

Non-trophic responses of algal communities to nutrient enrichment: interactions among coralline turfs, ephemeral algae and perennial fucoids

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ABSTRACT: Coastal eutrophication is known to promote the spread of fast-growing, ephemeral algae, with severe consequences for ecosystem health. Blooms of ephemeral algae within hard-bottom communities are facilitated by shifts from canopy to turf domination in degraded environments. In contrast to this pattern, however, turfs of articulated coralline algae have been shown to limit the development of ephemeral species, but the role of benthic habitat modification by coralline turfs in preventing nutrient-driven assemblage alterations has been scarcely investigated. Here, we tested whether coralline turfs can limit the growth of ephemeral algae in response to increased nutrient availability, and whether this can facilitate the recruitment of perennial canopy-forming fucoids. We manipulated coralline turf abundance and nutrient availability on an intertidal reef for 1 yr. The growth of ephemeral species was stimulated by nutrients, but only transiently during spring, and did not affect fucoid recruitment and final assemblage composition. The presence of the turfs was a major barrier to fucoid recruitment, and, although coralline turfs limited the growth of some ephemerals (*Ulva* spp.), they also facilitated the spread of others (*Colpomenia* spp.). These results highlight the resistance of fucoid assemblages to short-term nutrient stress and the threat posed by turf domination to the persistence of important habitat-forming species. Habitat modification by coralline turfs may both mitigate and exacerbate the biotic consequences of organic enrichment. Comparisons with the findings of previous studies indicate that local assemblage composition and the duration of disturbance can contribute to producing complex idiosyncratic responses to nutrient enrichment.

KEY WORDS: Algal blooms · Canopy · Coastal eutrophication · Disturbance · Facilitation · Habitat degradation · Resistance · *Ulva*

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INTRODUCTION

Human activities are altering the chemistry of the earth's atmosphere, soil and water at unprecedented rates (Vitousek et al. 1997). As a result, disproportionate quantities of macronutrients, mainly compounds of nitrogen and phosphorous, are being introduced into freshwater, estuarine and marine ecosystems because of agricultural practices, industrial runoffs and urban discharges (Carpenter et al. 1998, Cloern

2001). In New Zealand, for example, where the economy largely depends on agriculture and especially dairy farming, the increased accumulation of reactive nitrogen in the environment is altering the biogeochemical cycles of terrestrial, freshwater, coastal and oceanic ecosystems, with consequences for biodiversity and human health (Parfitt et al. 2008, Schiel & Howard-Williams 2015).

Large floristic changes can occur in coastal areas affected by excessive nutrient enrichment, with un-

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controlled blooms of fast-growing, ephemeral species (predominantly foliose and filamentous green and brown algae) causing severe and long-lasting impacts on the structure of benthic communities (Duarte 1995, Valiela et al. 1997, Eriksson et al. 2002, Herbert & Fourqurean 2008). Considerable research has been devoted to the identification of physical and biotic factors controlling the occurrence of macroalgal blooms. On temperate rocky shores, large canopy-forming macroalgae such as fucoids and kelps have been shown to exert a strong control on the spread of ephemeral species, thereby buffering the propagation of nutrient-driven alterations within hard-bottom communities (e.g. Russell & Connell 2005, Eriksson et al. 2006, 2007, Falkenberg et al. 2012). Because of coastal habitat degradation, however, fucoid and kelp canopies are in decline in many places worldwide, and intertidal and subtidal rocky reefs are increasingly dominated by low-lying, turf-forming algae (Benedetti-Cecchi et al. 2001, Airoidi et al. 2008, Connell et al. 2008). As a consequence, investigating the ecological role of algal turfs and their linkages with human disturbance is particularly important in order to achieve a better understanding of the conditions and mechanisms underlying large changes in the structure and functioning of benthic communities.

The loss of assemblage three-dimensional structural complexity caused by the shift from canopy- to turf-domination is often associated with a reduced resistance to nutrient-driven alterations, because algal turfs are generally unable to prevent the spread of opportunistic, fast-growing algae (Eriksson et al. 2002, Russell & Connell 2005, Bulleri et al. 2012). In contrast to this pattern, however, complex biogenic surfaces created by turfs of articulated coralline algae have been shown to limit the development of ephemeral green algae of the genus *Ulva* (Daleo et al. 2006). Coralline turfs are highly persistent components of intertidal assemblages and are known to obstruct the recruitment of large perennial macroalgae (Arenas et al. 2006, Bellgrove et al. 2010, Alestra et al. 2014). To the best of our knowledge, the findings of Daleo et al. (2006) are the only documented evidence suggesting that benthic habitat modification by coralline turfs may also play an important role in preventing nutrient-driven alterations in the structure of benthic assemblages, but this has not been further investigated.

The aim of this study was to test the influence of turf-forming, articulated corallines on the growth of ephemeral, fast-growing algae under increased nutrient loads, as well as the potential implications for

the recruitment of perennial habitat-forming fucoids. In particular, we tested (1) if coralline turfs can prevent nutrient-driven alterations in the structure of intertidal algal assemblages by limiting the growth of ephemeral algae in response to nutrient enrichment, and (2) whether reduced cover of ephemeral algae in the presence of corallines can facilitate the recruitment of slow-growing, perennial fucoids, or whether such a positive effect is offset by the impact of space pre-emption by the turfs on the settlement of the fucoids.

To test these hypotheses, we compared the structure (i.e. species composition and relative abundances) of intertidal algal assemblages recruiting on unoccupied substrates and on surfaces covered by coralline turfs, both under conditions of ambient and increased nutrient availability. We tested 4 scenarios (Fig. 1), which were hypothesized based on the literature testing the interactions among perennial macroalgae, ephemeral species and coralline turfs, as well as on prior knowledge of intertidal algal assemblages along the east coast of the South Island of New Zealand. The structure of these assemblages is mainly determined by non-trophic interactions (Lilley & Schiel 2006, Schiel & Lilley 2011). Coralline turfs tend to limit the abundance of both fucoids and ephemeral algae under ambient nutrient levels (Hurley 2009, Alestra 2014, Alestra et al. 2014; Fig. 1a). In the absence of coralline algae, both ephemerals and fucoids generally benefit from the increased availability of unoccupied primary substrate (indicated as bare rock), without interfering with each other (Hurley 2009, Alestra 2014, Alestra et al. 2014; Fig. 1b). Under enhanced nutrient concentrations, however, ephemeral algae may become more abundant and persist for longer periods of time on unoccupied substrates. This may impede the recruitment of the fucoids, or affect the plants already settled (Worm et al. 1999, 2001, Steen 2004, Alestra & Schiel 2014; Fig. 1c), and produce significant alterations to the structure of the entire assemblage (Eriksson et al. 2002, Kraufvelin et al. 2006). The presence of the corallines may prevent such nutrient-driven alterations by suppressing the abundance of the ephemerals (Daleo et al. 2006; Fig. 1d). The negative effect of the turfs on the ephemerals may increase the chances of recruitment of the fucoids by releasing them from the competition with ephemeral algae (Fig. 1d[a]); alternatively, this indirect positive effect may be outweighed by the impact of the turfs on the settlement of the fucoids (Fig. 1d[b]).

Direct positive and negative effects of nutrient enrichment on the early life history of fucoids have

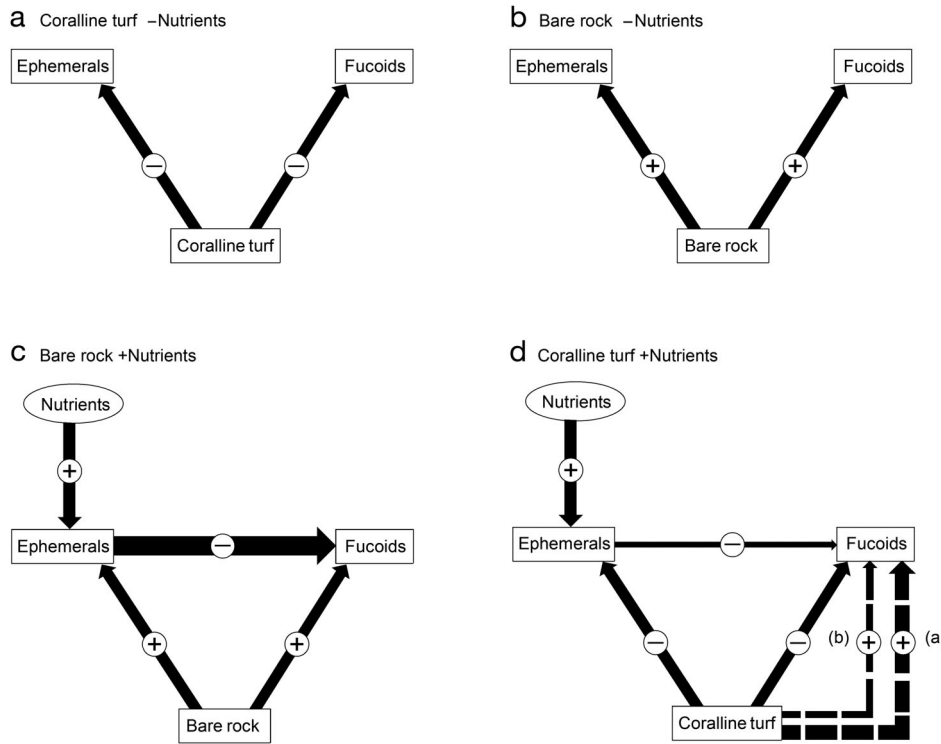


Fig. 1. Expected interactions among fucooid recruits and ephemeral algae in (a,d) the presence and (b,c) absence of coralline algae and under (a,b) ambient (-Nutrients) and (c,d) increased nutrient regimes (+Nutrients). Solid and dashed lines: direct and indirect interactions respectively; the intensity of positive (+) and negative (-) effects is indicated by arrows of different thicknesses. Lowercase letters in (d) distinguish between 2 alternative outcomes of indirect facilitation. See 'Introduction' for a detailed description of the 4 scenarios

also been observed in laboratory experiments (Kevekordes 2001, Steen 2004, Alestra & Schiel 2015), but such effects were considered to be negligible in the field (and are not shown in Fig. 1).

MATERIALS AND METHODS

Study site

The experiment was conducted at Wairepo Flats, Kaikoura (42° 25' S, 173° 42' E), on the northeast coast of the South Island of New Zealand. This site has a partially sheltered, large intertidal platform covered by canopies of various species of fucooids (predominantly *Cystophora torulosa* and *Hormosira banksii*, but *Carpophyllum maschalocarpum*, *Cystophora retroflexa* and *Cystophora scalaris* are also present in low abundances). Articulated coralline algae (mainly *Corallina officinalis* and *Jania* spp.) are the dominant primary space occupiers. Ephemeral green (*Ulva* spp.) and brown algae (*Adenocystis utricularis*, *Colpomenia* spp., *Ectocarpus* spp., *Scytosiphon lomentaria*, *Tinocladia novae-zelandiae*) tend to become abundant in spring and early summer, especially on unoccupied surfaces in the absence of fucooid canopies. Grazing invertebrates are generally small and do not play a dominant role in shaping the structure

of algal communities (Lilley & Schiel 2006, Hurley 2009, Schiel & Lilley 2011, Alestra 2014).

Average monthly sea surface temperatures in Kaikoura range between 9 and 18°C (Chiswell & Schiel 2001). The tidal regime is semi-diurnal, with a tidal range between 0.1 and 2.1 m above the lowest astronomical tide level (Land Information New Zealand 2015). Nutrients are likely to be a limiting factor for algal growth at this location, as the waters surrounding the east coast of New Zealand are known to be relatively nutrient-poor because of downwelling (Menge et al. 1999, 2003, Guerry et al. 2009).

Experimental design and data collection

Sixty 25 × 25 cm plots were haphazardly selected (ensuring that they were at least 2 m from each other) and marked in the low intertidal zone (about 0.3 m above the lowest astronomical tide level) along a stretch of shore of about 0.5 km. These plots were covered by mixed canopies of the fucooids *Cystophora torulosa* and *Hormosira banksii* (mean % cover ~50%), with a basal layer of articulated coralline algae (mean % cover ~95%; thickness ~10 mm). *C. torulosa* and *H. banksii* adult plants, along with all understory species, were removed by hand picking from 30 of

the plots, and from the area surrounding their immediate edges, to create experimental units of coralline turf alone. Furoid holdfasts were removed using a knife. The remaining 30 plots were cleared of all algae using a hammer and chisel to create denuded patches of bare rock. These plots were not recolonized by the coralline turfs during the experiment. Half of the replicates of each habitat type were assigned to the nutrient enrichment treatment and equipped with 2 polyethylene mesh dispenser bags attached in proximity to 2 opposite corners. Each dispenser was filled with 150 g of coated slow-release fertilizer pellets (Osmocote® Pro 3 to 4 mo release: 17, 4.8, 8.3 N-P-K), so that each plot was enriched with 300 g of fertilizer, a quantity shown to increase water nutrient concentration and stimulate macroalgal growth in a previous experiment done near Kaikoura (Guerry et al. 2009). The selected amount of fertilizer and the distance among the plots (at least 2 m from each other) reduced the chances of nutrient spillover, ensuring independent treatment effects (Worm et al. 2000). Osmocote pellets were replaced every 6 wk.

Twelve additional artefact control plots (6 coralline turf and 6 bare rock plots) were set up with dispenser bags filled with plastic beads of the same size and shape as the Osmocote pellets. These plots were compared with a randomly selected subset of no-enrichment plots (i.e. not surrounded by dispenser bags) from the main experiment to test for potential artefacts caused by the dispensers.

Before the start of the experiment, all plots were gently washed using a hose connected to a bilge pump to remove sediment and any algal propagules, so that all treatments were exposed to the same initial conditions. At this location, sediment is trapped in great abundance within the turfs, but this is unlikely to interfere with furoid recruitment. A previous study showed, in fact, that the rates of *H. banksii* recruitment in coralline turf plots did not differ under ambient and reduced levels of sediment accumulation (Alestra et al. 2014). The experiment was initiated at the beginning of the austral autumn (March 2012). At this location, both furoid reproduction and blooms of ephemeral species occur mainly during spring and early summer (Taylor & Schiel 2003, Lilley & Schiel 2006, Alestra 2014). The autumn start allowed a test of whether nutrient enrichment could stimulate algal blooms in the coldest seasons of the year and an assessment of the responses of furoids and ephemerals in spring and summer after prolonged exposure to increased nutrient loads.

The plots were sampled 4, 8 and 12 mo after the start of the experiment. On each occasion, all

algae were identified to the greatest possible taxonomic resolution and their % cover was recorded using a grid divided into 100 sub-quadrats. Water samples were collected once (3 wk after the start of the experiment) to test the efficacy of the enrichment treatment. This was done while the plots were covered by about 50 cm of water during a receding tide. A plastic syringe was used to withdraw 100 ml of seawater about 10 cm above the centre of 24 randomly selected plots (6 for each combination of habitat type and nutrient manipulation). Water samples were filtered in the field through 25 mm glass fiber filters, stored in acid-washed polyethylene vials, frozen, and successively analysed for nitrate, ammonium and phosphate using a spectrophotometer. Ammonium and phosphate were determined as described by Koroleff (1983a,b) and nitrate as per Parsons et al. (1984).

Statistical analyses

Differences in ammonium, nitrate and phosphate concentrations among treatments were analysed with a 2-way ANOVA with the fixed factors habitat (coralline turf vs. bare rock) and nutrients (enrichment vs. no-enrichment).

The % cover of the most abundant species of furoids and ephemeral algae colonizing the experimental plots was analysed after 8 and 12 mo using this same ANOVA design; α was Bonferroni-corrected to 0.025. Because of their slow growth rates, recruits of all furoids after 12 mo presented short, erect thalli (<2 cm long). This ensured that % cover reflected furoid rates of recruitment, as post-settlement growth was not a confounding factor (Alestra et al. 2014).

In addition, the relative interaction index (RII; Armas et al. 2004) was calculated, separately for different species of furoids, and used to describe the intensity and direction of their interactions with coralline turfs under ambient and increased nutrient levels at each sampling date. The RII is expressed as $RII = (B_w - B_o) / (B_w + B_o)$, where B_w and B_o are the % cover of furoid recruits in the presence and absence of coralline algae, respectively. The RII was calculated by randomly pairing each coralline turf plot with one bare rock plot, separately for the 2 nutrient levels. The RII ranges between 1 and -1, with negative values indicating competition and positive values showing facilitation. RII values relative to the final sampling date were analysed with a 1-way

ANOVA with the fixed factor nutrients (enrichment vs. no-enrichment).

The influence of coralline turfs and nutrient manipulation on assemblage composition was assessed with a combination of univariate and multivariate techniques. Differences in assemblage composition at the end of the experiment, expressed by Bray-Curtis dissimilarities calculated on untransformed data, were analysed with a permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) including the same combinations of habitat and nutrient levels used for univariate analyses. SIMPER analysis (Clarke 1993) was used to assess the contribution of individual taxa to multivariate dissimilarities. To describe the changes in assemblage composition that occurred throughout the experiment in coralline turf and bare rock plots under the 2 nutrient regimes, we calculated the average dissimilarity across all sampling dates for each experimental plot. The observations were first placed into Euclidean space by calculating principal coordinates (Gower 1966) from a Bray-Curtis dissimilarity matrix including the full set of data. Then, for each plot, we calculated and averaged the 3 Euclidean distances between consecutive sampling dates (start to 4 mo, 4 to 8 mo, 8 to 12 mo) to quantify the mean temporal change experienced by the algal assemblages. Finally, mean Euclidean distances were analysed with the 2-way ANOVA design previously described and displayed using non-metric multidimensional scaling (nMDS) plots showing the centroids of each treatment-by-time combination. The multivariate dispersion of the replicates of each treatment at each sampling date was expressed by the mean Euclidean distance to the treatment centroid and displayed in a separate graph.

To test for experimental artefacts, we compared the % cover of the most abundant species of furoids and ephemeral algae in artefact control plots (equipped with dispenser bags filled with plastic beads) and no-enrichment plots (not surrounded by dispenser bags) using a 2-way ANOVA with the fixed factors habitat (coralline turf vs. bare rock) and artefact control (dispenser bags filled with plastic beads vs. no dispensers).

In all analyses, data from individual sampling dates were independently analysed to avoid statistical procedures including repeated measures, which present complex assumptions and a less straightforward interpretation of the results (Murtaugh 2007). Before all univariate analyses, residual plots and Cochran's *C*-tests were used to assess the normality of error terms and the homogeneity of variances

respectively. Variance heterogeneity was removed with logarithmic transformation when required. When homogeneity of variances could not be achieved by transformation, significance was judged more conservatively ($\alpha = 0.01$). Student-Newman-Keuls (SNK) tests were performed for *a posteriori* comparisons of the means (Underwood 1997).

RESULTS

Efficacy of nutrient enrichment

Three wk after the first addition of fertilizers, water samples collected from enrichment plots had higher mean (\pm SE) levels of ammonium (18.90 ± 2.70 vs. $2.81 \pm 0.03 \mu\text{mol l}^{-1}$; $F_{1,20} = 33.29$, $p < 0.001$), nitrate (14.33 ± 2.03 vs. $1.29 \pm 0.33 \mu\text{mol l}^{-1}$; $F_{1,20} = 36.75$, $p < 0.001$) and phosphate (6.19 ± 0.71 vs. $0.17 \pm 0.02 \mu\text{mol l}^{-1}$; $F_{1,20} = 66.26$, $p < 0.001$) in comparison to no-enrichment plots. In both the enrichment and no-enrichment plots, no differences were detected between coralline turf and bare rock plots in the concentration of any of the macronutrients (ammonium: $F_{1,20} = 0.32$, $p = 0.58$; nitrate: $F_{1,20} = 0.06$, $p = 0.81$; phosphate: $F_{1,20} = 1.30 \times 10^{-3}$, $p = 0.97$). Nutrient levels in the enrichment plots aligned with the concentrations recorded in eutrophic coastal areas around New Zealand (Barr 2007).

Responses of furoids and ephemeral algae

Cystophora torulosa and *Hormosira banksii* were the most abundant furoids colonizing the experimental plots. The % cover of both species remained low for several months after the start of the experiment, with no differences among the experimental treatments after 8 mo (Table 1a, Fig. 2a,c). The abundance of both species increased significantly in the bare rock plots during the final 4 mo (spring-summer) to around 13%, while it remained below 4% in the coralline turf plots. No effects of nutrient enrichment were detected (Table 1b, Fig. 2a,c). Another furoid, *Cystophora retroflexa*, was also present with a low % cover, and was more abundant in bare rock compared to coralline turf plots after 12 mo (3.33 ± 1.05 vs. 0.40 ± 0.20 ; $F_{1,56} = 7.53$, $p < 0.01$).

Negative RII values after 8 and 12 mo indicated that the recruitment of *C. torulosa* and *H. banksii* was limited by substrate pre-emption by the turfs (Fig. 2b,d). The direction of coralline-furoid interactions did not vary with increased nutrient concen-

Table 1. ANOVA results for the % cover of *Cystophora torulosa* recruits, *Hormosira banksii* recruits, *Colpomenia* and *Ulva* recorded in (a,b) the main experiment and (c) the artefact control tests. The abundances of the 4 species under different combinations of habitat type (coralline turf vs. bare rock) and nutrient manipulation (enrichment vs. no-enrichment) were separately analysed at (a) 8 and (b) 12 mo in the main experiment. Artefact control tests (c) included analyses of *C. torulosa* and *H. banksii* recruit abundances at 12 mo and of *Colpomenia* and *Ulva* abundances at 8 mo in different habitat types (coralline turf vs. bare rock), both in the presence and absence of dispenser bags with no fertilizer. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. α was reduced to 0.025 to correct for repeated tests across sampling dates and to 0.01 when variance heterogeneity could not be removed through transformation

Source of variation	df	MS	F	MS	F	MS	F	MS	F
(a) Main experiment (8 mo)		<i>C. torulosa</i> recruits		<i>H. banksii</i> recruits		<i>Colpomenia</i>		<i>Ulva</i>	
Habitat (H)	1	10.00	0.46	0.06	0.20	2706.82	10.94**	29.20	64.61***
Nutrients (N)	1	7.00	0.32	0.21	0.65	5940.15	24.01***	20.94	46.33***
H × N	1	4.00	0.18	0.10	0.32	792.07	3.20	2.00	4.42
Residual	56			0.32		247.36		0.45	
(b) Main experiment (12 mo)		<i>C. torulosa</i> recruits		<i>H. banksii</i> recruits		<i>Colpomenia</i>		<i>Ulva</i>	
Habitat (H)	1	23.10	24.11***	31.05	51.97***	17.07	2.77	0.04	1.05
Nutrients (N)	1	0.54	0.56	0.22	0.37	9.60	1.56	1.20	33.72***
H × N	1	0.25	0.26	0.05	0.08	36.82	5.98	0.00	0.12
Residual	56	53.63		0.60		6.15		0.04	
(c) Artefact control tests		<i>C. torulosa</i> recruits (12 mo)		<i>H. banksii</i> recruits (12 mo)		<i>Colpomenia</i> (8 mo)		<i>Ulva</i> (8 mo)	
Habitat (H)	1	1283.34	82.12***	437.76	32.24***	882.09	8.64**	301.04	25.92***
Artefact control (AC)	1	3.76	0.63	41.34	3.05	78.84	0.39	6.00	0.52
H × AC	1	49.59	0.09	38.76	2.85	36.26	0.56	16.67	1.44
Residual	20	15.63				102.15		11.61	

trations, and after 12 mo RII values did not differ between nutrient levels both for *C. torulosa* ($F_{1,28} = 0.61$, $p = 0.44$; Fig. 2b) and *H. banksii* recruits ($F_{1,28} = 0.79$, $p = 0.38$; Fig. 2d).

Brown algae of the genus *Colpomenia* and green algae of the genus *Ulva* were the most abundant ephemeral species colonizing the plots. Both *Colpomenia* spp. and *Ulva* spp. (hereafter referred to as species and labelled as *Colpomenia* and *Ulva*) produced extensive blooms after 8 mo (spring), but were not abundant at the other sampling dates (Fig. 2e,f). After 8 mo the abundance of *Colpomenia* was independently enhanced by the presence of coralline algae and increased nutrient concentrations, with a cover >40% in coralline turf plots subjected to nutrient enrichment, and between 10 and 23% in all the other habitat–nutrient combinations (Table 1a, Fig. 2e). After 12 mo, however, the cover of *Colpomenia* was reduced to about 1% with no differences between habitats and nutrient levels (Table 1b, Fig. 2e). *Ulva* also strongly responded to nutrients after 8 mo, but it was more abundant in bare rock plots, where its cover was around 25%, compared to 1 to 5% under all other combination of treatments (Table 1a, Fig. 2f). After 12 mo the cover of *Ulva* was reduced to <1%, and although there were significant differences between enrichment and no-enrichment treatments (0.30 ± 0.05 vs. 0.02 ± 0.02 ; Table 1b, Fig. 2f), these were most likely biologically irrelevant.

Assemblage temporal variability and composition

In the absence of nutrients, assemblage composition varied little through time in the coralline turf plots (Fig. 3a), while there were larger variations in the bare rock plots (Fig. 3b) due to the greater recruitment of the dominant furoids and other algae compared to coralline plots. The addition of nutrients increased temporal variability of assemblage composition in both habitat types because of blooms of ephemeral algae after 8 mo (Fig. 3a,b; see Fig. 3c for estimates of multivariate dispersion around the centroids). The analyses of mean Euclidean distances showed interactive effects of habitat type and nutrient addition on assemblage composition through time (Table 2). Mean Euclidean distances were about 25% larger in the bare rock compared to the coralline turf plots in the absence of nutrients (Table 2, Fig. 3d). Mean Euclidean distances increased in both habitats under high nutrient levels and did not differ between bare rock and coralline turf plots, indicating that both habitats were prone to nutrient-driven structural changes (Table 2, Fig. 3d). At the end of the experiment, however, assemblage composition differed only between habitats and there were no effects associated with nutrient manipulation (Table 2), showing that nutrient-driven alterations were transient. SIMPER analysis indicated that the differences between habitats at the conclusion of the experiment were mainly driven by

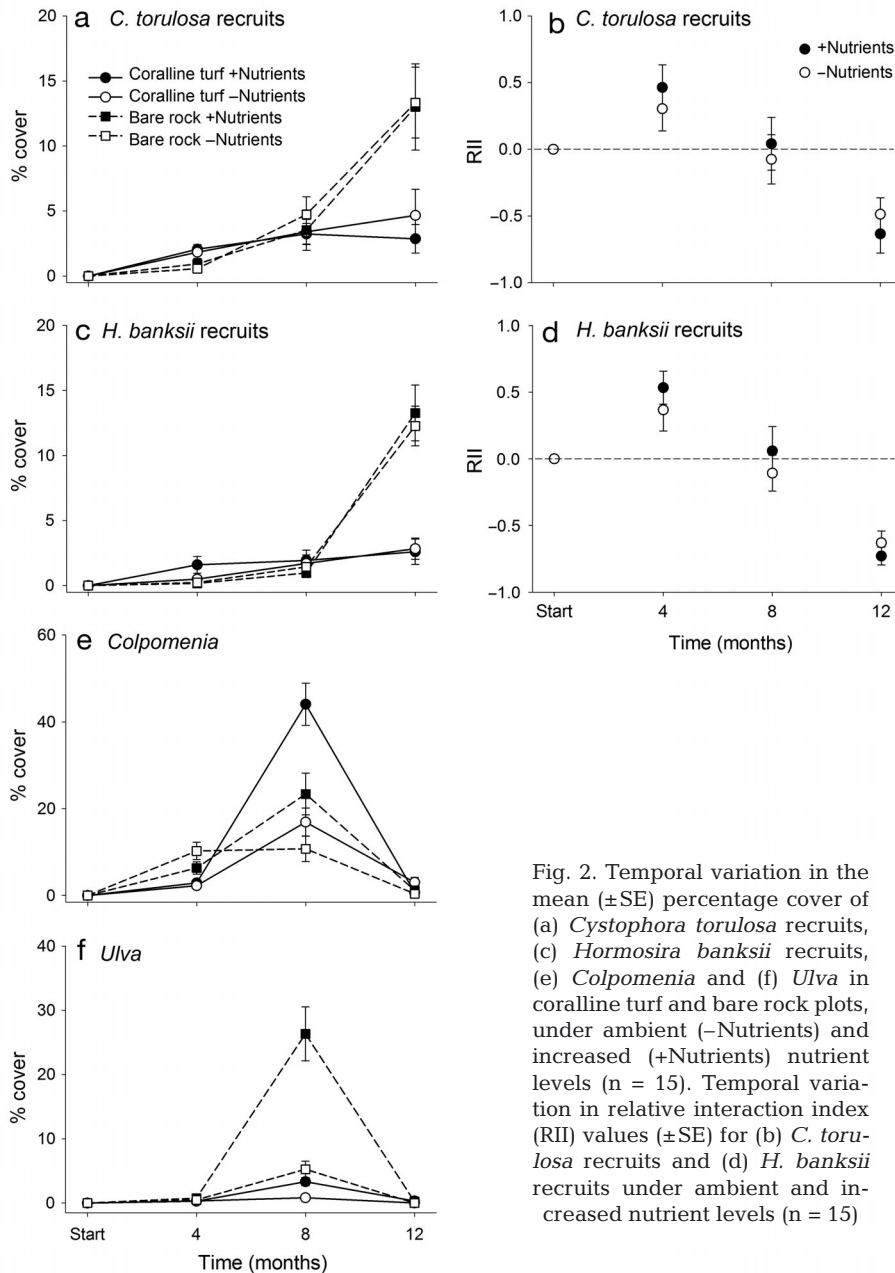


Fig. 2. Temporal variation in the mean (\pm SE) percentage cover of (a) *Cystophora torulosa* recruits, (c) *Hormosira banksii* recruits, (e) *Colpomenia* and (f) *Ulva* in coralline turf and bare rock plots, under ambient (-Nutrients) and increased (+Nutrients) nutrient levels ($n = 15$). Temporal variation in relative interaction index (RII) values (\pm SE) for (b) *C. torulosa* recruits and (d) *H. banksii* recruits under ambient and increased nutrient levels ($n = 15$)

fucoid patterns of recruitments, with 86.62% of the dissimilarity explained by the preferential recruitment of *H. banksii* (37.74%), *C. torulosa* (35.94%) and *C. retroflexa* (12.94%) in bare rock plots. Other less abundant taxa (mean % cover <3%) accounting for the remaining portion of variability among habitats at the conclusion of the experiment included *Adenocystis utricularis*, *Carpophyllum maschalocarpum*, *Cystophora scalaris*, *Colpomenia* spp., *Ectocarpus* spp., *Gelidium caulacanthum*, *Halopteris* spp., *Scytosiphon lomentaria*, *Tinocladia novaezelandiae* and *Ulva* spp.

Artefact control

Artefact control tests indicated that the use of the dispensers did not affect the results of the main experiment. Analyses on the abundance of *C. torulosa* and *H. banksii* recruits (at 12 mo) and of *Colpomenia* and *Ulva* (at 8 mo) did not show any difference between artefact control plots (equipped with dispenser bags filled with plastic beads) and plots not surrounded by dispenser bags (Table 1c).

DISCUSSION

This study examined whether algal assemblages dominated by turf-forming articulated coralline algae were able to withstand nutrient disturbance and potentially to revert to a state dominated by perennial canopies. Our results showed that nutrient-driven blooms in the abundance of ephemeral algae were short-lived and did not have any impact on the dominant fucoids (Fig. 4a,b) or on final assemblage composition over a year. *Cystophora torulosa* and *Hormosira banksii* recruited abundantly onto bare rock, even in the plots affected by elevated nutrient levels and increased abundance of ephemeral algae (Fig. 4a). The monopolization of primary space by the corallines was, however, a strong barrier to fucoid recruitment, and although coralline turfs limited the growth of

some ephemeral species (i.e. *Ulva*), they also facilitated the spread of others (i.e. *Colpomenia*; Fig. 4b). Collectively, these results contribute to a better mechanistic understanding of the interplay among 3 common components of temperate rocky systems (perennial fucoids, fast-growing ephemerals and algal turfs) in shaping the structure of benthic communities under altered environmental conditions.

Both in the presence and absence of coralline turfs on the substrate, there were large fluctuations in the composition of the assemblages recruiting under increased nutrient levels, due to the increase in the

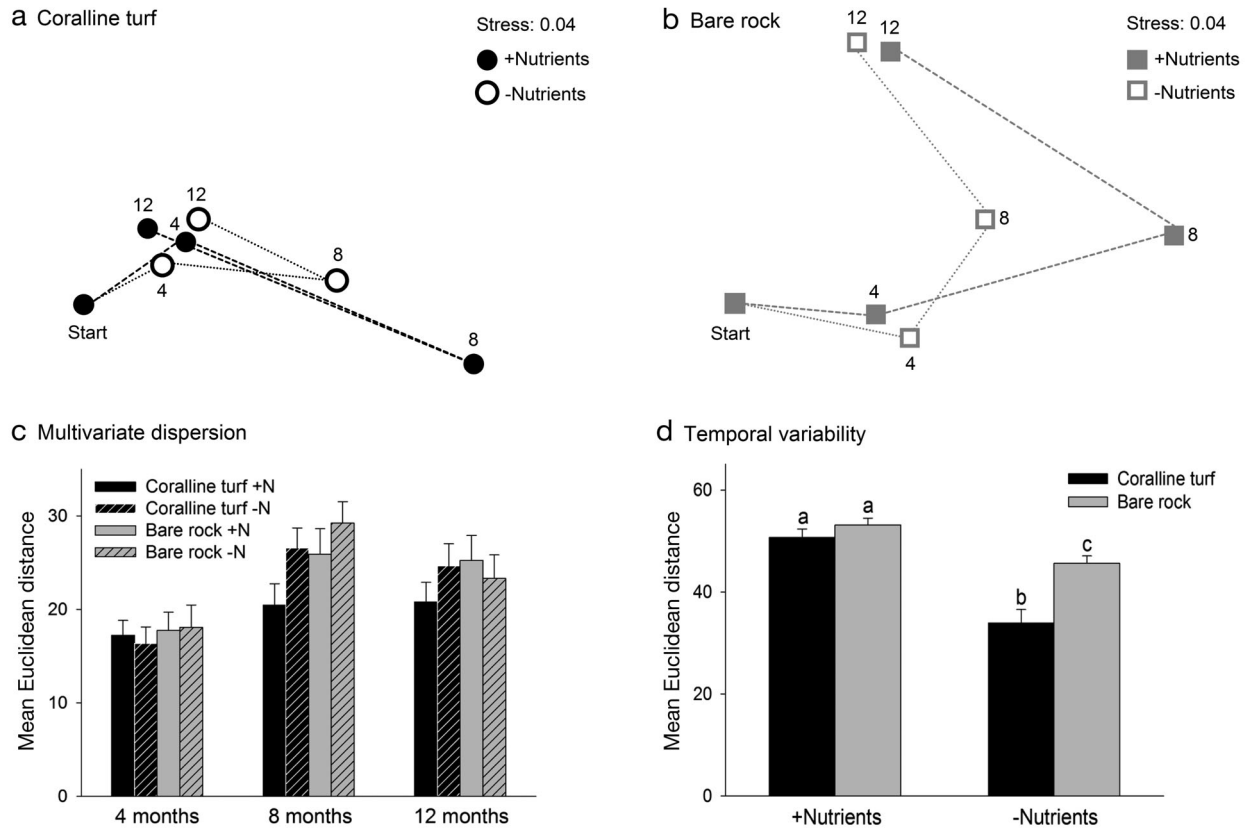


Fig. 3. Non-metric multidimensional scaling (nMDS) plots showing temporal changes in algal assemblages developing in (a) coralline turf and (b) bare rock plots under ambient (–Nutrients) and increased (+Nutrients) nutrient levels. Separate plots are presented for clarity, but they originated from the same nMDS. Symbols represent assemblage centroids under each combination of habitat and nutrient manipulation (n = 15) at each sampling date (numbers indicate months from the start of the experiment). (c) Mean (+SE) Euclidean distances to the centroids expressing the multivariate dispersion of the replicates of each treatment at each sampling date (n = 15). (d) Mean (+SE) Euclidean distances across all sampling dates expressing assemblage temporal variability under each combination of the experimental treatments (n = 15). Letters above bars: ranking of the means according to the Student-Newman-Keuls (SNK) tests

abundance of opportunistic species. Blooms of ephemeral algae were dominated by different species when occurring in the presence of the turfs or on unoccupied surfaces. Consistent with the findings of Daleo et al. (2006), *Ulva* had a limited ability to grow within the turfs which were, however, the most favourable habitat for the spread of *Colpomenia*. These results support the findings of Daleo et al. (2006), but also show that substrate monopolization by coralline turfs may not necessarily increase assemblage resistance against nutrient-driven alterations. This adds to a large body of evidence showing the limited ability of structurally simplified systems dominated by low-lying turfs to withstand perturbations such as mechanical disturbances (e.g. Bertocci et al.

2010), thermal stresses (e.g. Lilley & Schiel 2006), and exotic invasions (e.g. Bulleri et al. 2010). In addition, our results expand on the findings of Coleman (2003), who described positive effects of ephemeral species on coralline algae, showing that the

Table 2. ANOVA on mean Euclidean distances across all sampling dates and PERMANOVA on multivariate data of assemblage composition (after 12 mo) testing for differences between habitat types (coralline turf vs. bare rock) and nutrient regimes (enrichment vs. no-enrichment). *p < 0.05; **p < 0.01; ***p < 0.001

Source of variation	df	Mean Euclidean distance		Assemblage composition (12 mo)	
		MS	F	MS	Pseudo-F
Habitat (H)	1	755.30	17.92***	17828.00	26.00***
Nutrients (N)	1	2219.64	52.66***	783.11	1.14
H × N	1	319.29	7.57**	858.40	1.25
Residual	56	42.15		38418.00	

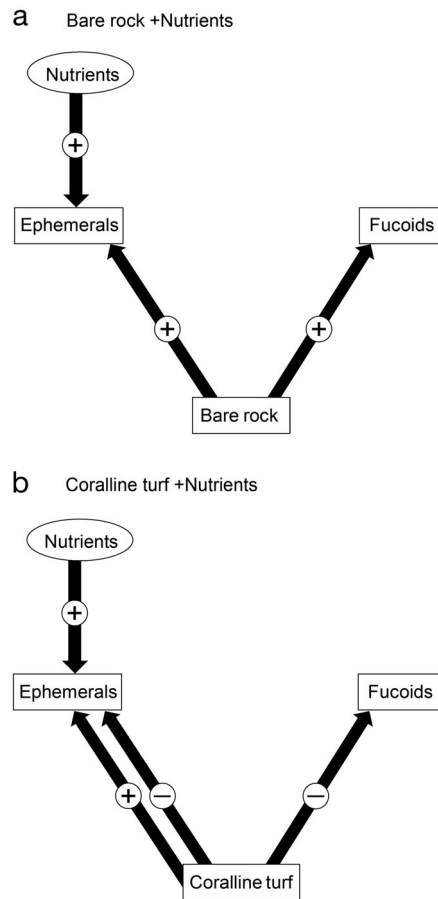


Fig. 4. Overview of the experimental results, showing the absence of any impact of ephemeral algae on fucooid recruitment, both in (a) bare rock and (b) coralline turf plots, despite their increased abundance in response to nutrient enrichment (+Nutrient). In (b), the interactions between coralline turfs and fucooids remained negative under increased nutrients loads, while both positive and negative effects of the turfs on the abundance of the ephemerals were observed. See 'Discussion' for a detailed description of the results

ephemerals may also be the beneficiary of facilitative interactions between the 2 groups.

Different morphological and physiological traits may explain the opposite outcome of *Colpomenia* and *Ulva* interactions with coralline turfs. Species with globular thalli such as *Colpomenia* are very tolerant to desiccation (Oates 1985, 1988) and are known for their ability to grow as epiphytes on articulated corallines (Oates 1989). On the other hand, the mechanisms underlying low abundances of *Ulva* on the corallines are still unclear, but Daleo et al. (2006) used artificial mimics to show that the negative impacts of coralline turfs on *Ulva* are related to their physical structure. This may be due to the higher topographic complexity of the turfs compared to un-

occupied surfaces (Granhag et al. 2004) and to increased desiccation at the surface of the corallines (Daleo et al. 2006).

Although habitat modification by coralline turfs had contrasting effects on the abundance of ephemeral algae, it posed a barrier to canopy recovery, with a dominant impact on fucooid recruitment. Despite the ability of *H. banksii* to invade short turfs of *Corallina officinalis* (10 mm thick or less) observed at this location (Schiel & Lilley 2011, Alestra et al. 2014) and elsewhere (Bellgrove et al. 2010), here the recruitment of both *H. banksii* and *C. torulosa* was extremely low in the presence of the corallines. This was probably due to the fact that in order to maximize the efficacy of the nutrient treatment, this experiment was set up in the low intertidal zone, where species with long, frondose branches (mainly *Jania* spp.) were particularly abundant and probably posed a bigger obstacle to fucooid recruitment compared to species with smaller fronds (Bellgrove et al. 2010, Schiel & Lilley 2011, Alestra et al. 2014). This pattern is consistent with the findings of numerous studies that have highlighted the importance of turf height and morphology in regulating the recruitment of a variety of benthic organisms (e.g. Birrell et al. 2005, Wieters 2005, Bellgrove et al. 2010).

Established communities dominated by fucooid canopies can be highly tolerant to increased nutrient loadings, resisting to the take-over by ephemeral algae for several months (Bokn et al. 2003). Here, we showed that fucooid assemblages may also be able to recover in spite of nutrient stress, as *C. torulosa*, *H. banksii* and the other species recruiting in the experimental plots were not affected by short-term (1 yr) nutrient enrichment and fluctuations in the abundance of ephemeral algae. This also indicates that the effects of ephemeral algae on perennial species may often be idiosyncratic (Viejo et al. 2008). Along European Atlantic shores, for example, Viejo et al. (2008) found that ephemeral green algae had opposite impacts on 2 fucooids, inhibiting the establishment of *Fucus vesiculosus* but facilitating the recruitment of *Himanthalia elongata*. In our study, in contrast, ephemeral green and brown algae had no effect on the recruitment of *C. torulosa* and *H. banksii*.

Colpomenia and *Ulva*, however, were not particularly abundant during most of our experiment. This suggests that increased nutrient availability alone may not be sufficient to maintain high biomass of ephemeral algae over extended periods. Although herbivory (Lilley & Schiel 2006, Schiel & Lilley 2011) and wave action (Taylor & Schiel 2003) are known to have a minor impact at this location, a variety of other

factors such as temperature, salinity, desiccation and light exposure may be implicated in the control of the abundance of ephemeral species (Fong et al. 1996, Kim et al. 2004). Furthermore, because of the 1 yr duration of this study, it was not possible to assess the long-term impacts of eutrophication, which often accumulate and escalate with time. The abundance of ephemeral green algae, for example, has been shown to build up with prolonged nutrient enrichment in long-term mesocosm experiments, leading to the collapse of furoid assemblages after several years (Kraufvelin et al. 2006). In addition, the establishment of propagule banks is also likely to foster ephemeral algae over longer time scales (Lotze et al. 2000, Worm et al. 2001).

Collectively, our results suggest that the interactions between coralline turfs and furoids are unlikely to switch from negative to positive in response to elevated nutrients, and that the trade-off between positive and negative effects of coralline turfs on the abundance of ephemeral species may either mitigate or exacerbate the biotic consequences of organic enrichment. Facilitative interactions have the potential to exert a destabilizing influence on community dynamics (Bulleri 2009, Butterfield 2009). Articulated corallines, in particular, are known to facilitate the settlement of the invasive kelp *Undaria pinnatifida* in intertidal assemblages in New Zealand (Thompson & Schiel 2012) and here we showed that they also are a favourable substrate for the growth of disturbance-oriented brown algae. To the best of our knowledge, there is no documented evidence of negative impacts of any species of *Colpomenia* and the influence of these algae on other benthic organisms deserves further investigation. *Colpomenia* spp. can, in fact, easily overgrow algae (Oates 1989) and corals (Coles 1988) and their extensive blooms can make large portions of the substrate inaccessible for other species.

In conclusion, comparisons of our findings with the results of previous research suggest that local assemblage composition and the duration of disturbance can contribute to producing complex idiosyncratic responses to nutrient enrichment. Different responses may well be expected in the presence of a different pool of species (e.g. turfs of filamentous algae in place of articulated corallines; Russell et al. 2009, Bulleri et al. 2012), and over longer temporal scales (Kraufvelin et al. 2006). Furthermore, synergisms between organic enrichment and other anthropogenic perturbations are likely to further add to this complexity (Gorgula & Connell 2004, Russell et al. 2009, Falkenberg et al. 2013), making short- and long-term consequences of eutrophication difficult to predict.

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