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RESEARCH ARTICLE

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Expansive covers of turf-forming algae on human-dominated coast: the relative effects of increasing nutrient and sediment loads

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Abstract Turf-forming algae form more extensive habitat on subtidal rock adjacent to urban than non-urban coast of South Australia. This pattern is frequently observed on the world's temperate coasts and is variously considered to be a result of enhanced concentration of nutrients or rates of sediment deposition on urban coasts. We experimentally tested which of three components of environmental change (increased nutrients in water, increased nutrients in sediments and increased sediment deposition) best explain the expansive covers of turf-forming algae on urban coasts. All three treatments had independent and positive effects on the percentage cover of turf-forming algae. The addition of nutrients from the water column had the largest influence ($\omega^2 = 0.55$), which was more than six times greater than the effect of nutrients added to sediments ($\omega^2 = 0.08$). An increase in rate of deposition of sediments had substantial effects ($\omega^2 = 0.35$), which were about one third less than those of water-borne nutrients. Importantly, the combined effect of all three treatments caused a 77% increase in percentage cover of turf-forming algae, which is comparable to the observed difference in covers between urban and non-urban coast in South Australia (93%). These results suggest that human activities that reduce water quality in both nutrient and sediment loads account for major change observed on human-dominated coasts. Despite this knowledge, we still lack complete information on the mechanisms that switch the primary subtidal habitat from canopy-forming algae to turf-forming algae on human-dominated coasts.

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Introduction

The domination of natural habitat by humans (Vitousek et al. 1997) has irrevocably changed the world and academic ecology (Tilman 1999). Novel environmental conditions created by human activity have altered habitats (Western 2001) and created great need for ecological predictions about the consequences of continuing human expansion. Many disturbances are local in nature and can obscure (Hulme et al. 1999) or even rival global climate change in their environmental and societal impacts (Vitousek et al. 1997).

Over the past few decades there has been a massive increase in terrestrial discharge of nutrients and sediments into coastal waters (Vitousek 1994; Carpenter et al. 1998; Airoldi 2003). Rocky shores represent one of the environments most vulnerable to these changes, given their close proximity to discharge and their phyletic diversity associated with canopy-forming algae (Smith et al. 1996). The novel conditions associated with terrestrial discharge appear to have caused an increase in the cover of turf-forming algae (filamentous assemblages of algae <5 mm in height) at the expense of canopy-forming algae (Airoldi et al. 1995; Benedetti-Cecchi et al. 2001; Eriksson et al. 2002; Airoldi 2003). Like many environmental changes, this change appears to favour a suite of species whose morphology, physiology and life history benefit from environments associated with human domination (Tilman and Lehman 2001).

The ability of turf-forming algae to dominate space on heavily populated coastlines appears to be a consequence of its ability to colonise rapidly and retain space under enhanced rates of sedimentation and nutrient input. Enhanced nutrient inputs enable this habitat to override the grazer control (Worm et al. 2001) and its sediment-trapping morphology (Stewart 1983; Kendrick 1991; Airoldi et al. 1995) to withstand heavy deposition of sediments (Airoldi 2003). Turf-forming algae inhibit the recruitment of canopy-forming algae (Kennelly 1987) and the global trend for replacement of the canopy with turf-forming algae on human-dominated coasts poses a serious threat to the biodiversity of coastal ecosystems. Canopy-forming algae constitute some of the temperate world's most extensive subtidal habitats (Dayton 1985; Goodsell et al. 2004) and their fragmentation and loss has major effects on the diversity of kelp-associated species (Goodsell and Connell 2002; Norderhaug et al. 2002).

For the same reasons that coastal nutrients loads are set to increase over the next 5 years (Tilman and Lehmann 2001), coastal sediment loads will also increase. Currently, little information exists on the relative and interactive effects of enhanced nutrients and sediment loads and the extent to which they drive the expansive covers of turf-forming algae on human-dominated coasts. Understanding the relative contribution of each of these factors will enable a more precise understanding of the cause of habitat change. Sediments are also an important source of nutrients (i.e. they accumulate during winter and storm events) and release nitrate into the water column in summer when photosynthetic demand is high and water stocks are low (Boynton et al. 1998). This synergy, combined with the physical facilitation of sediment on turf-forming algae (Airoldi 2003), may explain the spatial dominance of turfs on human-dominated coasts.

This research proceeded in two parts. First, we tested the hypothesis that the cover of turf-forming algae would be more extensive on subtidal rock on an urban coast compared to non-urban coasts of South Australia. Second, we experimentally tested which of three components of coastal change (increased sediment deposition, increased nutrients in water and increased nutrients in sediments) would best explain the expansive covers of turf-forming algae on urban coasts. This experiment enabled us to assess the extent to which this combination of environmental changes enables the percentage cover of turf-forming algae to approximate the cover observed on urban coast.

Materials and methods

Patterns of abundance on urban and non-urban coasts

To test the hypothesis that turf-forming algae occur more extensively adjacent to urban than non-urban coasts, the percentage cover of turf-forming algae was compared between the Adelaide metropolitan coast and two comparable coastlines without adjacent urban and/or aquaculture activities (Fig. 1). The Adelaide metropolitan coast consists of residential homes, hotels, marinas, light industry (e.g. retail outlets such as restaurants, mechanical repair and gas stations), and heavy industry (sewage treatment plants, power stations, international and industrial ports and an oil refinery). The potential magnitude and scales of influence of these activities is unknown and the locations chosen to represent urban coast were directly opposite residential housing and light industry. Media reports show conservation societies and SCUBA diving clubs to be concerned about massive but unquantified losses of canopy-forming algae (known as kelp forests) and their inhabitants (invertebrates and fishes) as a consequence of poorly managed water quality. These unquantified losses coincide with periods of major decline in water quality (A. Irving. personal communication) and the benthic assemblages in these locations do not appear representative of Australia's non-urban coast (Irving et al. 2004).

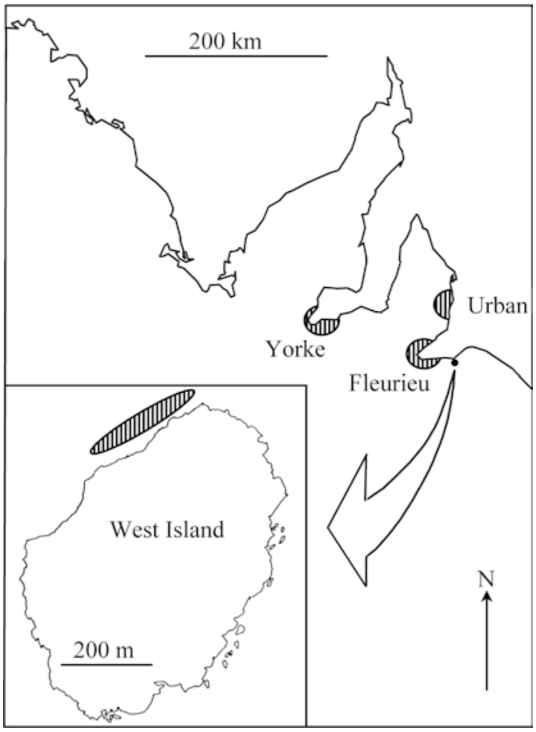

Fig. 1 Locations of urban (*urban*) and non-urban (*Yorke* and *Fleurieu* Peninsula) and the experimental study site (*West Island*) in South Australia

Within each locality (urban and non-urban), turf-forming algae were quantified along four transects (100 m×1 m) separated by at least 10 m and this was repeated at three sites separated by 1 km. Tape measures were laid out so that they were perpendicular to the shore and started as close to the low water mark as prevailing conditions would allow. Sampling stopped at 100 m irrespective of whether reef extended past this distance (to a maximum depth of 8–12 m). Observers swam along each tape and above all algae whilst recording the distance at which turf-forming algae occurred (as in Underwood et al. 1991). Percentage cover was calculated as the proportional distance that turf-forming algae occupied relative to the total distance of each tape. Turf-forming algae were defined as tightly packed filaments of algae combined with sediment (Stewart 1982).

Experimental effects of sediments and nutrients

At a non-urban study site, an experiment identified the components of water quality (increased sediment deposition, increased nutrients in water and increased nutrients in sediment) that primarily contributed to greater covers of turf-forming algae. The experiment was done on a boulder reef (5 m depth) in Abalone Cove, West Island, South Australia (35° 36′ S, 138° 35′ E). Boulders are composed of granite (approx. 300 mm across) and support extensive covers of encrusting coralline algae as understorey to monospecific canopies of the Laminarian kelp *Ecklonia radiata* (Connell 2003). Where canopies are absent, boulders are dominated by turf-forming algae and/or articulated coralline algae (Melville and Connell 2001). Turf-forming algae are comprised of numerous species of tightly packed erect filaments (B. Womersley, personal communication), which are generally 5-mm high and accumulate large amounts of sediment. The study site at West Island is characterised by low rates of sedimentation (Connell, unpublished data, c.f. Irving and Connell 2002).

The effects of sedimentation and two sources of nutrient enrichment (water column and sediment) were tested in a factorial design (2 sediment×2 water column nutrients×2 sediment nutrients; $n = 5$). Each of five replicate settlement plates was randomly assigned one of the eight treatment combinations (40 plates total) and the plates were deployed for 48 days (March 2003–April 2003). Sedimentation was manipulated so that the deposition of sediments was enhanced (addition) or left untouched (ambient). Nutrient enrichment was manipulated so that nutrients were enhanced (addition) or left untouched (ambient) for both enrichment of the water column and accumulated sediments. Replicates were separated by at least 1 m to ensure independence of treatments; nutrient concentrations ≥1 m from treatments of nutrient enhancement were equal to ambient concentrations (B. Russell, unpublished data from West Island using similar concentrations).

Settlement plates (12×12 cm) were attached to the upper surfaces of boulders so that they were oriented in the horizontal plane (i.e. the largest surface faced upwards). They were constructed from sheets of 4.5-mm fibre-cement (Hardi-flex) and all were covered with green shade cloth. The shade cloth acted as both the surface of the settlement plate and a structure to contain fertilizer pellets that diffused nutrients in an even and elevated concentration (Worm et al. 2000b). The application of fertilizer as Osmocote pellets follows the recommended protocol for sediment nutrient enrichment (Worm et al. 2000b) given the realistic and gradual nutrient release that tracks natural fluctuations in water and sediment.

Enhanced deposition of sediments was achieved by adding sediment (approx. 20g wet weight per settlement plate, equivalent to 10 g dry weight) collected from adjacent reef. Sediment was added to settlement plates (144 cm^{2}) so that sediment deposition was enhanced by approx. 144 g m^{-2}day^{-1} over 48 days. Total deposition on the day of application was estimated as approx. 515 g m^{-2} dry weight (144 g m^{-2} experimental addition plus 371 g m^{-2} deposition at the natural rate). This level of enhancement is within the natural range of sediment deposition observed on urban coast of South Australia [80–470 g m^{-2}day^{-1} dry weight (Greig 2000)] and its main harbour [323–2,033 g m^{-2}day^{-1} dry weight (Irving and Connell 2002)] where turf-forming algae dominate space. Sediments were added as fine “rain” (Airoldi and Virgilio 1998). Additions were carried out daily for the first 5 days and then weekly in each of the following 5 weeks (10 additions in total). Natural rates of sediment deposition at West Island [371 g m^{-2}day^{-1} dry weight (Connell, unpublished data)] have been observed to be more than 20% less than that of the urban coast [470 g m^{-2}day^{-1} dry weight (Greig 2000)]. These estimates were made with sediment traps [170 mm high×50 mm diameter, with an aspect ratio >3 as recommended by Häkanson et al. (1989)] over 22–24 days of December 1999–January 2000.

Nutrient enrichment of the water column was applied by adding 3 g Osmocote pellets into each of four nylon-mesh bags (1-mm mesh size). Concentrations of ammonia, nitrate, nitrite and phosphorus within enhanced (water and sediment source) treatments were increased by 88%, 58%, approx. 39% and approx. 38% respectively (see “Results”). Each bag was attached to the outer corners of the settlement plate and applied once at the beginning of the experiment. Nutrient enrichment of accumulated sediment was applied by fastening pellets onto the plate under the shade cloth. Potential artefacts associated with the physical presence of spherical balls of Osmocote pellets were tested by comparing plates without fastened Osmocote pellets with plates bearing glass balls of the same diameter and fastened in the same way. Testing for artefacts was done in a separate experiment in which the effects of glass balls (glass balls versus no balls) was compared in a crossed design with treatments of ambient and enhanced nutrients from the water column ($n = 5$ replicate plates for each of the four treatments).

To determine the actual concentrations of nutrients among treatments, water was sampled from the water column in mid-March 2003. Water column samples were taken using a 125-ml plastic bottle held directly above the settlement plate. On returning to the surface, samples were shaken and then filtered with a 0.45-µm filter. Samples were then immediately frozen in liquid nitrogen for transportation before analysis of ammonia, nitrate, nitrite and phosphorus concentrations (Australian Centre for Tropical Freshwater Research). Ambient and enhanced levels of dissolved inorganic nitrogen (DIN) (ammonia, nitrate and nitrite) at West Island were compared to those of the Adelaide urban coast in the same month (March) and the average of each March observation over 6 years (1998–2003) (data from the Environmental Protection Authority of South Australia).

Quantification and analysis of turf-forming algae and sedimentation

After 48 days (April 2003) each plate was placed in a sealable plastic bag for transportation to and quantification in the laboratory. Percent cover was estimated in situ using the point-intersect method (Meese and Tomich 1992) as applied to a grid of 25 evenly spaced points over the central 10×10 cm of the each plate. Sediment was also collected from each settlement plate, filtered with filter paper and oven dried to a constant weight at 70°C. Analysis of variance (ANOVA) and Student-Newman-Kuels (SNK) post-hoc tests were used to test for, and identify, differences among treatments according to Underwood (1997). The magnitude of effects (ω^{2}) was calculated (Vaughan and Corballis 1969) to assess which factor, or combination of factors, primarily contributed to expansive covers (percentage cover) of turf-forming algae under experimental conditions.

Results

Patterns of abundance on urban and non-urban coasts

The percentage cover of turf-forming algae was more extensive on the urban coast than comparable coasts without major urban or aquaculture development (Fig. 2; Table 1). Although there was substantial variation among sites at Yorke Peninsula (Fig. 2; Table 1), the percentage covers of turfs was approx. 15 times greater on the urban coast than on non-urban coasts.

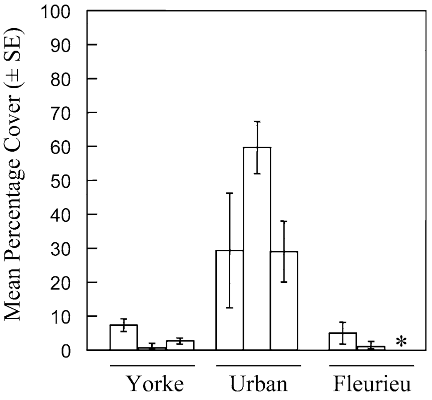

Fig. 2 The percentage cover of turf-forming algae (±SE) on South Australian rocky reefs on coastlines without urbanisation (Yorke and Fleurieu Peninsula) and with urbanisation (Adelaide metropolitan coast). Within each location (Yorke Peninsula, Adelaide metropolitan coast and Fleurieu Peninsula) percentage cover was estimated at three sites. *Asterisk* indicates zero value

Table 1 Two-way analysis of variance (ANOVA) testing for differences in percentage cover of turf-forming algae among three locations and at sites within each location (one urban coast and two non-urban coasts). Analysis treated location as fixed and site as random and nested within location. By the Student-Newman-Kuels (SNK) test, urban > Yorke Peninsula = Fleurieu Peninsula

Source	*df*	MS	*F*
Location	2	13.22	12.63**
Site (location)	6	1.05	2.86*
Residual	18	0.37	

$*P < 0.05$, $**P < 0.01$
df Degrees of freedom, *MS* mean square

Experimental effects of nutrients and sediments

After 48 days, experimental plates were covered with turf-forming algae that were primarily composed of the brown algae *Feldmannia lebelli* Crouan and Crouan and *F. globifera* Kuetzig. The concentrations of ammonia and nitrate in water were significantly greater within treatments of nutrient enhancement of the water column [0.32 ± 0.03 μmol l^{-1} ($\bar{x} \pm s_{\bar{x}}$) and 0.33 ± 0.01 μmol l^{-1}, respectively] and sediments (0.38 ± 0.03 μmol l^{-1} and 0.39 ± 0 μmol l^{-1}, respectively) compared to control treatments (0.06 ± 0 μmol l^{-1} and 0.17 ± 0.02 μmol l^{-1}, respectively) (Tables 2, 3). The concentrations of ammonia and nitrate were greatest within treatments of nutrient enhancement of both sources (water and sediment) (0.53 ± 0 μmol l^{-1} and 0.41 ± 0.01 μmol l^{-1}, respectively). Concentrations of nitrite and phosphorus in the water column were unaffected by the addition of any source of nutrients (results of ANOVA for nitrite were $F_{1,4} = 1$, $P > 0.25$ for both nutrient sources and their interaction; for phosphorus, $F_{1,4} = 3$, $P > 0.1$ for both nutrient sources and their interaction). Ambient concentrations of nitrite and phosphorus in the water column were 0.04 ± 0 μmol l^{-1} and 0.27 ± 0.02 μmol l^{-1}, respectively.

The percentage cover of turf-forming algae was greater in the treatments of enhanced sediment deposition and both treatments of nutrient elevation (water and sediment) (Fig. 3; Table 4). Importantly, there was no interaction among these treatments (Table 4), indicating that each of these effects occurred independently of each other. The treatment of largest influence was the addition of nutrients from the water column ($\omega^2 = 0.55$), which was more than six times greater than the effect of nutrients added to sediments ($\omega^2 = 0.08$). The effect size

Table 2 Two-way ANOVAs testing the effect of water column nutrients (enhanced vs. ambient) and sediment nutrients (enhanced vs. ambient) on the concentration of ammonia and nitrate in the water column

Source	*df*	Ammonia		Nitrate	
		MS	*F*	MS	*F*
Nutrients in water column (NW)	1	40.50	162.00**	120.12	87.36**
Nutrients in sediment (NS)	1	24.50	98.00**	105.12	76.45**
NW×NS	1	2.00	8.00*	15.12	11.00*
Residual	4	0.25		1.37	

All data are untransformed and the assumption of homogeneity met Cochran's *C*-test
Analysis treated all factors as fixed and orthogonal
$*P < 0.05$, $**P < 0.01$

Table 3 Results of SNK test showing pair-wise differences for the significant interaction term of ammonia and nitrate

Source	Result
Enhanced NW	Enhanced NS > ambient NS
Ambient NW	Enhanced NS > ambient NS
Enhanced NS	Enhanced NW > ambient NW
Ambient NS	Enhanced NW > ambient NW

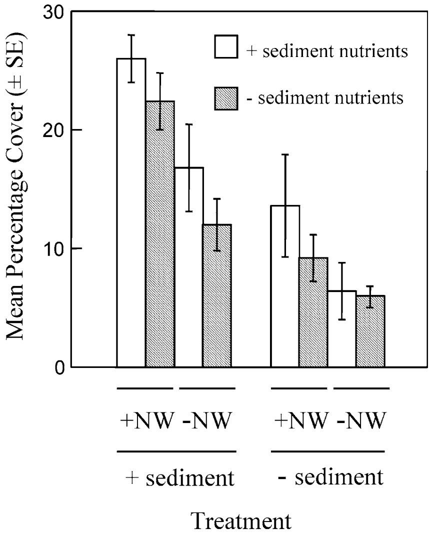

Fig. 3 The response of the percentage cover of turf-forming algae (± SE) among treatments of sedimentation (enhanced vs. ambient), nutrients added to the water column (*NW*) (enhanced vs. ambient) and nutrients added to the sediment (*NS*) (enhanced vs. ambient)

Table 4 ANOVA testing differences in the percentage cover of turf-forming algae (± SE) among treatments of sedimentation (enhanced vs. ambient), nutrients from the water column (enhanced vs. ambient) and nutrients added to the sediment (enhanced vs. ambient)

Source	*df*	MS	*F*	ω^2
Sediment (S)	1	592,435.60	15.41***	0.32
Nutrients water column (NW)	1	982,195.60	25.55***	0.55
Nutrients sediment (NS)	1	171,610.00	4.46*	0.08
S×NW	1	133,171.60	3.46 ns	0.05
S×NS	1	10,368.40	0.27 ns	0
NW×NS	1	15,210.00	0.40 ns	0
S×NW×NS	1	12,250.00	0.32 ns	0
Residual	32	38,435.60		

X^2 transformation was used to meet assumptions of homogeneity of data (Cochran's *C*-test)
All factors were treated as fixed and orthogonal
The magnitude of effects (ω^2) were calculated for each of the three factors tested (Vaughan and Corballis 1969; Graham and Edwards 2001)
ns Not significant ($P > 0.05$), $*P < 0.05$, $***P < 0.001$

associated with the addition of sediments ($\omega^2 = 0.35$) was substantially larger than the addition of nutrients to sediments ($\omega^2 = 0.08$). Potential artefacts associated with the physical presence of spherical Osmocote balls were not detected. The comparison between settlement plates with glass balls and plates without balls had no detectable influence on the percentage cover of turf-forming algae ($F_{1,6} = 1.01$, $P = 0.33$).

The dry weight (g) of sediment collected from the settlement plates was significantly greater in treatments of enhanced water column nutrients when the concentration of nutrients in sediments was ambient (Fig. 4). An interaction was detected (nutrients in water×nutrients in sediment; Tables 5, 6), indicating that the enhancement of nutrients in water can magnify the amount of sediment trapped by turf-forming algae when the surrounding sediments do not contain enhanced concentrations of sediment.

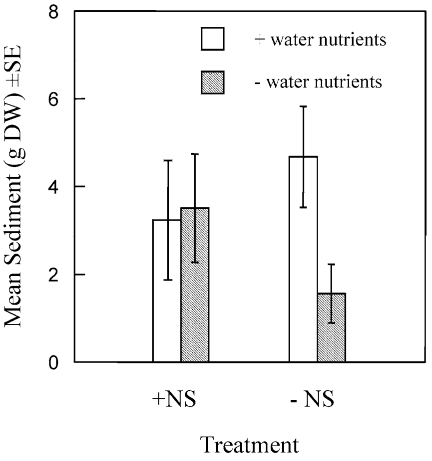

Fig. 4 The response of the mean amount of sediment [g dry weight (*g DW*) ± SE] collected from settlement plates (per 10×10 cm) among treatments of nutrients added to the water column [enhanced vs. ambient (*unshaded* and *shaded bars*, respectively)] and nutrients added to the sediment [enhanced vs. ambient (+*NS* and −NS, respectively)

Table 5 ANOVA testing the response of the amount (grams dry weight) of sediment collected from each settlement plate among treatments of sediment (enhanced vs. ambient), water column nutrients (enhanced vs. ambient) and sediment nutrients (enhanced vs. ambient)

Source	*df*	MS	*F*
Sediment (S)	1	0.02	0.02 ns
Nutrients water column (NW)	1	0.06	0.05 ns
Nutrients sediment (NS)	1	2.87	2.26 ns
S×NW	1	0.00	0.00 ns
S×NS	1	1.20	0.95 ns
NW×NS	1	6.85	5.40*
S×NW×NS	1	0.11	0.09 ns
Residual	32	1.27	

Ln(x) transformation used to meet assumption of homogeneity (Cochran's *C*-test)
Analysis treated factors sediment, nutrients from water column and nutrients from sediment as fixed and orthogonal
ns Not significant ($P > 0.05$), *$P < 0.05$

Table 6 Results of SNK test showing pair-wise differences for the significant interaction term

Source	Result
Enhanced NW	Enhanced NS = ambient NS
Ambient NW	Enhanced NS = ambient NS
Enhanced NS	Enhanced NW = ambient NW
Ambient NS	Enhanced NW > ambient NW

Discussion

Turf-forming algae formed more extensive habitats on subtidal rock of the urban than the non-urban coast of South Australia. This pattern is frequently observed on the world's temperate coasts (Benedetti-Cecchi et al. 2001) and is variously considered to be a result of enhanced concentrations of nutrients (Worm et al. 2000b; Eriksson et al. 2002) or rates of sediment deposition (Eriksson et al. 2002; Airoldi 2003). On non-urban coasts, kelp maintain understorey habitat (Connell 2003) that appear to facilitate kelp recruitment (Connell, personal observation), whereas on urban coasts, the novel environmental conditions that facilitate habitat (turf-forming algae) appear to inhibit recruitment of kelp (Worm et al. 1999; Airoldi 2003). Kelp may be better competitors for space under natural conditions, whereas the quick-recruiting, turf-forming algae seem better competitors for space under human-dominated conditions.

On the Adelaide metropolitan coast there has been much public concern about the loss of canopy-forming algae in favour of turf-forming algae as a consequence of enhanced sediment deposition and nutrient run-off (Cheshire et al. 1999). The current experiment provides new information on the relative contributions of sediment and nutrient enhancement to extensive covers of turf-forming algae. These results reveal that while both enhanced sedimentation and nutrients positively affect the covers of turf-forming algae, the addition of sediments and sediment-laden nutrients contributed a surprisingly small effect. Importantly, elevated nutrients in the water caused the greatest experimental increase in percentage cover of turf-forming algae. While increased sediment deposition was a major contributor to the overall increase, its contribution was almost half that of nutrients from water. It is likely that human activities in the coastal zone increase both nutrients and sediments together and this experiment highlights the need to consider both factors on human-dominated coasts.

Importantly, treatments of elevated nutrient and sediment loads recreated the extensive covers of turf-forming algae observed on the urban coast (Table 7). Within a short period of time (48 days), these treatments created covers (26 ± 2%) comparable to those on the urban coast (39 ± 8%). The experimental increase from ambient to enhanced conditions (77%) is also relatively

Table 7 Comparison of natural conditions in urban and non-urban environments to experimental conditions created to simulate urban and non-urban conditions: percentage cover of turf-forming algae, DIN [dissolved inorganic nitrogen (ammonia, nitrate and nitrite)] and rates of sediment deposition

Environment	Quantity	Natural	Experimental
Urban	Percentage cover ($\bar{x} \pm s_{\bar{x}}$)	39 ± 8	26 ± 2
	DIN (μmol l^{-1})	6.00[a]	1.01
	Sedimentation rate (g m^2 day^{-1})	470	515
Non-urban	Percentage cover ($\bar{x} \pm s_{\bar{x}}$)	3 ± 1	6 ± 1
	DIN (μmol l^{-1})	0.29	0.29
	Sedimentation rate (g m^2 day^{-1})	371	371

[a] Average DIN for six years (1998–2003) of samples taken in March was 2.44 μmol l^{-1} (Environmental Protection Authority of South Australia)

comparable to the "natural" difference between urban and non-urban reefs (93%). The similarity between experimental and natural effect-sizes suggests that elevated nutrient and sediment loads may explain much of the difference in percentage cover of turf-forming algae between urban and non-urban coasts. It is worth noting, however, that comparisons of percentage cover of turf-forming algae were done at different spatial scales. Also, the level of experimental enhancement of sediments was based on natural rates of sedimentation over a 12-month period at the study site some 24 months previously. Despite these caveats for comparison, the data provide some of the first insights into the magnitude and relative effects of different components of declining water quality on urban coasts.

Ambient concentrations of DIN at West Island are approx. 33–71 times less than at comparable parts of the temperate world [Western Baltic (Worm et al. 2000a), Sweden (Hillebrand 2003) and the North Western United States of America (Pfister and Van Alystyne 2003)]. This difference in nutrient concentrations suggests that South Australian coastal waters are relatively oligotrophic and the experiment highlights that even a slight increase in nutrient concentration in the water column is sufficient to trigger positive changes to the cover of turf-forming algae. In comparison, Worm et al. (1999) enhanced ammonium and nitrate concentrations by two times more than this study to achieve experimental increases in the percentage cover of algae.

Ecological theory predicts that human-dominated environments favour "weedy" plants, such that longer-lived and larger plants are displaced by small, fast-growing, "weedy" species (Tilman and Lehman 2001). These predictions match current concern that canopy-forming algae (e.g. kelp forests) have already undergone widespread and apparently irreversible replacement by turf-forming species along human-dominated shores (Worm et al. 1999). Kelp forests are generally longer-lived and physically larger than the fast-growing, small tightly packed filaments of "turf-forming algae". It is hypothesised that human-dominated environments favour "weedy" plants because their physiologies, morphologies and life histories enable them to be superior competitors under these changed conditions (Tilman and Lehman 2001). On human-dominated coasts, it appears that turf-forming algae have been favoured because their life-history and physiology is better suited to nutrient overloading (Worm et al. 1999) and their sediment-trapping morphology enables them to dominate space under heavy coastal sedimentation (Airoldi 1998).

The ability of turfs to withstand large amounts of sediment deposition may explain their spatial dominance over much of the world's temperate rocky reefs (Airoldi 2003). Not only are turf-forming algae better able to withstand the negative effects of sedimentation, but they also inhibit the recruitment of canopy-forming algae (Airoldi 2003). Turf-forming algae inhibit the recruitment of *E. radiata* (Kennelly 1987), which is Australia's most extensive species of canopy-forming algae (Goodsell et al. 2004). Kelp are well known to be lost through storm activity and it is possible, therefore, that their replenishment on urban coasts is slower because of the biological advantages turf-forming algae may have in rapid recruitment to and retention of bare space under heavy nutrient and sediment loads. This study suggests that nutrients can indirectly magnify the effects of sediments by enhancing turf-forming algae that trap sediment (i.e. greater weight of sediment per unit area) and further prevent colonisation by canopy forming-algae. This result points to a key interaction between two major human influences on temperate coasts and highlights a potential example of a feedback effect.

In summary, the dominance of turf-forming algae on urban coasts indicates that they are better able to colonise and retain space associated with human-altered environments. This experiment suggests that the human activities of concern include reduced coastal water quality as a function of increased nutrient and sediment loads. Despite this practical knowledge, we still lack detailed information on the mechanisms that switch the primary subtidal habitat from canopy-forming algae to turf-forming algae. We need to identify the specific mechanisms that enable turf-forming algae to colonise and retain space at a greater rate than canopy-forming algae. While a reduction in water quality can cause an increase in spatial extent of turf-forming algae, this knowledge is a necessary but insufficient step towards explaining why canopy-forming algae are unable to retain space as the primary habitat on human-dominated coast.

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