The prevalence and production of turf-forming algae on a temperate subtidal coast

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M. COPERTINO, S.D. CONNELL AND A. CHESHIRE. 2005. The prevalence and production of turf-forming algae on a temperate subtidal coast. *Phycologia* 44: 241–248.

This study shows that canopy-forming algae, composed mainly of fucoids and the kelp *Ecklonia radiata* (both Phaeophycea), dominated space on South Australian coasts relative to turf-forming algae. However, where canopy-forming algae are absent turf-forming algae are the primary occupiers of space (~ 70%). On some reefs where canopy-forming algae are restricted in spatial extent, turfs can occupy as much as 40% of reefs. Turf-forming algae are an abundant component of algal assemblages, but relatively little is known about their contribution to the primary productivity on temperate reefs, relative to canopy-forming species. This study reveals that net productivity rates of turfs at one South Australian location were very high across depths (1.3–2.9 g C m^{-2} day^{-1} or 23.2–88.0 mg C g ash-free dry weight^{-1} day^{-1}), comparable to the values discovered on tropical reefs. Although turf-forming algae are much more productive than canopy-forming algae on a biomass basis, the annual net production per area is two to seven times lower for turfs than for canopy-forming algae. However, if negligible exudation rates are assumed for turfs (up to 1%), the biomass of carbon produced by turf algae represents 44–71% of the carbon incorporated into biomass of kelps. Taken together, these results suggest that while canopy-forming algae can be correctly assumed to be the major source of total carbon produced on temperate reefs, the contribution of turf-forming algae may be substantial to the biomass production and turnover on South Australian reefs.

INTRODUCTION

Turf-forming algae are one of the most widespread and taxonomically diverse groups of algae occupying subtidal rock substratum and play key roles in the ecology of subtidal shores (Underwood *et al.* 1991; Airoldi 2003). Knowledge of the primary production by algal turfs, however, is primarily restricted to tropical waters (e.g. Borowitzka *et al.* 1983; Carpenter 1985, 1986; Adey & Goertemiller 1987; Adey 1998), probably in the belief that they are only a minor component of temperate reef algae (Westphalen & Cheshire 1997; Copertino 2002). The extensive body of studies on production ecology of temperate reefs have focused mainly on the spatially dominant group of canopy-forming macroalgae, particularly kelps (e.g. Lüning 1979; Mann *et al.* 1980; Gagné *et al.* 1982; Kirkman 1984; Larkum 1986; Wheeler & Druehl 1986; Hatcher *et al.* 1987; Kirkman 1989; Flores-Moya *et al.* 1993, among others). It is understandable, therefore, that the total carbon production on these reefs is thought to be a consequence of the extensive stands of the canopy-forming algae that contain a substantial portion of visible biomass (Mann *et al.* 1980).

Recent descriptions of the percentage cover of turf-forming algae across much of Australia's temperate coast suggest that these algae can form extensive mats in the absence of canopy-forming algae (Fowler-Walker & Connell 2002). Loss of canopy-forming algae often results in an increase in turf-forming

algae (Edwards 1998; Melville & Connell 2001), and turf algae also appear to increase their spatial extent in response to a decline in coastal water quality (Gorgula & Connell 2004). The idea that turf-forming algae may occupy large areas of temperate shores coupled with observations of phenomenal growth by turfs on tropical reefs, allowing turnover of their biomass once every 4–12 days (Carpenter 1985), suggests that some reassessment of the production ecology of this group is required.

The contribution of turf-forming algae to total carbon produced on temperate reefs may be substantial. This study assesses this idea in two steps. First, we assessed the areal extent of turf-forming algae relative to canopy-forming algae, as the latter are known to have negative effects on the cover of turf-forming algae in South Australia (Melville & Connell 2001). These estimates were derived from three sites within each of four locations spanning > 1000 km of continuous South Australian coast. Second, we assessed the biomass formation and the productivity rates at a locality in South Australia at different times.

MATERIAL AND METHODS

Prevalence

Relative cover of canopy-forming and turf-forming algae was quantified at or near the most exposed coast of South Australia's three peninsulas (within the latitudes 33°59'S and 35°51'S; Fig. 1) during the Austral summer of early 2002. Within each peninsula four sites were chosen so that they were of similar wave exposure and connected to the mainland.

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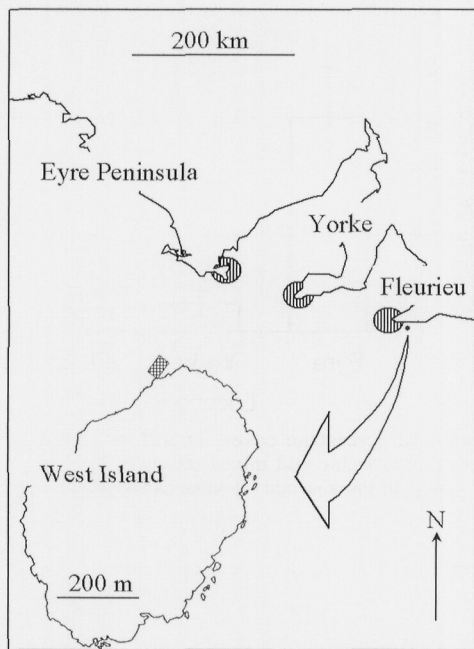
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Fig. 1. Map showing positions of sampling locations across the South Australian coastline. Locations from left to right are Port Lincoln, West Cape and Cape Jervis. Position of the experimental site (West Island) is also indicated.

Within each site, the relative cover of canopy vs turf-forming algae was quantified along four 100×1-m transects separated by at least 10 m. 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 into the subtidal irrespective of whether reef extended past this distance (maximum depth: 8–12 m). Observers swam along each tape and above all algae whilst recording the location at which canopy-forming and turf-forming algae occurred (same as Underwood *et al.* 1991). Canopy-forming algae were defined as algae that were the kelp (Laminariales) *Ecklonia radiata* (C. Agardh) J. Agardh or species of Fucales (mainly Cystoseiraceae and Sargassaceae) greater than 4 cm height. Turf-forming algae were defined as tightly packed multispecific short filaments, less than 1 cm, combined with sediment (Stewart 1983). Turfing algae also occur under canopies, albeit sparsely. The area of turf-forming algae under canopies was calculated from estimates made by Fowler-Walker & Connell (2002) at the same sites.

Production

Rates of primary productivity and standing biomass were quantified on turf-forming algae growing on settlement plates (11×11 cm, made of fibrous cement) at 4 m and 10 m depth at West Island ($35°36'25''$S, $138°35'27''$E; Fig. 1). Settlement plates were attached to a steel mesh grid fixed to the bottom at each depth. Settlement plates are ideal units to experimentally quantify biomass and productivity of turf-forming algae (e.g. Carpenter 1985; Irving & Connell 2002). Settlement plates were deployed in September 1998, and in February, June, September and December of 1999. Algal assemblages from both depths were sampled in September and December of 1999, and March and June of 2000, after 6 months growing

on plates. Assemblages of different ages were sampled in March 2000, corresponding to plates deployed for 3, 6, 9 and 18 months.

Primary productivity was quantified as oxygen evolution/consumption with an automated oxygen exchange apparatus (Cheshire Systems; The University of Adelaide, SA, Australia), similar in its major components to the system described by Chalker *et al.* (1985). Detailed description of the system used can be found in Cheshire *et al.* (1996). The model used comprised a data logger, a series of six UV-transparent acrylic sealed chambers (with a volume of 4 litres), six oxygen electrodes, six magnetic stirrers (fan type), two 2π quantum sensors (LICOR, USA), two temperature probes and a flushing system. An electrode, a stirrer and a flushing hose are connected to each chamber. The stirrers provided an average water flow around 20–25 cm s^{-1} over turf algal samples, which is higher than the saturating water velocities for photosynthesis and nutrient uptake measured on turfs from coral reefs (up to 22 cm s^{-1}; Carpenter *et al.* 1991). The apparatus was deployed on the reef at the depth of 4 m using scuba diving. Plates with turf algal communities were collected from the original depths and the associated macroinvertebrates attached were removed manually. Plates were sealed inside the chambers and oxygen concentrations in the chambers were recorded every 20 seconds during incubation periods of 20 minutes. At the end of each incubation chambers were flushed for 2 minutes, returning the water from within to surrounding ambient conditions. Oxygen consumption and production of turfs, photosynthetic photon flux density (PPFD) and temperature were measured over 24-hour periods. PPFD also was recorded daily by two fixed quantum sensors (LICOR, USA) at the depths of 2 m and 3 m. Thus, an attenuation coefficient (Kirk 1994) was calculated for each month, which was used to estimate PPFD values at the depth of 10 m.

A total of 35 successful deployments were performed from September 1999 to July 2000 and 182 samples (plates) were analyzed. The photosynthetic and respiratory rates (oxygen evolution/consumption) were expressed as µmol O$_2$ plate^{-1} min^{-1}. The photosynthesis–light relationship (P-E curve) was described for each sample, by adjusting an exponential model to the observations (Webb *et al.* 1974). The exponential model was used in preference to the hyperbolic tangent function (Jassby & Platt 1976) as it consistently provided a better mathematical representation of the data. Only fitted curves with r^2 greater than 0.8 were used in the analysis and to calculate the final values of production.

A previous taxonomical assessment of algae was done on fresh plates, with a maximum of 1 day after the experiment, and the main genera (rarely classified to species level) were identified. Extra plates were collected and fixed in 10% formalin for a more detailed study on species composition and community structure (Copertino 2002). Abundance of individual genera were measured as its occurrence on plates, and coded using a four-point scale. A generus was defined as rare if recorded on 10% or less of the combined plates, common if on 10–25%, abundant if on 25–50% and dominant if on more than 50% of the plates. Next, algal biomass on the plates was scraped off, dried at constant temperature (60°C) for 48 hours, weighed and then combusted in a muffle furnace at 550°C for 5 hours. Biomass values were obtained in grams of
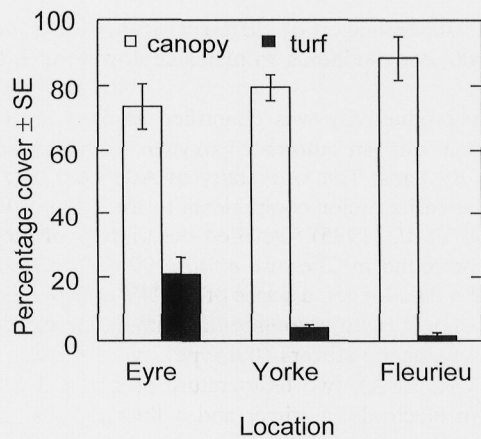
Fig. 2. Percentage cover of canopy-forming algae (*Ecklonia radiata* and fucoids > 4 cm in height) and turf-forming algae that occurred in the absence of canopy-forming algae.
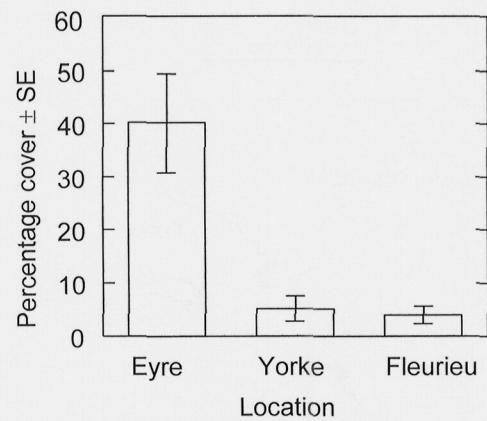

Fig. 3. Combined percentage covers of turf-forming algae that occurred under monospecific and mixed stands of *Ecklonia radiata* (> 4 cm height) and in the absence of other canopy-forming algae.

ash-free dry weight (AFDW) per plate and expressed in g AFDW m^{-2}.

Net productivity rates were estimated by integrating daily net photosynthesis obtained by the model over a standardized light field, which was calculated using the day length and maximum PPFD recorded in each deployment. The light field used to calculate production at 10 m was estimated with the attenuation coefficient obtained for each period. Oxygen values were converted to carbon assuming a photosynthetic quotient of 1 (1 μmol O_2 = 0.012 mg C). Production of a sampling period was normalized to both surface area (g C m^{-2} day^{-1}) and biomass (g C g $AFDW^{-1}$ day^{-1}). Complete turnover time of carbon (in days) was calculated as the ratio of biomass (g C) to daily productivity (g C day^{-1}) of a sample. Conversion of mass (g AFDW) to the carbon equivalent (g C) was estimated by assuming a carbon content of 36% of AFDW. This value was calculated based on the average carbon content (24.2% of dry weight) found for turfs and filamentous species (Atkinson & Smith 1983) and the average organic matter content (67% of dry weight) found for the present turfs (Copertino 2002). The mean daily productivity for one season was estimated from the average of the daily productivity rates found in two subsequent sampling periods. The total net production of a season was estimated as the sum of the average daily rates over a period of 90 days, which was used to calculate the annual net production. The total carbon losses during a season were estimated by subtracting the biomass balance during the season from the total net production of the respective period. Biomass balance within a season was assumed to be the difference in biomass between two sampling periods. Standing biomass and productivity data were analyzed using two-way ANOVA to compare depths and sampling periods for each dependent variable (biomass, productivity), with a *post hoc* Tukey test ($P < 0.05$) to verify significant differences between groups (Zar 1996). Homogeneity of variances was assessed with the Levene test for all of the analyses. Logarithmic transformation was applied to the dependent variables, in order to improve normality and homogeneity of variances. All analyses and tests were performed according to Zar (1996) and using the software package Statisca 5.1 (StatSoft, USA).

RESULTS

Prevalence

Percentage cover of turf-forming algae was substantially less than that of canopy-forming algae across the three localities sampled (Fig. 2). *Ecklonia radiata* comprised ~ 75% of the area that canopy-forming species occupied. Our figures provide a low estimate of the percentage cover of turf-forming algae (Fig. 2) because they also occur in sparse covers under canopies of *E. radiata* (Fowler-Walker & Connell 2002). To provide an upper estimate, we combined the lower estimate with published data on percentage covers of turf-forming algae under *E. radiata* at the same sites (Fowler-Walker & Connell 2002; within each site the understorey of monospecific stands of *E. radiata* were sampled within three 10 × 10-cm quadrats, within each of six 1-m^2 quadrats separated by 10 m). This upper estimate is shown in Fig. 3 (i.e. the combined percentage cover of turf-forming algae in both the absence of canopy-forming algae and presence of *E. radiata*). At these sites, turf-forming algae also occur under canopies of *E. radiata* mixed with fucoid algae (Cystoseiraceae and Sargassaceae) in similar covers to those under monospecific stands of *E. radiata* (Irving *et al.* 2004). This upper estimate, therefore, was based on estimated values of turfs under both monospecific and mixed canopies of *E. radiata* (*sensu* Goodsell *et al.* 2004) at each site. At one site the total percentage cover was as great as 54% of the rock surface (turfs occurring alone and under *E. radiata*).

Production

Turf algal communities in this study included representatives from the four major divisions (Chlorophyceae, Phaeophyceae, Rhodophyceae and Cyanophyceae). A total of 37 genera of macroalgae and assemblages of Cyanophyceae (small and spherical conglomerates, not identified) were observed on plates (Table 1). The dominant genera in terms of frequency, present on more than 50% of the plates sampled, were *Ectocarpus, Feldmania* (Phaeophyceae), *Ceramium, Gelidium* and *Lithothamnium* (Rodophyceae).

Turf algal communities growing on plates at West Island were highly productive all year around, with significant and

Table 1. List of algae recorded on settlement plates during the period of September 1999 to June 2000 in the present work and its frequency of occurrence.

Algal taxon	Occurrence[1]
Cyanophyceae	D
Chlorophyceae	
Caulerpa brownii	C
Caulerpa fastigiata	C
Caulerpa obscura	C
Cladophora	C
Chaetomorpha	R
Ulva	C
Phaeophyceae	
Colpomenia sinuosa	A
Colpomenia peregrina	A
Cystophora	A
Dictyota	R
Dictyopteris	R
Ectocarpus	D
Feldmania	D
Giffordia	A
Halopteris	C
Lobospira	C
Pachydictyon	R
Padina	R
Sargassum	C
Sphacelaria	C
Ralfsia	R
Rhodophyceae	
Cheilosporum	C
Asparagopsis armata	C
Botryocladia	R
Calophylis	R
Ceramium	D
Champia viridis	C
Corallina	A
Gelidiela	C
Gellidium pusillum (short form)	C
Gellidium sp	D
Griffithsia	R
Lithotamnium	D
Plocamium	R
Polysiphonia	A
Rhodymenia	C

[1] D, dominant; C, common; R, rare; A, abundant.

large differences between depths, and smaller differences between sampling periods. Biomass-specific net primary productivities (BeNPPs) were significantly higher in December and March, coinciding with the periods of lower standing biomass (Table 2), and higher light and water temperature (Fig. 4). Assuming negligible excretion rates for turfs (Hackney & Sze 1988), these productivity values represent a carbon incorporation of 7–28% and 0.8–6% of the standing biomass per day, for 4-m and 10-m plates, respectively. Net primary production (NPP) values on an areal basis ranged from 1.3 to 2.9 g C m^{-2} day^{-1} and from 0.14 to 0.6 g C m^{-2} day^{-1}, respectively, for 4-m and 10-m turfs, with lowest values occurring during June (winter) and highest during September (early spring) and December (early summer) (Table 2). Differences in standing biomass were not significant between depths, and higher values were found in September (88–100 g AFDW m^{-2} or 32–36 g C m^{-2}). Biomass turnover time (BTT) ranged between 4.6 and 14.1 days for turfs at 4 m, and from 22.3 to

159.3 days for turfs at 10 m. There was a trend of decreasing biomass and productivity rates with plate age, however differences were not significant due to the high variability found within groups (Table 2).

Total net production over the year ranged between 171 and 765 g C m^{-2} across depths. The total carbon produced was higher from spring to autumn, than it was from autumn to spring (Table 3). Estimated carbon losses were very high, accounting in general for 90–110% of the total carbon produced during a season (except for 10 m in winter), with lower rates of losses occurring during autumn and winter (Table 3).

DISCUSSION

Turf-forming algae form a conspicuous component of benthic algae observed on South Australian coasts. In one locality on the Eyre Peninsula turf-forming algae were the spatially dominant occupiers of space, but in most localities these algae only occupied less than 10% of the available rock. These observations indicate that while canopy-forming algae are the major occupiers of subtidal rock, turf-forming algae can be extensive. Although canopy-forming algae represented the dominant space occupiers, there has been a trend for loss of these habitats with increasing coastal sedimentation and eutrophication and their replacement by turf-forming algae on local South Australian coasts (Cheshire & Turner 2000; Gorgula & Connell 2004) and globally (Airoldi & Virgilio 1998; Worm *et al.* 1999).

Turf-forming algae act as habitat for a diverse suite of mobile invertebrates, which primarily form the diet of some fish (e.g. Wellenreuther & Connell 2002). In South Australia reduction in the spatial extent of turfing-algae profoundly reduces the distribution and abundance of invertebrates whose abundance effects the foraging activities of fish (Connell 2002; Wellenreuther & Connell 2002). Despite this importance of turf-forming algae, ecologists have primarily considered the consequences of changes to canopy-forming algae on invertebrates (e.g. Goodsell & Connell 2002; Goodsell *et al.* 2004) and fish (Choat & Ayling 1987). The current study adds weight to the emerging importance of turf-forming habitats and the need to understand their spatial and temporal prevalence and productivity.

Assemblages of turf-forming algae at West Island were extremely productive, with daily rates comparable to the values identified on tropical reefs obtained by similar methodology (Table 4). The reasons for such a high productivity under lower average light and temperature of South Australian rock reefs are still unclear.

Production is not only a function of light and temperature, but also of nutrient status, water motion and grazer pressure (Lobban & Harrison 1997). High nitrogen levels found in turf algal tissue during the study period raised the hypothesis that production is not nitrogen-limited at West Island (Copertino 2002). However, the low levels of nutrients found in the water and recent experimentation on nutrient enrichment of benthic communities suggest that turf production is nutrient-limited on South Australian reefs, including West Island (Gorgula & Connell 2004; B.D. Russell & S.D. Connell, unpublished data). Productivity is also characteristically high on high-energy shores (Lobban & Harrison 1997), such as the temperate

Table 2. Standing biomass, net primary production on areal (NPP) and biomass basis (BeNPP), ratio of gross daily production to total daily respiration (GPP:R) and biomass turnover time (BTT) for turf algal communities growing on plates averaged per month (after 6 months of growth) and per plate age (recorded only in March 2000) for the depths of 4 m and 10 m. Standard error values are given in parentheses.[1]

	Biomass (g AFDW m⁻²)		BeNPP (mg C g AFDW⁻¹ day⁻¹)		NPP (g C m⁻² day⁻¹)		GPP:R		BTT (days)	
	4 m	10 m	4 m	10 m	4 m	10 m	4 m	10 m	4 m	10 m
Month										
Sep.	100.5	88.4	34.3	8.6	2.9	0.6	2.4	1.3	11.3	47.2
	(8.04)	(11.80)	(3.58)	(1.50)	(0.16)	(0.08)	(0.06)	(0.03)	(0.92)	(39.43)
Dec.	50.1	60.9	67.2	11.9	2.0	0.6	2.4	1.6	7.8	33.0
	(10.18)	(8.20)	(14.57)	(1.65)	(0.21)	(0.06)	(0.13)	(0.06)	(0.96)	(4.05)
Mar.	31.9	41.8	88.0	19.8	2.4	0.6	3.9	2.8	4.6	22.3
	(5.43)	(4.98)	(10.06)	(3.06)	(0.40)	(0.07)	(0.36)	(0.94)	(0.48)	(11.75)
Jun.	46.9	49.7	23.2	2.5	1.3	0.1	3.6	1.3	14.1	159.3
	(3.97)	(4.42)	(1.23)	(0.53)	(0.07)	(0.04)	(0.27)	(0.07)	(0.46)	(27.78)
Plate age (months)										
3	44.7	60.9	73.0	21.0	2.2	0.6	2.6	1.6	6.5	32.5
	(16.32)	(16.40)	(12.48)	(3.58)	(0.36)	(0.12)	(0.63)	(0.12)	(1.79)	(5.89)
6	39.9	39.3	49.2	20.2	1.5	0.6	1.6	1.9	8.5	21.5
	(13.01)	(11.89)	(8.45)	(6.93)	(1.16)	(0.23)	(0.58)	(2.60)	(1.57)	(5.08)
9	33.9	44.6	64.0		1.9		5.4	2.0	5.7	
	(9.08)	(11.89)	(4.20)		(0.13)		(0.45)	(0.23)	(1.12)	
18	25.5	67.5	57.3	27.6	1.7	0.8	3.0	1.9	4.8	27.2
	(4.56)	(21.54)	(6.80)	(4.45)	(0.22)	(0.12)	(0.40)	(0.23)	(0.89)	(6.41)

[1] AFDW, ash-free dry weight.

coast of South Australia (Womersley 1990). While high water motion enhances nutrient uptake and photosynthetic rates of turfs, due to the reduction of the boundary layer effects over algal patches (Carpenter *et al.* 1991; Williams and Carpenter 1998), the role of this factor on the production of turfs cannot be evaluated from the present study. Grazing pressure can affect productivity rates by removing excessive biomass, which reduces self shading, and enhances water flow and nutrient availability. However, grazer pressure on turfs is low in South Australian reefs (Fowler-Walker & Connell 2002) including West Island (S.D. Connell, unpublished data). More detailed studies should be done before evaluation of the main abiotic and biotic factors affecting productivity rates of turfs on these reefs.

Net production did not accumulate as standing biomass, being removed or lost at high rates. From September to March (during spring and summer), the total net production was estimated in 418 (± 189) and 108 (± 46) g C m⁻², respectively,

Fig. 4. Average maximum photosynthetic photon flux density (PPFD) per month (right axis) at the depths of 4 m (solid line) and 10 m (dashed line), temperature per month (left axis, dotted line) and day length in hours (numbers at the top) during the study period.

for 4-m and 10-m turfs. At the end of this 6-month period, the observed standing biomass of 6-month-old plates averaged 10.2 (4 m) and 13.4 (10 m) g C m⁻², which represents 2% and 12% (respectively) of the total net production. The cause of this loss was not determined.

Grazers are a key cause of loss of turf-forming algae in many parts of the world (Littler & Littler 1984; Andrew 1993; Sala & Boudouresque 1997). While such grazing pressure in South Australia appears weak (Fowler-Walker & Connell 2002), molluscan grazers at West Island (Clarkson & Shepherd 1985) are likely to be the most effective grazers of filamentous turfs. During the peak season of production of filamentous turfs at West Island, however, molluscan grazing has negligible effects under ambient nutrient concentrations (B.D. Russell & S.D. Connell, unpublished experimental data). It is worth noting, however, that molluscs can reduce percentage cover of filamentous turfs (by up to ~15%) when nutrient concentrations are enhanced to match those on human-dominated coast (S.D. Connell, unpublished data). We suggest that the observed loss of turf-forming algae on a 'natural' coast of South Australia is a consequence of physical processes that we are yet to fully understand, but whose timing occurs with striking predictability.

Daily rates of *in situ* productivity for subtidal turfs on temperate coasts are scarce (but see Westphalen & Cheshire 1997). Rates of net productivity per hour observed in this study (3.2–5.4 mg C g AFDW⁻¹ h⁻¹) are comparable to functional groups of sheet-like algae (2–11 mg C g DW⁻¹) and filamentous algae (0.5–5.5 mg C g DW⁻¹) growing on intertidal rock (Littler & Arnold 1982; Littler & Littler 1984). Average productivity at West Island is higher than the average for filamentous species found in previous studies, even considering a conversion of dry weight to ash-free dry weight. One reason for this difference could be the higher clumping
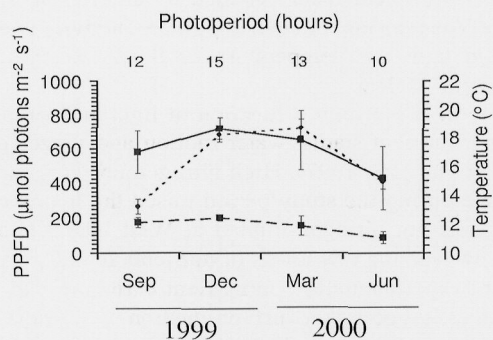
Table 3. Total net primary production (T-NPP), biomass gain (difference in standing biomass between two sampling periods) and estimated carbon losses for turfs during each season (90 days between two sampling periods). Standard error values are given in parentheses.

	T-NPP (g C m^{-2} 90 days^{-1})		Biomass balance[1] (g C m^{-2} 90 days^{-1})		Carbon losses			
					(g C m^{-2} 90 days^{-1})		% of T-NPP	
	4 m	10 m	4 m	10 m	4 m	10 m	4 m	10 m
Winter	189	32	19.3	13.9	169.7	18.1	90	61
(Jun. to Sep.)	(45)	(18)	(2)	(6.4)	(41)	(11)		
Spring	220	54	−18.1	−9.9	238.1	63.9	110	116
(Sep. to Dec.)	(72)	(23)	(12.9)	(4)	(77)	(27)		
Summer	198	54	−6.6	−6.6	204.6	60.6	103	111
(Dec. to Mar.)	(117)	(23)	(4.4)	(3.3)	(120)	(26)		
Autumn	166	31	5.4	2.8	160.6	28.2	98	92
(Mar. to Jun.)	(90)	(19)	(1.21)	(0.6)	(87)	(17)		

[1] Conversion factor from ash-free dry weight (AFDW) to carbon is 0.36.

of some monospecific stands of filamentous algae in the studies by Littler & Arnold (1982) and Littler & Littler (1984), decreasing the surface-area : volume ratios and photosynthetic efficiency.

Standing biomass and productivity rates for turfs are compared to the values found for canopy-forming algae at West Island, which were obtained using the same methodology (Table 5). Indeed, values for the kelp *E. radiata* were obtained over the same sampling periods (Fairhead 2002). Productivity rates for canopy-forming algae at West Island are similar to those found in Northern Hemisphere temperate macroalgae (5–10 g C m^{-2} day^{-1}; Mann *et al.* 1980). Although turfs were much more productive on a biomass basis, their production per area is lower compared to the local kelp and fucoids (Table 5). Total net production of turfs at a depth of 4 m (773 g C m^{-2} yr^{-1}) is about two and seven times lower than the values obtained for fucoids (Cheshire *et al.* 1996) and for the kelp *E. radiata* (Fairhead 2002), respectively. The obvious reason for that difference is the much higher biomass of the large macroalgae. However, the proportion of carbon incorporated into biomass of large macroalgae can be much lower, due to the high exudation rates that can vary between 10% and 40% of the net production of the algae, depending on nutrient conditions and carbon metabolism (see Mann *et al.* 1980 and Lobban & Harrison 1997 for a review). Through

measurements of productivity rates (oxygen evolution) and growth (elongation and biomass accumulation), it has been estimated that carbon incorporated into biomass of *E. radiata* in West Island accounts for 20–42% (across depths) of annual net production, with the balance released as exudates (Fairhead 2002). Exudation rates for turfs are considered negligible by some authors (Carpenter 1985), not being more than 1% of the net production (estimated for filamentous algae; Hackney & Sze 1988). Thus, the amount diverted into biomass of turfs is probably not less than 765 (4 m) and 169 (10 m) g C m^{-2} yr^{-1}, which represents 71% and 44% of the total carbon incorporated into biomass of kelps at the depths of 3 m and 10 m, respectively. While complete biomass turnover for turfs ranged between 29 (4 m) and 79 (10 m) times in a year, it has been estimated that the tissues of the kelp and fucoids can turnover on average 2.6 (Fairhead 2002) and 5.8 times per year (Cheshire *et al.* 1996). We acknowledge that productivity can vary greatly in space and time given such differences in light, grazing and exposure to wave action (Klumpp & McKinnon 1989, 1992; Russ & McCook 1999), but the values we report are counter to the idea that the productivities of turfs are considered negligible relative to larger canopy-forming algae.

In conclusion, we accept that productivity of turf-forming algae is likely to vary greatly from place to place and time to

Table 4. Standing biomass, net primary productivity rates (NPP) and biomass specific net productivity (BeNPP) in percentage of biomass found for turfs in tropical and temperate regions.

Geographic region	Depth (m)	Biomass (g C m^{-2})	NPP (g C m^{-2} day^{-1})	BeNPP	Reference
Great Barrier Reef	1	2.6–3.9	0.3–1.4	11–36	Borowitzka *et al.* 1983[1]
	~2	23–32	1.2–1.7	3.3–5.6	Klumpp & McKinnon 1989[1]
	10	13–22	0.8–1.2		Klumpp & McKinnon 1989[1]
	~2	25–35	0.7–2.5	3.0–1	Klumpp & McKinnon 1992
	10	15–20	0.4–0.8	2.5–5	Klumpp & McKinnon 1992
Caribbean reefs	2	5.6–11.2	2.1–3.1	21–46	Carpenter 1985[1]
	5		1.7		Carpenter 1985
	10		1.1		Carpenter 1985
	1.5–2	6.2–12.4	1.5–2.1	17–24	Carpenter 1986[1]
South Australia	4		0.1–0.9		Westphalen & Cheshire 1997
(West Island)	4	10–32	1.3–2.9	7–28	Present work
	10	13–28	0.1–0.6	0.8–6	Present work

[1] Values converted from dry weight (original data) to carbon by applying a factor of 0.32 (Carpenter 1985).

Table 5. Standing biomass (g C m^{-2}), net primary productivity rates per day (NPP; g C m^{-2} day^{-1}), biomass specific net primary productivity rates per day (BeNPP; % of biomass), total net production per year (TNPP; g C m^{-2} y^{-1}), estimated exudation rates (Exu; proportion of NPP) and total biomass production per year (TBP; g C m^{-2} y^{-1}) for a dominated fucoid community, the kelp *Ecklonia radiata* and turfs growing on plates at West Island.

	Depth (m)	Biomass	NPP	BeNPP	TNPP	Exu[1]	TBP	Reference
Fucoids	4	225	2.6–6	0.9–3	1444	0.10–0.40	866–1299	Cheshire *et al.* 1996
Kelp	3	410	14.8	2.7–4.4	5470	~0.80	1079	Fairhead 2002
	10	241	2.5	0.09–0.36	921	~0.58	384	
Turfs	4	10–32	1.3–2.9	7–28	773	up to 0.1	765	Present work
	10	13–28	0.1–0.6	0.8–6	171		169	

[1] Exudation rates for fucoids and turfs are based on literature values.

time, as the species composition within this functional group is notoriously diverse (Carpenter 1986; Scott & Russ 1987; Copertino 2002). Nevertheless, the average productivity values found at West Island and the extensive covers of turfs found on some reefs suggests that the contribution of turfs to the total carbon produced in a temperate reef can be extremely high, particularly considering the production of carbon incorporated into biomass. As turf-forming algae increase their spatial extent on the world's temperate reefs (Gorgula & Connell 2004), a more detailed consideration of their ecology and ecophysiology is essential to understand the relative role of the biotic and abiotic factors affecting the production, distribution and abundance of these communities.

ACKNOWLEDGEMENTS

REFERENCES

Adey W.H. 1998. Coral reefs: algal structured and mediated ecosystems in shallow turbulent, alkaline waters. *Journal of Phycology* 34: 393–406.

Adey W.H. & Goertemiller T. 1987. Coral reef algal turfs: master producers in nutrient poor seas. *Phycologia* 26: 374–386.

Airoldi L. 2003. The effects of sedimentation on rocky shore assemblages. *Oceanographic, Marine and Biological Annual Review* 41: 161–236.

Airoldi L. & Virgilio M. 1998. Responses of turf-forming algae to spatial variations in the deposition of sediments. *Marine Ecology Progress Series* 165: 271–282.

Andrew N.L. 1993. Spatial heterogeneity, sea urchin grazing, and habitat structure on reefs in temperate Australia. *Ecology* 74: 292–302.

Atkinson M.J. & Smith S.V. 1983. C:N:P ratios of benthic marine plants. *Limnology and Oceanography* 28: 568–574.

Borowitzka M.A., Day R. & Larkum A.W.D. 1983. The importance of primary production by turf and crustose algal communities in

One Tree Lagoon. In: *Great Barrier Reef Conference* (Ed. by J. Baker, R. Carter, P. Sammarco & K. Stark), pp. 287–292. James Cook University and Australian Institute of Marine Science, Townsville, Australia.

Carpenter R.C. 1985. Relationships between primary production and irradiance in coral reef algal communities. *Limnology and Oceanography* 30: 784–793.

Carpenter R.C. 1986. Partitioning herbivory and its effects on coral reef algal communities. *Ecological Monographs* 56: 345–363.

Carpenter R.C., Hackney J.M., & Adey W.H. 1991. Measurements of primary productivity and nitrogenase activity of coral reef algae in a chamber incorporating oscillatory flow. *Limnology and Oceanography* 36: 40–49.

Chalker B.E., Carr K. & Gill E. 1985. Measurement of primary production and irradiance in coral reef algal communities. *Limnology and Oceanography* 30: 784–793.

Cheshire A.C. & Turner D.J. 2000. Effect of dispersed sediment plumes from beach sand replenishment dredging on recruitment of phaeophycean algae to rocky reefs in Gulf St. Vincent, South Australia II: 1999 surveys. In: *The impact of sand dredging on benthic community structure at the Port Stanvac dredge site*, vol. 5. The University of Adelaide, A Report for Environmental Protection Authority, Adelaide, Australia.

Cheshire A.C., Westphalen G., Wenden A., Scriven L.J. & Rowland B.C. 1996. Photosynthesis and respiration of phaeophycean-dominated macroalgal communities in summer and winter. *Aquatic Botany* 55: 159–170.

Choat J.H. & Ayling A.M. 1987. The relationship between habitat structure and fish faunas on New Zealand reefs. *Journal of Experimental Marine Biology and Ecology* 110: 257–284.

Clarkson P.S. & Shepherd S.A. 1985. Distribution and feeding of archaeogastropods in a boulder habitat at West Island, South Australia. *Journal of the Malacological Society of Australia* 7: 35–44.

Connell S.D. 2002. Effects of a predator and prey on a foraging reef fish: implications for understanding density-dependent growth. *Journal of Fish Biology* 60: 1551–1561.

Copertino M. 2002. Production ecology and ecophysiology of turf algal communities on a temperate reef (West Island, South Australia). PhD thesis. The University of Adelaide, Adelaide, Australia. 293 pp.

Edwards M.S. 1998. Effects of long-term kelp canopy exclusion on the abundance of the annual alga *Desmarestia ligulata* (Light F.). *Journal of Experimental Marine Biology and Ecology* 228: 309–326.

Fairhead A.V. 2002. The ecophysiology and production ecology of the kelp *Ecklonia radiata* (C. Agardh) J. Agardh, at West Island, South Australia. PhD thesis. The University of Adelaide, Adelaide, Australia. 166 pp.

Flores-Moya A., Fernandez J.A. & Niell F.X. 1993. Reproductive phenology, growth and primary production of *Phyllariopsis purpurascens* (Phyllariaceae, Phaeophyta) from the Straits of Gibraltar. *European Journal of Phycology* 28: 223–230.

Fowler-Walker M.J. & Connell S.D. 2002. Opposing states of subtidal habitat across temperate Australia: consistency and predict-

ability in kelp canopy–understorey associations. *Marine Ecology Progress Series* 240: 49–56.

GAGNÉ J.A., MANN K.H. & CHAPMAN A.R.O. 1982. Seasonal patterns of growth and storage in *Laminaria longicruris* in relation to differing patterns of availability of nitrogen in the water. *Marine Biology* 69: 91–102.

GOODSELL P.J. & CONNELL S.D. 2002. Can habitat loss be treated independently of habitat configuration? Implications for rare and common taxa in fragmented landscapes. *Marine Ecology Progress Series* 239: 37–44.

GOODSELL P.J., FOWLER-WALKER M.J., GILLANDERS B.M. & CONNELL S.D. 2004. Variations in the configuration of algae in subtidal forests: implications for invertebrate assemblages. *Austral Ecology* 29: 350–357.

GORGULA S.K. & CONNELL S.D. 2004. Expansive covers of turf-forming algae on human-dominated coast: the relative effects of increasing nutrient and sediment loads. *Marine Biology* 145: 613–619.

HACKNEY J.M. & SZE P. 1988. Photorespiration and productivity rates of a coral reef algal turf assemblage. *Marine Biology* 98: 483–492.

HATCHER B.G., KIRKMAN H. & WOOD W.F. 1987. Growth of the kelp *Ecklonia radiata* near the northern limit of its range in Western Australia. *Marine Biology* 95: 63–72.

IRVING A.D. & CONNELL S.D. 2002. Interactive effects of sedimentation and microtopography on the abundance of subtidal turf-forming algae. *Phycologia* 41: 517–522.

IRVING A.P., CONNELL S.D. & GILLANDERS B.M. 2004. Local complexity in patterns of canopy–benthos associations produce regional patterns across temperate Australasia. *Marine Biology* 144: 361–368.

JASSBY A.D. & PLATT T. 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. *Limnology and Oceanography* 21: 540–547.

KIRK J.T.O. 1994. *Light and photosynthesis in aquatic environments.* Cambridge University Press, Cambridge. 509 pp.

KIRKMAN H. 1984. Standing stock and production of *Ecklonia radiata.* *Journal of Experimental Marine Biology and Ecology* 76: 119–130.

KIRKMAN H. 1989. Growth, density and biomass of *Ecklonia radiata* at different depths and growth under artificial shading off Perth, Western Australia. *Australian Journal of Marine and Freshwater Research* 40: 169–178.

KLUMPP D.W. & McKINNON A.D. 1989. Temporal and spatial patterns in primary production of a coral-reef epilithic algal community. *Journal of Experimental Marine Biology and Ecology* 131: 1–22.

KLUMPP D.W. & McKINNON A.D. 1992. Community structure, biomass and productivity of epilithic algal communities on the Great Barrier Reef: dynamics at different spatial scales. *Marine Ecology Progress Series* 86: 77–89.

LARKUM A.W.D. 1986. A study of growth and primary production in *Ecklonia radiata* (Laminariales) at a sheltered site in Port Jackson, New South Wales (Australia). *Journal of Experimental Marine Biology and Ecology* 96: 177–190.

LITTLER M.M. & ARNOLD K.E. 1982. Primary productivity of marine macroalgal functional-form groups from southwestern North America. *Journal of Phycology* 18: 307–311.

LITTLER M.M. & LITTLER D.S. 1984. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. *The American Naturalist* 116: 25–44.

LOBBAN C.S. & HARRISON P.J. 1997. *Seaweed ecology and physiology.* Cambridge University Press, Cambridge. 366 pp.

LÜNING K. 1979. Growth strategies of three *Laminaria* species (Phaeophyceae) inhabiting different depth zones in the sublittoral region of Helgoland (North Sea). *Marine Ecology Progress Series* 1: 195–207.

MANN K.H., CHAPMAN A.R.O. & GAGNÉ J.A. 1980. Productivity of seaweeds: the potential and the reality. In: *Primary productivity in the sea* (Ed. by P. G. Falkowski), pp. 363–379. Plenum, New York.

MELVILLE A.J. & CONNELL S.D. 2001. Experimental effects of kelp canopies on subtidal coralline algae. *Austral Ecology* 26: 102–108.

RUSS G.R. & McCOOK L.J. 1999. Potential effects of a cyclone on benthic algal production and yield to grazers on coral reefs across the central Great Barrier Reef. *Journal of Experimental Marine Biology and Ecology* 235: 237–254.

SALA E. & BOUDOURESQUE C.F. 1997. The role of fishes in the organization of a Mediterranean sublittoral community. 1. Algal communities. *Journal of Experimental Marine Biology and Ecology* 212: 25–44.

SCOTT F.J. & RUSS G.R. 1987. Effects of grazing on species composition of the epilithic algal community on coral reefs of the central Great Barrier Reef. *Marine Ecology Progress Series* 39: 293–304.

STEWART J.G. 1983. Fluctuations in the quantity of sediments trapped among algal thalli on intertidal rock platforms in southern California. *Journal of Experimental Marine Biology and Ecology* 73: 205–211.

UNDERWOOD A.J., KINGSFORD M.J. & ANDREW N.L. 1991. Patterns in shallow subtidal marine assemblages along the coast of New South Wales. *Australian Journal of Ecology* 6: 231–249.

WEBB W.L., NEWTON M. & STARR D. 1974. Carbon dioxide exchange of *Alnus rubra*: a mathematical model. *Ecologia* 17: 281–291.

WELLENREUTHER M. & CONNELL S.D. 2002. Response of predators to prey-abundance: separating the effects of prey-density and patch-size. *Journal of Experimental Marine Biology and Ecology* 273: 61–71.

WESTPHALEN G. & CHESHIRE A.C. 1997. Quantum efficiency and photosynthetic production of a temperate turf algal community. *Australian Journal of Botany* 45: 343–349.

WHEELER W.N. & DRUEHL L.D. 1986. Seasonal growth and productivity of *Macrocystis integrifolia* in British Columbia, Canada. *Marine Biology* 90: 181–186.

WILLIAMS S.L., & CARPENTER R.C. 1998. Effects of unidirectional and oscillatory water flow on nitrogen fixation (acetylene reduction) in coral reef algal turfs, Kaneohe Bay, Hawaii. *Journal of Experimental Marine Biology and Ecology* 2: 293–316.

WOMERSLEY H.B.S. 1990. Biogeography of Australian marine macroalgae. In: *Biology of marine plants* (Ed. by M.N. Clayton & R.J. King), pp. 367–382. Longman Cheshire, Melbourne, Australia.

WORM B., LOTZE H., BOSTROM C., ENGKVIST R., LABANAUSKAS V. & SOMMER U. 1999. Marine diversity shift linked to interactions among grazers nutrients and propagule banks. *Marine Ecology Progress Series* 185: 309–314.

ZAR J.H. 1996. *Biostatistical analysis.* Prentice Hall, Upper Saddle River, NJ, USA. 662 pp.