 0.005$ for all three dates). Changes in the number of primary laterals were not significantly different between the sediment removal treatment and the unmanipulated (control) sediment treatment, since neither changed significantly during the experiment. In contrast, there was a significant loss of primary laterals in the sediment addition treatment, both over the time course of the experiment, and compared to the other two treatments.

Comparisons of the size distributions of primary laterals of *S. microphyllum* again indicate that sediment addition reduced the ability of small *S. microphyllum* fronds to survive and grow into larger size classes (Fig. 6). In all treatments, the smallest size class decreased as fronds grew into larger size classes. However, after nine months, increases in the larger size classes were much greater where sediment was removed

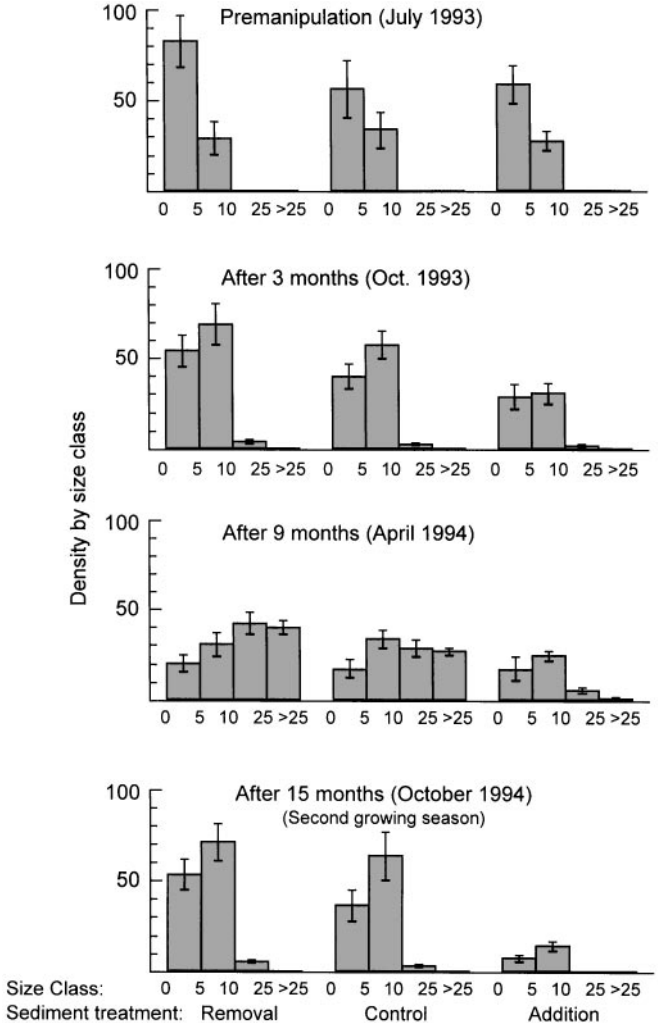

Fig. 4 The effect of sediment on the size distributions for *S. microphyllum* populations (experiment 2). Size distribution before and 3, 9 and 15 months after commencement of the experiment. Data include both pre-existing and recruited plants, and are density (fronds per 0.25 m^2) of primary laterals in each size class (see experimental design section), expressed as mean ($\pm$SE) of 5 replicates; size classes are in cm

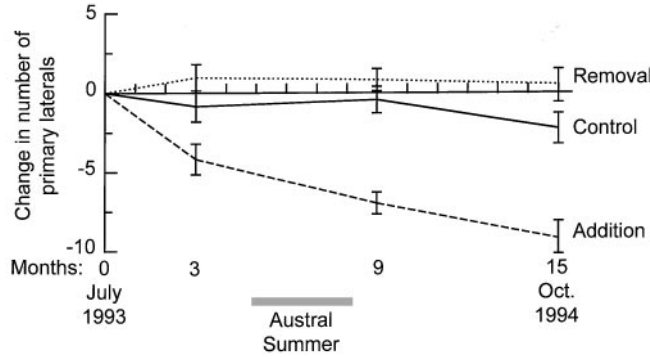

Fig. 5 The effect of sediment on changes in the frond number of individually tagged *S. microphyllum* (experiment 3). Data are the differences between number of the primary laterals before and 3, 9 and 15 months after commencement of the experiment (July 1993), expressed as means ($\pm$SE) of 15 replicates

or unmanipulated (control) than where sediment was added.

Experiments 4 and 5

There was no significant effect of sediment level on degeneration of *S. microphyllum* . In all three treatments, average primary lateral length for each thallus decreased by a similar amount (27–32 cm; ANOVA, $P = 0.42$). Similarly, percent cover and density were not significantly affected by the different sediment regimes (ANOVA, $P = 0.78$ and 0.30 respectively).

Experiment 6

In each of the three sediment treatments, thallus damage significantly reduced the vegetative regeneration of *S. microphyllum* in terms of proportion of degenerated thalli which regenerated (Fig. 7; $P < 0.001$). Sediment treatment effects were also significant ($P < 0.001$), as sediment addition led to less regeneration than unmanipulated (control) or sediment removal treatments. There was no significant interaction between sediment treatment and thallus damage ($P = 0.92$). The effects on proportional regeneration were closely reflected in effects on % cover and density, with significantly less regeneration of cut thalli, and thalli in the sediment addition treatment, and no interaction between factors.

Notwithstanding the effects of sediment addition, or thallus damage, a high proportion of thalli regenerated. Even cut holdfasts with added sediments had more than 50% recovery during the period of the experiment, and recovery was as high as 98% for uncut thalli with sediments removed (Fig. 7).

Discussion

The results of this study reveal that recruitment, growth, survival, and seasonal regeneration of *S. microphyllum* at Geoffrey Bay were significantly affected by an increase in sediment load. Each of these processes was significantly decreased where sediment was added, although populations were never completely killed. In contrast, the effects of sediment removal were rarely significant and the only significant difference for sediment removal (experiment 1) was small compared to the effect of sediment addition. This suggests that the abundance of *S. microphyllum* is not significantly affected by current sediment levels at the study site. A twofold increase in thickness of sediments covering the substratum apparently would reduce *Sargassum* abundance considerably, but probably would not cause local extinction. The consistent direction of treatment

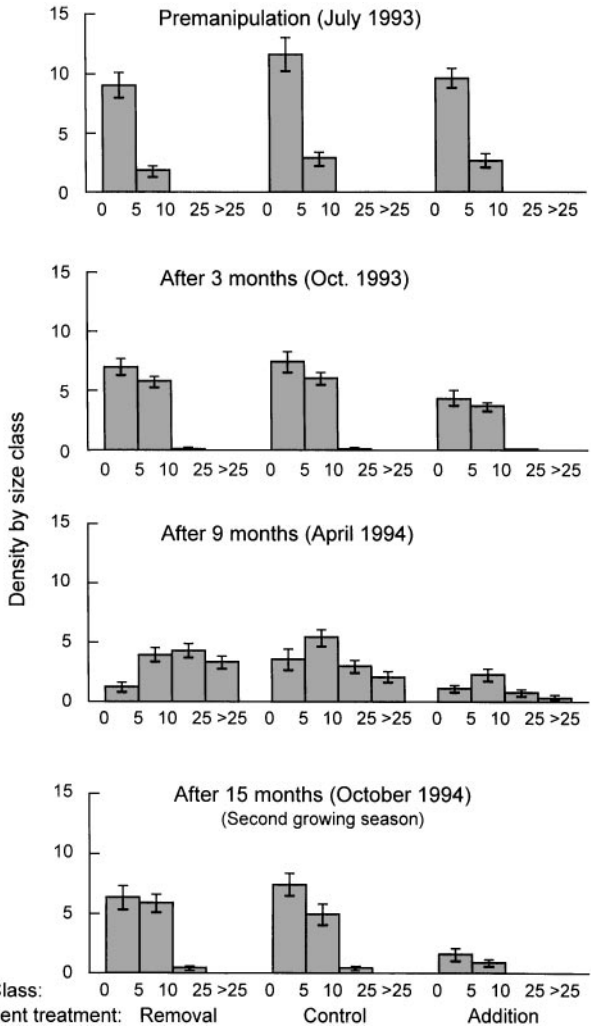

Fig. 6 The effect of sediment on the size distributions of primary laterals of individually tagged *S. microphyllum* (experiment 3). Size distributions before and 3, 9 and 15 months after commencement of the experiment. Data are numbers of primary laterals in each size class, expressed as means (±SE) of 15 replicates; size classes are in cm

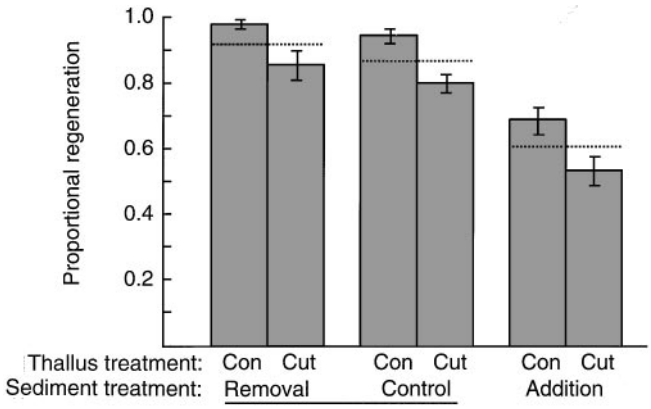

Fig. 7 The effect of sediment and thallus damage on regeneration of *S. microphyllum* (experiment 6). Data are proportion of original "degenerated" thalli to show regrowth 3 months after commencement of the experiment (June 1994), expressed as means (±S.E.) of 5 replicates. *Dashed lines* indicate means for sediment treatments, averaged across both thallus treatments. *Con*, control. *Solid line* indicates sediment treatments which were not significantly different

effects for the different life history stages is strong evidence that the overall success of the alga would be generally inhibited by sediment deposition, as a direct effect.

The effects on recruitment probably include effects on settlement and attachment of new embryos, and on growth of already settled, microscopic plants into adult populations. Fertile *Sargassum* is rare at this site between July and October (but it does occur, Martin-Smith 1993b, Vuki and Price 1994), so that most recruits which appeared by October 1993 were probably already attached when the experiment was established. Recruitment data for April and October 1994 would include both new settlement and growth of the previous cohort.

The range of treatments and responses in these experiments appear broadly relevant to the local distribution of *S. microphyllum*. *Sargassum* spp. are not found in areas with sediment deposits much deeper than our addition treatment (personal observation), presumably because they only attach to hard substrata. The alga is unlikely to be inhibited by thinner sediment deposits than our removal treatment. Sediment deposits vary considerably between and within reefs in this area, ranging from bare carbonate pavement with no sediment deposits, through coarse, oxic carbonate sands on offshore reefs, to deep, anoxic terrigenous mud on inshore reef flats bordered by mangroves. Thus our sediment treatments include most of the range of sediment conditions in which *Sargassum* occurs, and are intermediate to the range of conditions available on local reefs.

The results of experiment 6 also show that *S. microphyllum* has an impressive ability to regenerate from basal tissues, even after experimental removal of all erect parts. Regeneration was significantly reduced in these damaged thalli, indicating that damage to *S. microphyllum* thalli, whether due to natural or anthropogenic disturbance, would reduce regeneration of the species. This would particularly be true for plants subject to other stresses, such as increased sediment load. Nonetheless, the ability of *S. microphyllum* to regenerate from damaged thalli (holdfasts only) is likely to be important during recovery from disturbance, especially since recruitment is relatively low (experiment 1). The importance of vegetative regeneration in fucoid populations has been established for species of *Sargassum* (Ang 1985c; Kendrick 1994), and *Fucus* (McCook and Chapman 1992).

Previous studies of the effects of sedimentation have also found sediment load to be detrimental to corals (e.g. Hodgson 1990a) and to algae. High sediment load on the substratum has been reported to decrease

Macrocystis recruitment, by preventing propagule attachment (Devinny and Volse 1978) and reduce the biomass of *Fucus* (Vogt and Schramm 1991). Espinoza and Rodriquez (1987) also found a reduction in thallus size and reproductive capability of *Sargassum sinicola* subjected to an increase in sediment load in the southern Gulf of California. However, the present study is the first to demonstrate experimental effects of sediment on tropical macroalgae, and also the first to examine sediment effects on all the major life history stages.

There are several indications that the main mechanisms by which added sediments inhibited *S. microphyllum* at Geoffrey Bay involved smothering short fronds and recruits, and preventing attachment of new recruits. Comparison of the size distributions of *S. microphyllum* before and after treatments within the same growing season suggest that added sediments inhibited the survival of small fronds and recruits and their growth into larger size classes (experiments 2 and 3). Similarly, the inhibition of regeneration of short thalli (experiment 6) contrasted with the lack of a significant effect on degeneration of tall fronds (experiments 4 and 5). This proportionally higher mortality of shorter fronds is unlikely to result from sand scour, microbial infection, or from suspended sediments increasing turbidity or deposition on distal tissues, although such effects have been found for other algae and reef organisms (e.g. Devinny and Volse 1978; Ang 1985a; Hodgson 1990b; Rogers 1990). Indeed suspended sediments are unlikely to have differed much between treatments.

The results of this study contrast with the observation that macroalgae such as *Sargassum* are more abundant in reef areas with relatively high sedimentation (e.g. McCook et al. 1997). This suggests that abundant *Sargassum* in areas with higher sediment load is not due to direct effects of sediments, but must be caused either by other factors correlated with sediments (e.g. nutrients, Schaffelke and Klumpp 1997b), or indirectly by the effects of sediments on other organisms. For example, if sedimentation kills other species such as hard corals, the space available for the algae may increase considerably. Similarly, if suspended sediments or sediment deposition inhibit herbivorous fish, then algae may be enhanced overall by sediments. Certainly, *Sargassum* is not dependent on the physical/chemical environmental conditions on the inshore reef flats where it is normally most abundant (McCook 1996, 1997). Thus, macroalgae such as *Sargassum* may merely be opportunistic beneficiaries of the detrimental effects of sediments on other organisms, rather than being favoured by high sediment loads.

In summary, the results of the present study provide evidence that sediment deposits inhibit the recruitment, growth, survival and vegetative regeneration of *S. microphyllum*. It appears that current sediment levels (<10 mm thickness) at Geoffrey Bay are not inhibiting *Sargassum* significantly. However, a twofold increase in sediment thickness would strongly reduce the success of the species. This has important implications for management of reefs exposed to dredging and other anthropogenic increases in sediments. It suggests that algal overgrowth during reef degradation may in fact be an indirect effect of increased nutrient or substratum availability, or decreased herbivory, rather than resulting from direct enhancement of algal populations.

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