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Nutrients increase epiphyte loads: broad scale observations and an  
experimental assessment

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Running head: Epiphytes of kelp and nutrients

## Abstract

There is a global trend towards elevated nutrients in coastal waters, especially on human-dominated coasts. We assessed local to regional scale relationships between the abundance of epiphytic algae on kelp (*Ecklonia radiata*) and nutrient concentrations across much of the temperate coast of Australia, thus, assessing the spatial scales over which nutrients may affect benthic assemblages. We tested the hypotheses that (1) percentage cover of epiphytic algae would be greater in areas with higher water nutrient concentrations, and (2) that an experimental enhancement of nutrient concentrations on an oligotrophic coast, to match more eutrophic coasts, would cause an increase in percentage cover of epiphytic algae to match those in more nutrient rich waters. Percentage cover of epiphytes was most extensive around the coast of Sydney, the study location with the greatest concentration of coastal chlorophyll *a* (a proxy for water nutrient concentration). Elevation of nitrate concentrations at a South Australian location caused an increase in percentage cover of epiphytes that was comparable to percentage covers observed around Sydney's coastline. This result was achieved despite our inability to match nutrient concentrations observed around Sydney (< 5 % of Sydney concentrations), suggesting that increases to nutrient concentrations may have disproportionately larger effects in oligotrophic waters.

## Introduction

Enhancement of nutrients in coastal waters is likely to cause large changes to benthic assemblages, such as a shift from slow growing macroalgae to fast growing turf-forming algae (Pedersen and Borum 1996, Worm et al. 1999, Gorgula and Connell 5 2004). Nutrient inputs can be point-source (e.g. sewage outfall: Littler and Murray 1975) and non-point source (see review by Carpenter et al. 1998), modifying habitat in aquatic systems over large scales (i.e. 100s to 1000s kms) (Vitousek et al. 1997, Carpenter et al. 1998, Eriksson et al. 2002). Nutrient inputs across large scales can adversely affect entire ecosystems (Duarte 1995, Eriksson et al. 2002), hence, 10 understanding the relationship between nutrient concentrations and ecosystem effects from local through regional scales may not only identify areas of interest, but also place these patterns within their regional context.

Enhanced nutrient concentrations have strong positive effects on assemblages of fine 15 filamentous algae that comprise ‘turfs’ (Gorgula and Connell 2004), which appear to be favoured on human-dominated coasts because their life-history and physiology are better suited to nutrient overloading (Hein et al. 1995, Pedersen and Borum 1996).

Assemblages of turf-forming algae can respond to seemingly minor physical differences in substratum (Irving and Connell 2002). We chose to compare percentage cover of turf- 20 forming algae on the most comparable substratum we could find, the laminae of *Ecklonia radiata* sourced from stands of similar age and density. The canopy-forming alga *Ecklonia radiata* is common and extensively distributed across temperate Australia (Fowler-Walker and Connell 2002, Goodsell et al. 2004). These stands form predictable associations with the benthos (Connell 2003, Irving et al. 2004) and represent a 25 common habitat on which to base regional comparisons of benthic algae.

Perennial epiphytes on seagrass and macroalgae are often more abundant on the older portions of the host (Whittick 1983, Borowitzka and Lethbridge 1989). Kelp grows upwards from the meristem (located near the bottom of the stipe); thus, laterals at the top of each individual are the oldest (Kain 1963, Bolton and Anderson 1994). From this algal growth pattern, the upper part of individual kelp would be most likely to have greatest cover of epiphytes. Vertical gradients of perennial epiphyte abundance on kelp stipes exist (Whittick 1983), but it is not known whether such a gradient exists on the laterals of kelp. In contrast, a gradient may not exist with ephemeral epiphytes, such as turf-forming algae, because there will not be accumulation of these epiphytes across years, as occurs with perennial epiphytes (Whittick 1983). Furthermore, it is unknown whether gradients of epiphyte abundance are altered by the concentration of nutrients in the water.

We assessed local to regional scale relationships between the abundance of epiphytic algae on kelp (*Ecklonia radiata*) and chlorophyll *a* (proxy for nutrient concentrations) across much of the temperate coast of Australia, to assess the locations and spatial scales over which nutrients may affect benthic assemblages. While *E. radiata* and their epiphytic turfs appear ideally suited for detecting spatial scales and localities likely to be affected by elevated nutrients, we acknowledge that any perceived relationship constitutes a correlation and may be explained by a host of alternate models. Hence, we took the additional step and directly tested the hypothesis that if we elevated nutrient concentrations in an oligotrophic system to match the most eutrophic system, the percentage cover of turfs in the nutrient poor system would increase to match those observed in the nutrient rich system.

## Materials and methods

### Regional epiphyte data

Percentage cover of turf-forming algae growing as epiphytes on *Ecklonia radiata* was  
5 quantified across temperate Australia in the Austral summer of 2001/2002. Sampling  
was constrained to the latitudinal limits of 33°37'S – 37°06'S so as not to be strongly  
influenced by latitudinal gradients. Sampling was done at hierarchal nested spatial  
scales of regions, locations, and sites; regions were separated by 1000s of kilometres,  
locations (within regions) separated by 100s of kms, and sites (within locations)  
10 separated by 1 – 10 km (Fig. 1). Within each site, replicate *E. radiata* separated by 1 –  
10 m ( $n = 5$ ) were collected from approximately 3 – 10 m depth. Percentage cover of  
epiphytic turf-forming algae was quantified on the laterals of *E. radiata* at three heights  
from the holdfast (bottom, middle and top). Laterals on the lower half of the algae  
represent the “bottom”. The remainder of the algae was then divided in half again and  
15 defined as “middle” and “top” relative to the algal holdfast. Percentage cover of  
epiphytic turf-forming algae was estimated for the point of attachment to *E. radiata*  
within a 10 mm<sup>2</sup> quadrat haphazardly placed within each lateral height ( $n = 5$ ).

### Coastal chlorophyll concentrations

20 A positive correlation can exist between water nutrient concentration and chlorophyll *a*  
concentrations in the water column (Evgenidou and Valiela 2002, Nedwell et al. 2002,  
Nielsen et al. 2002, Muslim and Jones 2003). We obtained a remotely sensed SeaWiFS  
satellite chlorophyll *a* image, spanning temperate Australia, from the Australian CSIRO  
Remote Sensing Facility. All satellite passes over the region during January 2002 were  
25 formed into a single monthly composite image. The month of January was selected,

because it represented conditions half way through the regional sampling. The image spanned all regions and was analysed at a resolution of 1 km pixels. Study sites could not be accurately plotted on the image, thus, chlorophyll *a* concentrations were quantified for 10 pixels spanning across all sample sites at each location, and taken as a mean chlorophyll *a* concentration ( $\mu\text{g L}^{-1}$ ) for each location.

#### Experimental manipulation of nutrients

The effect of elevated nutrients on turf-forming algae growing on *E. radiata* was experimentally tested at West Island, South Australia (35°36'S, 138°35'E), by comparing *E. radiata* from experimental reefs with different nutrient treatments (ambient *v.* elevated;  $n = 5$  / treatment). Nutrient concentrations were manipulated on experimental reefs from December 2002 to March 2003 (Austral summer). Percentage cover of turf-forming algae on *E. radiata* was quantified at the peak of summer (beginning of March 2003), to avoid confounding effects of algal senescence with the onset of cooler water temperatures and shorter days (Worm et al. 2002). *E. radiata* was collected and percentage cover of turf-forming algae quantified using the same method as for the regional scale study.

Experimental reefs were made from metal frames on a concrete base (60 × 60 cm) set on sand and separated from the natural reef. Boulders were collected from the natural reef and placed on each experimental reef in November 2002, before the experiment commenced. Boulders were selected so that *E. radiata* were on experimental reefs in natural densities (9 – 11  $\text{m}^{-2}$ ).

Treatments of elevated nutrients were manipulated by the addition of 12 g of Osmocote Plus<sup>®</sup> slow release fertilizer per nutrient reef (6 month release: 15,5,10 N-P-K).

Nutrients were supplied in four nylon mesh bags (1mm mesh size) filled with

Osmocote<sup>®</sup> pellets and attached to stakes on the reef corners at the beginning of the

5 experiment. Bags containing nutrient pellets were replaced every two months to ensure a continuous supply of nutrients; this approach has been tested and suggested to be the most appropriate method of elevating nutrients in subtidal experiments (Worm et al. 2000) and has been successfully used in a previous experiment at the study site (Russell and Connell 2005). Control reefs were identical, without the addition of nutrients.

10 Experimental reefs were separated by at least 5 m to ensure treatments were independent.

Water samples were collected at the end of February 2003 to ascertain whether nutrients were supplied at elevated concentrations on the experimental reefs. To test whether the

15 nutrient treatments on neighbouring reefs were independent, water samples were taken from nutrient elevated reefs, their closest ambient (control) reef, as well as distant to all reefs (ambient water column nutrients) ( $n = 4$ ). Samples were collected in 120ml vials 10 cm above the experimental boulders. Ambient water column samples were taken at the same height above the natural substratum. On returning to the surface, all samples

20 were filtered through 0.45  $\mu\text{m}$  filters and frozen. Samples were sent to the Australian Water Quality Centre (South Australia) for analysis. It was assumed that if nutrient concentrations on control reefs did not differ from ambient water column concentrations, then nutrients were not flowing from elevated reefs to control reefs.

## Analyses

The mensurative hypothesis was tested using a four-factor ANOVA; factors: region, location (nested within region), site (nested within region and location), and height on *E. radiata* (orthogonal). Region and height were treated as fixed factors, and site and  
5 location as random. Arc-sine transformation was used to reduce heterogeneity in the data, but variance remained heterogeneous, so significance was judged at the more conservative  $\alpha = 0.01$  (Underwood 1997).

The experimental hypothesis was tested in two steps. First, a two-factor ANOVA tested  
10 for differences in percentage cover of epiphytes between nutrient concentrations (ambient *v.* elevated) among the three heights on the algae (bottom *v.* middle *v.* top). Both factors were fixed and orthogonal. Again, arc-sine transformation was used to reduce heterogeneity in the data, but variance remained heterogeneous, so significance was judged at  $\alpha = 0.01$ . Second, a two-factor ANOVA tested the extent to which  
15 percentage cover of epiphytes in treatments of elevated nutrients matched the covers observed around Sydney. Because replication differed between the mensurative and manipulative experimental designs, we compared the mean percentage cover of epiphytes at each of the four Sydney sites (i.e. sites were used as replicate samples) with the experimental responses (replicate samples were randomly reduced from 5 to 4 by  
20 deleting one replicate). Arc-sine transformation was successfully used to reduce heterogeneity in the data, and significance judged at  $\alpha = 0.05$ .

## Results

The turf-forming algae quantified had similar morphology, as identification to species  
25 requires examination of specimens under microscopes (which was impossible in field

conditions). All turf-forming algae quantified were filamentous brown algae that grew in mats, generally to a vertical height of  $\leq 20$  mm. In South Australia, these algae were primarily composed of *Feldmannia lebelli* and *F. globifera*, which were morphologically similar to the turf-forming algae in WA and EA.

5

In southern Australia (SA) and western Australia (WA) the percentage cover of epiphytic turf-forming algae did not differ with lateral height on *E. radiata*, but turf-forming algae in eastern Australia (EA) showed different patterns, according to proximity to Sydney (Fig. 2, Table 1; significant height  $\times$  location interaction; SNK

10 tests). In EA, there were no differences among heights at the most distant location from Sydney (Eden), whereas at the two closer locations (Batemans Bay and Jervis Bay) the percentage cover was greater at the top and middle than bottom. At the Sydney location, the percentage cover of epiphytic algae was greatest on the top laterals and showed a clear gradient to the bottom laterals (top  $>$  middle  $>$  bottom). Percentage cover of

15 epiphytic algae was more extensive in Sydney than all other locations in EA, SA, and WA (Fig. 2, Table 1) and no differences were observed among locations in SA and WA.

In locations with higher water nutrient concentrations (see next paragraph) there was greater percentage cover of turf-forming algae on the top laterals of *E. radiata*. There was also higher variability in cover of epiphytes at locations with increasing water

20 nutrient concentrations, causing significant site and location terms (Table 1).

There was a positive correlation between chlorophyll *a* concentration in the water column and mean percentage cover of epiphytic algae at locations ( $r = 0.96$ ,  $P < 0.001$ ;

Fig. 3). This correlation was partly driven by the Sydney location, and even though the

25 relationship was non significant ( $r = 0.58$ ,  $P = 0.06$ ) when Sydney was removed from

the analysis, there was still a positive trend. When SA was removed from the analysis, there was a strong correlation between chlorophyll *a* concentration and percentage cover of epiphytic algae ( $r = 0.89$ ,  $P = 0.007$ ). In EA, there was a north to south decrease in chlorophyll concentration. Chlorophyll *a* concentration was higher at  
5 Sydney than Jervis Bay, Batemans Bay, and Eden, and was > 3 times higher than all locations in SA and WA.

Experimental conditions created nitrate concentrations that were approximately 89 % higher on nutrient elevated (mean  $0.121 \pm 0.04 \mu\text{mol L}^{-1}$ ) than ambient (mean  $0.064 \pm$   
10  $0.01 \mu\text{mol L}^{-1}$ ; ANOVA:  $F_{2,5} = 16.78$ ,  $P < 0.03$ ) reefs. Student Newman Keuls (SNK) comparison of means demonstrated that nitrate levels differed between elevated and ambient water samples, but did not differ between ambient nutrient reefs and water column samples, indicating that nutrients from elevated reefs were not detectable on  
15 control reefs, so the distance between experimental reefs was great enough that elevated and control reefs were independent of each other. Phosphate levels did not differ between ambient ( $0.19 \pm 0.005 \mu\text{mol L}^{-1}$ ) and nutrient elevated reefs ( $0.19 \pm 0.01$   
 $\mu\text{mol L}^{-1}$ ; ANOVA:  $F_{2,5} = 3.1$ ,  $P > 0.15$ ). The failure to detect enriched phosphorus is likely due to filtering of water samples, which removes most of the ionic phosphorus. The failure to detect elevated phosphate concentrations is not considered a problem  
20 because nitrogen, not phosphorus, is generally considered the nutrient limiting algal growth in marine waters (Hecky and Kilham 1988, Carpenter et al. 1998, Hodgkiss and Lu 2004).

Percentage cover of epiphytic algae was greater on *E. radiata* exposed to elevated  
25 nutrient concentrations than on those exposed to ambient concentrations of water

nutrients (Fig. 4, Table 2a). SNK comparison of means showed that percentage covers of epiphytic algae on *E. radiata* exposed to elevated nutrients did not differ from those observed on *E. radiata* around Sydney (Fig. 4; Table 2b). Height on *E. radiata* also had a significant effect on the percentage cover of epiphytic algae, but there was no  
5 significant interaction with nutrient treatment (Fig. 4; Table 2b).

## Discussion

Local through broad scale observations are fundamental to identifying localities and scales of patterns and the processes underlying them. Little information is currently  
10 available on the scales at which abundance of epiphytes vary. A key finding of this study was that the cover of epiphytic algae on *E. radiata* did not differ between southern Australia and western Australia. Importantly, the percentage cover of epiphytic algae in eastern Australia tended to increase from south to north, with covers at the Sydney location being greater than all other locations across temperate Australia, indicating that  
15 epiphyte covers can vary over scales of 100s kms. Abundance of epiphytes on seagrass and some macroalgae has been shown to vary on the scale of kms, which is the scale of variation of physical environmental gradients (Lavery and Vanderklift 2002, Rindi and Guiry 2004). In this study, there was variation in cover among sites (kms) but the greatest differences were seen among locations (100s kms). Importantly, it is over this  
20 larger scale that we detected large differences in the concentration of ambient chlorophyll *a*.

The pattern of chlorophyll concentrations showed a positive relationship with the percentage cover of epiphytic algae. Chlorophyll concentrations were greatest at the  
25 Sydney location, which also showed the highest cover of epiphytic algae. Although

chlorophyll *a* concentrations may not directly relate to the concentration of nutrients available to turf-forming algae (because of nutrient use by phytoplankton), a separate broad-scale study in 2004 showed ambient water nutrient concentrations above the substrate were higher in Sydney than in locations of comparable latitude in South  
5 Australia and Western Australia (mean  $\pm$  SE; Sydney  $3.8 \pm 0.89$ ; SA  $0.26 \pm 0.036$ ; WA  $0.59 \pm 0.091 \mu\text{mol L}^{-1}$ ; Connell, S.D. unpubl. data). As turf-forming algae can benefit from increased nutrient levels (Rönnerberg et al. 1992, Hein et al. 1995, Worm and Sommer 2000), we suggest that the greater nutrient concentrations observed around Sydney cause the greater covers of epiphytic algae observed in that location.

10

At most locations in this study there was no pattern in the vertical distribution of turf-forming algae on *E. radiata* laterals. However, in EA locations with the highest chlorophyll *a* concentrations, an increase in cover of turf-forming algae with increasing height on *E. radiata* was found. It is unknown why higher nutrient levels should cause  
15 this vertical pattern. It is unlikely that there is an increase in the cover of epiphytes with age of the host, because the turf-forming algae are ephemeral and not likely to increase biomass across years. Epiphytes have been shown to preferentially settle at specific sites on the host, such as wounded parts (Pearson and Evans 1990) and the apices of seagrass, possibly because the apices receive the most sunlight (Borowitzka and  
20 Lethbridge 1989). It is possible that with increased nutrients epiphytes show an increase in photosynthetic productivity and either settle or survive in greater abundance on the upper laterals of *E. radiata*, causing a change in the vertical distribution. The pattern in vertical distribution of epiphytes also seems to vary, depending on the host. Perennial epiphytes can show greater abundances on the older parts of kelp stipes (Whittick 1983)  
25 and seagrasses (Borowitzka and Lethbridge 1989). However, no pattern of zonation was

observed in a study of the epiphytes of furoid algae (*Cystoseira* spp.: Beleggratis et al. 1999).

Our experimental enhancement of nutrient concentrations under field conditions  
5 resulted in an increase in the percentage cover of epiphytic algae, which was  
comparable to the covers observed at Sydney. Elevated water nitrate concentrations in  
this experiment were approximately 80 % greater than ambient water concentrations.  
Ambient nitrate concentrations were higher in Sydney than locations of comparable  
latitude in South Australia and Western Australia (Connell, S.D. unpubl. data, see  
10 previous paragraph). Mean nitrate concentration at a Sydney site in January 2000  
(records were unavailable for 2002) was  $3.36 \pm 1.6 \mu\text{mol L}^{-1}$  (CSIRO Port Hacking  
record station), indicating that the elevated concentrations used in this experiment were  
< 4 % of the ambient concentrations recorded at Sydney in January 2000 and 2004.  
Even with this relatively low concentration of nutrients, we were able to achieve covers  
15 of epiphytic algae similar to those recorded at the Sydney location. This  
disproportionate response to increased nutrients may be a function of nutrient limitation  
(Neckles et al. 1993, Hein et al. 1995, Karez et al. 2004) and level of response may be  
greater when in nutrient limited waters. As the growth response of epiphytes is not  
proportional to the increase in nutrients (Duarte 1995), response of epiphytes in  
20 oligotrophic waters (such as South Australia: Gorgula and Connell 2004; Russell and  
Connell 2005) is likely to be greater than in waters with higher nutrient concentrations  
(such as Sydney and other human dominated coasts). Therefore, nutrient inputs on  
oligotrophic coasts may have larger effects than on coasts with high ambient nutrient  
concentrations (such as regions of seasonal nutrient upwelling), or coasts already  
25 impacted by human nutrient inputs (e.g. Western Baltic: Worm et al. 2000).

Although anthropogenic nutrient inputs surrounding Sydney are large (e.g.  $9.2 \times 10^8 \text{ L d}^{-1}$  of sewage discharged at Port Hacking; Dela-Cruz et al. 2003), there is some seasonal upwelling in summer that cannot be dismissed as a source of nutrients (Gibbs 2000, Oke and Middleton 2001, Roughan and Middleton 2002). This wind driven upwelling is localised in extent (Pritchard et al. 2003), and is not associated with major upwelling caused by the East Australia Current, which splits off from the coast at about  $32^\circ \text{ S}$  (compared to Sydney at  $\sim 34^\circ \text{ S}$ ; Gibbs 2000). During upwelling events, sewage and estuarine nutrients make up only  $\sim 10\%$  of the total water nutrients (Pritchard et al. 2003). However, sources of nutrients are difficult to separate, possibly because of variability in hydrological conditions and difficulty in determining chemical signatures (e.g. Dela-Cruz et al. 2003). Thus, phytoplankton blooms and chlorophyll *a* concentrations in the Sydney region can be caused by anthropogenic (i.e. sewage outfall, Dela-Cruz et al. 2003), estuarine (Dela-Cruz et al. 2003), and upwelling nutrients (Dela-Cruz et al. 2002). It seems likely that because upwelling events can be short lived (McClellan-Padman and Padman 1991), anthropogenic and estuarine sources of nutrients are important, especially during the non-upwelling season (Pritchard et al. 2003), but more study is needed.

Eutrophication has been proposed as a cause of greater epiphyte abundance and biomass on developed coasts (Philippart 1995, Wear et al. 1999) and near point-source nutrient enriched areas, such as fish farms (Rönnerberg et al. 1992). Increased epiphytic cover may adversely affect health of host algae and seagrasses through reduced photosynthesis (e.g. Sand-Jensen 1977) and incidental consumption of host tissue by increased grazing on epiphytes (Williams and Ruckelshaus 1993, Karez et al. 2000).

This reduction in the health of the host algae and plant has been shown for kelp (Scheibling et al. 1999), furoid macroalgae (D'Antonio 1985, Karez et al. 2000, Worm and Sommer 2000), and seagrass (Sand-Jensen 1977, Sand-Jensen et al. 1985).

5 Much of our knowledge about the ecology of *E. radiata* is from eastern Australia (see Irving et al. 2004 for a review of published studies), especially from sites close to and around Sydney. However, there is increasing evidence that generalisations based on information from this area may not be directly applicable to other regions of Australia (e.g. Fowler-Walker and Connell 2002, Irving et al. 2004). We have shown that  
10 generalisations based on the percentage cover of turf-forming algae from Sydney are not indicative of patterns across temperate Australia. Furthermore, experiments on the effects of elevated nutrients, were they to be done in Sydney, may lead to different results than we found in the oligotrophic waters of South Australia, because nutrient concentrations are already elevated around Sydney. A limited response of epiphytic  
15 algae may be seen if ambient levels of nutrients are high relative to experimental increases (Karez et al. 2004). Indeed, predictions based on the effects of experimentally elevated nutrients may be limited to areas with similar nutrient regimes. Thus, generalisations about nutrient effects in oligotrophic waters can not be obtained from studies in already nutrient rich areas (natural or human impacted).

20

In summary, the cover of turf-forming algae growing on *E. radiata* was greater in Sydney than the rest of temperate Australia. Epiphytic algal abundance was correlated to chlorophyll *a* concentration, and thus, higher water nutrient concentration. We were able to show that elevated nutrients positively affect the abundance of turf-forming  
25 algae by experimentally elevating nitrate concentrations. These experimental results

also suggest that increased nutrient concentrations have large effects on oligotrophic coasts, which requires further investigation. Understanding the different effects of elevated nutrients is important when considering management of coasts close to large sources of nutrients, such as agricultural and urbanised areas.

5

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15

**Table 1** Results of four-factor ANOVA testing differences in percentage cover of turf-forming algae growing as epiphytes at different heights on *Ecklonia radiata* laterals among regions, locations and sites within Australia. *df* degrees of freedom, *MS* mean square, *F*-ratio, *P* probability.

5

Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Region	2	6064.98	3.79	NS
Location (Region)	9	1600.56	7.32	***
Site (Region × Location)	36	218.72	5.08	***
Height	2	718.73	5.41	NS
Region × Height	4	325.02	2.44	NS
Height × Location (Region)	18	132.94	2.64	**
Height × Site (Region × Location)	72	50.35	1.17	NS
Residual	576	43.03		

NS not significant ( $P > 0.01$ ), \*\*  $P < 0.005$ , \*\*\*  $P < 0.0001$ . Arc-sine transformation was used to reduce heterogeneity in the data, but variance remained heterogeneous, so significance was judged at  $\alpha = 0.01$  (Underwood 1997).

10

**Table 2** Results of a two-way ANOVAs testing the effects of experimental elevation of nutrients on the percentage cover of turf-forming algae growing as epiphytes at different heights on *Ecklonia radiata* laterals, (a) all experimental reefs compared (ambient v. elevated; n = 5 / treatment) and, (b) comparison of experimental reefs with Sydney (ambient v. elevated v. Sydney; n = 4 / treatment). Differences in replication ((a) v. (b)) reflect differences in mensurative and manipulative experimental designs (see Methods).

(a) Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Nutrient	1	6087.69	28.75	***
Height	2	196.59	0.93	NS
N × H	2	74.45	0.35	NS
Residual	24	211.76		

NS not significant ( $P > 0.01$ ), \*\*\*  $P < 0.0001$ . Arc-sine transformation was used to

10 reduce heterogeneity in the data, but variance remained heterogeneous, so significance was judged at  $\alpha = 0.01$  (Underwood 1997).

(b) Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Nutrient	2	1671.98	11.16	**
Height	2	542.02	3.62	*
N × H	4	76.10	0.51	NS
Residual	27	149.76		

NS not significant ( $P > 0.05$ ), \*  $P < 0.05$ , \*\*  $P < 0.001$ . Arc-sine transformation was used to reduce heterogeneity in the data (Underwood 1997).

## Figure Legends

**Fig. 1** Map showing the locations sampled within regions across southern Australia.

Regions: WA = western Australia, SA = southern Australia, EA = eastern Australia.

5 Locations: CL = Cape Leeuwin, A = Albany, BrB = Bremer Bay, Es = Esperance,  
El = Elliston, PL = Port Lincoln, WC = West Cape, CJ = Cape Jervis, Ed = Eden,  
BaB = Batemans Bay, JB = Jervis Bay, and S = Sydney.

**Fig. 2** The percentage cover of turf-forming algae growing as epiphytes on (a) top, (b)

10 middle and (c) bottom laterals of *E. radiata* across regions and locations (mean  $\pm$  SE).

For region and location abbreviations see Fig. 1. \* = 0 % cover.

**Fig. 3** The relationship between concentration of chlorophyll *a* (mean  $\pm$  SE) and

percentage cover of turf-forming algae (mean  $\pm$  SE) growing as epiphytes on *E. radiata*

15 at all sampling locations across temperate Australia.

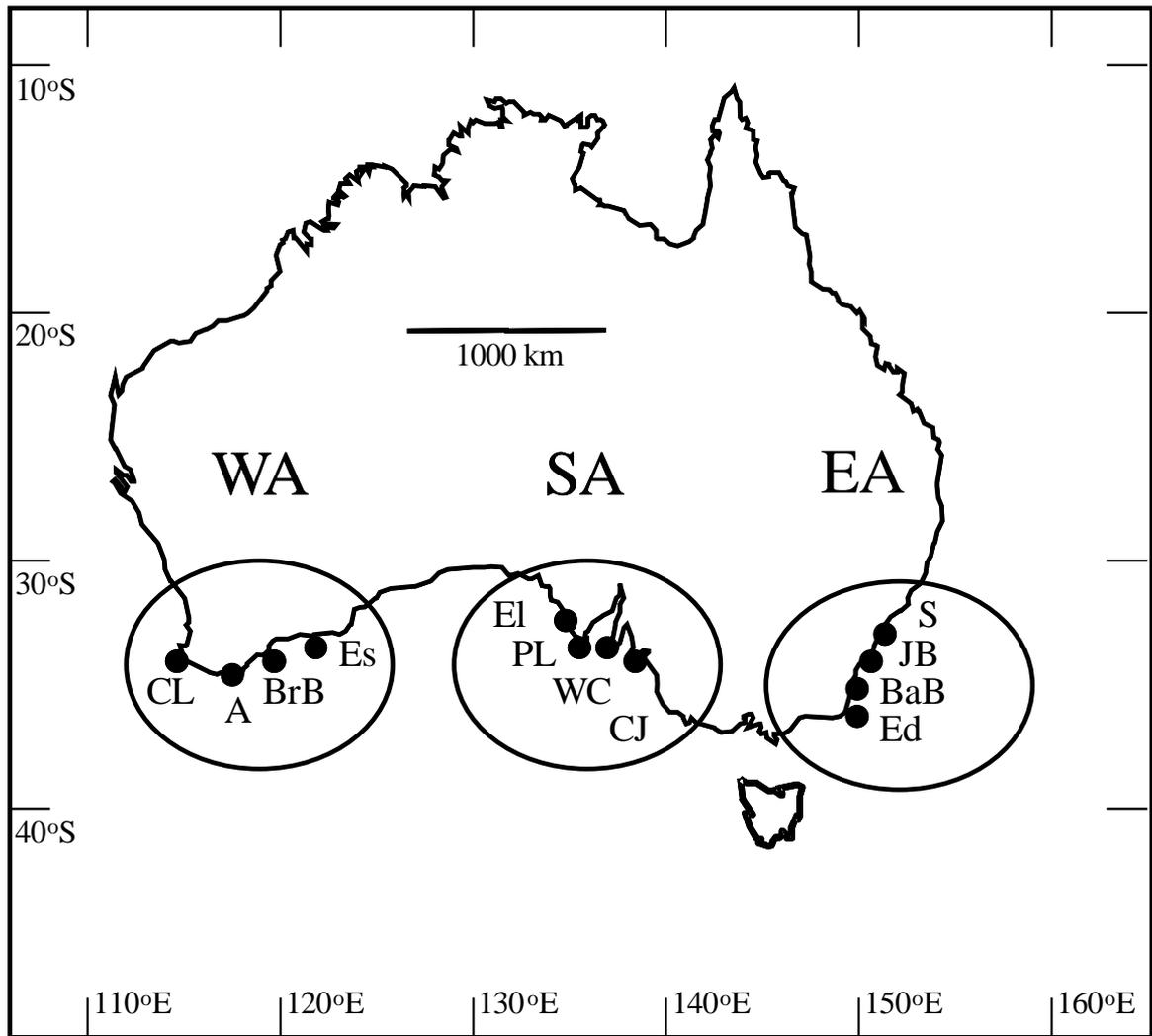
**Fig. 4** The effect of nutrients (ambient *v.* elevated) on the percentage cover of turf-

forming algae growing as epiphytes on the top, middle, and bottom laterals of

*E. radiata*, compared to natural percentage cover at Sydney.

20

Fig. 1



**Fig. 2**

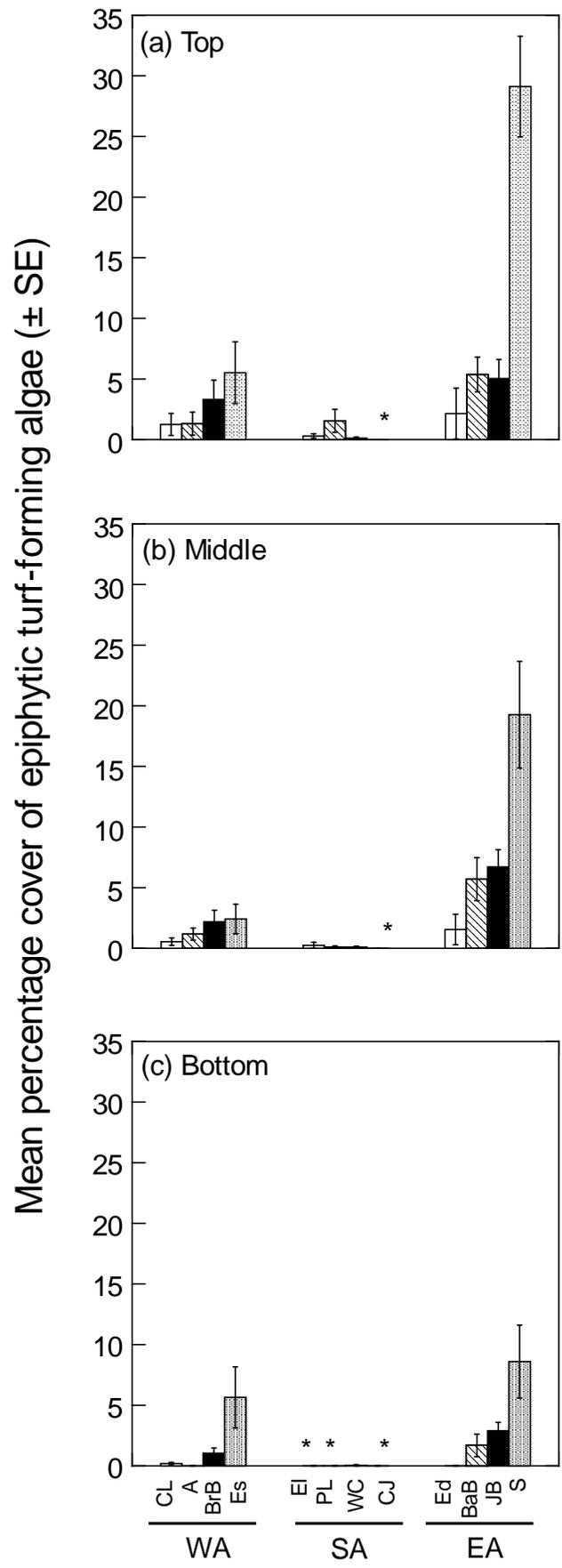


Fig. 3

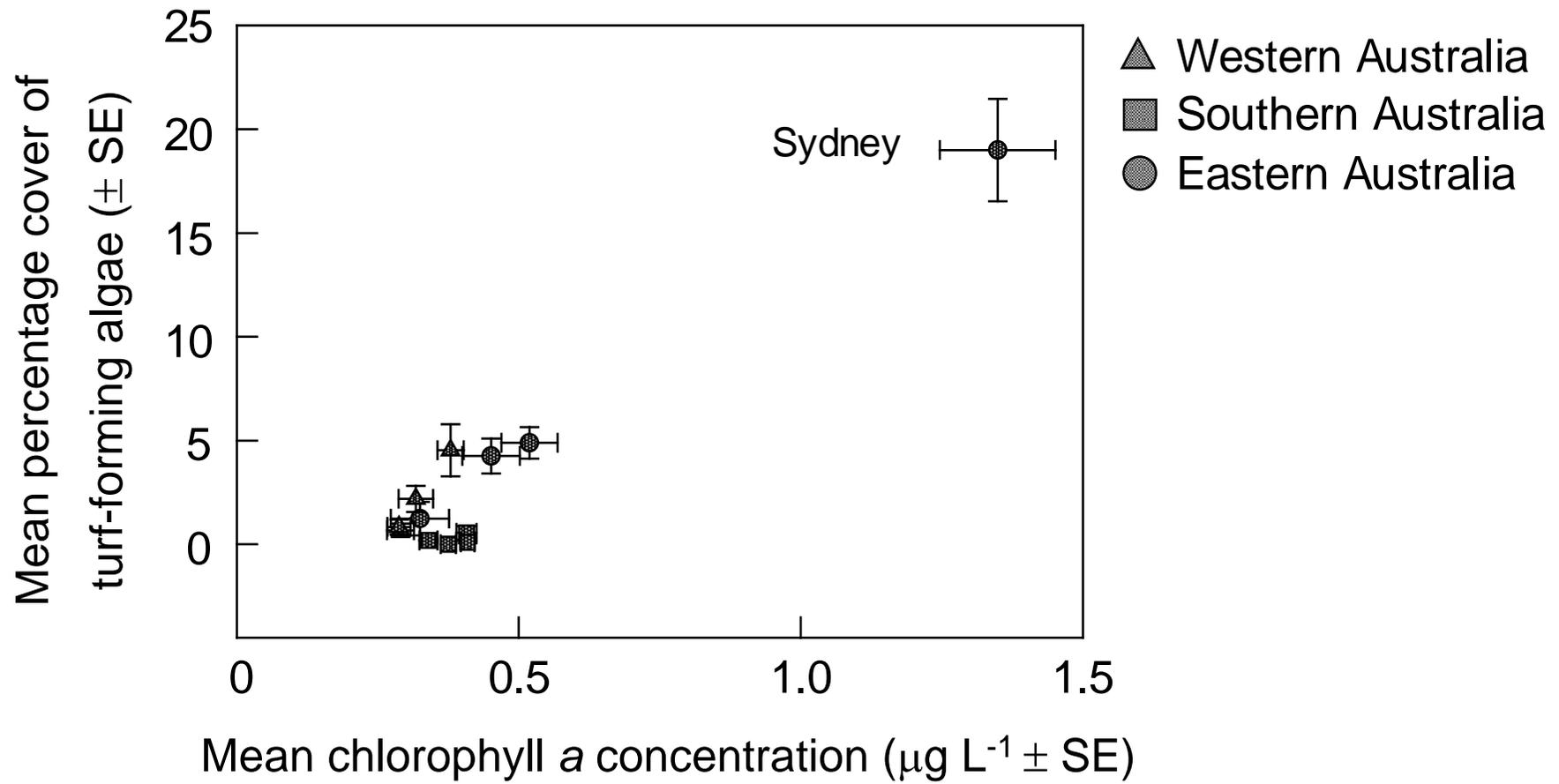


Fig. 4

