

Biological traits and taxonomic composition of invertebrate assemblages associated with coralline turf along an environmental gradient

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ABSTRACT: Biological traits relating to the behaviour, morphology and life history of organisms can influence ecological functioning, and this principle is becoming increasingly used to examine the functional response of communities to environmental variation. We quantified the taxonomic and biological traits composition, and the overall abundance and richness, of small (1–8 mm) mobile invertebrate assemblages inhabiting subtidal coralline algal turf (*Corallina officinalis*) along an environmental gradient ranging from (1) relatively deep, wave-exposed sites with short turf containing a low proportion of fine sediment to (2) shallow wave-sheltered sites with taller turf containing a higher proportion of fine sediment. Turf fauna were diverse (118 taxa) and abundant (12 000–53 000 ind. m⁻²), with assemblages dominated by amphipods and gastropods. Total abundances of invertebrates were higher at the wave-exposed sites. When analysed in multivariate space using proportional abundance, replicates based on taxonomic composition grouped more strongly by site along the overall gradient than those based on traits. As proportions of biological traits remained relatively stable along the gradient, numbers of all traits possessed by individuals were higher at the wave-exposed end of the gradient. Although some environmental variables contributed significantly to explaining multivariate trait and taxa patterns, most individual correlations between environmental variables and traits and taxa were weak. This study shows that biological traits can be shared between taxonomically distinct assemblages of turf-dwelling invertebrates, and indicates a relatively small influence overall of environmental variables on the composition of traits and taxa.

KEY WORDS: Temperate rocky reef · Diversity · Algal morphology

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INTRODUCTION

The functioning of systems is strongly influenced by the biological traits, i.e. aspects of behaviour, life history and morphology, of the organisms that inhabit them (Diaz & Cabido 2001, Bremner 2008). As these traits cannot necessarily be predicted by taxonomic relatedness, they have the potential to provide greater insight into community functioning than can be inferred from the taxonomic composition of the community alone (Bremner et al. 2003, Frid et al. 2008). The analysis of species traits can be used to compare func-

tioning across assemblages that are not taxonomically equivalent (Bremner et al. 2006a), to estimate functional redundancy and therefore predict the resilience and stability of a community (Hewitt et al. 2008), and to determine the functional response of communities to habitat variability (Bremner 2008). Originally developed for freshwater (e.g. Townsend & Hildrew 1994, Doledec et al. 1999) and terrestrial (e.g. Olf et al. 1994, McIntyre et al. 1995) systems, biological traits analysis (BTA) is increasingly being applied to marine habitats (Bolam & Eggleton 2014), where it is often used to determine the functional response of

communities to natural and anthropogenic variation in environmental factors (e.g. Bremner et al. 2006a, Paganelli et al. 2012). In the sea, BTA has largely been used on soft-sediment fauna (e.g. Bremner et al. 2003, Hewitt et al. 2008, Oug et al. 2012), usually to investigate anthropogenic impacts such as fishing (e.g. Tillin et al. 2006) and dredging (e.g. Bolam 2014). Comparatively little attention has been paid to animals inhabiting marine hard substrates (but see Munari 2013), including the fauna living amongst seaweeds on rocky reefs (but see Thrush et al. 2011, Törnroos et al. 2013).

Coralline algal turfs occur on shallow rocky substrates worldwide (Nelson 2009, Connell et al. 2014). They host an abundant and diverse assemblage of small (<10 mm) mobile invertebrates (Taylor 1998, Kelaher & Castilla 2005, Cowles et al. 2009) that contribute strongly to the flux of materials through reef ecosystems (Taylor 1998), control algal epiphytes through their grazing (Berthelsen & Taylor 2014), and are a major food source for higher trophic levels such as fish (e.g. Wellenreuther & Connell 2002). These important roles are potentially vulnerable to changes in the relative abundances of functional traits caused by natural or anthropogenic environmental variation. Previous studies have highlighted the strong influence of environmental variables on the taxonomic structure of turf-dwelling invertebrate assemblages (e.g. Dommasnes 1968, Kelaher & Castilla 2005). We aimed to determine changes in biological traits and taxonomic composition and overall invertebrate abundance, along an environmental gradient driven by variation in physical factors and host morphology for mobile invertebrates inhabiting subtidal coralline turf.

MATERIALS AND METHODS

Field

We sampled 7 sites spanning ~8.5 km along the southern coast of the Tawharanui Peninsula in temperate northeastern New Zealand (36° S, 174° E; Fig. 1). Reefs at the eastern end of the peninsula were exposed to prevailing ocean swells, deep, and relatively free of fine sediment, while reefs at the western end were wave-sheltered, shallow, and subject to sedimentation. The reefs were dominated by coralline turf (*Corallina officinalis*) and brown macroalgae (mostly the laminarian *Ecklonia radiata* and fucaleans of the genus *Carpophyllum*).

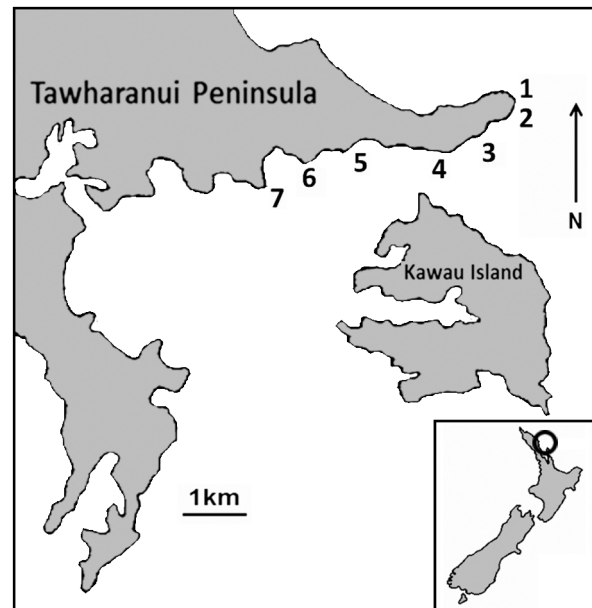


Fig. 1. Sites from which coralline turf and associated invertebrates were collected, along the southern side of Tawharanui Peninsula in northeastern New Zealand: 1: Takatu Point, 2: Elephant Point, 3: Bluebell Point, 4: Unnamed Point, 5: Mata-tuahu Point, 6: Motutara Point and 7: Karangatuoro Point

During autumn 2012, samples were taken from patches of *Corallina officinalis* (the only coralline turf species present) between the depths of 0 and 10 m (below mean low tide). At each of the 7 sites, coralline turf and associated fauna were scraped and vacuumed from a haphazardly selected 50.3 cm² area (n = 5) into a 0.2 mm mesh bag, using the suction sampler of Taylor et al. (1995). In association, sediment samples (n = 5) were collected by sliding a knife under a container with a 13.9 cm² mouth pushed through the turf down to the underlying rock, collecting any remaining sediment with a syringe, and placing the overall sample in a Ziploc bag. Lengths of 5 fronds from each turf patch were also measured *in situ*. The relative wave exposure of each site was estimated by summing values of distance to the nearest land mass (to a maximum of 300 km) at 10° intervals. The depth-averaged maximum tidal current speed for each site on a 1 km × 1 km grid was obtained from www.niwa.co.nz.

Laboratory

Faunal samples were washed through an 8 mm mesh sieve to establish an upper size limit for the individuals studied. The few individuals retained on the 8 mm sieve (mostly hermit crabs, nereid poly-

chaetes and ophiuroids) comprised <3% of the total abundance of mobile invertebrates sized between 1 and 8 mm and were not considered further. Individuals <8 mm were washed over a 1 mm mesh sieve, and all mobile invertebrates retained were identified as far as possible (see Gordon 2009, 2010 for taxonomic authorities) and counted. These were also washed over a 2.8 mm mesh sieve to split them into size classes for BTA. Fauna <1 mm were excluded from this study due to the difficulty of identifying individuals of this size. Turf fronds were removed from sediment samples and oven-dried at 60°C for 48 h to determine dry weight (algal biomass). The remaining sediment from each sample, from which large fauna were also removed, was wet-sieved into 3 size fractions: coarse (>1 mm), medium (0.125–1 mm) and fine (0.063–0.125 mm), each of which was oven-dried at 60°C to determine dry weight. Frond density was calculated by dividing the mean algal biomass by the mean frond length, as in Kelaher (2003), for each site. Turf frond widths were measured for 10 thalli haphazardly chosen from 1 frond per faunal sample, and the resulting values pooled to create an overall mean thallus width value per frond (as in Taylor & Cole 1994).

Biological traits

Faunal assemblages were defined using 8 biological trait categories (encompassing 23 traits) based on morphology, body size, life history and behaviour (Table 1). All trait categories were chosen for their potential ability to influence ecological functioning as recommended by Frid et al. (2008), although choice of these was limited by information availability. The definition of traits within each category was carefully considered in order for these to be relevant to all faunal taxa in our samples. Trait information was based on adults of all taxa and derived from the literature, with the exception of body size and body shape, which were determined during the study. If information on a taxon was unavailable, we used the most closely related taxon for which data existed. If no information was available (this occurred for <1% of assigned trait values), equal values were given across all traits. If taxa exhibited a number of traits within a category, fuzzy coding (Chevenet et al. 1994) was applied, where values were assigned to multiple traits within each category such that they summed to 1 (as in Hewitt et al. 2008). Each trait score for each taxon was then multiplied by the abundance of that taxon, and these abundance-

Table 1. Biological trait categories and traits that were used to conduct biological traits analysis on mobile invertebrates inhabiting subtidal coralline turf in northeastern New Zealand

Biological trait category	Trait
Feeding method	Grazer
	Detritus/deposit feeder
	Scavenger
	Predator
	Suspension feeder
Trophic level	Herbivore
	Carnivore
	Omnivore
Treatment of eggs	Brooded
	Substrate attached
	Planktonic
Larval mobility	High (planktonic)
	Low (does not swim)
Adult mobility	High (free-living, can swim)
	Moderate (tube/burrow, can swim)
	Low (does not swim)
Body size	Large (2.8–8 mm)
	Small (1–2.8 mm)
Body shape	Globose
	Flattened
	Vermiform
Calcareous exterior	Calcareous
	Not calcareous

weighted values summed across all taxa within each replicate to obtain a frequency value for each trait. These values were also expressed as a proportion of the total number of individuals in the replicate to prevent variation in total abundance from obscuring trends in composition. Numbers scaled in this way are hereinafter referred to as 'proportional', while unscaled numbers are referred to as 'raw'.

Statistical analyses

In order to elucidate fine-scale patterns that did not necessarily follow the gradient, univariate relationships between individual taxa and biological trait frequencies were assessed against all environmental/turf morphology variables individually using Pearson correlations on replicate-level data. Correlation strengths were defined as weak, $r < |0.5|$; medium/moderate, $r = |0.5|$ to $|0.8|$; and strong, $r > |0.8|$. Distance-based linear model (DistLM) analyses based on multivariate trait and taxa data (details below in this section) were also assessed using individual environmental variables.

In order to determine broad-scale patterns along the gradient as a whole, and to more easily visualise these patterns graphically, both multivariate principal coordinates (PCO) analyses using taxonomic and traits composition, and univariate measures of invertebrate abundance and richness (total number of taxa), were assessed in relation to the overall environmental gradient, for which distance from the easternmost point on the Tawharanui Peninsula was used as a proxy.

To examine multivariate patterns in taxonomic composition, the abundances of taxa were scaled to the proportion of total individuals that they comprised in their sample at the level of the site replicate. These data were then subjected to a PCO analysis run on a Bray-Curtis dissimilarity matrix (Anderson et al. 2008). This was run on untransformed, square-root- and 4th-root-transformed data with only the analysis run on untransformed data presented, as transformation made little difference to the result. The same analysis was performed on the biological traits frequency data (also converted to the proportion of total individuals). To determine whether significant differences in taxonomic and trait composition existed between sites, a 1-way (with site as the factor) permutational multivariate analysis of variance (PERMANOVA) with pairwise tests based on unrestricted permutations was conducted on the same multivariate data used in the PCOs.

The ability of environmental variables to explain patterns in taxonomic and biological traits composition was determined using a DistLM analysis. Marginal tests were performed individually for all environmental variables to test potential relationships between these and the multivariate data. Sequential tests were then conducted, in which the amount of variability explained by each variable added to the model depended on the variables already included in the model. The environmental variables 'percent medium sediment' and 'algal biomass' were excluded from the sequential test due to their strong Pearson correlations with 'percent coarse sediment' ($r = -0.88$) and 'frond density' ($r = 0.88$) respectively (Clarke & Gorley 2006). The DistLM model used a stepwise selection procedure and adjusted r^2 selection criterion and was based on the same biological data and similarity measures used in the PCO analyses and environmental/turf morphology data (normalised). Results of PERMANOVA and DistLM marginal tests were considered significant if $p < 0.05$. All multivariate analyses were run using the software package PRIMER v.6 (Clarke & Gorley 2006) and its add-on PERMANOVA+ (Anderson et al. 2008).

RESULTS

Environmental gradient

Environmental factors and turf structure changed to varying degrees along the Tawharanui Peninsula (Fig. 2). In terms of the overall environmental gradient, fetch ($r = -0.90$), depth ($r = -0.81$) and thallus width ($r = -0.65$) were negatively related to distance from Takatu Point (the wave-exposed easternmost site), while algal biomass ($r = 0.83$), percentage fine sediment ($r = 0.76$) and frond height ($r = 0.59$) were positively related to distance from Takatu Point. Relationships with distance from Takatu Point were weak ($r < |0.5|$) for frond density, percentage medium sediment, current speed, total sediment, and percentage coarse sediment.

Abundance and taxonomic richness

A total of 118 mobile taxa (size: 1–8 mm) were recorded from subtidal *Corallina officinalis* (Table S1 in the Supplement at www.int-res.com/articles/suppl/m530p015_supp.pdf). These included arthropods (56 taxa), molluscs (38 gastropods, 2 bivalves and 6 Polyplacophora), polychaetes (11 taxa), echinoderms (4 taxa) and nematodes (1 taxon). Total abundance was moderately negatively correlated with distance from Takatu Point ($r = -0.76$), with site means ranging from $12\,225 \pm 1355$ SE ind. m^{-2} at the wave-sheltered end to $53\,643 \pm 4203$ SE ind. m^{-2} at the wave-exposed end (Fig. 3a). Richness was also moderately negatively correlated with distance from Takatu Point ($r = -0.62$), with site means ranging from 20.2 ± 2.2 to 33.2 ± 1.5 SE total taxa (Fig. 3b). Arthropods (mostly amphipods) and molluscs (mostly gastropods) were numerically dominant at all sites, and relationships between proportional abundances of each of the broad taxonomic groups and the overall environmental gradient were weak ($r < 0.5$), except for polychaetes, which had a moderate positive correlation with distance from Takatu Point (Fig. 3c).

Taxonomic composition

The PCO analysis (Fig. 4) run on proportional abundances of taxa showed moderately tight clustering of replicates by site along the overall environmental gradient, with significant differences existing between all of the sites (PERMANOVA: $p < 0.05$, all pairwise tests: $p < 0.05$, data not shown), and with site explaining

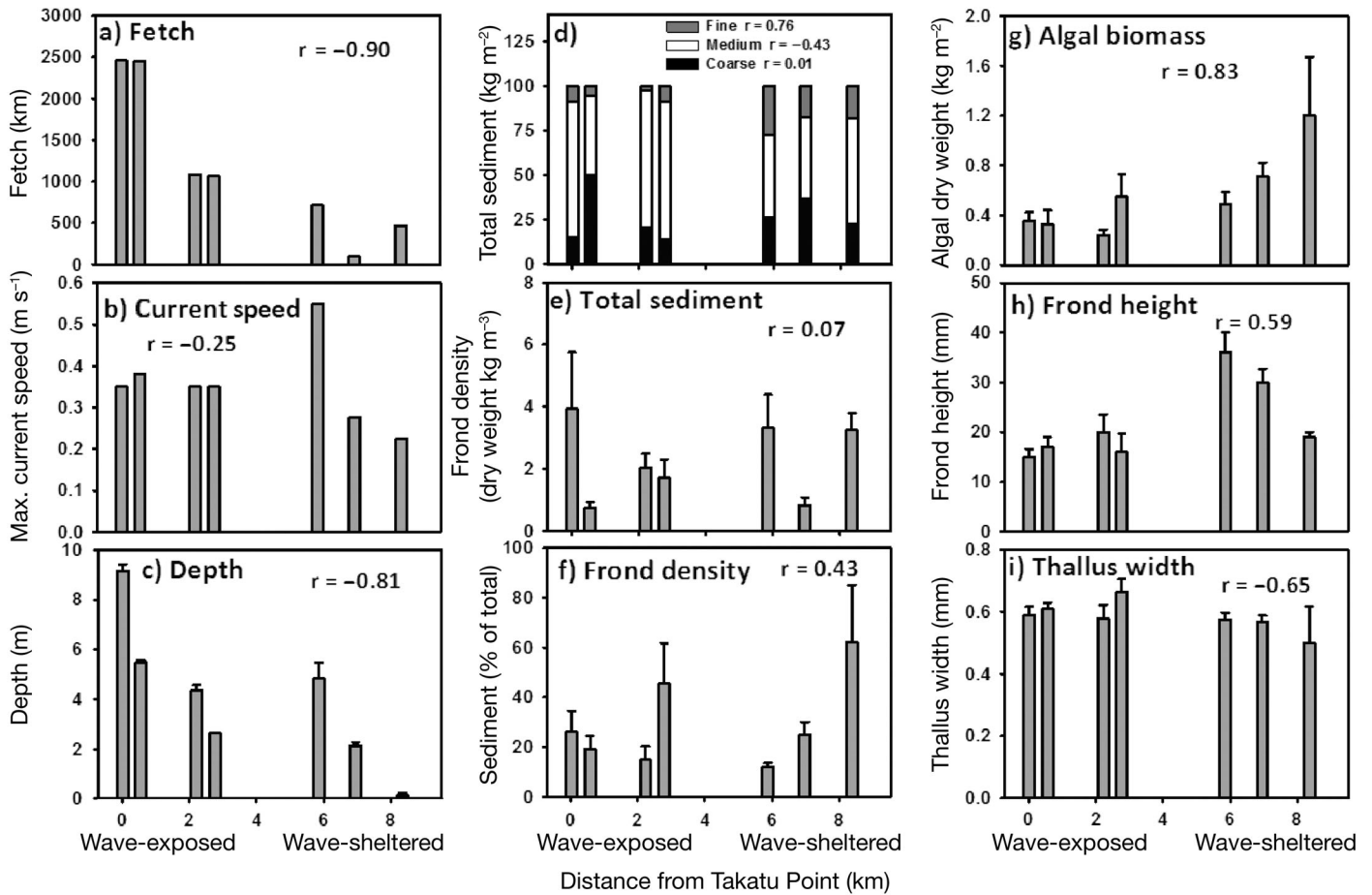


Fig. 2. Environmental variables and features of algal morphology associated with subtidal *Corallina officinalis* turf at sites along the southern side of Tawharanui Peninsula. Values are means; error bars represent SE; $n = 5$. Sediment size fractions are coarse (>1 mm), medium (0.125–1 mm) and fine (0.125–0.063 mm)

39% of the variation (Fig. 4a). The positioning of the sites in the PCO generally mirrored site positioning along the overall gradient, with wave-sheltered sites grouping on the left end of the x-axis (i.e. more negative values of principal coordinate [PC] 1) and wave-exposed sites on the right. The DistLM marginal test was significant for fetch, depth, current speed, percentage coarse sediment, percent medium sediment, percentage fine sediment, frond height and frond density (Table 2a). A combination of environmental variables (physical factors and turf morphology) explained $r^2 = 0.41$ (DistLM adjusted r^2) of the variation in taxonomic composition, and of these, fetch (17% of variation) and depth (11% of variation) were the most powerful. Overall, 96% (1249 from a total of 1298) of correlations between taxa abundances (proportion of total) and all individual environmental/turf morphology variables were weak ($r < |0.5|$), although 4% (49 from a total of 1298) were of medium strength ($r = |0.5|$ to $|0.8|$). A number of taxa (of which >10 individuals

were recorded during the study) had stronger than weak (all were moderate, $r > |0.5|$ to $|0.8|$) correlations with individual environmental variables (that were significant in the DistLM marginal test). *Eatoniella limbata*, *Fictonoba rufolactea*, *Cyclaspis* sp. and *Protohyale* sp. were positively correlated, and *Rissoina* sp. negatively correlated with fetch (Fig. 5a). *Eunice* spp. and *Gammaropsis* sp. were positively correlated and *Rissoina* sp. negatively correlated with current speed (Fig. 5b). *Paradexamine houtete*, *Eunice* spp. and *Halicarcinus cookii* were positively correlated, and Ostracoda negatively correlated, with percent fine sediment (Fig. 5c). *Nereis falcaria* and Ostracoda were positively correlated with percent medium sediment (Fig. 5d). *F. rufolactea*, *Cyclaspis* sp. and *Protohyale* sp. were positively correlated, and *Rissoina* sp. negatively correlated, with depth (Fig. 5e). Syllidae was positively correlated with algal biomass (Fig. 5f). *Fictonoba carnosus* and Syllidae were positively correlated with both frond height and frond density (Fig. 5g,h).

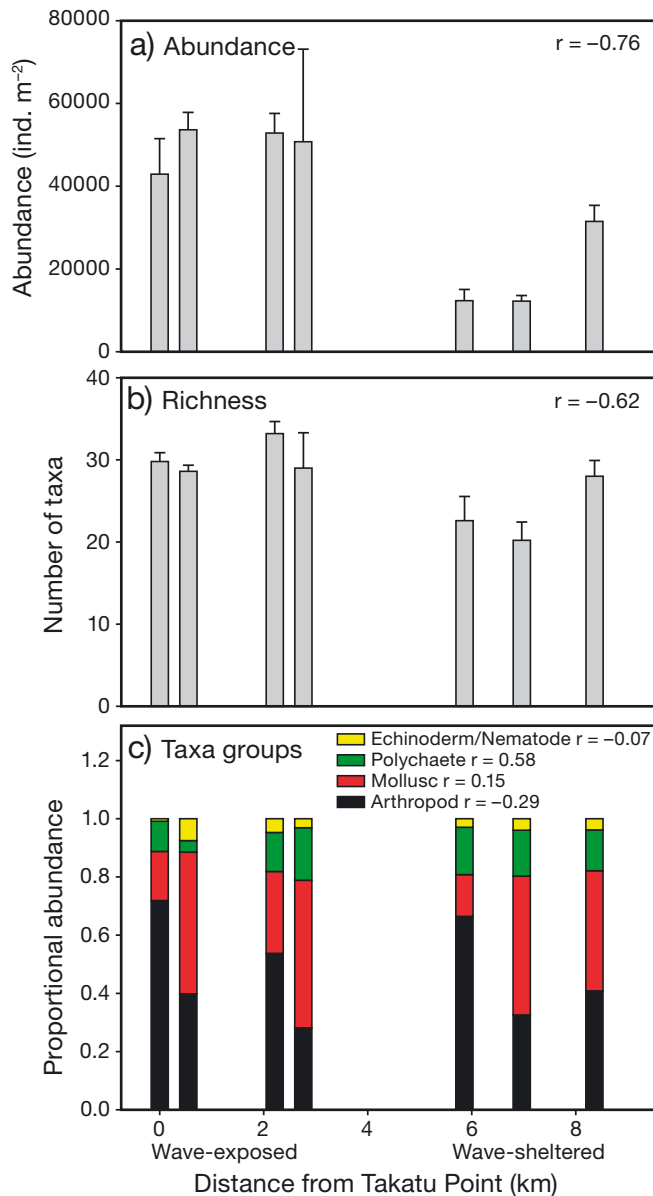


Fig. 3. (a) Abundance, (b) taxonomic richness and (c) proportional abundance of broad taxonomic groups of mobile invertebrates inhabiting subtidal *Corallina officinalis* turf at sites along an environmental gradient. Values are means; error bars represent SE; $n = 5$

Biological traits

The PCO run on proportional biological traits frequencies (Fig. 4b) yielded weaker patterns in terms of replicates clustering by site, and the overall gradient, than were seen for the proportional taxonomic data (Fig. 4a). Although significant differences existed between some (14 from a total of 21), but not all, sites (PERMANOVA: $p < 0.05$, 14 from a total of 21 pairwise tests: $p < 0.05$, data not shown), site ex-

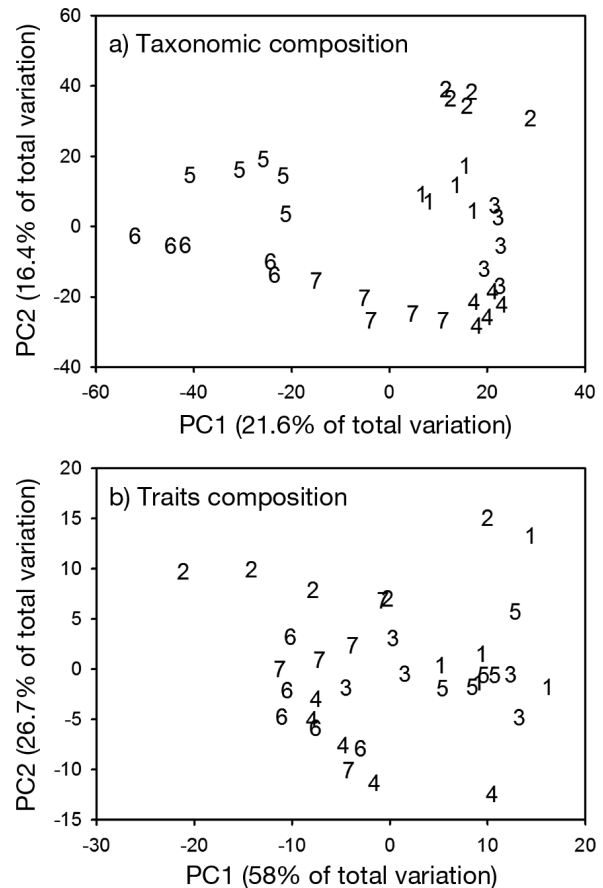


Fig. 4. Principal coordinate analysis (Bray-Curtis similarity) of faunal assemblages inhabiting subtidal coralline turf based on (a) proportional taxonomic composition and (b) proportional biological traits composition. Site numbers correspond to those in Fig. 1, with low numbers at the wave-exposed end of the gradient

plained only 9% of the variation. All 23 biological traits were represented in at least 1 individual invertebrate at every site (Fig. S1 in the Supplement). Traits that were more commonly exhibited across all sites, relative to other traits in their category, were: small (1–2.8 mm) size, globose shape, calcareous exterior, detritus/deposit-feeding mode, omnivory and low larval mobility. Traits that were uncommonly exhibited across all sites, compared to others in their category, included carnivorous diet, large (2.8–8 mm) size, non-calcareous exterior and moderate adult mobility. The DistLM marginal test was significant for fetch, depth, current speed, percent coarse sediment and percent medium sediment (Table 2b). Environmental variables accounted for $r^2 = 0.43$ (DistLM adjusted r^2) of the variation in biological traits composition, and of these, depth (19% of variation) and percentage coarse sediment (12% of varia-

Table 2. Distance-based linear model (DistLM) marginal and sequential tests describing the association between environmental variables and patterns in (a) proportional taxonomic composition and (b) proportional biological traits composition of faunal assemblages occupying subtidal coralline turf along an environmental gradient. Significant results ($p < 0.05$) in the marginal test are shown in **bold**. Prop. var. = proportion of variation; Prop. cum. var. = cumulative proportion of variation

	Marginal test				Sequential test			
	Pseudo- <i>F</i>	<i>p</i>	Prop. var.		Pseudo- <i>F</i>	<i>p</i>	Prop. var.	Prop. cum. var.
(a) Taxa								
Fetch	6.9	0.001	0.17	Fetch	6.9	0.001	0.17	0.17
Depth	4.7	0.001	0.12	Depth	4.8	0.001	0.11	0.28
Current speed	3.2	0.002	0.09	Current speed	3.7	0.002	0.08	0.36
% Coarse sediment	2.2	0.012	0.06	% Coarse sediment	3.2	0.002	0.06	0.42
% Medium sediment	3.8	0.001	0.10	% Fine sediment	2.5	0.005	0.05	0.46
% Fine sediment	4.5	0.001	0.12	Frond height	1.9	0.019	0.03	0.50
Total sediment	1.0	0.429	0.03	Thallus width	1.5	0.105	0.03	0.52
Frond height	4.6	0.001	0.12	Frond density	1.5	0.109	0.03	0.55
Thallus width	1.2	0.242	0.04	Adjusted $r^2 = 0.41$				
Algal biomass	1.6	0.093	0.05					
Frond density	1.9	0.031	0.05					
(b) Traits								
Fetch	5.2	0.005	0.14	Depth	7.6	0.001	0.19	0.19
Depth	7.6	0.001	0.19	% Coarse sediment	5.4	0.005	0.12	0.31
Current speed	5.4	0.004	0.14	Current speed	2.9	0.048	0.06	0.37
% Coarse sediment	4.4	0.01	0.12	Frond density	3.2	0.039	0.06	0.43
% Medium sediment	3.6	0.022	0.10	Fetch	2.9	0.048	0.05	0.48
% Fine sediment	1.3	0.257	0.04	Thallus width	2.4	0.097	0.04	0.52
Total sediment	2.8	0.054	0.08	% Fine sediment	1.8	0.177	0.03	0.55
Frond height	1.3	0.279	0.04	Frond height	1.1	0.341	0.02	0.56
Thallus width	0.6	0.6	0.02	Adjusted $r^2 = 0.43$				
Algal biomass	1.2	0.314	0.04					
Frond density	1.7	0.181	0.05					

tion) explained the most variation. Overall, 91 % (216 from a total of 238) of correlations between all proportional traits frequencies and all individual environmental/turf morphology variables were weak ($r < |0.5|$), although 9 % (22 from a total of 238) were of medium strength ($r = |0.5|$ to $|0.8|$), and these (that involve environmental variables significant in the DistLM marginal test) are listed as follows. In regards to feeding methods: detritus/deposit feeding was negatively correlated with current speed, depth and fetch (Fig. 6a,f,n). In regards to trophic level: herbivory was negatively correlated, and omnivory positively correlated, with depth (Fig. 6g). In regards to adult mobility: moderate adult mobility was positively correlated with current speed, and high adult mobility was positively correlated, and low adult mobility negatively correlated, with depth (Fig. 6c,i). In regards to larval mobility: high larval mobility was positively correlated with percentage of medium sediment and negatively correlated with percentage of coarse sediment, while low larval mobility was positively correlated with percent coarse sediment

and negatively correlated with percent medium sediment (Fig. 6e,l). In regards to treatment of eggs: planktonic eggs was positively correlated with percent medium sediment and negatively correlated with percent coarse sediment, while brooding was positively correlated, and substrate attached negatively correlated, with depth and current speed (Fig. 6b,d,h,k). In regards to body shape: flattened was positively correlated with depth, and vermiform was negatively correlated with fetch and percent coarse sediment (Fig. 6j,m,o). All raw biological trait frequencies (i.e. not scaled to overall abundance) were negatively correlated with distance from Takatu Point, with r -values (based on means) ranging from -0.25 to -0.87 .

DISCUSSION

Overall, the proportional taxonomic composition of faunal assemblages inhabiting subtidal coralline turf exhibited a higher level of variation between sites

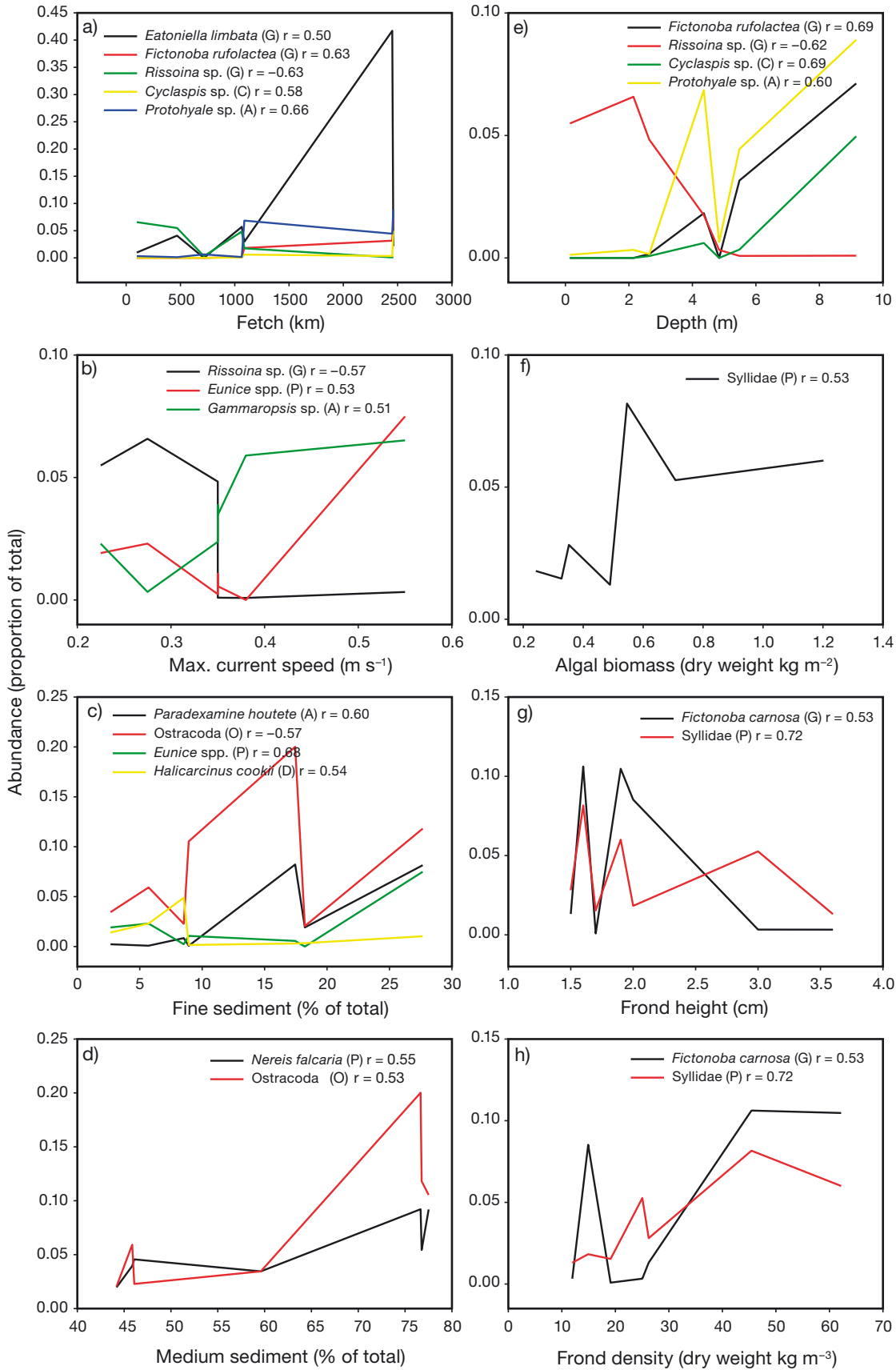


Fig. 5. Relationships between proportional abundance of mobile invertebrate taxa in *Corallina officinalis* turfs and environmental variables. Taxa were only included if >10 individuals were recorded throughout the study and if they had a correlation higher than 0.51 with any of the environmental variables that were significant in a distance-based linear model (DistLM) marginal test. Taxa letter codes: A = amphipod, C = cumacean, D = decapod, G = gastropod, O = ostracod and P = polychaete

along an overall environmental gradient than did the proportional biological traits composition. This result supports the idea that species turnover can occur within the constraints imposed upon biological traits (Usseglio-Polatera et al. 2000, Bremner et al. 2006a) and that ecological functioning can be shared amongst assemblages that are taxonomically distinct (e.g. Hewitt et al. 2008, Verissimo et al. 2012, Munari 2013). The ability of assemblages differing in taxonomic composition to function in a similar manner allows BTA to be used across different taxonomic groups of organisms (Bremner et al. 2006a), and also across large geographical scales where different species contribute to the overall make-up of assemblages (Bremner et al. 2003, Hewitt et al. 2008). In our study, only a small (9%) number of individual traits were responsive to environmental variables (when trait frequencies were expressed as proportions of total abundance), and the ability of BTA as a whole (in its multivariate form) to detect changes in environmental conditions along the overall gradient was limited due to the unresponsive nature of the majority of traits. In contrast, other studies have demonstrated that BTA can detect environmental changes, possibly due to the larger magnitude/scale of environmental variation in these studies, e.g. those occurring along a pollution gradient of heavy metals (Oug et al. 2012) and a large-scale river system (e.g. Usseglio-Polatera et al. 2000). The strong influence of total abundances on biological trait frequencies along the overall gradient (i.e. all traits were present in higher frequencies at the wave-exposed end of the gradient) highlights the ability of changes in invertebrate density to drive ecological function (Hewitt et al. 2008, Paganelli et al. 2012).

The subtidal coralline turfs examined in this study hosted an abundant (12 225–53 643 ind. m⁻²) and diverse (118 taxa) assemblage of mobile invertebrates (size 1–8 mm) dominated by amphipods and gastropods, with total invertebrate abundances being much higher at the wave-exposed sites. The ability of the turf to ameliorate wave stress by providing recesses to hide in and fine structures to cling to (Dommasnes 1968) may have facilitated the high invertebrate abundances at wave-exposed sites. This likely allowed invertebrates to benefit from factors associated with strong water movement, e.g. replenishment of organic particles in the water column for suspension feeders (Fenwick 1976) and a reduction in harmful fine sediment (Airoldi 2003, Prathep et al. 2003). The presence of lower invertebrate densities at the sheltered end of the gradient may have detrimental impacts for foraging fish as these can be sen-

sitive to the density of their turf-dwelling invertebrate prey (e.g. Wellenreuther & Connell 2002).

While a number of environmental variables were significantly linked to multivariate patterns in taxonomic composition, when expressed as a proportion of total abundance, most (96%) individual taxa were only weakly correlated with environmental variables. This is surprising, as the influence of environmental/turf structural variables on fauna is well documented for subtidal (e.g. Dommasnes 1968) and intertidal (e.g. Grahame & Hanna 1989, Kelaher et al. 2001, Kelaher & Castilla 2005) coralline turfs. However, similarly to our results, Thrush et al. (2011) also found a limited ability of algal turf complexity to explain the distribution of fauna in intertidal turfs. In our study, the 2 variables that best explained overall patterns in proportional taxonomic composition were fetch (a proxy for wave action) and depth. Fetch and depth have been shown to influence the distribution of coralline turf fauna in other studies (Dommasnes 1968 and Bussell et al. 2007, respectively). In our study, the potential reasons for relationships between some taxa and fetch and depth are unknown. However, *Protohyale* sp., a herbivorous amphipod (Brawley 1992) whose abundance was positively correlated with wave exposure in our study, is likely to have benefitted from the algal growth often found at wave-exposed sites (Krapp-Schickel 1993). These amphipods are strong swimmers and have the ability to cling to the fronds to avoid dislodgment (Tararam & Wakabara 1981). The gastropod *Eatoniella limbata*, also a herbivore (Ponder 1965) and positively associated with wave exposure in our study, likely shelters amongst the turf fronds to prevent being washed away (Morley & Hayward 2010). *Rissoina* sp., a gastropod negatively associated with wave exposure, may feed on detritus and was likely advantaged by the habitat and food supplied by the higher percentage of detritus associated with more sheltered conditions (Prathep et al. 2003).

When expressed as a proportion of total abundance, 91% of traits were only weakly correlated with environmental variables, indicating their relative stability in the face of changing environmental conditions (e.g. Bremner et al. 2006a). The influence of environmental variables on the biological traits of turf-dwelling invertebrates have been little studied; however, Thrush et al. (2011) also found generally weak relationships between traits related to feeding and mobility, and environmental conditions. The 2 variables that best explained multivariate patterns in biological traits composition were depth and the percentage of coarse sediment. While the reasons for

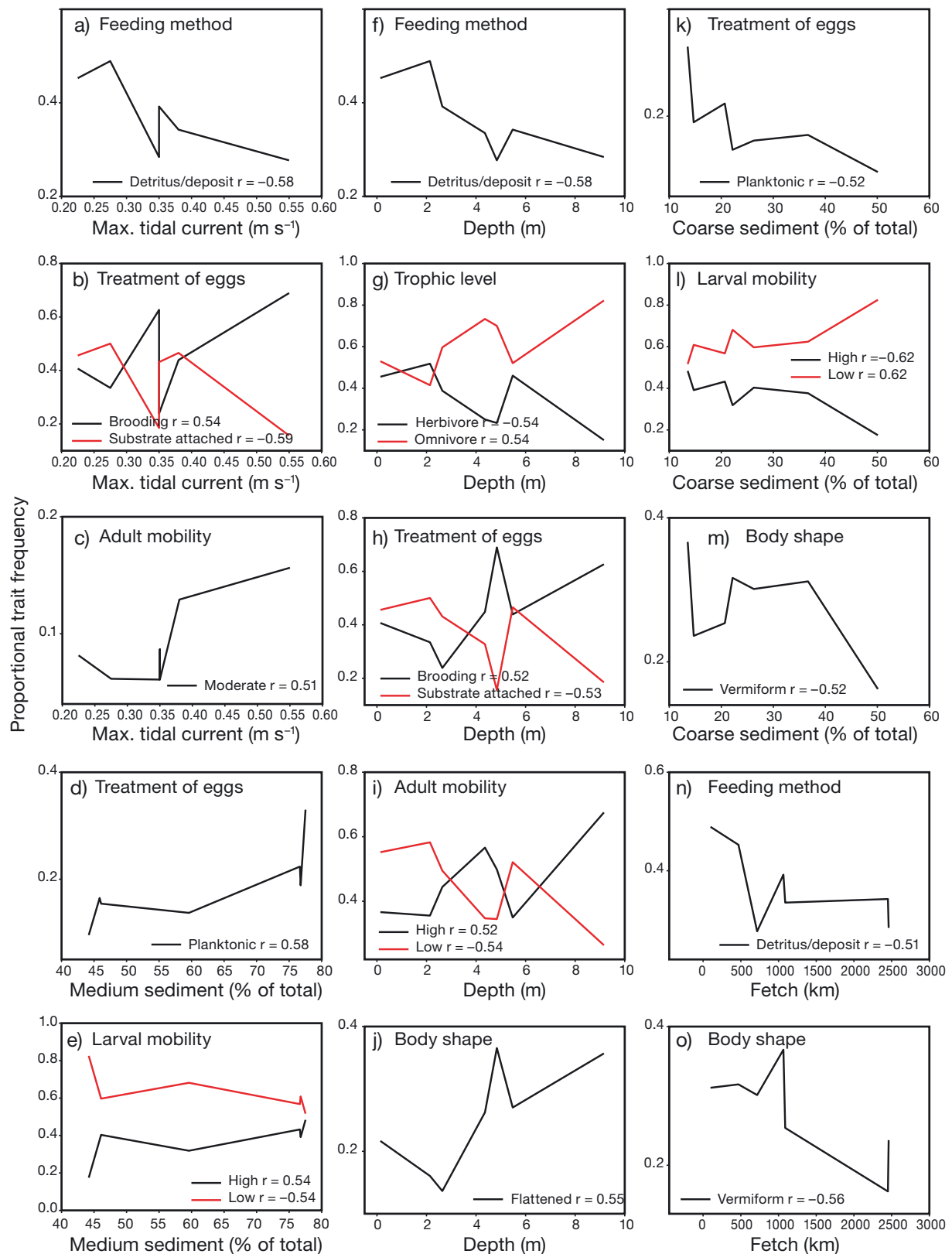


Fig. 6. Relationships between proportional biological trait frequencies of mobile invertebrates in *Corallina officinalis* turf and environmental variables. Traits were only included if they had a correlation higher than 0.51 with any of the environmental variables that were significant in a distance-based linear model (DistLm) marginal test

many of the relationships between traits in our study and depth and percent coarse sediment are unclear, these traits have the potential to strongly influence ecosystem function. Biological traits relating to feeding methods are often responsible for distinguishing assemblages (Oug et al. 2012) and detritus/deposit feeding, negatively correlated with depth in our study and often associated with organically rich fine sediment (Olabarria & Chapman 2001, Prathep et al. 2003), is functionally important as it incorporates uneaten primary production into the food web (Bremner 2008). Vermiform shape, negatively correlated with percentage coarse sediment in our study, may be advantageous for moving within fine sediment, and this trait was also positively correlated with percent fine sediment in a BTA of benthic assemblages in Italy (Paganelli et al. 2012).

A number of biological traits distinguished turf-associated faunal assemblages by being consistently more common than others within the same trait category across all sites. The general small (1–2.8 mm) size of fauna and the high occurrence of detritus/deposit feeding is likely explained by the complex structure of *Corallina officinalis* turf, which offers only small spaces for fauna to dwell (Dommasnes 1968), and which can trap detritus/fine sediment within its branches (Cowles et al. 2009). The high level of omnivory exhibited by turf fauna reflects an ability to utilise a variety of food sources, and could suggest they occupy relatively wide niches (Thrush et al. 2011). Low, as opposed to high, larval mobility was also frequently exhibited by fauna, which is in contrast to the findings of Thrush et al. (2011), but similar to those of Hagerman (1966) for algal-dwelling fauna and Boström et al. (2010) for seagrass fauna. In our turfs, this was driven by the high number of brooding peracarid crustaceans and egg-laying gastropods with direct larval development, e.g. eatoniellids. Low dispersal suggests that the persistence of populations of turf-dwelling invertebrates relies on the immigration of adults from nearby turfs and/or the recruitment of juveniles from within the turf. As high larval mobility can indicate an unstable habitat (Paganelli et al. 2012), the frequent occurrence of low larval mobility suggests that the habitat provided by the turf is relatively stable, possibly due to the perennial nature of the turf and its ability to ameliorate environmental stresses such as wave action (Dommasnes 1968). Traits may strongly map onto taxonomic relationships (Munari 2013), and the frequent occurrence of the traits calcareous exterior and globose shape in the present study reflects the numerical dominance of molluscs (calcareous and

often globose) and arthropods (calcified, albeit lightly) within the turf.

BTA has the potential to shed light on the functioning of communities in marine habitats (Bremner et al. 2006b, Van der Linden et al. 2012). However, its overall effectiveness is heavily influenced by the choice and definition of traits, which are in turn dependent on the availability of detailed and accurate data (Usseglio-Polatera et al. 2000). This is currently lacking for many marine communities (e.g. Paganelli et al. 2012, Munari 2013), including those in our study, where many traits with strong links to ecosystem function, e.g. life span, growth rate and fecundity (Bremner et al. 2006b) could not be included. In regards to the definition of traits, differences in function can exist within these if they are broadly defined, possibly obscuring fine-scale patterns and misleading predictions of functional redundancy. For example, functional redundancy does not necessarily exist between different marine grazing species (Aguilera et al. 2013), even though 'grazer' and 'herbivore' are traits commonly used in marine BTA studies.

We therefore suggest that more research into quantifying a larger number of faunal traits and understanding the links between these and functioning, followed by careful consideration of the definition of these traits, be undertaken in order to utilise BTA to its full potential.

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