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Effects of algal turfs and sediment accumulation on replenishment and primary productivity of fucoid assemblages

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ABSTRACT: As a result of anthropogenic habitat degradation worldwide, coastal ecosystems are increasingly dominated by low-lying, turf-forming species, which proliferate at the expense of complex biogenic habitats such as kelp and fucoid canopies. This results in dramatic alterations to the structure of the associated communities and large reductions in primary productivity. The persistence of turf-dominated systems has been attributed to the impacts of the turfs on the recovery of algal canopies and also to the different susceptibility of canopy- and turf-forming algae to altered physical conditions, in particular increased sedimentation. Here we tested the impacts of turfing geniculate coralline algae and sediment on fucoid recovery dynamics and their influence on assemblage net primary productivity (NPP). The recruitment of the habitat-forming fucoid *Hormosira banksii* on bare substrata was significantly higher than in treatments in which sediments, coralline turfs or turf mimics covered the substratum, indicating that sediment deposition and space pre-emption by algal turfs can synergistically affect the development of fucoid beds. NPP of coralline turfs was much lower than that of fucoid-coralline assemblages, which included a *H. banksii* canopy, and was reduced further by sediment accumulation. When devoid of sediment, however, coralline algae contributed to enhance fucoid-coralline assemblage NPP, because of synergistic interactions among the components of the multi-layered assemblage in optimizing light use. Our findings amplify extensive research addressing the global loss of macroalgal canopies and highlight key processes involving sediment accumulation in the benthic environment and effects on the replenishment and productivity of fucoid stands.

KEY WORDS: Canopy · Coralline algae · Habitat structure · Intertidal · Macroalgae · Photosynthesis · Sediment · Turf-forming

INTRODUCTION

Nearshore ecosystems are increasingly under pressure from anthropogenic activities, many of which have the potential to cause widespread changes to ecosystem structure and functioning (Halpern et al. 2008, Crain et al. 2009, Schiel 2009). The fragmentation and loss of structurally complex habitats, shaped by canopy-forming macroalgae (kelps and fucoids), for example, have been reported worldwide (Steneck et al. 2002, Airoldi et al. 2008, Connell et al. 2008, Raybaud et al. 2013). In degraded environments, the recovery of algal canopies is usually inhibited by the rapid proliferation of low-lying, turf-forming algae, resulting in dramatic shifts to simplified systems with long-term impacts on community structure (Kennelly 1987, Connell et al. 2008, Bellgrove et al. 2010) and functioning (Tait & Schiel 2011a).

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Turf-forming algae are a widespread and taxonomically diverse group of species with variable morphologies, ranging from filamentous to calcareous-articulated forms (Airoldi 2001, Connell et al. 2014). Independent of their composition, algal turfs are abundant in disturbed areas because of their ability to tolerate stressful conditions, such as elevated nutrient and sediment loads (Airoldi & Virgilio 1998, Gorgula & Connell 2004). Sediment, in particular, is considered a structural component of algal turfs because it is often trapped in great abundance within their densely packed, mat-like structure (Airoldi & Virgilio 1998, Airoldi 2003). Differences among taxa in their ability to tolerate sediment may explain the concomitant increase in spatial dominance of algal turfs and regression of canopy stands (Airoldi et al. 2008, Connell et al. 2008). Increased sediment loads can have strong impacts on the early life stages of kelps and fucoids (Vadas et al. 1992, Schiel & Foster 2006, Schiel et al. 2006, Irving et al. 2009), and many studies have suggested that turfs and sediments may provide positive feedbacks to each other, thereby contributing to preventing the recovery of algal canopies (Airoldi & Virgilio 1998, Connell 2005, Bellwood & Fulton 2008).

Such processes may be particularly relevant to New Zealand's coastlines, which are affected by exceptionally high sediment loads originating from geological and climatic processes as well as human land use (Griffiths & Glasby 1985, Goff 1997). Algal assemblages in mid-intertidal regions in New Zealand are occupied by canopies of the fucoid macroalga *Hormosira banksii*, while algal turfs composed of geniculate coralline algae are usually the main benthic space occupiers (Schiel 2004, 2006). *H. banksii* is a key foundation species, and research in New Zealand and Australia has described dramatic structural changes following its loss, with a rapid monopolization of the substratum by extensive mats of articulated coralline algae (Lilley & Schiel 2006, Bellgrove et al. 2010, Schiel & Lilley 2011). These studies highlighted negative impacts of coralline turfs on the recruitment of *H. banksii*, showing how increasing abundance and thickness of the turfs can contribute to the decline of this fucoid. None of them, however, tested the influence of sediment accumulation within the turfs on *H. banksii*. Furthermore, little is known about the consequences of sediment build-up within coralline turfs on assemblage productivity. The primary productivity of coralline algae is generally considered negligible compared to canopy-forming species (Littler & Arnold 1982, Tait & Schiel 2011b). As a consequence, the loss of structural complexity associated with the advent of coralline turfs is likely to result in a substantial and long-lasting loss of ecosystem function (Tait & Schiel 2011a,b), especially under elevated sediment loads.

Here we examined the influence of sediment on the interactions between *H. banksii* and turf-forming coralline algae and their implications for the functioning of intertidal autotrophic assemblages. We first tested how coralline turfs can affect the recruitment of *H. banksii* by altering the physical properties of the benthic environment and the dynamics of sediment accumulation. Algal turfs are known to competitively exclude other algal species through the monopolization of primary substratum and the creation of a complex biogenic surface unsuitable for colonization (Britton-Simmons 2006, Daleo et al. 2006). We expected sediment to compound the impact of coralline turfs on the recruitment of *H. banksii*, both by accumulating within the turfs and through the deposition on unoccupied substrata. In addition, using *in situ* and laboratory photorespirometry techniques (Tait & Schiel 2010), we evaluated the contribution of coralline algae to assemblage net primary productivity (NPP) and the impacts of sediment accumulation within coralline turfs. We expected coralline turf NPP to be significantly lower than that of experimental assemblages including *H. banksii* canopy, especially in the presence of sediment.

MATERIALS AND METHODS

Field experiments were done at Wairepo Reef, Kaikoura, New Zealand (42° 25′ S, 173° 42′ E), a large intertidal platform where fucoid species and turfs of geniculate coralline algae (predominantly *Corallina officinalis*) coexist in high abundance (see Lilley & Schiel 2006 for full site description), providing the opportunity to investigate the nature and strength of their interactions. Because of coastal erosion and riverine inputs, the waters surrounding Kaikoura are characterized by elevated sediment loads, with large quantities of sediment (mainly fine sand; grain size 100 to 250 µm) accumulating in the benthic environment in many places, especially within the turfs (Schiel et al. 2006, Hurley 2009). Previous studies in Kaikoura highlighted a negative relationship between the recruitment of fucoid macroalgae, including *Hormosira banksii*, and the abundance of turf-forming species and deposited sediment in the benthic environment (Schiel et al. 2006, Hurley 2009).

Impacts of coralline turfs and sediment on *H. banksii* recruitment

To examine the mechanisms regulating the impacts of algal turfs on canopy recovery, we tested the influence of 3 distinctive traits of coralline turfs on the recruitment of *H. banksii*: (1) the rapid preemption of primary substrata; (2) the creation of morphologically complex habitats; and (3) the retention of sediment. To tease out the impact of each of these factors on *H. banksii*, we monitored its recruitment over a period of 12 mo in 5 experimental habitat types: (1) coralline turf; (2) bare rock; (3) artificial turf; (4) artificial turf control; and (5) fucoid-coralline assemblage. Along a 1 km stretch of shore, twelve 25 × 25 cm replicate plots of each habitat were set up in the mid-intertidal zone (0.5 to 1 m above the lowest astronomical tide level). Coralline turf plots were occupied by articulated corallines only (with a mean percentage cover ~90 %), while all other algal species (which were in low abundances) were removed. Bare rock plots were obtained through the complete clearing of all algal species. The artificial turf plots were patches of synthetic grass glued to fibrolite plates and were fitted flush with the substratum using a hammer and chisel to create a depression. This material is considered to be a reasonably good mimic for coralline turfs, as it is characterized by an analogous dense mat-like structure (Kelaher 2002). The artificial fronds were 10 mm long, similar to the branches of coralline algae at our study site, and produced a 3-dimensional matrix that was capable of trapping sediment. We compared *H. banksii* recruitment rates between coralline turf and bare rock plots to assess the impact of space preemption by the turfs, and between coralline turfs and artificial mimics to evaluate the importance of the physical complexity of the corallines, separating it from the influence of alternative mechanisms such as the release of allelopathic compounds (Jeong et al. 2000, Kim et al. 2004), or the breakage of the fronds. In addition, we used artificial turf control plates with the fronds removed to ensure that the effects produced by such artificial habitats were related to their morphological complexity. Finally, we also included fucoid-coralline assemblage plots consisting of a basal layer of coralline turf (mean percentage cover ~90 %) and a canopy of *H. banksii* (mean percentage cover ~85 %), because at our study site, zones covered exclusively by corallines alternate with zones where *H. banksii* canopies and turfs coexist. These fucoid-coralline assemblage plots were used to tease out the influence of coralline turfs from that of the overlying canopy.

Before the start of the experiment, new recruits of *H. banksii* were absent from all habitats, and all experimental units were cleared of sediment using a hose connected to a bilge pump, to ensure the initial conditions were the same for all treatments. To evaluate the impact of sediment accumulation in the benthic environment, half of the replicates of each habitat were assigned to periodic sediment removal throughout the duration of the experiment (12 mo). Every 2 wk, the sediment was gently washed from the plots, ensuring that coralline algae and *H. banksii* recruits were not affected. Similar sediment manipulation procedures were previously used at this location without any impact on small fucoid recruits (Hurley 2009).

Rates of sediment deposition were estimated before the start of the experiment by measuring the dry weight of sediment accumulating within 12 additional 25 × 25 cm coralline turf plots. These plots were first simultaneously cleared of sediment, and sediment samples were collected from 3 of them to establish a baseline level. Successively, all plots were again cleared of sediment, 4 at a time at intervals of 5 d (15 d in total) and sediment was collected to estimate its rate of accumulation. The rate of sediment accumulation per plot was around 9 g d^{-1} (equivalent to 144 g m^{-2} d^{-1}) and after 15 d the amount of sediment trapped within the turfs was back to the original levels of around 150 g per plot (equivalent to 2400 g m^{-2} d^{-1}). These estimates are in line with the rates of sediment deposition previously recorded in Kaikoura (Schiel et al. 2006, Hurley 2009).

The percentage cover of *H. banksii* recruits colonizing the 5 experimental habitats under ambient and reduced sedimentation was measured after 3, 6, 9 and 12 mo from the start of the experiment. In the coralline turf and fucoid-coralline assemblage plots, there were small patches of unoccupied substratum; we recorded only the percentage cover of the recruits growing within the turfs in these plots. Because of their slow growth rates, the recruits were always clearly distinguishable from the adults. In contrast to the frondose, canopy-forming structure of the adults (with thalli 15 to 20 cm long), the recruits presented short, erect, tubular thalli (< 2 cm long), and their percentage cover accurately reflected their density. At the end of the experiment, however, we also counted the number of the recruits within each plot, and we measured the lengths of 10 randomly selected recruits in each plot.

Net primary productivity

To test the impact of coralline algae and sediment on assemblage primary productivity, we measured changes in dissolved oxygen as a proxy for net primary productivity (NPP) for 2 habitat types: fucoid-coralline assemblages (i.e. coralline turf + *H. banksii* canopy) and coralline turf alone, each with 2 levels of sediment in the turf (present/removed). NPP of both fucoid-coralline assemblages and coralline turfs was determined by incubating algae in sealed photorespirometry incubation chambers filled with seawater. The chambers were composed of a clear Perspex cylinder closed on top by a lid and could be fitted around macroalgal assemblages attached to the reef surface, or used in the laboratory to incubate algae removed from the shore (Tait & Schiel 2010 for details). For both habitat types, coralline algae occupied ~90% of the substratum enclosed within the chambers (276 cm^2), while *H. banksii* canopy, when present, had a percentage cover of ~85%. To evaluate the interactions between coralline turf and the *H. banksii* canopy, other sub-canopy species, which can add substantially to the NPP of intact assemblages (Tait & Schiel 2011b), were removed from the experimental plots by carefully picking them off by hand. These included the fucoids *Cystophora torulosa* and *Carpophyllum maschalocarpum* and several ephemeral species.

NPP of both habitat types was estimated through *in situ* and laboratory incubations. In the field, the chambers were fixed around existing macroalgal assemblages, randomly assigned to 1 of the 4 combinations of experimental treatments (fucoid-coralline assemblage + sediment; fucoid-coralline assemblage − sediment; coralline turf + sediment; coralline turf − sediment), each replicated 4 times. The incubations were completed under full sunlight (1500 to 2000 µmol photons m^{-2} s^{-1}) during the summer months (from December 2010 to February 2011). Irradiance was measured with a LiCor meter (LI-192 quantum sensor). Each replicate in the field was incubated on 2 different days at approximately the same time (between 10:00 and 13:00 h) for no longer than 40 min. This ensured that super-saturation of oxygen did not occur and that essential nutrients were not depleted (Tait & Schiel 2010). In the replicates allocated to sediment removal, coralline algae were cleared of sediment immediately before the incubations using the procedures outlined in the previous subsection.

Field incubations were performed during periods of partial emersion between consecutive high tides to assess the influence of the experimental factors on NPP during periods of similar light conditions. However, to account for potential variability in the light conditions, we tested the effects of different light levels on the experimental habitats under controlled laboratory conditions. Representative assemblages containing adult individuals of *H. banksii* and patches of coralline algae were removed from the reef surface and used to recreate coralline and fucoid-coralline assemblages for laboratory incubations. The 2 habitat types were incubated at 5 light intensities (0, 150, 800, 1500, 2000 µmol photons m^{-2} s^{-1}), both in the presence and absence of sediment within the corallines (n = 6 for each combination of habitat and sediment manipulation), in order to generate their light response curves (*P-E* curves) and determine key photosynthetic parameters (Tait & Schiel 2011b). Dark respiration was measured by covering the chambers to omit light.

Both in the field and in the laboratory, water samples were extracted from the chambers using a syringe, and oxygen concentration was measured using a Hach LDO meter (Model HQ40d). NPP was estimated as the increase in oxygen concentration after 20 and 40 min of incubation (Tait & Schiel 2010). Changes in dissolved oxygen over time were converted to changes in carbon uptake using a P:Q (photosynthetic quotient) ratio of 1:1 (Kirk 1994) and standardized to carbon uptake per m^2 of reef surface (g C m^{-2} h^{-1}). Before each incubation, all visible invertebrates were removed from the corallines to limit the influence of heterotrophic respiration. Following laboratory incubations, the algae were dried for 24 h in a conventional oven at 60°C and their dry weight (DW) was recorded. The dry weight of algae was used to standardize NPP also by dry biomass of algal material (mg C gDW^{-1} h^{-1}), thereby accounting for any differences in the amount of biomass between fucoid-coralline assemblages and coralline algae alone. In the laboratory we also recorded the dry weight of the sediment contained within coralline turfs and fucoid-coralline assemblages assigned to the +sediment treatment and, from 6 of these sediment samples, the dry biomass of the invertebrates that could not be removed before the incubations.

Statistical analyses

The effects of coralline turfs and sediment deposition on percentage cover, number and length of *H. banksii* recruits recorded after 12 mo were analysed with a 2-way ANOVA with the fixed factors Habitat (5 levels: coralline turf, bare rock, artificial turf, artificial turf control, fucoid-coralline assemblage) and Sediment (2 levels: present and removed). Only the final percentage cover data (recorded after 12 mo) were formally analysed as they were representative of the temporal trends observed under each combination of treatments throughout the experiment. This enabled us to avoid statistical analyses including repeated measures, which present complex assumptions and allow for a less straightforward interpretation of the results (Murtaugh 2007).

Data of NPP recorded in the field were analysed with a 2-way ANOVA with the fixed factors Habitat (2 levels: fucoid-coralline assemblage and coralline turf) and Sediment (2 levels: present and removed). Data from laboratory incubations, standardized both per-area and per-biomass, were used to generate photosynthesis-irradiance (*P-E*) curves, separately for each replicate incubation. Several photosynthetic parameters were calculated from the *P-E* curves (Walsby 1997), including P_m (the maximum photosynthetic rate at light saturating irradiances), *R* (the rate of respiratory oxygen production), α (the light-use efficiency observed at light-limiting irradiances) and β (the negative gradient due to photoinhibition). When saturation in photosynthesis did not occur, the value of P_m was designated as the highest level of irradiance tested (i.e. 2000 µmol photons m^{-2} s^{-1}). For each replicate incubation, the NPP gradient at light-limiting irradiances was calculated as the slope of a linear regression between 0 and 150 µmol photons m^{-2} s^{-1}. Similarly, photoinhibition was calculated as the slope of a linear regression between the 2 irradiances at which photoinhibition occurred. When photoinhibition did not occur, we still calculated the direction of change between 1500 and 2000 µmol photons m^{-2} s^{-1} to give an indication of non-saturation at high light levels. A further parameter, E_c (the irradiance at compensation, i.e. where net photosynthesis = 0) was also calculated using the linear regression of light-use efficiency to determine the irradiance at which $y = 0$. The influence of habitat type and sediment manipulation on these photosynthetic parameters was examined with a 2-way ANOVA analogous to the one used to analyse *in situ* NPP data.

Before all the analyses, variance heterogeneity was tested with the Cochran's *C*-tests and removed with log transformation when required. Student-Newman-Keuls (SNK) tests were performed for *a posteriori* comparisons of the means (Underwood 1997).

RESULTS

Impacts of coralline turfs and sediment on *Hormosira banksii* recruitment

The 1 yr field experiment showed an effect of treatments over time, beginning at around 3 mo, and by the end of the experiment there was a clear interaction between the factors Habitat and Sediment ($F_{4,50}$ = 6.34, p < 0.001; Fig. 1A,C). SNK tests showed that, at the end of the experiment, the influence of sediment removal on the abundance of the recruits varied among the experimental habitats. In the fucoid-coralline assemblages, the combination of a fucoid canopy and coralline algae suppressed the cover of *H. banksii* recruits to near zero, both in the presence (Fig. 1A) and absence of sediment (Fig. 1C). Under ambient sedimentation, the percentage cover of *H. banksii* recruits was similar in all other habitats, ranging between 28 and 33% at the end of the experiment (Fig. 1A). When sediment was removed, the recruitment of *H. banksii* increased significantly only in bare rock and artificial turf control plots compared to the cover levels observed under ambient sedimentation (Fig. 1C). With reduced sediment loads the final cover of the recruits in bare rock and artificial turf control plots was around 40 to 50% and was significantly higher compared to all other habitats (Fig. 1C). The percentage cover of the recruits, on the contrary, was reduced to 20 and 24% in coralline turf and artificial turf plots allocated to sediment removal, respectively, but SNK tests did not highlight these differences as significant (Fig. 1C).

The number of recruits per plot at the end of the experiment was also a product of an interaction between Habitat and Sediment ($F_{4,50}$ = 6.53, p < 0.001; Fig. 1B,D). The few *H. banksii* recruits present under the canopy in both sediment treatments reflected their poor cover (Fig. 1B,D). In all other habitats, the erect growth habit of the recruits allowed them to reach extremely high densities (between 225 and 550 ind. $plot^{-1}$). Under ambient sedimentation, the density of the recruits did not differ among coralline turf, artificial turf, bare rock and artificial turf control plots. With reduced sedimentation, recruit number increased in bare rock and artificial turf control plots compared to the densities recorded under ambient sediment loads, and these 2 habitats had significantly more recruits compared to all others (Fig. 1D). Following sediment removal there was also a reduction in the number of recruits in coralline turf and artificial turf plots, which was not statistically significant according to SNK tests, however (Fig. 1D). Differ-

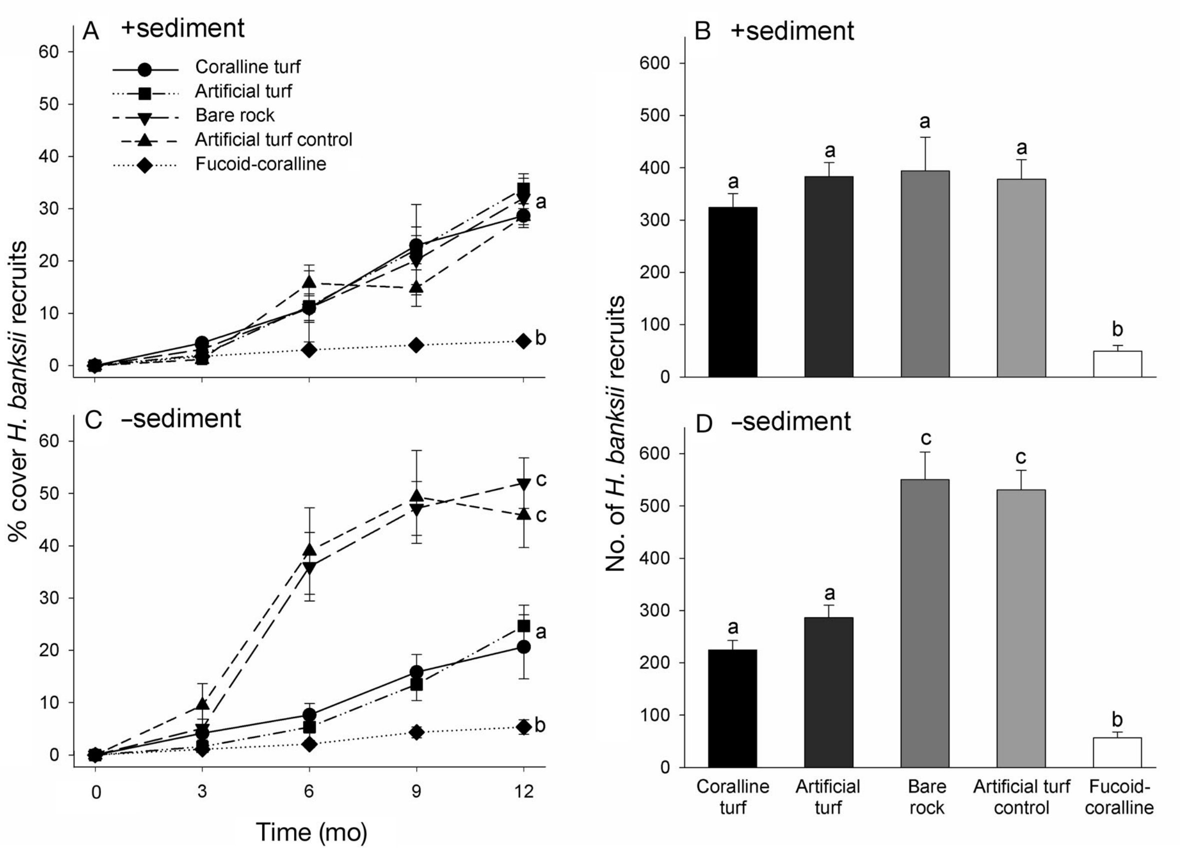

Fig. 1. Temporal variation in the mean percentage cover (±SE) of *Hormosira banksii* recruits in coralline turf, artificial turf, bare rock, artificial turf control and fucoid-coralline assemblage plots, under (A) ambient and (C) reduced levels of sediment accumulation, and (B,D) mean number of *H. banksii* recruits per plot recorded after 12 mo under the same combinations of habitat and sediment manipulation (all n = 6). Shared letters next to lines and above bars indicate that groups are not significantly different (Student-Newman-Keuls post hoc test, $p > 0.05$)

ences in recruit cover did not result from variable growth rates among treatments, as the length of the recruits after 12 mo (mean ± SE: 13.48 ± 0.14 mm) did not differ among habitats ($F_{4,50} = 1.49$, $p = 0.22$) or sediment levels ($F_{1,50} = 0.22$, $p = 0.64$).

Net primary productivity

There was a significant interaction between Habitat and Sediment in NPP dynamics *in situ* ($F_{1,12} = 5.14$, $p < 0.05$; Fig. 2). Fucoid-coralline assemblages, both in the presence and absence of sediment, had the greatest NPP at ca. 1.3 g C m^{-2} h^{-1}. Coralline turfs showed reduced NPP compared to fucoid-coralline assemblages, with plots containing sediment having less than half the productivity (at ca. 0.4 g C m^{-2} h^{-1}) of coralline plots without sediment (Fig. 2).

Consistent with *in situ* results, data from laboratory incubations, standardized on a per-area basis, showed that fucoid-coralline assemblages had higher

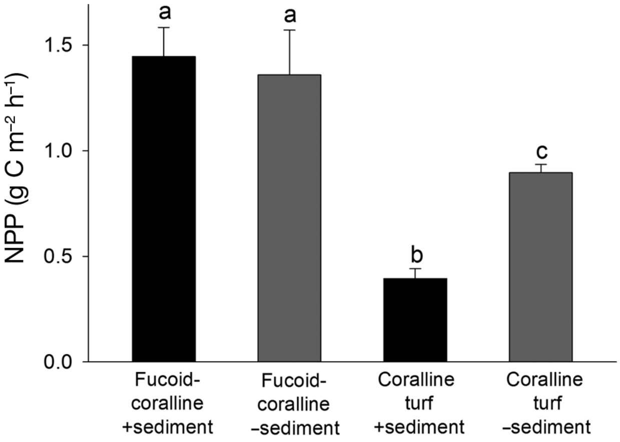

Fig. 2. Net primary productivity (NPP) standardized by area of reef (+SE) of fucoid-coralline assemblages and coralline turfs incubated in the field under full sunlight (1500 to 2000 µmol photons m^{-2} s^{-1}) in the presence and absence of sediment (n = 4). Shared letters above bars indicate that groups are not significantly different (Student-Newman-Keuls post hoc test, $p > 0.05$)

maximum photosynthetic rates (P_m) than coralline turfs (Tables 1 & 2). P_m of both habitats (i.e. with and without a *H. banksii* canopy) was reduced by sediment load within the corallines (Tables 1 & 2, Fig. 3A,B). In the presence of sediment, photoinhibition was more severe and started at lower irradiance (ca. 1000 µmol photons m^{-2} s^{-1}) in the coralline turfs compared to fucoid-coralline assemblages (>1500 µmol photons m^{-2} s^{-1}; Tables 1 & 2, Fig. 3A,B). Fucoid-coralline assemblages also required higher light intensities to reach a net carbon gain (i.e. compensating irradiance) and were characterized by higher levels of respiration compared to coralline turfs (Tables 1 & 2, Fig. 3A,B). For both coralline and fucoid-coralline assemblages, respiration rates did not differ in the presence and absence of sediment, suggesting that the influence of the heterotrophic organisms associated with the sediment was negligible. The dry biomass of invertebrates isolated from the sediment samples (4.75 ± 0.34 g, n = 6) was, in fact, very low compared to the amount of sediment contained within the turfs (142.49 ± 4.10 g, n = 12) and the biomass of algal material used in the incubations (91.05 ± 2.82 and 145.12 ± 7.67 g for coralline and fucoid-coralline assemblages, respectively, n = 12).

Laboratory experiments also allowed comparisons between treatment effects assessed on a per-area and per-biomass basis. The response curves under the 2 standardisations were virtually identical both for fucoid-coralline assemblages (Fig. 3A vs. 3C) and coralline turfs (Fig. 3B vs. 3D). The analyses confirmed that differences in NPP between habitats were not driven by variations in biomass alone. Even on a per-biomass basis, fucoid-coralline assemblages had higher maximum photosynthetic rates than coralline turfs ($F_{1,20}$ = 6.59, $p < 0.05$; Fig. 3C,D). Photoinhibition was stronger in the coralline turfs ($F_{1,20}$ = 6.66, $p < 0.05$; Fig. 3C,D), but the corallines reached the compensation point at lower irradiances ($F_{1,20}$ = 32.40, $p < 0.001$; Fig. 3C,D). The only exceptions were respiration and light-use efficiency. With the data standardized by dry weight of algae, the respiration rates of the 2 habitats did not differ ($F_{1,20}$ = 0.09, p = 0.77; Fig. 3C,D), indicating that the differences observed on a per-area basis were affected by the higher biomass of fucoid-coralline assemblages compared to coralline turfs. Per-biomass results also showed differences among habitats in the values of α ($F_{1,20}$ = 8.16, $p < 0.01$; Fig. 3C,D), with coralline turfs showing higher light-use efficiency at low irradiance.

DISCUSSION

This study showed an important interplay between coralline turfs and sediment in influencing replenish-

Table 1. Photosynthetic parameters (mean ± SE) estimated during laboratory incubations of fucoid-coralline assemblages and coralline turf in the presence or absence of sediment from data standardized on a per-area basis, separately for each combination of the experimental factors. P_m: maximum photosynthetic rate; R: respiration; α: slope at light-limiting irradiance; β: slope at saturating irradiance; E_c: irradiance at compensation

Experimental treatments	P_m (g C m^{-2} h^{-1})	R (g C m^{-2} h^{-1})	α (g C m^{-2} h^{-1})	β (g C m^{-2} h^{-1})	E_c (µmol photons m^{-2} s^{-1})
Fucoid-coralline + sediment	0.54 ± 0.15	−0.74 ± 0.06	0.0021 ± 0.0007	−0.0005 ± 0.0004	499.10 ± 107.28
Fucoid-coralline − sediment	1.02 ± 0.17	−0.68 ± 0.08	0.0021 ± 0.0007	0.0010 ± 0.0002	480.07 ± 56.21
Coralline turf + sediment	0.15 ± 0.19	−0.41 ± 0.07	0.0027 ± 0.0006	−0.0010 ± 0.0001	148.88 ± 27.52
Coralline turf − sediment	0.40 ± 0.15	−0.51 ± 0.11	0.0042 ± 0.0013	−0.0001 ± 0.0003	120.79 ± 23.69

Table 2. ANOVA testing the influence of habitat type (fucoid-coralline assemblage and coralline turf) and sediment manipulation (sediment present and removed) on the photosynthetic parameters estimated during laboratory incubations from data standardized on a per-area basis. See Table 1 for definitions of photosynthetic parameters. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

Source of variation	df	P_m		R		α		β		E_c	
		MS	F	MS	F	MS	F	MS	F	MS	F
Habitat (H)	1	1.52	9.38**	0.38	9.67**	<0.001	2.41	<0.001	6.87*	9.71	31.57***
Sediment (S)	1	0.79	4.88*	0.01	0.06	<0.001	0.72	<0.001	18.28**	0.01	0.02
H × S	1	0.08	0.49	0.04	1.04	<0.001	0.69	<0.001	1.29	0.17	0.55
Residual	20	0.16		0.04		<0.001		<0.001		0.31	

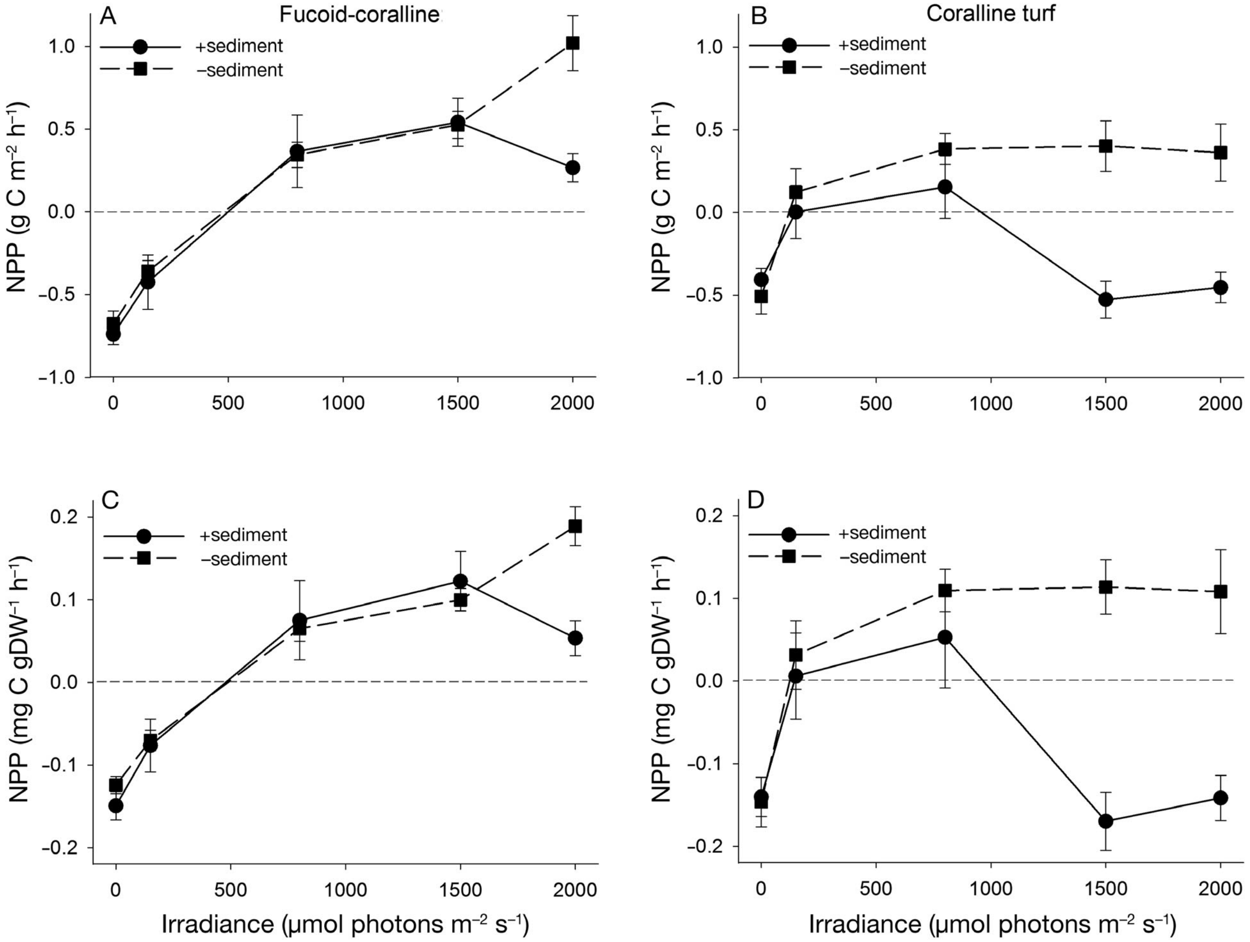

Fig. 3. Net primary productivity (NPP) variations (±SE) across irradiance levels in (A,C) fucoid-coralline assemblages and (B,D) coralline turfs incubated in the laboratory in the presence and absence of sediment (all n = 6). Data are standardized by (A,B) area of reef or (C,D) dry weight of algae

ment and productivity of macroalgal stands. Sediment deposition on unoccupied substrata combined with space preemption by low-lying algal turfs to suppress the recruitment of the dominant fucoid, and its accumulation within the turfs greatly altered primary production dynamics. These results contribute to a better mechanistic understanding of the implications of processes affecting rocky shores worldwide, such as the spread of benthic turfs and increased sediment loads in the coastal zone.

The suppressive effects of algal canopies on intra- and interspecific recruitment of kelps and fucoids have been widely documented (Vadas et al. 1992, Schiel & Foster 2006), but less so those relating to the conditions in the benthic environment. In our study, sediment accumulation on bare substrata reduced the recruitment of the dominant fucoid to the same levels as in the presence of the turfs (both coralline and artificial). Sediment is known to override the influence of habitat heterogeneity (Balata et al. 2007), eliminating biotic differences generated by the presence of distinct physical elements in the environment, such as substrata with different inclination and topography. Our results show a homogenizing effect of sediment deposition across substrata with different structural complexity. In addition, the absence of differences between coralline turfs and artificial mimics confirms the importance of the physical properties of such biogenic habitats in regulating fucoid recruitment.

Contrary to our expectations, reduced sedimentation did not increase the recruitment of *Hormosira banksii* in coralline and artificial turf plots. Turfs are known to stabilize sediment accumulation, by retaining elevated sediment loads independently of its fluctuations in the surrounding environment (Stewart 1983, Airoldi & Virgilio 1998). Despite the fortnightly removal treatment, therefore, sediment possibly re-accumulated quickly within the turfs compared to the other habitats. Furthermore, percentage cover and number of the recruits decreased both in coralline and artificial turf plots when sediment was removed. Even if not statistically significant, these variations suggest that the recruits may have been loosely attached within the turfs, making them more prone to the impact of natural disturbances (e.g. wave force; Taylor & Schiel 2003) and potential artifact perturbations due to sediment removal.

Our results add to a growing body of research on the impacts of sediment on recruitment of fucoids (Vadas et al. 1992, Schiel et al. 2006, Irving et al. 2009). In laboratory experiments, Schiel et al. (2006) showed that a light dusting of sediment reduced the settlement of *H. banksii* by 34 % relative to controls, and complete sediment cover prevented attachment altogether. In the present study, however, *H. banksii* did recruit under ambient levels of sedimentation. This and other field investigations at this location (Hurley 2009) suggest that temporal fluctuations in the sediment environment may open windows of opportunity for fucoid recruitment, allowing the persistence of abundant adult stands. Furthermore, *H. banksii* was able to recruit also within the turfs (both coralline and artificial), provided there was no fucoid canopy, indicating that turfs of small thickness (~10 mm) may not present an insurmountable barrier for this species. These results are in line with the findings of Bellgrove et al. (2010) who showed that thick mats of corallines (3 to 4 cm high) are virtually inaccessible for *H. banksii*, but that *H. banksii* can be highly abundant in areas colonized by less developed turfs (ca. 10 mm thick or less). Similarly, Schiel & Lilley (2011) observed that the long-term recovery of *H. banksii* canopies is influenced by the composition and morphological traits of the turfs, with slower recovery rates in the presence of articulated corallines with long, frondose branches (e.g. *Jania* spp.). Our study shows that the effects of shorter turfs (*Corallina officinalis*) may not be as strong. In addition, the length of the recruiting plants was not affected by the properties of the habitats or sedimentation levels, suggesting that once juvenile individuals overcome the critical bottleneck represented by settlement and early post-settlement phases, the nature of the substratum and the deposition of sediment may have limited influence on their development.

Net primary productivity was regulated by a combination of biotic (i.e. canopy–understory interactions; Tait & Schiel 2011b) and abiotic factors (i.e. sediment deposition). In the field, fucoid-coralline assemblages were more productive than coralline turfs, both in the presence and absence of sediment. Analogously, in the laboratory coralline algae alone could not match the photosynthetic rates reached by fucoid-coralline assemblages, despite showing higher light-use efficiency at low irradiance, probably as a result of their adaptation to shaded subcanopy conditions (Irving et al. 2004, Gattuso et al. 2006).

Both field and laboratory incubations highlighted a detrimental impact of sediment on NPP of coralline turfs and, under controlled laboratory conditions, this also compromised the functioning of fucoid-coralline assemblages at elevated light intensities. In the presence of sediment, *P-E* curves of coralline algae and fucoid-coralline assemblages showed photoinhibition under increasing irradiance, with coralline turfs shifting into net respiration beyond 1000 µmol photons m^{-2} s^{-1}. This was most likely due to photoinhibitive mechanisms within the turfs, induced by the accumulation of sediment. Sediment constitutes a clear physical obstruction for low-lying benthic taxa like coralline algae, as only small portions of their thalli are exposed to direct sunlight (Fig. 4A). The simplification of the 3-dimensional structure of the latticed coralline algae likely reduces their ability to make use of the full irradiance gradient. Turfs with

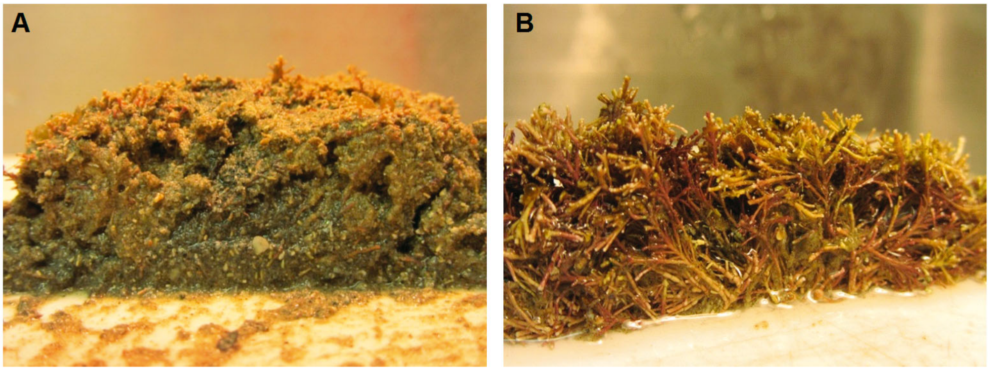

Fig. 4. Cross-sections of a patch of coralline turf (ca. 10 mm thick) collected in the field and used for laboratory incubations: (A) a high sediment load obstructing the thalli of the corallines and (B) the same patch following sediment removal (showing the potential for increased light penetration)

little sediment obstructing photosynthetic tissues (Fig. 4B), on the other hand, seem able to maintain their photosynthetic capacity at relatively high irradiance, possibly through increased self-shading and a higher leaf area index. Complex assemblages have a greater ability to convert incoming photons into carbon fixation at the higher end of the irradiance gradient, because although some components will be undergoing photo-inhibition, others will be photosynthesizing efficiently (Binzer et al. 2006). In addition, the instantaneous response of coralline turfs to sediment removal suggests a remarkable recovery or persistence of photosynthetic activity. Analogously, various species of crustose corallines have been shown to restore their photosynthetic capacity quickly after sedimentation stress (Harrington et al. 2005).

Collectively, the NPP dynamics described here indicate that even if the photosynthetic capacity of coralline algae is limited in comparison with *H. banksii* canopies, depending on the light environment, these species have the potential to exert a strong influence over assemblage functioning. When devoid of sediment, coralline algae contributed to enhance fucoid-coralline assemblage NPP, highlighting the importance of synergistic interactions among the components of multi-layered macroalgal assemblages in optimizing light use (Binzer et al. 2006, Tait & Schiel 2011b). Similarly, Chisholm (2003) has shown that crustose corallines make a larger contribution to organic production on coral reefs than previously thought. Our results, however, also highlight the consequences of sediment accumulation within the turfs, and stronger impacts on assemblage photosynthetic processes are likely to occur when larger amounts of sediment are suspended in the water column, a scenario commonly observed in coastal areas in New Zealand and worldwide (Airoldi 2003, Thrush et al. 2004).

The overwhelming influence of anthropogenic perturbations is reshaping the structure of coastal systems worldwide, and a better mechanistic understanding of the causes and the effects of these alterations is often advocated (Airoldi et al. 2008, Connell et al. 2008, Foster & Schiel 2010). Our study sheds light on the influence of altered physical and biotic conditions on the persistence and functioning of benthic assemblages dominated by macroalgal canopies. It also highlights the potential implications of the impairment of key ecological processes within these complex biogenic habitats. The combined impacts of multiple perturbations, however, remain difficult to predict, and synergies among stressors may be critical for the outcome of the interactions between canopy- and turf-forming algae (Connell & Russell 2010, Falkenberg et al. 2012, 2013). Further studies will no doubt clarify the effects of altered sediment dynamics in combination with other anthropogenic influences acting across global to local scales.

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