# Survival strategies in *Polysiphonia adamsiae* and *P. strictissima* (Rhodophyta, Rhodomelaceae) subjected to sediment deposition and grazing pressure

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Abstract Adaptive strategies of *Polysiphonia* adamsiae and P. strictissima living in conditions subject to sand deposition and amphipod grazing were investigated by in situ field observations and experimental culture in southern New Zealand between September 2001 and July 2003. The findings from this study showed that for both species, branches regenerated from prostrate axes and fragments grew 7 to 10 times faster than sporelings under the same culture conditions. Also, prostrate axes exhibited extensive creeping growth and produced dense upright branches. In contrast, sporelings exclusively grew upright until they reached c. 1-2 cm. These findings indicate that vegetative propagules have a much higher probability of forming algal turf than sporelings. In addition, prostrate axes survived darkness longer than sporelings, implying that algal thalli might be protected from amphipod grazing by sediments. This study shows that vegetative modes of reproduction predominated over sporic modes in both species. Vegetative reproduction might be advantageous for thalli to survive amphipod grazing under turf-trapped sand.

**Keywords** amphipod; growth differences; sporic reproduction; turf; vegetative reproduction

### INTRODUCTION

Sediment deposition significantly influences benthic algal distribution patterns in coastal environments (Daly & Mathieson 1977; Littler et al. 1983; Stewart 1983; D'Antonio 1986; McQuaid & Dower 1990; Airoldi et al. 1995; Airoldi 1998). Sediment accumulation, interacting with light intensity and microtopography, often acts as a negative factor on the abundance of algae (Irving & Connell 2002a,b). In addition to sediment load (Eriksson & Johansson 2003), sediment quality also determines growth and survival of seaweeds (Chapman & Fletcher 2002; Gorgula & Connell 2004). In habitats with sediment disturbances, some species may become dominant because of their relative ability to resist disturbance agents. For example, some intertidal habitats are inundated seasonally by sand and covered for several months, and only a few species of red algae are able to survive such periods (Airoldi 2003 and references therein; Balata et al. 2005). However, field observations have shown that turf-forming algae can be abundant on sedimentinfluenced rocky shores (Airoldi 1998, 2000), and the ability of vegetative reproduction is important in maintaining algal turfs (D'Antonio 1986; Airoldi & Cinelli 1997; Airoldi 2003). In some species, vegetative propagation appears to be the only form of reproduction (Airoldi et al. 1995). To date, however, few experiments have been conducted to measure the difference in turf-forming ability between spores and vegetative propagules in species that perform both sporic reproduction and vegetative progagation. Furthermore, despite the ability of algal turfs to entrap large amounts of sediment, the hypothesis that this ability could also limit grazing by herbivores has not been supported by experimental data.

Decreased algal species diversity is also associated with areas of intensive amphipod grazing activity (Slocum 1980; Brawley & Adey 1981; Hay 1981; Jara & Moreno 1984; D'Antonio 1985, 1986). Where grazing is intense, all but the toughest algae are removed (Kain & Norton 1990). Amphipods occur in both tropical and temperate environments (Greze

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1968; Moore 1975; Brenner et al. 1976; Young et al. 1976). Previous experiments have demonstrated that intensive grazing by amphipods can eliminate turf-forming algal species, such as *P. havanensis*, *Centroceras clavulatum*, and *Ceramium flaccidum* (Brawley & Adey 1981; Hay 1981).

There are many turf-forming red algal species on intertidal beaches in southern New Zealand where sand covers the substratum in a layer that varies in depth throughout the year (Adams 1994; Schiel et al. 2006). *Polysiphonia adamsiae* Womersley is the most abundant among turf-forming species, and this species normally occupies intertidal rocks protruding from sandy beaches (Adams 1994). *Polysiphonia strictissima* Hook. f. et Harvey covers intertidal rocky platforms where sediment fluctuations are not apparent (authors' pers. obs.). Both species exhibit seasonal differences in the amount of thalli present (authors' pers. obs.).

In the natural habitats of *P. adamsiae* and *P. strictissima* used in this study, the most abundant macro-invertebrate species in algal beds of both species is the amphipod *Hyale rubra* (Thompson 1879), which is frequently found during all growing seasons, whereas few other grazers occur in these habitats (authors' pers. obs.).

In this study, we used a series of field and laboratory experiments to test the effects of sediment deposition and amphipod grazing on *P. adamsiae* and *P. strictissima* in New Zealand. First, we tested the hypothesis that regeneration of the upright portion from a remnant base and from damaged branches plays an important role in establishing and maintaining algal turf. Second, we experimentally tested the hypothesis that sand cover protects algae from amphipod grazing. Third, we tested the hypothesis that prostrate axes of the algae are able to tolerate darkness caused by sand burial.

#### MATERIALS AND METHODS

#### Study sites

*Polysiphonia adamsiae* was studied on a sandy beach ("Lab Rocks") in front of the University of Canterbury field station in Kaikoura (42°25′08″S, 173°41′45″E), South Island, New Zealand. The study site was 2 m seaward and extended approximately 12 m parallel to the shoreline. In this intertidal zone, vertical rock surfaces offer habitat to a number of macroscopic algal species, and two turf-forming algae, *P. adamsiae* and *C. clavulatum* predominate in this area (Adams 1994; Schiel et al. 2006). Gametophytes of *Gigartina decipiens* were also present (Adams 1994). *Polysiphonia strictissima* was studied on "Seal Reef" ( $42^{\circ}25'28''S$ ,  $173^{\circ}42'$ 55''E), 5 km south of the field station. It is a wide, intertidal rocky platform extending  $\geq 60$  m seaward and approximately 80 m parallel to the shoreline. The bottom is a flat, siltstone platform, which supports a turf assemblage consisting mostly of *P. strictissima*, intermixed with *C. clavulatum* (Adams 1994). Algae with other morphologies, such as *Ulva pertusa* Kjellman, also occur in the turf (Adams 1994; authors' pers. obs.). The major similarities of the two sites were that dense patches of algal turf and high densities of grazing amphipods were present.

Lab Rocks is characterised by seasonal sediment loads. The intensity of sediment deposition varies greatly through time; maximum deposition generally occurs in summer when the algal turf is subjected to complete burial (authors' pers. obs.). Seal Reef is characterised by a low sediment load and sediment fluctuations are not apparent. Contrary to Seal Reef, the algal turf does not get completely buried (Schiel et al. 2006).

## Field study

Observations were made between September 2001 and July 2003 for *P. adamsiae*, and between June 2002 and June 2003 for *P. strictissima*. Four 4 m<sup>2</sup> stations for each algal species were selected at random at each study site. The minimum distance between stations was 0.5 m. At each station four thalli were selected at random and harvested every month. Thalli were kept in sea water and assessed under a microscope (40× magnification) within an hour of collection to determine where new branches originated from and whether thalli developed reproductive structures. The lengths ( $\pm 1$  mm) of the thalli were measured at the same time.

To assess sediment deposition rates for *P*. *adamsiae* at Lab Rocks, sand depth relative to the rock beneath was measured directly each month, by inserting a 40-cm long pin into the sand at four points randomly selected at each station.

#### Laboratory culture experiments

Pilot studies established that optimum growth rates for both species were attained using a photoperiod 12h:12h light:dark, light level of 40  $\mu$ mol photons m<sup>-2</sup> s<sup>-1</sup>, and temperature of 15°C (Mei & Schiel unpubl. data). Therefore, unless otherwise stated, all cultures in this study were grown at 15 ± 1°C under 40  $\mu$ mol photons m<sup>-2</sup> s<sup>-1</sup>, using white fluorescent tubes with a 12h:12h light:dark photoperiod. The growing medium (Van der Meer & Bird 1985) was renewed each week.

To compare growth rates, turf-forming ability and response to amphipod grazing between sporic and vegetative reproduction, sporelings, regenerated and erect branches from prostrate axes of both species were used. To obtain sporelings, mature thalli collected in the field in April 2002 were submerged in growing medium overnight. Released spores were settled onto glass slides (2.5 cm  $\times$  7.0 cm) and fibre plates (cement with a fibreglass matrix; see further details in Taylor & Schiel 2003) in 20-litre buckets. The glass slides were removed to conduct experiments 1 and 3, and the fibre plates remained in the buckets at temperatures of 12.4-16.5°C and light intensities of 0-80  $\mu$ mol photons m<sup>-2</sup> s<sup>-1</sup> for use in experiment 4 and for in situ culture. To obtain regenerated branches and fix them onto plates for subsequent experiments, erect branches and prostrate axes of mature thalli of both species collected in the field were cut into fragments of c. 6 mm length. Fragments were left for 2 days in buckets containing growing medium to settle onto glass slides and fibre plates. The glass slides were removed to complete experiment 2, whereas fibre plates were left in the buckets for use in experiment 4 and for in situ culture.

#### **Experiments 1 and 2**

To determine growth rates of sporelings and of regenerated branches, 18 spore-covered, 18 fragmentcovered and 18 prostrate axes-covered glass slides were selected and 3 slides each were placed into 6 flasks per cover type (each containing 800 ml medium). The slides were cultured under optimum conditions as described above. After 12 weeks, 3 sporelings and 3 regenerated branches from fragments and 3 erect branches from prostrate axes were randomly selected from each of 6 randomly selected slides and their lengths measured ( $\pm 1$  mm).

#### Experiment 3

Darkness resistance of *P. adamsiae* in response to sediment burial was examined in newly released spores, sporelings and basal portion fragments. Three groups of slide coverings were separated with 12 flasks each containing slides covered with newly released spores, slides with 14-day old sporelings, and slides with 10 mm long basal portions cut from adult *P. adamsiae* collected in the field. Each flask contained three slides and 400 ml medium, and was wrapped with two layers of black plastic (for complete darkness) and kept at  $15 \pm 1^{\circ}$ C. Every two weeks, to a maximum of 12 weeks, two flasks of

each group were randomly selected and cultured for 1 week at  $15 \pm 1^{\circ}$ C under light of 40  $\mu$ mol photons m<sup>-2</sup> s<sup>-1</sup> to assess recovery or regeneration.

## **Experiment 4**

To examine the effects of different growth forms of P. adamsiae and P. strictissima, and of sediment deposition on amphipod grazing, two sets of experiments were conducted. Each set was conducted in two plastic tanks, 1.5 m long, 1.2 m wide and 0.4 m deep, located in a covered area. Tanks were supplied with running sea water at a temperature close to the natural habitat of the algae (12.4–16.5°C) and illuminated by ambient natural light (0–80  $\mu$ mol photons m<sup>-2</sup> s<sup>-1</sup>). There were three types of algal cover on the fibre plates for each species. For *P. adamsiae*, plates were covered with sporelings, 2–7 mm high, or with fragments bearing regenerated branches 2–5 mm high, or with creeping axes derived from prostrate fragments, bearing erect branches 1-5 mm high. For P. strictissima, plates were covered with sporelings 2–5 mm high, or with fragments bearing regenerated creeping axes and erect branches, 2–10 mm high, or with algal mats. To obtain amphipods, P. adamsiae thalli were collected from Lab Rocks on 23 June 2002, immediately dried with paper towels, and submerged in sea water 20-60 s later. Resident invertebrates were collected as they dispersed from the thalli. To assess the effect of sediment deposition on amphipod grazing, sediment was taken from the natural habitat from Lab Rocks and dried to constant weight at 11.5-20.0°C. The dry sand was then spread onto the fibre plates to a depth of 3-5 mm, thus covering thalli on the plates. There were two treatments for each type of algal cover (i.e., with and without sediment), and three replicate plates for each treatment. Therefore 18 plates (3 types of algal cover  $\times$  2 treatments (sediment or no sediment addition)  $\times$  3 replicates) for each species were randomly placed within each tank. Eighty amphipod H. rubra (total length 7-10 mm) were released into one tank, whereas the second tank contained no amphipods (control). Before and after each experiment, the number of undamaged branches was determined by viewing damp plates under a dissecting microscope ( $20 \times$ magnification) and counting five random 1-cm<sup>2</sup> quadrats. Percentage survival for each type of cover per treatment was calculated by counting the sum of undamaged branches within those five quadrats after the experiment and dividing this number by the same count taken before the experiment. Two runs of the experiment were conducted (so n = 6 for each type of algal cover under each treatment). The duration of the experiments was based on the time that examined materials could survive. For *P. adamsiae*, no algae were left after 5 days except the prostrate axes from the previous year, so that the experiments were conducted over 5 days. For *P. strictissima*, fragments and regenerated branches had survived for nearly 10 days, so that this experimental set continued for 15 days.

### In situ culture

To test differences in survival between sporelings and regenerated branches for each species, plates covered with sporelings and with regenerating fragments were cultured for 8 and 4 weeks, respectively under laboratory conditions as described above. In June 2002, plates were transplanted to the study sites where the parent thalli had been collected. Plates were fenced using stainless-steel mesh (9 holes per cm<sup>2</sup>, 0.7 mm gauge wire) to prevent macro-grazer access. Fences were  $12 \times 12$  cm and approximately 5 cm high with the top edge bent outward to provide a 2 cm lip. The experiments lasted for 4 weeks, after which thalli lengths ( $\pm 1$  mm) were measured.

## Data analysis

Sediment depth and algal growth data from the field study were analysed for each species across seasons by one-way ANOVA (Stewart 1983). Algal growth data of different cover types in experiments 1 and 2 were analysed for each species by one-way ANOVA (sporelings versus regenerated branches versus erect branches from prostrate axes) (Airoldi 1998). Survival of different cover types in experiments 3 and 4 were also analysed by one-way ANOVA after 4 and 12 weeks of darkness treatment (experiment 3) and between cover types of both algae with or without sediment addition (experiment 4) (Airoldi 1998). Cochran's C tests were performed to assess homogeneity of variances before ANOVA and  $\log_{10}$ -transformations were applied when necessary (Chapman & Fletcher 2002). Unless stated otherwise, arithmetic means of replicate measurements are provided with SD as the measure of precision.

# RESULTS

# Field study

A marked seasonal pattern was evident in sediment deposition at *P. adamsiae* stations over the study period. The sand level began to build in late December and remained at high levels throughout the summer with sediment depth varying significantly between seasons (log<sub>10</sub>-transformed,  $F_{22,345} = 2737$ , P < 0.01, Fig. 1). Algal habitats on rocks became buried until March to May (autumn), when storms removed the sand.

Individual erect axes of *P. adamsiae* grew to lengths of 60 mm or more and seasonal differences in thallus length were significant ( $F_{22,345} = 2962, P <$ 0.01, Fig. 1). Erect axes were absent by November, when most algae were dying back. During summer (January, February, March), basal portions (prostrate axes with broken branches <10 mm in length) from the previous growth season were covered by sediments. New erect axes protruded through the sediments when the sediment levels reduced in autumn. There were two types of thalli at the sites. One type was light brown, with erect branches developed from basal portions that had survived the preceding summer. Another type was crimson and new crimson branches grew from light-coloured prostrate axes and appeared to have originated from spores. The crimson patches only occurred at one of the four experimental stations. Only 1.25% (2 of 16 samples) of *P. adamsiae* thalli in the population were estimated to have developed from spores.

The growth of P. strictissima was seasonal and differences in thallus length were significant between seasons ( $F_{12,195} = 554$ , P < 0.01, Fig. 2). Adult plants formed distinct patches among C. clavulatum from June to November (winter and spring). Mature plants bearing tetrasporangia or carposporangia were abundant from July to October. From this time, branches weaved together, forming several mats for each plant. In January (summer), prostrate axes, mats and fragment clusters were only evident if sand was removed as they were buried or partly buried. Turf, composed of visible young plants and sand grains, appeared in March. Examination under the microscope of randomly selected samples from the study site, showed all new small thalli (100%  $\pm 0\%$ , n = 35) developed from prostrate axes that regenerated from dark pigmented fragments, which, in turn, were portions of mats, prostrate axes and fragment clusters that had survived the preceding summer. No thalli that resembled algae developed from sporelings were found.

#### Laboratory culture experiments

After 12 weeks culture, *P. adamsiae* reached a length of 1–2 cm, and some branches from the lower portions of the main axes produced rhizoids which attached to the substratum. Subsequently, these branches grew horizontally and functioned

Fig. 1 Average length (+SD, n = 16) of *Polysiphonia adam*siae (open bars) and average depth (+SD, n = 16) of sediments (closed bars) at Kaikoura, New Zealand from September 2001 to July 2003.



as prostrate axes. Similarly, *P. strictissima* did not produce any prostrate axes from main axes until the latter reached 1 cm height. Sporelings of *P. adamsiae* and *P. strictissima* obtained average growth rates of  $0.25 \text{ mm/day} (\pm 0.077 \text{ mm/day}, n = 18)$  and  $0.18 \text{ mm/day} (\pm 0.020 \text{ mm/day}, n = 18)$ , respectively. Cultured material exhibited the basic morphology of field algae in *P. adamsiae*, but varied in some features in *P. strictissima*. In *P. strictissima*, wild algae bore numerous branches whereas cultured algae seldom branched. Also, in cultured algae the distinction between creeping axes and erect branches was usually not as clear as in material collected in the wild.

New sprouts arose from broken sections of base portions and fragments for both species, similar to regeneration observed in the field, whereas other new sprouts generated from groups of pericentral cells in contiguous segments of prostrate axes and fragments. Most fragments of both species attached to the fibre plates by numerous rhizoids that developed from uninjured pericentral cells of the fragments without the formation of any separating walls. They were unbranched, but developed into flattened discs when



Fig. 2 Average length (+SD, n = 16) of *Polysiphonia* strictissima at Kaikoura, New Zealand from June 2002 to June 2003.





**Fig. 3** Comparison of growth rates (mean +SD, n = 18) of sporelings, regenerated branches (RB) and erect branches from prostrate axes (EP) of *Polysiphonia adamsiae* (closed bars) and *P. strictissima* (open bars) cultured under a photoperiod 12h:12h light:dark at 40  $\mu$ mol photons m<sup>-2</sup> s<sup>-1</sup>and at 15 ± 1°C.

**Fig. 4** Survival (%) (mean  $\pm$ SD, n = 6) of different cover types of *Polysiphonia adamsiae* after darkness treatment for different lengths of time at 15  $\pm$  1°C.

**Table 1** Results of one-way ANOVA of growth rates between sporelings, regenerated branches from fragments (RB) and erect branches from prostrate axes (EP) of *Polysiphonia adamsiae* and *P. strictissima* under laboratory culture with a photoperiod 12h:12h light:dark under 40  $\mu$ mol photons m<sup>-2</sup> s<sup>-1</sup> and at 15 ± 1°C.

Source of variation	MS	F <sub>1,34</sub>	Р	
Polvsiphonia adamsiae				
Sporelings and RB	32.32	176.70	< 0.01	
Sporelings and EP	2.85	13.72	< 0.01	
RB and EP	0.32	0.84	>0.05	
Polysiphonia strictissima				
Sporelings and RB	63.68	259.72	< 0.01	
Sporelings and EP	26.32	363.53	< 0.01	
RB and EP	8.12	25.61	< 0.01	

they attached themselves to the substratum. The apical cells for both species, which had stopped dividing in matured plants, resumed dividing to form new branches after the apical branches were cut off and cultured. The regenerated sprouts of *P. adamsiae* grew into normal branches that grew upright and did not produce rhizoids. In contrast, regenerated sprouts of *P. strictissima* grew into branched or unbranched prostrate proliferations, which eventually produced erect axes and rhizoids. The erect growth did not start until the prostrate proliferations reached 2–5 cm length. Average growth rates of regenerated branches from fragments and erect branches from prostrate

axes were 2.14 mm/day ( $\pm$  0.60 mm/day, n = 18) and 1.95 mm/day ( $\pm$  0.64 mm/day, n = 18) for *P. adamsiae*, 8.56 times and 7.80 times, respectively, the growth rates of sporelings. Average growth rates of regenerated branches from fragments and erect branches from prostrate axes of *P. strictissima* were 2.84 mm/day ( $\pm$  0.70 mm/day, n = 18) and 1.89 mm/day ( $\pm$  0.38 mm/day, n = 18), 15.78 times and 10.50 times, respectively, the growth rates of sporelings cultured under the same conditions (Fig. 3). One-way ANOVA showed significant differences in growth rates between cover types of each species (Table 1).



**Fig. 5** Survival (%) (mean  $\pm$  SD, n = 6) of: **A**, *Polysiphonia adamsiae* under amphipod grazing with and without sediment cover over 5 days; **B**, *Polysiphonia strictissima* under amphipod grazing with and without sediment cover over 15 days. (RB, regenerated branches from fragments; EP, erect branches from prostrate axes; PP, prostrate axes of preceding growth season.)

Table 2	Results of one-way ANOV	'A of survival (p	ercentage) of	Polysiphonia	adamsiae and	d P. strictissim	a under
sediments	and amphipod grazing. (R	B, regenerated bi	ranches from t	fragments; PP,	prostrate axe	s of preceding	growth
season.)							

Source of variation	MS	F <sub>1,10</sub>	Р
Polysiphonia adamsiae			
Sporelings with and without sediments	4845.40	4.97	< 0.05
RB with and without sediments	28227.54	6.97	< 0.05
PP with and without sediments	158794.58	1.29	>0.05
Polysiphonia strictissima			
Sporelings with and without sediments	25389.00	9.27	< 0.05
RB with and without sediments	206667.06	111.08	< 0.01
Mat with and without sediments	102.23	1.56	> 0.05

Following 4 weeks of darkness and further culture under light for 1 week, 5% (± 1%, n = 6) of *P. adamsiae* spores germinated, 21% (± 9%, n = 6) of sporelings resumed growth and 26% (± 8%, n = 6) of prostrate axes fragments regenerated within 1 week. Differences in survival between spores, sporelings and prostrate axis fragments were significant ( $F_{2,15}$ = 5.32, P < 0.05). No spores or sporelings survived darkness treatment for 6 or more weeks, but 10% (± 4%, n = 6) of prostrate axis fragments produced new erect axis within 1 week of further culture under light (Fig. 4).

In the grazing experiments without sediment, amphipods grazed all the sporelings, fragments and newly regenerated branches of *P. adamsiae* within 5 days, and only prostrate axes of the previous year were left. Differences in survival between growth forms were significant ( $F_{2,15}$  = 48.25, P < 0.01, Fig. 5A, Table 2). Erect branches did not grow more than 2 mm high before being grazed by amphipods. In *P. strictissima*, amphipods consumed sporelings preferentially, which were completely grazed within 5 days. Fragments and regenerated axes were grazed completely within 10 days. The least preferred diet of the amphipods appeared to be algal mat material, which remained ungrazed after 15 days (Fig. 5B, Table 2). Sediment addition resulted in a significant effect on survival of sporelings and regenerated branches of both species under amphipod grazing pressure, whereas sediments appeared to have no

significant effect on survival of prostrate axes of the preceding growth season of *P. adamsiae* or algal mats of *P. strictissima* (Table 2). In the tank without amphipods (control), average survival percentage of every growth form was >95% and there were no significant differences between growth forms at the end of the experiment.

#### In situ culture

All plates placed in the field were covered with sediment to a depth of approximately 3 mm. After 4 weeks in the field, regenerated branches from fragments of *P. adamsiae* grew up to 3–5 cm high, with lower parts of the plant covered by sediment. No sporelings of *P. adamsiae* were found on the plates, nor did any sporelings or regenerating fragments of *P. strictissima* survive.

## DISCUSSION

Results of experiments 1 and 2 support the hypothesis that basal axes, instead of sporelings, might play an important role in establishing and maintaining algal turf. The horizontal distribution of prostrate axes through creeping growth and the fast growth of upright branches from such axes may be related to persistence of algal turfs.

Results of experiments 2, 3 and 4 indicate that the prostrate basal axes of both species and the mats of *P. strictissima* had some advantages over sporelings. For example, branches generated from prostrate axes grew 7 to 10 times faster than sporelings, enabling them to recover faster following amphipod grazing. Secondly, prostrate axes of the preceding growth season were relatively resistant to amphipod grazing, thus increasing their survival rate. Thirdly, prostrate axes of the previous year occupied the suitable locations for recruitment of the species and might preclude the establishment of competitive algae, including sporelings from the same species. Fourthly, prostrate forms in darkness survived longer than sporelings.

Survival strategies of red algae in response to macro-grazers have been relatively well documented. Littler & Kauker (1984) emphasised that *Corallina officinalis* adapted to sea urchin grazing by heterotrichy. Hay (1981) found that turf forms of algae lost less biomass to fish and urchins than did individuals. However, any advantage of heterotrichy or turf growth when living within areas predominantly affected by macro-grazers such as amphipods has not been previously shown. Amphipods consume a variety of seaweeds (Cruz-Rivera & Hay 2001) and have a strong effect on their preferred host (Cronin & Hay 1996), as well as on the macroalgal community structure in general (Duffy & Hay 2000). Amphipods in the algal beds, unlike other crustaceans or small gastropods which are eliminated by sand burial (D'Antonio 1986), remain active after sand deposition, possibly using the sediment as a refuge from fish grazing (Young & Young 1978; Stoner 1979). Brawley & Adey (1981) reported that P. havanensis survived heavy grazing of amphipods by virtue of its extensive basal system, which was rarely completely eliminated by grazers. However, their study did not consider how newly formed branches, which are unlikely to have chemical defence or physical differences from young sporelings, were protected from grazers living on them all the time.

The results of the field study and the *in situ* culture indicated that sporelings contributed little to the size of the algal populations, and they had little chance to survive in the field. Only 1.25% of *P. adamsiae* thalli and 0% of *P. strictissima* thalli appeared to originate from sporelings in the natural habitat. A possible explanation for this unexpected outcome is that turf construction of sporelings seemed to be deterred by the slow growth rate of sporelings and the delay in horizontal extension as shown in experiment 1. Therefore, the sporelings would be unlikely to benefit from any protection afforded by sediments entrapped in the algal turf during growth seasons.

Dixon (1965) was among the first to provide insight into the ecological significance of vegetative propagation in algae. Although other studies have highlighted the adaptive importance of vegetative reproduction (e.g., Lobban & Harrison 1994), there is relatively little knowledge about the extent to which algae rely on vegetative reproduction as opposed to sporic reproduction. At our study sites, the recruitment of the two turf-forming red algae was apparently dominated by vegetative propagation as indicated in the field study. The field study also demonstrated that reproduction by means of perennial prostrate axes of P. adamsiae and P. strictissima and algal mats of P. strictissima predominated over sporic reproduction. Only 1.25% of *P. adamsiae* thalli originated from spores, although both tetraspores and carpospores of the two species are able to germinate and grow in a wide range of temperatures, light intensities and photoperiods under laboratory culture (Mei & Schiel unpubl. data).

Sediment deposition decreases light available to algal species. The ability of *P. adamsiae* to adapt to

sand burial seems to be facilitated by the method of reproduction and the resistance of basal portions to darkness. The ability of this alga to withstand sand coverage observed in our study is consistent with findings in other studies (Dahl 1971; Daly & Mathieson 1977; Stewart 1983; D'Antonio 1986). The tolerance of sediment burial includes regeneration of upright potions from remnant bases and physiological adaptations to withstand darkness (Airoldi 2003).

The influence of physical and biological processes such as sediment deposition and amphipod grazing on algal recruitment patterns may have serious consequences for higher levels of organisation, that is, for benthic marine assemblages in this area. Changes to water quality in this region may lead to an increase in sedimentation of nearshore waters (Schiel et al. 2006). If sediment deposition does not leave time for colonisation of underlying substratum or is continual, reproduction of habitat forming algae such as Hormosira banksii through zygotes and germlings may become untenable (Schiel et al. 2006). Therefore sediment increase may potentially affect species shifts as a consequence of differential sediment susceptibility between turf-forming species such as Polysiphonia sp. and non-turf-forming species such as H. banksii.

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