

Biomass and species richness relationships in macroalgal communities that span intertidal and subtidal zones

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ABSTRACT: Investigations of the strong environmental gradients within intertidal and subtidal rocky reefs have contributed significantly to our understanding of ecological processes, but studies exploring how algal community structure responds to the extreme environmental transition of the intertidal–subtidal interface are rare. Our objective was to examine patterns in macroalgal distribution and species richness with depth on temperate rocky reefs. Standing algal biomass and richness were measured on 6 representative reefs in southern New Zealand, across 5 depth strata from the high intertidal zone, 1.5 m above mean low water (MLW), to the subtidal zone, 10 m below MLW. We found a unimodal relationship between algal richness and biomass across the depths, where maximum species richness occurred at intermediate levels of biomass. These results are consistent with many terrestrial plant studies across strong environmental gradients. Biomass decreased down the shoreline, with the exception of the high intertidal where the lowest biomass was recorded, whilst species richness increased down the shoreline. Additionally, strong patterns of dominance were observed, with a single species (not always the same species) contributing >56% of the total biomass across all depth strata examined. This dominance could have important implications for ecosystem provisioning across this system, particularly if dominant species are found to be vulnerable to the impacts of local and/or global change. The strong environmental gradients that characterise the intertidal–subtidal transition on rocky reefs over relatively small and experimentally tractable spatial scales enable opportunities to further advance our understanding of the mechanisms controlling the distribution of biodiversity.

KEY WORDS: Kelp · Seaweed · Macroalgae · New Zealand · Temperate rocky reef · Species richness · Biomass · Hump-shaped curve · Biomass-diversity · Unimodal relationship

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1. INTRODUCTION

Understanding patterns of biodiversity and the processes driving them is a core objective of ecology. Metrics such as biomass (often used as a proxy for productivity) and species richness are commonly

employed to characterise community structure across a range of different systems and habitat types (e.g. Johnson & Bell 1976, Bhattarai et al. 2004, Alves et al. 2010, Konar et al. 2010). While biomass trends across environmental gradients have been studied extensively in many ecosystems, results suggest

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that relationships are often specific to the system being investigated (e.g. Whittaker & Niering 1975, Johnson & Bell 1976, Alves et al. 2010). Studies in terrestrial plant systems have shown a variety of often contradictory biomass trends, such as decreasing (Whittaker & Niering 1975), increasing (Alves et al. 2010) or non-linear (Johnson & Bell 1976) relationships to disturbance gradients. However, most terrestrial studies agree in that one or 2 dominant species make up the majority of the total community biomass (Danin 1976, Kutiel & Danin 1987, Walker et al. 1999).

Similarly, species richness exhibits a variety of trends across environmental gradients and between differing systems (Danin 1976, Pollock et al. 1998). Richness observed across an environmental gradient has been associated with mechanisms linked to biotic interactions (i.e. interspecific competition and facilitation) and/or adaptations to environmental stressors (Grime 1973, Menge & Sutherland 1987, Bruno et al. 2003, Michalet et al. 2006). Species richness is often examined in relation to biomass, and has been studied in a range of terrestrial ecosystems (e.g. Kutiel & Danin 1987, Bhattarai et al. 2004, Espinar 2006), and a unimodal relationship showing a peak in biomass at intermediate species richness is most commonly reported, although highly debated (Mittelbach 2010, Whittaker 2010, Fraser et al. 2015). This relationship was traditionally explained by alterations in competition and resource use under differing stress conditions (Grime 1973, Connell 1978). However, in the last 20 yr other mechanisms influencing this unimodal relationship have been proposed (Oksanen 1996, Michalet et al. 2006, Pärtel & Zobel 2007, Zobel & Pärtel 2008).

In the marine environment, biomass and richness trends have been examined across environmental gradients including nutrient, light and turbulence conditions (Irigoien et al. 2004). The majority of studies investigating biomass and richness patterns have focussed on invertebrates (Rex 1981, Witman et al. 2008, Leduc et al. 2012, van Denderen et al. 2014) and plankton (Irigoien et al. 2004, Spatharis et al. 2008), where a unimodal relationship between biomass and richness is also commonly described (e.g. Irigoien et al. 2004, Graham & Duda 2011, van Denderen et al. 2014).

Rocky reefs dominated by macroalgae are considered one of the most productive ecosystems globally (Mann 1973, Harrer et al. 2013) and provide significant ecosystem services for marine organisms and coastal communities (e.g. Duggins et al. 1989, Steneck et al. 2002, Teagle et al. 2017),

therefore underpinning the need to improve our understanding of the structure of these communities. In algal-dominated rocky reef systems, species distribution and biomass patterns have historically received a large amount of attention, but the majority of these studies focus on either intertidal (Stephenson & Stephenson 1949, Sousa 1979a, Schonbeck & Norton 1980, Raffaelli & Hawkins 1996, Bustamante et al. 1997) or subtidal habitats (Aleem 1973, Valdivia et al. 2015) (but see Coleman 2003, Konar et al. 2009, 2010). In the intertidal, both the diversity (Stephenson & Stephenson 1949, Scrosati & Heaven 2007) and biomass (Bustamante et al. 1997, Ingólfsson 2005) of macroalgae have been described to decline with increasing elevation. In contrast, varying trends in macroalgal diversity have been documented with depth (Pedersen & Snoeijs 2001, Goldberg & Kendrick 2004, Balata & Piazzzi 2008), and biomass has been observed to decline with depth (Aleem 1973, Konar et al. 2009). Patterns in macroalgal biomass and richness have been examined in response to disturbances, most commonly wave exposure (e.g. Sousa 1979a,b, Goldberg & Kendrick 2004) or region/latitudinal trends (e.g. McQuaid & Branch 1984, Konar et al. 2010). However, the vast majority of studies have focussed on either intertidal or subtidal habitats, despite the linkages between these systems and the need for their integrated management (Bustamante et al. 1995, Rilov & Schiel 2006).

Temperate rocky reefs exhibit strong environmental gradients from the intertidal down into subtidal depths, whereby the depth gradient is accompanied by a change in abiotic factors such as light and water motion. Thus, these systems are ideal for furthering knowledge about ecological patterns and processes across gradients. In terrestrial and rocky reef systems, a range of co-occurring and interacting stressors exists along environmental gradients. While gradients in terrestrial systems (e.g. elevation gradients) typically occur over comparatively larger scales, the transition across the intertidal–subtidal interface of rocky reef systems is much more compressed in comparison.

Our objectives were to investigate patterns in algal community structure, biomass and species richness across the entire intertidal–subtidal gradient across multiple rocky reefs in southern New Zealand. In particular, we aimed to investigate the relationship of biomass and species richness across this transition by examining depths from the high intertidal down to 10 m (generally the deepest extent of rocky reef sys-

tems within this region) (Shears & Babcock 2007, Hepburn et al. 2011). Through this research, we aimed to achieve a better understanding of richness and biomass trends across the entire intertidal–subtidal interface and to put these results in context with the more widely studied terrestrial plant-dominated ecosystems.

2. MATERIALS AND METHODS

2.1. Study region

Algal composition and species richness were quantified at 6 representative rocky reefs of bedrock and/or boulder substrate in southern New Zealand. These sites ranged in their degree of exposure and slope. Three sites were located on the south-eastern coast of New Zealand's South Island and 3 were located on the coast of Stewart Island (Fig. 1). Within each site, 3 subtidal and 2 intertidal depth strata were assessed. The subtidal depth strata represent distinct macroalgal communities that are typical across New Zealand temperate reefs (Shears & Babcock 2007). The intertidal depths selected represent globally defined vertical zonation habitats (Stephenson & Stephenson 1972). These strata include high intertidal (1–2 m above mean low water [MLW]), low intertidal (0–0.5 m above MLW), 2 m (1–3 m below MLW), 5 m (4–7 m below MLW) and 10 m (9–12 m below MLW).

2.2. Field collection and survey

The survey was conducted in autumn (March to May 2017) using a single 20 m weighted transect line run parallel to the shore. The transect was positioned in the middle of each depth stratum using depth measurements adjusted to levels below MLW. Six 0.25 m² quadrats were randomly positioned along the length of the transect. All sub-canopy fleshy macroalgae, including articulated coralline algae, within the 0.25 m² quadrats were harvested by hand or using a fine metal blade, then placed into a mesh bag. Large canopy forming *Durvillaea antarctica* and *Macrocystis pyrifera* were excluded from the collection due to difficulty in collecting the thalli. However, smaller sub-canopy individuals of these species were sampled. Note that *D. antarctica* was only present in the low intertidal depth stratum and *M. pyrifera* was relatively uncommon along the transects (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m654p067_supp.pdf).

Macroalgal samples were identified by experienced algal taxonomists. When possible, specimens were identified to species level or to genus if material was sterile or fragmentary (e.g. *Halopteris* spp. and *Phycodrys* spp.), or if the genus included multiple species not yet described (e.g. *Plocamium* spp. and *Zonaria* spp.) or when molecular data are necessary for species identification (e.g. *Ulva* spp.). For each species (or species group), excess water was shaken off and the wet weight was recorded to the nearest g.

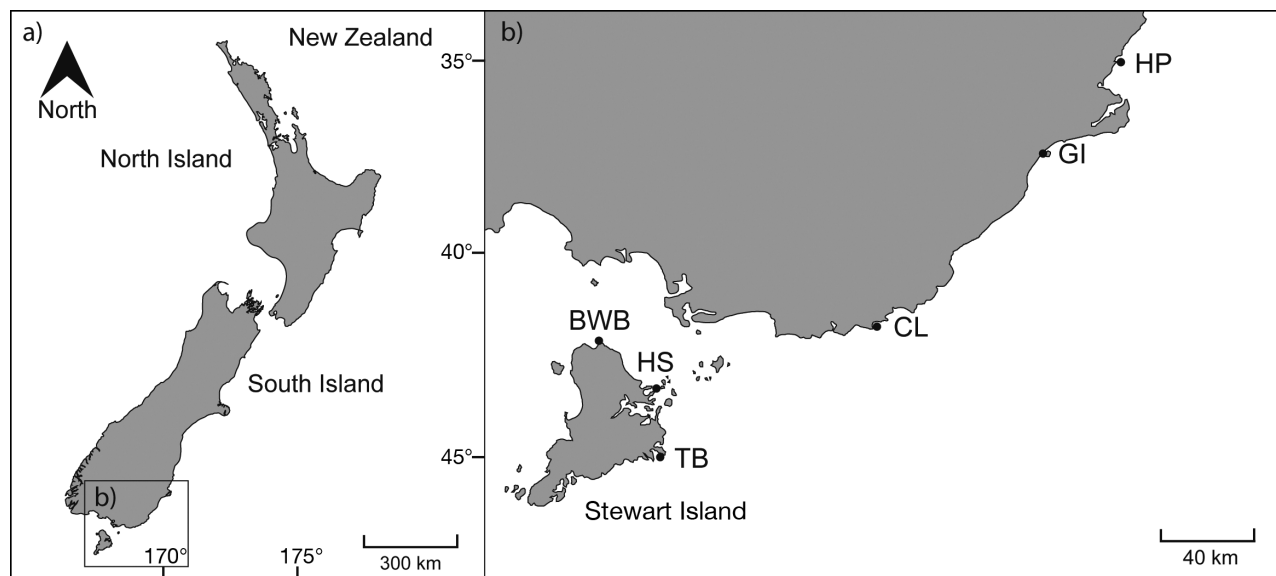


Fig. 1. (a) New Zealand and (b) southern New Zealand showing the location of algal biomass collection sites. HP: Huriawa Peninsula; GI: Green Island; CL: Chaslands; BWB: Black & White Bay; HS: Horseshoe Bay; TB: Tikotatahi Bay

Voucher specimens were retained and lodged in the herbarium of the Museum of New Zealand Te Papa Tongarewa (WELT; Thiers 2018).

2.3. Data analysis

All statistical analyses were performed using the R statistical software platform v.3.3 (R Core Team 2017) and associated packages. Assemblages were analysed using both univariate and multivariate statistics to determine generalised trends in biomass (g wet weight per 0.25 m²), species richness (average number of species) and community structure across depths.

Mixed effect models were used to examine differences in total biomass and species richness of all taxa per quadrat across depth strata, with depth treated as a fixed effect and site as a random effect. Biomass was analysed using a linear mixed effects model, fitted with the 'lme' function from the 'nlme' package (i.e. nlme::lme v.3.1.131; Pinheiro et al. 2017). Prior to analysis, model assumptions of normality (Shapiro Wilk test) and homoscedasticity (Bartlett test) were checked, resulting in biomass values being transformed using a Box-Cox transformation in order to satisfy requirements. Figures were produced from back-transformed data. A generalised linear mixed regression model with negative binomial family link for the species count data was used to examine species richness, as the data were found to be over-dispersed, preventing the use of the Poisson family link (lme4::glmer.nb v.1.1.18; Bates et al. 2014). In both analyses, post hoc multiple comparisons (Tukey's procedure) were performed when depth was found to be significant to identify differences between depths (multcomp::glht v.1.4.8; Hothorn et al. 2008).

To assess the dominance of individual species across depths, the cumulative percentage of total biomass within each depth (quadrats pooled across depth at a site) was plotted against the number of species, with species ranked in order of percentage biomass contribution. These plots were separated by depth and fitted with a scaled and shifted Michaelis-Menten function (Bolker 2008) of the form:

$$y = \frac{(100 - yint)(x - 1)}{(km / 3) + (x - 1)} + yint \quad (1)$$

where x is the number of species in each depth for a given site, $yint$ is the average percentage of biomass contributed by the most abundant species ($x = 1$) and km denotes the number of additional species required to account for 75% of the remaining increase in biomass. Taken together, $yint$ and km determine

the overall shape of the curve. An algal community where a small number of species dominate may have a high $yint$ and/or low km and a curve that increases steeply. A community with biomass more evenly distributed across a number of species may have a low $yint$ and/or a high km and a correspondingly flat curve that increases slowly. This curve was fitted using a non-linear mixed effect modelling approach (nlme::nlme v.3.1.131; Pinheiro et al. 2017) with depth strata (factor, 5 levels) as a fixed effect and site (factor, 6 levels) as a random effect. To visualise broad taxonomic trends with depth, species were coded based on taxonomic groupings of red (Phylum Rhodophyta), green (Phylum Chlorophyta) or brown (Phylum Ochrophyta) algae. Comparisons of $yint$ and km among depth strata were made whilst controlling the Type I error rate using single-step adjustments (multcomp::glht v.1.4.6; Hothorn et al. 2008).

Algal community structure across depth (fixed factor) and sites (random factor) was analysed using non-metric multidimensional scaling ordination and permutational multivariate analysis of variance (PERMANOVA, vegan::adonis v.2.4.3; Oksanen et al. 2017) based on fourth-root transformed biomass data (to achieve normality) and a Bray-Curtis similarity matrix. PERMANOVA was also used to conduct pairwise comparisons between depth strata using Bonferroni-adjusted p-values. Species indicator analysis (indispes::multipatt v.1.7.6; Dufrene & Legendre 1997, De Cáceres & Legendre 2009) was then used to determine algae significantly associated with each depth, assessed using a Monte Carlo permutation approach with 999 random permutations.

To examine the relationship between richness and biomass across the key environmental gradient in this study (depth), algal species richness was plotted against logged biomass values (Leduc et al. 2012). Prior to analysis, quadrats for each depth at a given site were averaged. Additionally, separate plots were produced to determine the relationship between biomass and species richness of all taxa per quadrat at each site individually. To test for evidence of a curved ('hump-shaped') relationship over this gradient, a quadratic model was compared to a linear model and null model. Akaike's information criterion (AIC) and R^2 values were used to assess the best model and model fit (Burnham & Anderson 2003, Johnson & Omland 2004).

3. RESULTS

A total of 101 species of macroalgae (Table S1) were identified from the 180 quadrats sampled over

this study (approximately 50 % of the flora reported from this region; Nelson et al. 2013). Of these macroalgae, 70 were red, 27 were brown and 4 were green. Both biomass and species richness differed significantly among depths (Table S2). The high intertidal had significantly lower biomass than all other depths (Fig. 2, Table S3), and the 10 m depth stratum had significantly lower biomass than the 2 m and low intertidal strata. Similarly, species richness was significantly lower in the high intertidal compared with all other depths (Fig. 2, Table S3). In contrast with total biomass, species richness was significantly higher in the 10 m stratum compared to the low intertidal and 2 m depths, and the 5 m depth stratum also had significantly higher species richness than the low intertidal stratum.

On average, across all depth strata, the proportion of total biomass accounted for by the most dominant species (irrespective of identity) (*yint*) within a depth stratum was 56.5 % (± 4.1 %). In the low intertidal depth stratum, the most dominant species (not always the same species) accounted for 71.9 % of the total biomass, significantly greater than at all other depths (a difference of 13.2, 21.4, 22.7, 19.7 % for high intertidal, 2, 5 and 10 m, respectively, $p < 0.008$ for all comparisons; Fig. 3). On average, slightly more than 2 species were required to account for 75 % of the remaining biomass ($km = 2.5 \pm 0.5$ species) with no statistically significant difference between the high intertidal, low intertidal, 2 and 5 m depth strata ($km = 1.6, 3.1, 1.8$ and 1.5 , respectively). However, total biomass in the 10 m depth stratum was distributed more evenly among species,

which was reflected in a significantly higher *km* at this depth (4.0) compared to the high intertidal, 2 and 5 m depth strata (a difference in *km* of 2.4, 2.2 and 2.5, respectively; $p < 0.005$ for all comparisons).

Species of brown algae contributed to over half of total biomass (>57.9 %) for all depth strata except for the high intertidal (Fig. 3), which was dominated by red algae. In the 10 m depth stratum, red and green algae were more dominant (contributing to 42.1 % of total biomass combined) compared to the low intertidal (15.9 %), 2 (2.2 %) and 5 m (13.4 %) depth strata.

Community composition differed significantly between the depth strata examined (Table S4). When accounting for differences among sites, significant differences in species composition occurred among all depths, except between the 5 and 10 m depth strata (Fig. 4). Indicator species analysis showed that 17 species had significant indicator values for the defined depths strata (Table S5), although only 6 of these species accounted for more than 10 % of the total biomass in a given depth.

The AIC values indicated that the quadratic model, compared to a linear and null model, was the best fitting model for explaining the relationship between biomass and species richness across all sites (Fig. 5). An R^2

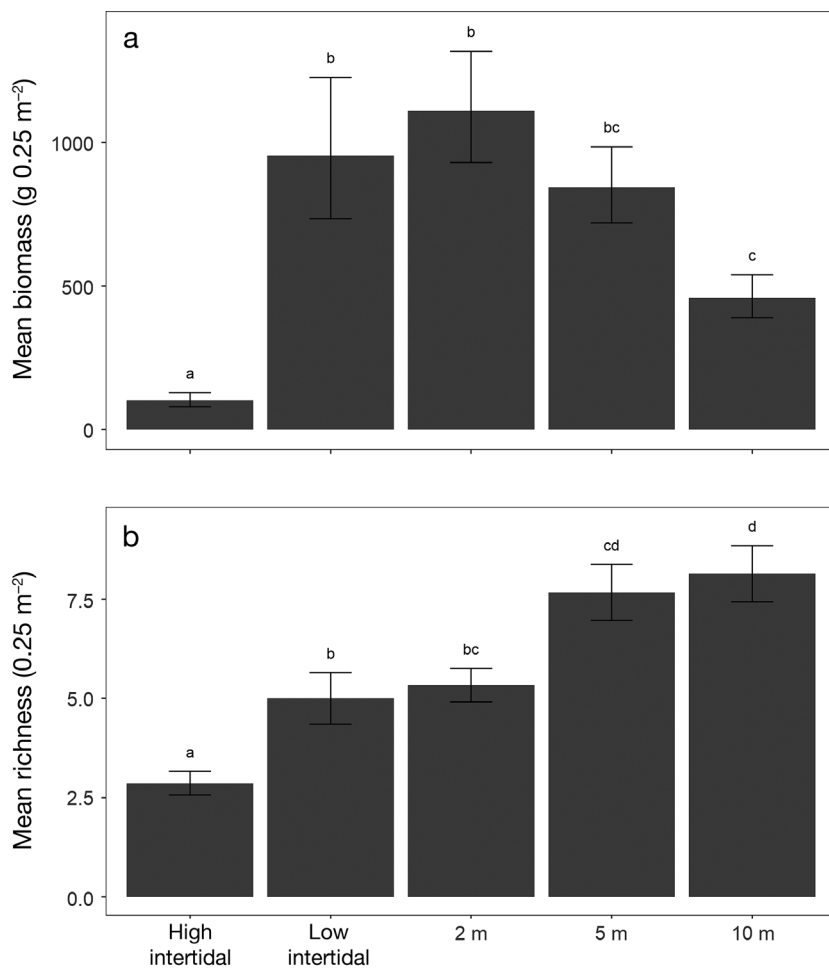


Fig. 2. Mean (± 1 SE) algal (a) biomass and (b) species richness for the 5 different depths across rocky reefs in southern New Zealand ($n = 36$). Different letters represent significant differences ($p < 0.05$) based on Tukey's post hoc test using linear mixed effects models (with a negative binomial family link for species richness) with depth treated as a fixed effect and site as a random effect

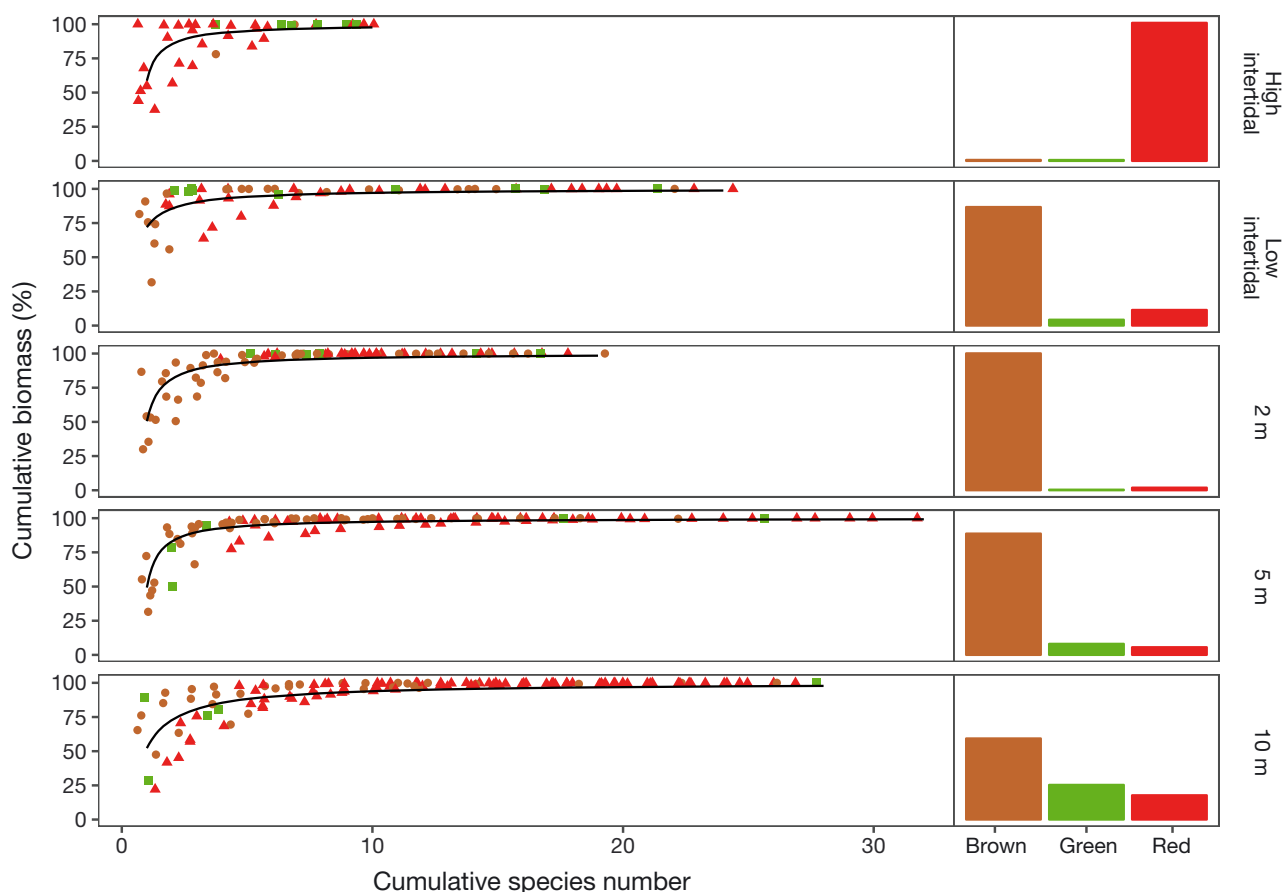


Fig. 3. Cumulative biomass (percentage of total) against the ranked (in order of decreasing contribution) species, within each depth stratum. The 3 taxonomic orders of algae are shown with different colours and symbols: brown (Phylum Ochrophyta), green (Phylum Chlorophyta) and red (Phylum Rhodophyta). Lines are scaled and shifted Michaelis-Menten curves fitted using non-linear least squares regression (see Section 2.3 for details). For visualisation, values are jittered along the x-axis to avoid over-plotting. The percentage contribution of the 3 algal taxonomic orders towards total biomass are shown on the right of the plot. Note that the y-axis for these bar plots represents contribution towards total biomass (%) and not cumulative biomass (%)

squared value of 0.31 for the quadratic model showed a moderate fit of this curve. This result provides some support for a unimodal relationship over the gradient examined here, where species richness increased as biomass increased to a maximum at intermediate levels of biomass and then gradually decreased thereafter (Fig. 5). When examining the relationship between biomass and species richness for each of the 6 sites individually, 4 showed that a unimodal quadratic curve was the best fitting model, with R^2 values ranging from 0.12–0.19 (Fig. S2). The 2 sites (Green Island and Huriawa) where a unimodal quadratic fit was not the best supported model showed an increasing linear relationship between biomass and species richness as the best model (Fig. S2). However, these sites both showed the lowest total biomass observed for any one quadrat out of all the sites.

4. DISCUSSION

4.1. Biomass vs. species richness

This study suggests a unimodal relationship between macroalgal biomass and species richness across a depth gradient spanning the intertidal–subtidal interface on rocky reefs in southern New Zealand. Specifically, species richness peaked at intermediate levels of biomass when looking at all sites combined across a depth gradient from the high intertidal down to 10 m depth. This unimodal pattern is the most commonly reported relationship in plant-dominated terrestrial systems and in marine phytoplankton environments (Kutiel & Danin 1987, Irigoien et al. 2004, Espinar 2006, Graham & Duda 2011, Fraser et al. 2015). To our knowledge, this is the first

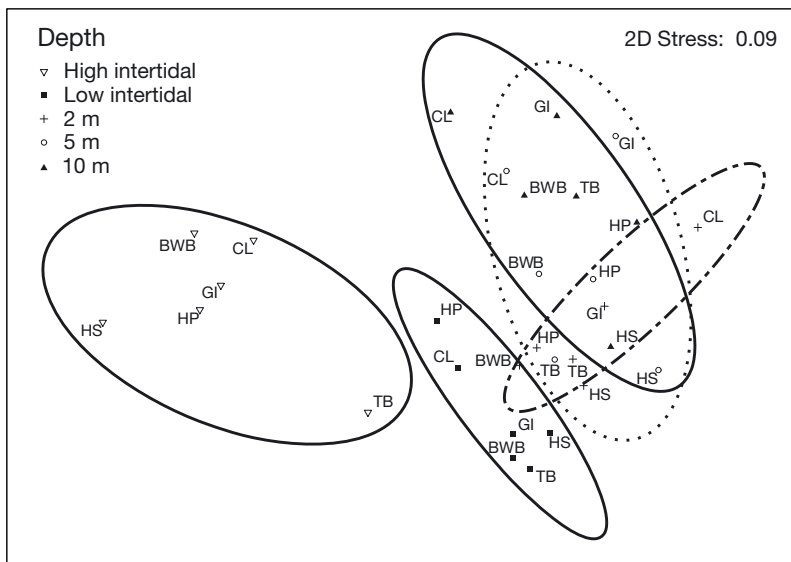


Fig. 4. Non-metric multidimensional scaling ordination plot examining the difference in community biomass composition among depths and sites (all quadrats within each depth stratum at each site are pooled). Ellipses show the mean hull distance; overlapping ellipses are shown with differing dashed lines for clarity. HP: Huriawa Peninsula; GI: Green Island; CL: Chaslands; BWB: Black & White Bay; HS: Horseshoe Bay; TB: Tikotatahi Bay

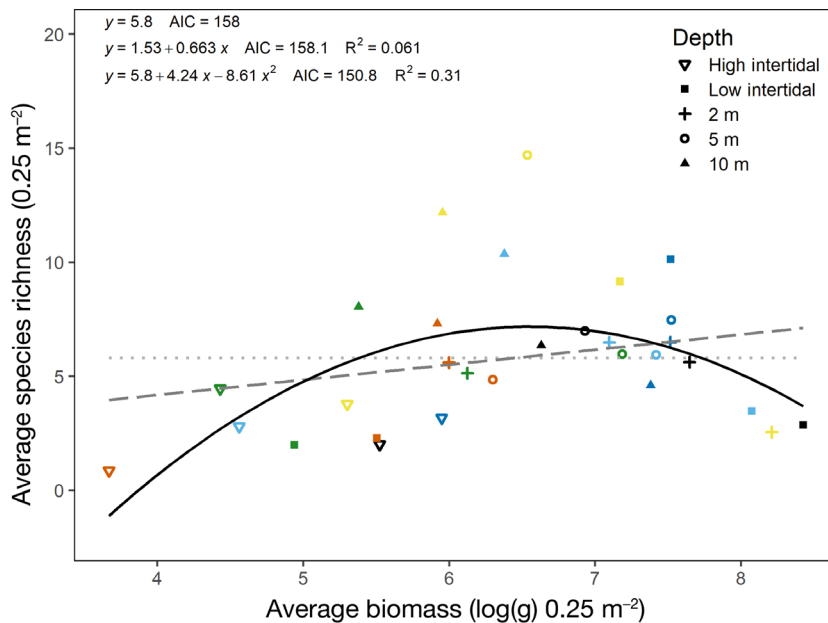


Fig. 5. Species richness (number of species) versus total biomass shown on a log scale from the high intertidal down to 10 m depth across 6 rocky reef systems in southern New Zealand. The 6 sites are shown with different colours: black, Black & White Bay; yellow, Chaslands; green, Green Island; light blue, Horseshoe Bay; brown, Huriawa Peninsula; dark blue, Tikotatahi Bay. Data points are averages from the 6 quadrats within each depth stratum. Dotted light grey line: null model (richness = intercept); dashed grey line: linear model (richness = intercept + biomass); solid black line: quadratic model (richness = intercept + biomass + biomass²)

instance where this pattern has been described for benthic macroalgal communities. There are a number of underlying mechanisms that could contribute to a unimodal pattern, including competitive exclusion, tolerance of species to extreme conditions and facilitation (Grime 1973, Michalet et al. 2006).

Although there is large support for a unimodal relationship, there has been debate about the universality of this relationship across differing systems (Mittelbach 2010). Other relationships, including U-shaped, positive linear, negative linear or no relationship, have also been observed in a number of terrestrial plant studies (Mittelbach et al. 2001, Roxburgh et al. 2004, Mittelbach 2010, Whittaker 2010). These divergent patterns seen across studies could be modulated by differences in the intensity, frequency and duration of a disturbance and interactions among these parameters (Shea et al. 2004). Furthermore, differences in the extent of the environmental gradient examined among studies could contribute to differences in the observed relationship. Although we did not quantify the intensity of abiotic gradients in this study, it is widely accepted that the environmental gradient spanning the high intertidal to deep subtidal is strong and encompasses a wide range of disturbance and stress patterns over a relatively short distance (Leigh et al. 1987, Raffaelli & Hawkins 1996, Pritchard et al. 2013, Desmond et al. 2015). Notwithstanding any debate about the universality of biomass–species richness relationships, there is general agreement that the greater the gradient of the disturbances (i.e. the greater the range in the type, severity and/or frequency of disturbances) and where studies include observations transitioning across community types, the more likely it is to observe a unimodal relationship (Waide et al. 1999, Mittelbach et al. 2001, Fridley et al. 2012). Our data are consistent with this view,

in that the algal communities transitioning the intertidal–subtidal interface are subjected to strong gradients in a range of different types of disturbances. This includes steep light gradients that are typical in the reef systems we studied (Hepburn et al. 2011, Pritchard et al. 2013, Desmond et al. 2015), strong gradients in the degree of desiccation experienced down the shore in the intertidal (Schonbeck & Norton 1980, Raffaelli & Hawkins 1996), varying impacts of wave energy and differences in grazer abundance and pressure typical of temperate rocky reefs (Leigh et al. 1987, Korpinen et al. 2007, Shears & Babcock 2007, Desmond et al. 2015). In terrestrial systems, strong environmental gradients typically occur over larger spatial scales in contrast to the strong gradient observed over short spatial scales on rocky reefs across intertidal–subtidal interfaces. However, despite this difference, there appears to be a consistency in the type of pattern observed between the 2 systems.

Examining trends across the whole intertidal–subtidal gradient may allow for better comparisons with terrestrial systems, where trends across the entirety of strong environmental gradients have been investigated. Previous studies examining biomass and richness patterns of benthic macroalgae have focussed on either the intertidal or subtidal, often reporting biomass and richness trends separately (e.g. Goldberg & Kendrick 2004, Valdivia et al. 2015), and thus these studies have examined a reduced environmental gradient which may limit the likelihood for a unimodal pattern (Waide et al. 1999, Mittelbach et al. 2001, Fridley et al. 2012, Fraser et al. 2015). An exception is a study by Konar et al. (2010), who observed a positive linear relationship between algal biomass and species richness across the intertidal–subtidal interface when examining a number of Northern Hemisphere rocky reef sites. However, Konar et al. (2010) averaged biomass and richness values across individual sites (i.e. one biomass and richness value obtained for a given site). This averaging excluded the effect of depth on this relationship, which, together with the accompanying strong environmental gradients, is the likely reason a different biomass richness relationship was observed.

When examining the species richness and biomass relationship at an individual site level, all sites showed a unimodal relationship except the Huriawa and Green Island sites, where a linear relationship was observed. A likely explanation for this deviation from a unimodal relationship at these sites may be due to the exclusion of adult *Durvillaea* spp. and *Macrocystis pyrifera* (which was not collected in this

study due to logistical reasons). Separate 1 m² quadrats completed at all the sites (Fig. S1) revealed the density of these species to be high in the low intertidal at both sites and to a lesser degree in the 2 m depth at Huriawa. The inclusion of adult thalli of these species would likely result in high biomass and similar species richness for the quadrats in these depths. This would result in the intermediate biomass and low species richness points observed for the low intertidal moving to become high biomass low species richness points (i.e. moving the low intertidal points to the far right for the Huriawa and Green Island sites; Fig. S2.). This, in turn, would likely result in a more unimodal relationship of the data at these sites. It is less clear how the inclusion of these adult canopy forming species may influence the unimodal relationship observed across all sites, but a similar trend would likely occur with the low intertidal sites increasing in biomass to different degrees (i.e. dragged to the right in Fig. 5). The measurement of dry biomass as opposed to fresh biomass (used in this study due to the remote sampling sites locations) may affect the general trends observed in this study due to differences in the capacity of different algal species to retain water. However, the use of wet weight is consistent and comparable with other studies of this scale (e.g. Goldberg & Kendrick 2004, Konar et al. 2010).

4.2. Dominant species

Another pattern that was consistently observed across depths in this study was the dominant contribution of biomass by a single species (not always the same species) to community biomass which, on average, constituted >56 % of community biomass within a depth stratum. Different algal species dominated biomass across the depth strata, with red algae dominant in the upper intertidal and brown algae dominant contributors to biomass from the low intertidal zone to the 10 m stratum, with increasing contributions from red and green algae with depth. Dominance of a single taxon is a commonly observed phenomenon in terrestrial plant systems (e.g. Kutiel & Danin 1987, Walker et al. 1999, Kumar & Ram 2005). The dominance of a single species in biomass is hypothesised to be due to the competitive ability of that species to exploit the available resources under the given environmental conditions (Kutiel & Danin 1987). Similarly, in marine benthic algal systems, the theme of dominance by a single species is not a new concept, but is rarely tested and quantified (e.g.

Sousa 1979b, McQuaid & Branch 1984, Goldberg & Kendrick 2004). It is unclear what the effect of the exclusion of *M. pyrifera* or *Durvillaea* spp. would have on the value of this dominance, but given the large size of these canopy forming species, it is likely they would dominate biomass and potentially result in higher contribution of one species towards community biomass values for the low intertidal and 2 m depth strata where these species were more abundant (Fig. S1). While ecosystem stability and resilience are generally considered to be tightly linked to biodiversity (Walker et al. 1999, Steneck et al. 2002, Worm et al. 2006), there is an increasing body of literature suggesting dominant species contribute a disproportionately greater part to some ecosystem functions than less dominant (or rare) species (Smith & Knapp 2003, Winfree et al. 2015, Lohbeck et al. 2016). Furthermore, it is believed that dominant species play an important role in mediating short-term ecosystem resistance to disturbance (Smith & Knapp 2003). In the low intertidal zone, the dominant species contributed significantly more (on average 71.9%, likely underestimated—see above) towards total biomass than all other depth strata examined. Kumar & Ram (2005) concluded, from examination of several forest types in the Himalayas, that an increase in dominance of plant biomass of one species was seen in environments with fewer disturbances. This was attributed to a mixing of different succession states reducing competitive dominance. A similar pattern was observed in an experimental mesocosm study on freshwater algae by Weis et al. (2007). Mesocosms in late stable successional stages showed that one species accounted for the majority of biomass through mechanisms of interspecific competition. This is likely not the case in this study, as the low intertidal can be considered to have high levels of disturbance from increased wave action and periods of desiccation.

4.3. Biomass trends

Our observations of highest biomass occurring in the 2 m depth and decreasing with depth and with elevation into the intertidal are consistent with a range of other studies examining rocky reef biomass (Aleem 1973, Bustamante et al. 1997, Konar et al. 2010). As alluded to above, the inclusion of adult *Durvillaea* spp. and *M. pyrifera* would have likely bolstered the biomass in the low intertidal and to a lesser degree the 2 m depth (Fig. S1). It is likely that biomass patterns are driven by extremes of abiotic gradients (Menge & Sutherland 1987). Organisms on

the high shore are exposed to extreme environmental conditions such as desiccation stress, limited access to nutrients and high (often damaging) light that would likely cause reductions in productivity (Lamote et al. 2012). In contrast, deeper benthic algae are limited by light, with a 77% reduction in photosynthetically active radiation at 10 m compared to 2 m in southern New Zealand (Desmond et al. 2015). Between these extremes, depth strata at the intertidal–subtidal interface are subjected to highly variable environmental conditions. High wave energy can cause physical damage and detachment of organisms which can lead to increased mortality and, in turn, reduce total biomass (Vogel 1984, Gaylord et al. 1994). However, our observations are more consistent with studies that have observed high biomass with enhanced wave action, potentially due to an associated increase in nutrient availability (Leigh et al. 1987, Bustamante et al. 1997, Hepburn et al. 2007). Similarly, wave action has been shown to reduce grazer abundances, which in turn results in higher macroalgal biomass (Leigh et al. 1987, Korpinen et al. 2007). However, differences in grazer abundance among depth strata in this study are unlikely to account for the observed patterns in biomass. Supplementary surveys at each of the sites (eight 1 m² quadrats within each depth stratum) revealed low abundances of potentially influential grazers of *Evechinus chloroticus* (sea urchin), *Haliotis* spp. (abalone) and *Scutus breviculus* (limpet) (Table S6). While sessile invertebrates can also compete for space with marine macroalgae (Dayton 1971), these invertebrates only occupied a small proportion of the available space (<20% on average; Table S6), which suggests that light and nutrient availability could be the primary factors driving algal biomass (Carpenter 1990).

4.4. Species richness and community composition

In contrast with biomass, species richness increased linearly with depth down the shore. This pattern has previously been shown for intertidal macroalgal-dominated communities where the low intertidal has a greater number of species on average than the high intertidal (Ingólfsson 2005, Scrosati & Heaven 2007). The high intertidal is a harsh environment where individuals are exposed to high levels of UV light and subjected to increased desiccation stress (Raffaelli & Hawkins 1996). For this reason, only a few well adapted species may be able to tolerate this environment resulting in low species richness as well

as biomass. The red algal species *Apophlaea lyallii* and *Bostrychia arbuscula*, which dominated this depth, have physiological adaptations that enable them to tolerate the high environmental stress levels experienced in this zone, such as surviving incomplete turgor regulation, faster recovery of photosynthetic rates post-desiccation and increased nitrogen uptake abilities (Brown 1987, Phillips & Hurd 2004). The low intertidal and upper subtidal (2 m depth stratum) had markedly different community compositions than the deeper depths, with larger brown algal species dominating the shallower depth strata and a combination of red, green and brown algae found in deeper depth strata, typical of New Zealand reefs, and contributing to greater species richness at the deeper strata (Brown 1987, Shears & Babcock 2007, Hepburn et al. 2011, Desmond et al. 2015). Differences in species richness and composition with depth may be due to relatively narrow fluctuations (i.e. greater stability) in environmental conditions (e.g. temperature and wave action) at 10 m compared to large fluctuations seen in the upper subtidal, for example (Menge & Sutherland 1987). In terrestrial plant systems, species richness is typically thought to result from the adaptability of species to harsh or varying abiotic conditions (Michalet et al. 2006), the competitive ability of species to monopolise resources in low stress conditions (Grime 1973, Menge & Sutherland 1987) and facilitation processes in which stress-tolerant species alter the conditions for stress-intolerant species to occupy the space (Bruno et al. 2003, Michalet et al. 2006). The relatively stable environment at the 10 m depth stratum in comparison to the upper subtidal may have enabled a large number of species to adapt and colonise this environment.

4.5. Conclusions

This research provides new and important information on how benthic phototrophic organisms vary across the strong environmental gradient spanning the intertidal–subtidal interface. To our knowledge, this is the first instance of a unimodal relationship being observed for benthic marine algal communities across this range of depths, representative of rocky reef habitats as a whole. Additionally, we observed and quantified a high proportion (56.5%) of total community biomass resulting from a single species. Overall, these results provide useful baseline data for a better understanding of current and future variability/fluctuations in the composition and bio-

diversity of these dynamic coastal systems that are increasingly experiencing the impacts of human-induced change at local and global scales. In our view, there is still much to learn from these coastal marine systems, particularly where marine ecologists can work alongside experts in taxonomy and terrestrial plant ecology.

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