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# Limited effects of grazer exclusion on the epiphytes of *Posidonia sinuosa* in South Australia

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## Abstract

The role of grazing in regulating the abundance and biomass of epiphytes of the seagrass *Posidonia sinuosa* Cambridge et Kuo was investigated at an oligotrophic site in lower Spencer Gulf, South Australia. Prosobranch gastropods >7 mm in size were excluded from 0.25 m<sup>2</sup> plots of seagrass for 3 months with four steel mesh cages, compared with four partial cages used to control for cage artefacts, and also four uncaged control plots. Abundances of epiphytic algae, invertebrates and epiphytic mass (DW, AFDW and calcium carbonate) were recorded regularly. The indirect effect of grazer exclusion on seagrass leaf mortality (necrosis) was also measured. Grazing effects on the epiphytic assemblage were detected despite some cage artefacts. Filamentous algal abundance and epiphytic biomass (AFDW) increased in response to grazer exclusion. Caging per se reduced crustose coralline algal cover and calcium carbonate during the experimental period but, after 3 months, no artefact or treatment effect was discernible. Abundances of invertebrate taxa were little affected by grazer exclusion although caging per se reduced the density of spirorbid polychaetes. Grazer exclusion did not affect seagrass necrosis. In comparison with similar studies and given the duration of exclusion, the sum of treatment effects on epiphytes and seagrass was small. Rather, the role of epiphyte grazing in this nutrient-poor area appears to be limited to the maintenance of an epiphytic assemblage that is free of filamentous algae and dominated by crustose corallines.

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## 1. Introduction

Epiphytes are ubiquitous in macrophyte-dominated ecosystems and can contribute substantially to their primary production (Cattaneo and Kalff, 1980; Morgan and Kitting, 1984;

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Silberstein et al., 1986; Moncreiff et al., 1992). Conversely, they can outcompete host macrophytes such as seagrass for light and solute resources (Sand-Jensen, 1977; Sand-Jensen et al., 1985; Silberstein et al., 1986). The accumulation of epiphytic biomass is partially controlled by nutrient supply, and overgrowth in response to eutrophication has been implicated in declines of submerged aquatic vegetation (Orth and Moore, 1983; Twilley et al., 1985). Nonetheless, epiphytes often dominate the diets of herbivorous epifauna (Fry, 1984; Kitting et al., 1984; Morgan and Kitting, 1984; Klumpp et al., 1989). Regulation of epiphytic biomass and productivity by grazers can therefore mitigate the negative impacts of epiphytes on their hosts (Orth and van Montfrans, 1984; Brönmark, 1985; Hootsmans and Vermaat, 1985; Howard and Short, 1986; Williams and Ruckelshaus, 1993).

Despite their acknowledged importance to aquatic macrophytes, grazer–epiphyte interactions remain poorly understood (Jernakoff et al., 1996). The impacts of grazing are known to vary among grazer taxa (Jernakoff and Nielsen, 1997) and with regard to different components of the epiphytic assemblage (Mazzella and Russo, 1989; Neckles et al., 1994; Jernakoff and Nielsen, 1997; Jones et al., 2000). The outcome of interactions can also shift spatially or seasonally with temperature, light and nutrient levels (Neckles et al., 1993; Williams and Ruckelshaus, 1993). Experimental results obtained in lab conditions may therefore poorly reflect those in the field (Williams and Ruckelshaus, 1993; Jernakoff and Nielsen, 1997). However, few investigations of grazer–epiphyte interactions have been conducted in situ (e.g. Robertson and Mann, 1982; Borum, 1987; Philippart, 1995; Gacia et al., 1999; Fong et al., 2000).

Temperate Australia contains some of the world's largest seagrass meadows, yet research on grazer–epiphyte interactions has been limited to the Western coastline (e.g. Nielsen and Lethbridge, 1989; Jernakoff and Nielsen, 1997). This is the first study in the fully marine seagrass meadows of South Australia's Spencer Gulf (33–35°S, 136–138°E). The objective was to determine whether grazing regulated the abundance or biomass of epiphytes of *Posidonia sinuosa* Cambridge et Kuo. To do this, I excluded large gastropods from seagrass in situ and measured the response of the epiphytic assemblage over a 3 month period.

## 2. Methods

### 2.1. Experimental site and species

The study was conducted in a 1 m deep (MHLW) meadow of *P. sinuosa* Cambridge et Kuo at Louth Bay, an open embayment of Spencer Gulf (34°43'S, 135°51'E). Located near the Gulf's entrance, the Bay experiences oceanic temperature, salinity and wave energy (Shepherd and Robertson, 1989) and ambient nutrient levels in the region are notably low (Smith, 1991). *P. sinuosa* shoots have 1–2 strap-like leaves of 7–9 mm width and up to 70 cm length, that are distinctly curved in cross-section (Cambridge and Kuo, 1979; Trautman and Borowitzka, 1999). Shoot densities range from 1500 to 2000 m<sup>-2</sup> in the Louth Bay meadow and a group of comparatively large herbivorous gastropods (up to 20 mm shell width) dominate the seagrass epifauna (unpublished data). This group comprises six prosobranchs: *Austrocochlea odontis* (Wood 1828), *Thalotia conica* (Gray 1827), *Clanculus philippi* (Koch 1843), *Phasianotrochus irisodontes* (Quoy et Gaimard 1834) (all F. Trochidae), *Phasianella*

*australis* (Gmelin 1791) and *Astraliium aureum* (Jonas 1844) (both F. Turbinidae). Their combined density usually exceeds  $100 \text{ m}^{-2}$  of sediment area (this study).

## 2.2. Experimental setup

Wire mesh cages (four vertical sides plus roof) were used to exclude the gastropod group from plots of seagrass, and partial cages served as procedural controls. First, 12 plots of  $0.5 \text{ m} \times 0.5 \text{ m}$  were marked out haphazardly over an area of  $15 \text{ m} \times 20 \text{ m}$ , allowing  $>3 \text{ m}$  separation between plots (Fig. 1). Herbivorous gastropods were removed from four of the plots and full cages (length, width and height  $0.5 \text{ m}$ ) of galvanised steel mesh (size  $6.5 \text{ mm}$ ) were anchored over these (hereafter “F plots”). For further exclusion, a  $30 \text{ cm}$  wide apron of insect-screen mesh (size  $1 \text{ mm}$ ) was attached at the base of each side, any seagrass beneath the apron cut at sediment level, and the apron laid out and secured with stakes (see Fig. 1). Pilot trials demonstrated the efficacy of this design in excluding the gastropod group from the plots for several months. Partial cages (anchored over a further four “P

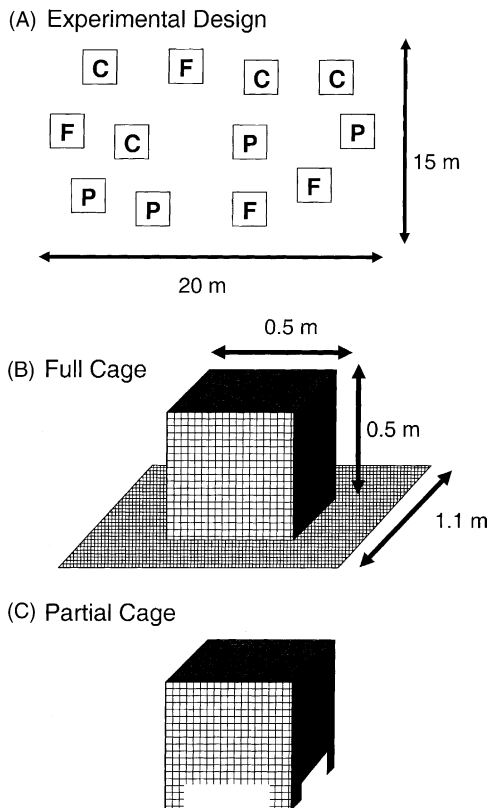


Fig. 1. Experimental design. (A) Diagram of plot arrangement (not to scale). F: full cage (gastropod exclusion), P: partial cage (procedural control), C: control. (B) Diagram of full cage with insect-screen mesh apron extending from base. (C) Diagram of partial cage showing sections removed from base. See text for details.

plots”) had no apron, and 250 mm × 70 mm sections of the cage were removed from the base of each side. This design allowed gastropod access but still provided alteration to light and hydrodynamic regimes. The remaining four plots were left as open controls (“C”). Treatments were assigned to plots in a completely randomised design.

### 2.3. Sampling

Initial reference samples ( $n = 4$ ) were taken outside of the experimental plots immediately before exclusion began in late September 2001. Sampling then occurred in three subsequent months of the austral spring after which the experiment was terminated on 29 December. At each sampling time, 10 randomly chosen shoots were removed at the rhizome from each plot and frozen for later analysis of epiphytes and seagrass (see Section 2.4). The F plots were searched for herbivorous gastropods and those found were recorded and removed. Gastropod density was only qualitatively assessed in P and C plots, to minimise the confounding disturbance of searching for, removing and replacing individuals. However, background gastropod densities were recorded in 25 quadrats (area = 180 cm<sup>2</sup>) outside plots. To measure the cages’ impact on the light regime, PAR was recorded with a LI-COR spherical sensor attached to a Datasonde 4a (Hydrolab Corporation, Austin, TX, USA) within C, F and P plots. Background water temperature was recorded hourly for the duration of the experiment with a HOBO logger (Onset Computer Corporation, Bourne, MA, USA).

### 2.4. Lab analysis

For each shoot, leaf length and width were measured, and each leaf was fully divided into 10 cm sections (from the apical end; final section  $\leq 10$  cm) for measurement of epiphytic abundance. Note that *epiphytes* are defined here as those forms visible to the naked eye, as distinct from *periphyton*, the assemblage in the mucus-like layer adherent to the leaf (following van Montfrans et al., 1984; Jernakoff et al., 1996; Jernakoff and Nielsen, 1997). The noted algal diversity in southern Australia (Womersley, 1990) coupled with taxonomic uncertainty suggested that species identification of epiphytic algae and invertebrates would be problematic. Instead, I recorded the abundance of algal morphotypes based on the functional groups of Steneck and Dethier (1994), and for invertebrates I recorded the abundance of coarse taxa. Where the abundance of filamentous algae on a section exceeded what was practicably countable ( $\approx 100$  basal attachments), a conservative count of 100 was assigned (3% of sections). The percent of necrotic (coloured brown to black) seagrass leaf area was also recorded. All data were pooled per plot. Variation within leaves, within shoots, and among shoots will be treated in a separate publication.

The epiphytic material scraped from the seagrass leaves was pooled per plot, dried to constant weight at 80 °C to determine dry weight (DW) then combusted at 550 °C for 4 h to determine ash-free dry weight (AFDW). A further combustion at 950 °C for 2 h allowed for the stoichiometric determination of calcium carbonate mass, as the carbonate combusts to calcium oxide and carbon dioxide at about 825 °C (Paine, 1964; P. Lavery, personal communication). This method assumes that the contribution of other carbonates is not significant, which is credible here given the domination of the epiphytic assemblage by crustose coralline algae. Standards were included to account for combustion inefficiencies

(Kendrick and Lavery, 2001). Seagrass leaf area (shoot length  $\times$  width  $\times$  2) was used to standardise the epiphytic abundance and mass data.

### 2.5. Statistics

Graphical interpretation of the data was supported by repeated-measures ANOVA of October to December samples. Treatment (C, P, F) was the between-subjects term; time (October, November, December) and the treatment-time interaction were within-subjects terms (Table 1). Assumptions of sphericity for the within-subjects factors were accommodated by conservative (Greenhouse–Geisser) and liberal (Huynh–Feldt) adjustments to original  $P$ -values (von Ende, 1993). The statistical significance (at  $\alpha = 0.05$ ) of adjusted and original values was equivalent for all variables, hence only the Greenhouse–Geisser values are reported. The a priori hypotheses: C = P plots (no caging artefact) and C = P < F plots (treatment effect) were tested orthogonally (at  $\alpha = 0.05$ ) with linear contrasts of final plot means following ANOVA (factor: treatment). Assumptions of normality and homoscedasticity were verified visually by inspecting residuals.

## 3. Results

Experimental cages remained intact except for one P plot cage, which was damaged by wave action and replaced at the time of the November sample. The cages successfully excluded most (>85%) of the gastropods from the plot area (Fig. 2A). All species of the gastropod group were present at approximate background densities in the P and C plots (personal observation). Abundances of other herbivores (and specifically small crustacea) had not obviously increased in caged plots in the absence of gastropods (personal observation).

In the repeated-measures ANOVA, treatment, time as well as their interaction were always significant (Table 1). However, for most variables and sampling times considered, mean values from P plots were similar to either F or C plots, demonstrating presence or absence of treatment artefacts, respectively. PAR measured at the start of the experiment was reduced by 20–30% in caged plots. Fouling of the cage mesh further reduced light intensity to 50% by the end of November in some plots. Thereafter cages were scrubbed weekly. Seagrass necrosis, which was similar in F and P plots, always exceeded the mean values in C plots (linear contrast of final means: C  $\neq$  P,  $P < 0.01$ ; Fig. 2B). However, this difference was less than the temporal increase related to seasonal changes in irradiation, emersion time and water temperature. The daily maximum water temperature increased from 13.7 to 24.4 °C during the experiment. Caging also depressed crustose coralline algal cover (and calcium carbonate mass) during the experimental period. However, the effects were considerably reduced after cage fouling was regularly removed, and final plot means were not significantly different for either cover (ANOVA: among treatments  $F_{2,9} = 3.548$ ,  $P = 0.073$ ) or mass ( $F_{2,9} = 4.060$ ,  $P = 0.055$ ).

Crustose coralline algae and spirorbid polychaetes (F. Serpulidae) were the dominant algal morphotype and invertebrate taxon, respectively, recorded on seagrass leaf sections. Crustose coralline cover ranged from 0 to 95% of a section and spirorbid density ranged from 0 to 19 individuals  $\text{cm}^{-2}$  of leaf. The clearest effect of grazer exclusion was on the

Table 1  
Summary ANOVA table of variables used in repeated-measures analysis

	DF	Filamentous algae		Crustose coralline algae		Spirorbids		DW		AFDW		Calcium Carbonate	
		MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>
Treatment	2	3.950	<0.001	328.9	0.002	5.553	<0.001	0.551	0.019	0.105	0.004	0.265	0.015
Error	9	0.199		23.88		0.259		0.086		0.010		0.038	
Time	2	5.785	<0.001	115.9	0.024	13.13	<0.001	0.542	0.002	0.176	<0.001	0.060	0.027
Interaction	4	0.744	0.001	72.44	0.045	1.985	0.001	0.159	0.018	0.016	0.044	0.102	0.001
Error	18	0.079		19.31		0.144		0.033		0.004		0.012	

Greenhouse–Geisser adjusted probability values are reported for time and interaction.

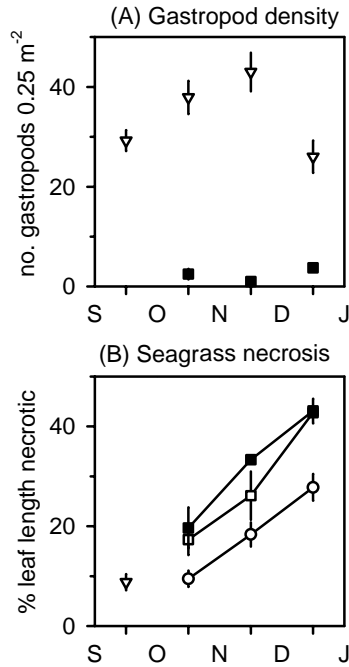


Fig. 2. (A) Herbivorous gastropod densities in background of study site ( $n = 25$  quadrats; symbol  $\nabla$ ) and found in F plots ( $n = 4$  plots; symbol  $\blacksquare$ ), both expressed as number per plot area ( $0.25 \text{ m}^2$ ). (B) Seagrass necrosis (percent of leaf length per plot). Symbols: ( $\nabla$ ) background; ( $\circ$ ) C plots; ( $\square$ ) P plots; ( $\blacksquare$ ) F plots. All values are mean  $\pm$  S.E.

abundance of filamentous algae (Fig. 3A), which occurred on 16% of leaf sections (mostly in the later months). Abundance was consistently and significantly greater in F plots than in P and C plots (final mean  $\approx 2.5 \times$  greater;  $C = P < F$ ,  $P < 0.01$ ). Filamentous algal abundance increased in F plots every month during the experiment whereas it only increased substantially in P and C plots during the last month. Phaeophytes such as *Sphacelaria*, *Feldmannia* and *Hincksia* were dominant members of the filamentous morphotype. The treatment effect on the crustose corallines was not interpretable beyond the cage artefact and cover varied little over time in F and C plots (Fig. 3B). Grazer exclusion did not consistently affect the abundance of the four most common invertebrate taxa, namely spirorbids, foraminiferans, bryozoans and hydroids. However, caging per se reduced the density of spirorbids (Fig. 3C). Abundances in F and P plots were always lower than those in C plots, particularly at the end of December (final mean of P plots  $\approx 1/4$  of C plots;  $C \neq P$ ,  $P < 0.001$ ).

Epiphytic DW had increased at the end of the experiment for all treatments but differences among treatments were inconsistent over time (Fig. 3D). At the end of the experiment all three treatment means were comparable in value. Clearer treatment contrasts were discernible for AFDW (Fig. 3E). Epiphytic AFDW in F plots consistently exceeded that in both P and C plots. By the end of December the difference amounted to  $\sim 0.23 \text{ mg cm}^{-2}$  of seagrass leaf,  $\sim 50\%$  higher than control values ( $C = P < F$ ,  $P < 0.01$ ). There was no

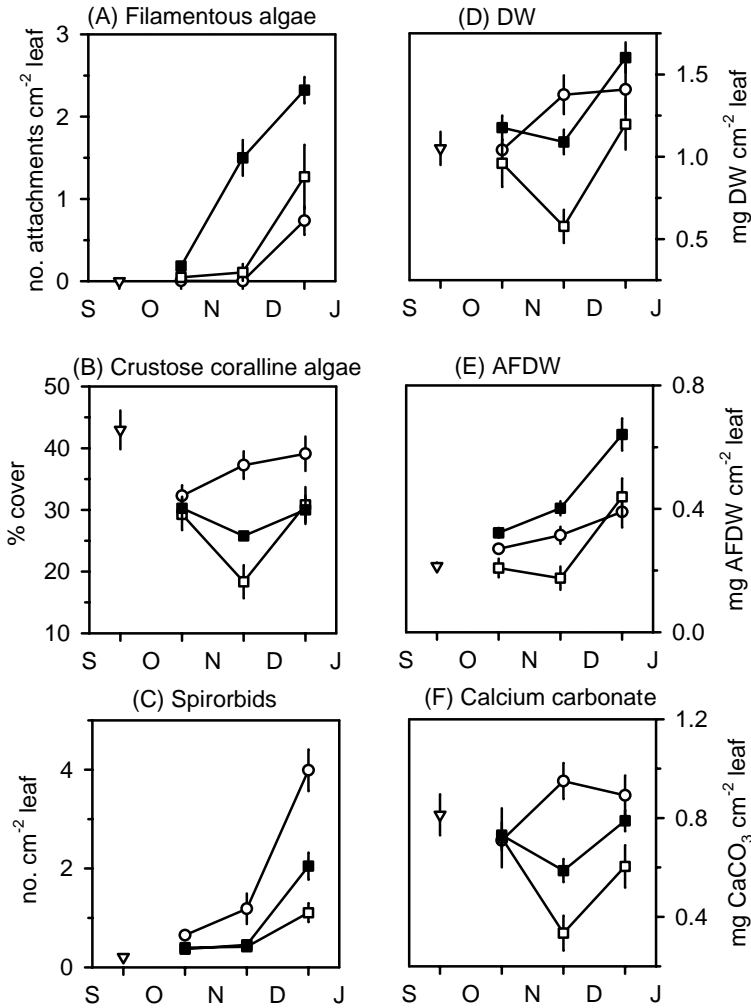


Fig. 3. Abundance of (A) filamentous algae (number of basal attachments cm<sup>-2</sup> leaf), (B) crustose coralline algae (percent cover), (C) spirorbids (number cm<sup>-2</sup> leaf). Mass of epiphytes (mg cm<sup>-2</sup> leaf) as (D) DW, (E) AFDW, (F) calcium carbonate. All values are mean ± S.E. per plot. Symbols and notation as for Fig. 2B.

consistent effect of grazer exclusion on the mass of calcium carbonate and (as noted above) all three final treatment means were alike (Fig. 3F). Grazer exclusion did not affect seagrass necrosis beyond the cage artefact discussed above (Fig. 2B).

#### 4. Discussion

The objective of this experiment was to determine if caging gastropod grazers out of plots of seagrass at Louth Bay would lead to changes in epiphytic abundance and, consequently,

epiphytic biomass. Cage artefacts have tended to overshadow treatment effects in some experiments (e.g. Jernakoff and Nielsen, 1997). However artefacts were relatively small in this study and well accounted for by procedural controls. The decreased spirorbid density in caged plots was noteworthy given the observed discrimination of this taxon for shaded settlement sites in an adjacent gulf (Saunders and Connell, 2001). Nonetheless, the cage mesh probably reduced water flow and the supply of spirorbid larvae to the seagrass plots (Virmstein, 1978; Dayton and Oliver, 1980). Beyond any cage artefact, the abundance of filamentous algae, and consequently epiphytic biomass, increased substantially in response to grazer exclusion. However, total epiphytic mass was relatively unaffected by that response. The most parsimonious explanation for such a result is that filamentous epiphytic growth was limited by nutrient supply in the oligotrophic waters of Louth Bay. The balance of the competition between seagrass and epiphytes has been predicted to shift in favour of the macrophyte in nutrient-poor situations (Borum, 1985; Duarte, 1995; Alcoverro et al., 1997; Fong et al., 1997).

Exclusion of the gastropod epifauna increased the density of filamentous algae amongst the epiphytic assemblage on *P. sinuosa*. Periphyton and detrital material were also more conspicuous on ungrazed leaves (personal observation), supporting previous findings (e.g. Robertson and Mann, 1982). Conversely, the cover of crustose corallines as a group was unaffected and remained relatively high. Prosobranch gastropods often consume simpler algal morphologies in preference to crustose coralline algae (Jacobs et al., 1983; Howard and Short, 1986; Klumpp et al., 1992; but see Nielsen and Lethbridge, 1989), being limited in part by the action of their rhipidoglossan radula (Steneck and Watling, 1982). Epiphytic assemblages from seagrass meadows neighbouring Louth Bay but naturally lacking the same gastropods are morphologically more diverse—the abundance of fleshy algal morphotypes is higher but coralline cover is lower (unpublished data). An analogous situation may exist on coral reefs where grazing maintains dominance by competitively inferior, slower growing corallines (Steneck, 1983, 1988).

Epiphytic biomass (AFDW) increased in fully caged plots in the experiment, but the magnitude of effect was considerably less than that found in comparable studies (Robertson and Mann, 1982; Jernakoff and Nielsen, 1997; Fong et al., 2000; but see Hootsmans and Vermaat, 1985 for *Littorina littorea* grazing). Given the duration of exclusion and the slow leaf turnover of *P. sinuosa* (Jernakoff et al., 1996), this contrast is even more marked. Exclusion of *Thalotia conica* (a grazer also in this study) from *P. sinuosa* in Western Australia resulted in double the effect size for AFDW than was found at Louth Bay, in only one third of the time period (Jernakoff and Nielsen, 1997). Ambient gastropod density was also higher in the present study than in theirs, with over 90% of individuals at Louth Bay consistently recorded as being active on the seagrass leaves (unpublished data). Presumably, water-column nutrient concentrations were higher in Jernakoff and Nielsen's (1997) lagoonal location (they provided no data) than in Louth Bay. Conversely, they were surprised that their measured impacts of grazing were not more pronounced, based on laboratory grazing rates. Jernakoff and Nielsen (1997) only measured presence-absence of algal species in their experiment, and so comparisons of compositional responses to exclusion with this study are difficult. Nonetheless, they concluded that gastropod grazers did not significantly affect epiphytic species richness, and crustose corallines were only present under amphipod-grazed treatments.

The lack of an indirect impact on seagrass tissue mortality from grazer exclusion was unsurprising given the relatively small increases in algal abundance and biomass. Those amounts fell far short of the values associated with impaired seagrass performance in eutrophic meadows (Silberstein et al., 1986; Neverauskas, 1987). Although my experiment spanned only one season, direct or indirect impacts of exclusion are unlikely to be greater at other times for several reasons. Seasonal fluctuations in gastropod density and total epiphytic biomass are relatively small and *P. sinuosa* leaf turnover is no lower at other times of the year (unpublished data). Grazing is therefore suggested to be of secondary importance to the low ambient nutrient concentration as a regulator of total epiphytic biomass on *P. sinuosa* at Louth Bay. Nutrient inputs to Louth Bay from land and sea have been comparatively low to date but may increase over time in concert with anthropogenic activity. Nonetheless, under the current nutrient regime I conclude that epiphyte grazing determines the broad composition and organic matter content of epiphytic assemblages on *P. sinuosa* in Louth Bay, but has a limited impact on total epiphytic mass.

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## References

- Alcoverro, T., Duarte, C.M., Romero, J., 1997. The influence of herbivores on *Posidonia oceanica* epiphytes. *Aquat. Bot.* 56, 93–104.
- Borum, J., 1985. Development of epiphytic communities on eelgrass (*Zostera marina*) along a nutrient gradient in a Danish estuary. *Mar. Biol.* 87, 211–218.
- Borum, J., 1987. Dynamics of epiphyton on eelgrass (*Zostera marina* L.) leaves: relative roles of algal growth, herbivory, and substratum turnover. *Limnol. Oceanogr.* 32, 986–992.
- Brönmark, C., 1985. Interactions between macrophytes, epiphytes and herbivores: an experimental approach. *Oikos* 45, 26–30.
- Cambridge, M.L., Kuo, J., 1979. Two new species of seagrasses from Australia, *Posidonia sinuosa* and *P. angustifolia* (Posidoniaceae). *Aquat. Bot.* 6, 307–328.
- Cattaneo, A., Kalf, J., 1980. The relative contribution of aquatic macrophytes and their epiphytes to the production of macrophyte beds. *Limnol. Oceanogr.* 25, 280–289.
- Dayton, P.K., Oliver, J.S., 1980. An evaluation of experimental analyses of population and community patterns in benthic marine environments. In: Tenore, K.R., Coull, B.C. (Eds.), *Marine Benthic Dynamics*. University of South Carolina Press, Columbia, pp. 93–120.
- Duarte, C.M., 1995. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* 41, 87–112.
- Fong, C.W., Lee, S.Y., Wu, R.S.S., 2000. The effects of epiphytic algae and their grazers on the intertidal seagrass *Zostera japonica*. *Aquat. Bot.* 67, 251–261.
- Fong, P., Jacobson, M.E., Mescher, M.C., Lirman, D., Harwell, M.C., 1997. Investigating the management potential of a seagrass model through sensitivity analysis and experiments. *Ecol. Appl.* 7, 300–315.
- Fry, B., 1984.  $^{13}\text{C}/^{12}\text{C}$  ratios and the trophic importance of algae in Florida *Syringodium filiforme* seagrass meadows. *Mar. Biol.* 79, 11–19.
- Gacia, E., Littler, M.M., Littler, D.S., 1999. An experimental test of the capacity of food web interactions (fish-epiphytes-seagrasses) to offset the negative consequences of eutrophication on seagrass communities. *Estuar. Coastal Shelf Sci.* 48, 757–766.

- Hootsmans, M.J.M., Vermaat, J.E., 1985. The effect of periphyton-grazing by three epifaunal species on the growth of *Zostera marina* L. under experimental conditions. *Aquat. Bot.* 22, 275–285.
- Howard, R.K., Short, F.T., 1986. Seagrass growth and survivorship under the influence of epiphyte grazers. *Aquat. Bot.* 24, 287–302.
- Jacobs, R.P.W.M., Hermelink, P.M., Van Geel, G., 1983. Epiphytic algae on eelgrass at Roscoff, France. *Aquat. Bot.* 15, 157–173.
- Jernakoff, P., Brearley, A., Nielsen, J., 1996. Factors affecting grazer–epiphyte interactions in temperate seagrass meadows. *Oceanogr. Mar. Biol. Annu. Rev.* 34, 109–162.
- Jernakoff, P., Nielsen, J., 1997. The relative importance of amphipod and gastropod grazers in *Posidonia sinuosa* meadows. *Aquat. Bot.* 56, 183–202.
- Jones, J.I., Moss, B., Eaton, J.W., Young, J.O., 2000. Do submerged aquatic plants influence periphyton community composition for the benefit of invertebrate mutualists. *Freshwat. Biol.* 43, 591–604.
- Kendrick, G.A., Lavery, P.S., 2001. Assessing biomass, assemblage structure and production of algal epiphytes on seagrasses. In: Short, F.T., Coles, R.G. (Eds.), *Global Seagrass Research Methods*. Elsevier, Amsterdam, pp. 199–222.
- Kitting, C.L., Fry, B., Morgan, M.D., 1984. Detection of inconspicuous epiphytic algae supporting food webs in seagrass meadows. *Oecologia* 62, 145–149.
- Klumpp, D.W., Howard, R.K., Pollard, D.A., 1989. Trophodynamics and nutritional ecology of seagrass communities. In: Larkum, A.W.D., McComb, A.J., Shepherd, S.A. (Eds.), *Biology of Seagrasses: A Treatise On the Biology of Seagrasses with Special Reference to the Australian Region*. Elsevier, Amsterdam, pp. 394–457.
- Klumpp, D.W., Salita-Espinosa, J.T., Fortes, M.D., 1992. The role of epiphytic periphyton and macroinvertebrate grazers in the trophic flux of a tropical seagrass community. *Aquat. Bot.* 43, 327–349.
- Mazzella, L., Russo, G.F., 1989. Grazing effect of two *Gibbula* species (Mollusca, Archaeogastropoda) on the epiphytic community of *Posidonia oceanica* leaves. *Aquat. Bot.* 35, 357–373.
- Moncreiff, C.A., Sullivan, M.J., Daehnick, A.E., 1992. Primary production dynamics in seagrass beds of Mississippi Sound: the contributions of seagrass, epiphytic algae, sand microflora, and phytoplankton. *Mar. Ecol. Prog. Ser.* 87, 161–171.
- Morgan, M.D., Kitting, C.L., 1984. Productivity and utilization of the seagrass *Halodule wrightii* and its attached epiphytes. *Limnol. Oceanogr.* 29, 1066–1076.
- Neckles, H.A., Wetzel, R.L., Orth, R.J., 1993. Relative effects of nutrient enrichment and grazing on epiphyte-macrophyte (*Zostera marina* L.) dynamics. *Oecologia* 93, 285–295.
- Neckles, H.A., Koepfler, E.T., Haas, L.W., Wetzel, R.L., Orth, R.J., 1994. Dynamics of epiphytic photoautotrophs and heterotrophs in *Zostera marina* (eelgrass) microcosms: responses to nutrient enrichment and grazing. *Estuaries* 17, 597–605.
- Neverauskas, V.P., 1987. Monitoring seagrass beds around a sewage sludge outfall in South Australia. *Mar. Poll. Bull.* 18, 158–164.
- Nielsen, J., Lethbridge, R., 1989. Feeding and the epiphyte food resources of gastropods living on leaves of the seagrass *Amphibolis griffithii* in south-western Australia. *J. Malac. Soc. Aust.* 10, 47–58.
- Orth, R.J., Moore, K.A., 1983. Chesapeake Bay: an unprecedented decline in submerged aquatic vegetation. *Science* 222, 51–53.
- Orth, R.J., van Montfrans, J., 1984. Epiphyte-seagrass relationships with an emphasis on the role of micrograzing: a review. *Aquat. Bot.* 18, 43–69.
- Paine, R.T., 1964. Ash and calorie determinations of sponge and opisthobranch tissues. *Ecology* 45, 384–387.
- Philippart, C.J.M., 1995. Effects of periphyton grazing by *Hydrobia ulvae* on the growth of *Zostera noltii* on a tidal flat in the Dutch Wadden Sea. *Mar. Biol.* 122, 431–437.
- Robertson, A.I., Mann, K.H., 1982. Population dynamics and life history adaptations of *Littorina neglecta* Bean in an eelgrass meadow (*Zostera marina* L.) in Nova Scotia. *J. Exp. Mar. Biol. Ecol.* 63, 151–172.
- Sand-Jensen, K., 1977. Effect of epiphytes on eelgrass photosynthesis. *Aquat. Bot.* 3, 55–63.
- Sand-Jensen, K., Revsbach, N.P., Jørgensen, B.B., 1985. Microprofiles of oxygen in epiphyte communities on submerged macrophytes. *Mar. Biol.* 89, 55–62.
- Saunders, R.J., Connell, S.D., 2001. Interactive effects of shade and surface orientation on the recruitment of spirorbid polychaetes. *Austral. Ecol.* 26, 109–115.
- Shepherd, S.A., Robertson, A.I., 1989. Regional Studies—Seagrasses of South Australia, Western Victoria and Bass Strait. In: Larkum, A.W.D., McComb, A.J., Shepherd, S.A. (Eds.), *Biology of Seagrasses: A Treatise On the Biology of Seagrasses with Special Reference to the Australian Region*. Elsevier, Amsterdam, pp. 221–229.

- Silberstein, K., Chiffings, A.W., McComb, A.J., 1986. The loss of seagrass in Cockburn Sound, Western Australia. III. The effect of epiphytes on productivity of *Posidonia australis* Hook. f. *Aquat. Bot.* 24, 355–371.
- Smith, S.V., 1991. Stoichiometry of C:N:P fluxes in shallow-water marine ecosystems. In: Heal, O.W., Grime, J.P. (Eds.), *Comparative Analysis of Ecosystems: Past Lessons and Future Directions*. Springer, New York, pp. 259–286.
- Steneck, R.S., 1983. Escalating herbivory and resulting adaptive trends in calcareous algal crusts. *Paleobiology* 9, 44–61.
- Steneck, R.S., 1988. Herbivory on coral reefs: a synthesis. In: *Proceedings of the Sixth International Coral Reef Symposium, Australia 1*, pp 37–49.
- Steneck, R.S., Dethier, M.W., 1994. A functional group approach to the structure of algal-dominated communities. *Oikos* 69, 476–498.
- Steneck, R.S., Watling, L., 1982. Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. *Mar. Biol.* 68, 299–319.
- Trautman, D.A., Borowitzka, M.A., 1999. Distribution of the epiphytic organisms on *Posidonia australis* and *P. sinuosa*, two seagrasses with differing leaf morphology. *Mar. Ecol. Prog. Ser.* 179, 215–229.
- Twilley, R.R., Kemp, W.M., Staver, K.W., Stevenson, J.C., Boynton, W.R., 1985. Nutrient enrichment of estuarine submersed vascular plant communities. I. Algal growth and effects on production of plants and associated communities. *Mar. Ecol. Prog. Ser.* 47, 145–152.
- van Montfrans, J., Wetzel, R.L., Orth, R.J., 1984. Epiphyte-grazer relationships in seagrass meadows: consequences for seagrass growth and production. *Estuaries* 7, 289–309.
- Virnstein, R.W., 1978. Predator caging experiments in soft sediments: caution advised. In: Wiley, M.L. (Ed.), *Estuarine Interactions*. Academic Press, New York, pp 261–273.
- von Ende, C.N., 1993. Repeated-measures analysis: growth and other time-dependent measures. In: Scheiner, S.M., Gurevitch, J. (Eds.), *Design and Analysis of Ecological Experiments*. Chapman and Hall, New York, pp. 113–137.
- Williams, S.L., Ruckelshaus, M.H., 1993. Effects of nitrogen availability and herbivory on eelgrass (*Zostera marina*) and epiphytes. *Ecology* 74, 904–918.
- Womersley, H.B.S., 1990. Biogeography of Australasian marine macroalgae. In: Clayton, M.N., King, R.J. (Eds.), *Marine Botany: An Australian Perspective*, Longman, Melbourne, pp. 292–307.