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Mrowicki, R. J., & O'Connor, N. E. (2015). Wave action modifies the effects of consumer diversity and warming on algal assemblages. *Ecology*, 96(4), 1020-2029. <https://doi.org/10.1890/14-0577.1>

Published in:
Ecology

Document Version:
Publisher's PDF, also known as Version of record

Queen's University Belfast - Research Portal:
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Wave action modifies the effects of consumer diversity and warming on algal assemblages

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Abstract. To understand the consequences of biodiversity loss, it is necessary to test how biodiversity–ecosystem functioning relationships may vary with predicted environmental change. In particular, our understanding will be advanced by studies addressing the interactive effects of multiple stressors on the role of biodiversity across trophic levels. Predicted increases in wave disturbance and ocean warming, together with climate-driven range shifts of key consumer species, are likely to have profound impacts on the dynamics of coastal marine communities. We tested whether wave action and temperature modified the effects of gastropod grazer diversity (*Patella vulgata*, *Littorina littorea*, and *Gibbula umbilicalis*) on algal assemblages in experimental rock pools. **The presence or absence of *L. littorea* appeared to drive changes in microalgal and macroalgal biomass and macroalgal assemblage structure. Macroalgal biomass also decreased with increasing grazer species richness, but only when wave action was enhanced. Further, independently of grazer diversity, wave action and temperature had interactive effects on macroalgal assemblage structure.** Warming also led to a reversal of grazer–macroalgal interaction strengths from negative to positive, but only when there was no wave action. Our results show that hydrodynamic disturbance can exacerbate the effects of changing consumer diversity, and may also disrupt the influence of other environmental stressors on key consumer–resource interactions. These findings suggest that the combined effects of anticipated abiotic and biotic change on the functioning of coastal marine ecosystems, although difficult to predict, may be substantial.

Key words: biodiversity–ecosystem functioning; climate change; disturbance; environmental context; facilitation; interaction strength; multiple stressors; rocky intertidal; trophic interactions.

INTRODUCTION

Ongoing biodiversity loss has profound implications for the functioning of ecosystems on a global scale (Pimm et al. 1995, Hooper et al. 2012). Over the last two decades, biodiversity–ecosystem functioning research has focused increasingly on the multi-trophic effects of biodiversity change (see reviews by Duffy et al. 2007, Gamfeldt and Hillebrand 2008), acknowledging the complexity of biotic interactions in natural ecosystems. Impacts of biodiversity change are complicated further by changes in a suite of environmental variables (Stocker et al. 2013), which are affecting the nature of biological interactions via climate-driven species range shifts and modification of ecophysiological processes (Parmesan 2006). Therefore, in addition to incorporating processes occurring across trophic levels, we should address the role of environmental context if we are to understand the consequences of species loss against a background of global environmental change (O'Connor and Donohue 2013).

Consumer diversity effects on resources may be driven by changes in consumer identity or species richness per se (O'Connor and Crowe 2005). Two main classes of mechanism may underlie the emergent effects of altered consumer species richness. First, sampling or selection effects occur when a particular consumer species, characterized by traits begetting high performance and competitiveness, comes to dominate resource use within an assemblage. Second, complementarity effects involve increased total resource use by an assemblage as a result of either resource partitioning or facilitative interactions (Loreau and Hector 2001). The basis for resource partitioning among consumer species is provided by differentiation in terms of traits related to resource capture, such as body size, mobility, and food preference, which may be manifested in the directions and strengths of trophic interactions (Duffy 2002). If such traits, and therefore interaction strengths, are differentially sensitive to changes in environmental conditions, then we should expect the role of consumer diversity change to be context dependent. In general, testing how environmental factors modify the relative strengths of key consumer–resource interactions will advance our mechanistic understanding of the community-level effects of biodiversity change (Duffy 2002, Agrawal et al. 2007).

Manuscript received 26 March 2014; revised 11 August 2014; accepted 4 September 2014. Corresponding Editor: J. H. Grabowski.

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Warming may strengthen plant–herbivore interactions by elevating metabolically driven consumption rates to a greater extent than primary productivity rates, resulting in increased top-down control and changes in community structure (O'Connor et al. 2009). Conversely, physical disturbance, such as that arising from wave action in coastal marine systems, can disrupt the foraging activity of consumers, potentially leading to a weakening of trophic interactions and reduced top-down control (Nielsen 2001). The extent to which trophic groups are affected differentially by environmental stressors, and therefore the sensitivity of trophic interactions, can vary according to the type and intensity of the stressor itself (Menge and Sutherland 1987). Additionally, the effects of consumer diversity on resource assemblages depend on resource species diversity (Bruno et al. 2008) and on environmental heterogeneity (Griffin et al. 2009), both of which may be regulated by abiotic stressors. Therefore, the combined effects of biodiversity change and multiple stressors on ecosystem processes are difficult to predict without studies that address them simultaneously.

Rocky shores are highly productive environments, functionally connected to other marine habitats via trophic processes and the transport of biological materials (Raffaelli and Hawkins 1996). These important coastal habitats are subjected to a range of interacting biotic and abiotic stressors, which have potentially large impacts on the dynamics of their constituent ecological communities. Loss of species on local and regional scales owing to anthropogenic pressures including overexploitation of organisms, nutrient enrichment, and habitat alteration (Thompson et al. 2002) is combined with larger-scale changes in assemblage composition and diversity resulting from climate-driven species range shifts (Harley et al. 2006).

In the UK and Ireland, more poleward range extensions of southern, warmer water species have been recorded than range contractions of northern, colder water species, thus changes in the richness and abundance of rocky intertidal grazers are predicted (Mieszkowska et al. 2005, Hawkins et al. 2009). Mean sea surface temperatures, currently at the highest levels recorded, are also increasing, and may rise a further 2°C by the mid-21st century (Hulme et al. 2002, Hiscock et al. 2004). This warming is likely to be accompanied by substantial changes in the nearshore hydrodynamic environment. For example, extreme weather events are expected to become more frequent, resulting in stormier seas and enhanced wave action in coastal habitats (Hulme et al. 2002, Stocker et al. 2013). Overall, these climate-related biotic and abiotic changes may have profound effects on the dynamic balance of rocky shore ecosystems in the north east Atlantic. The combination of altered gastropod grazer diversity and increased hydrodynamic disturbance may result in decreased algal biomass, reducing intertidal biodiversity, and thus

limiting detrital exports to other marine habitats (Hawkins et al. 2009).

Empirical research has begun to address consumer diversity effects in relation to multiple stressors in marine systems (e.g., Blake and Duffy 2012, Eklöf et al. 2012). Although previous studies have assessed the effects of grazer diversity on ecosystem processes in rocky shore habitats in the northeast Atlantic (O'Connor and Crowe 2005, Griffin et al. 2010), little work has been done to examine the context dependency of these effects in relation to abiotic variables reflecting predicted environmental change. We investigated how increased wave disturbance and ocean warming may alter the effects of changing grazer diversity on algal production and assemblage structure in rocky intertidal ecosystems. The composition and richness of gastropod grazer assemblages, including the limpet *Patella vulgata*, periwinkle *Littorina littorea*, and topshell *Gibbula umbilicalis*, were manipulated simultaneously with wave action and temperature to test the following hypotheses: (1) The effects of grazers on algal biomass and assemblage structure (a) differ according to grazer identity and (b) increase with grazer species richness; and (2) these effects are context dependent with respect to the influences of both enhanced wave action and increased temperature. Further, we aimed to determine whether, under conditions where there are significant effects of grazer identity and species richness, there are differences among grazer species in terms of the strengths of their interactions with algal resources.

MATERIALS AND METHODS

Experimental setup and design

The experiment was conducted in outdoor flow-through mesocosms at Queen's University Marine Laboratory, Portaferry, Northern Ireland for four weeks beginning on 7 February 2013. Three factors were manipulated in a factorial design: wave action (two levels, low and enhanced), temperature (two levels, ambient and elevated), and gastropod grazer diversity (five levels, no grazers, monocultures of *Patella vulgata*, *Littorina littorea*, and *Gibbula umbilicalis*, and a polyculture containing all three species). Each of the 20 treatment combinations was replicated five times and assigned randomly among 100 experimental units. Mesocosms were opaque propylene boxes (internal dimensions 55.5 cm long × 35.5 cm wide × 22.0 cm height) enclosed with lids of opaque plastic mesh (size 5 mm), arranged in shallow tables (10 per table) supplied with sand-filtered seawater from the adjacent Strangford Lough. Light levels were quantified in a subsample of 10 mesocosms around midday on a sunny day using an underwater photosynthetically active radiation (PAR) sensor (LI-192; LI-COR, Lincoln, Nebraska, USA) positioned centrally within each tank, providing readings averaged over 15 s. Although PAR was lower in experimental mesocosms ($539 \pm 121 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ [mean ± SE]) compared to ambient conditions measured

simultaneously ($1654 \pm 13 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), mean light levels in natural rock pools are likely to be reduced by the shading effects of macroalgal canopies (Reed and Foster 1984).

Grazer diversity was manipulated using a modified substitutive design, whereby the densities of species in polyculture (one *Patella*, three *Littorina*, and four *Gibbula* per mesocosm) were determined by dividing the respective monoculture densities (*Patella*, 3; *Littorina*, 9; *Gibbula*, 12) by the total number of species (Griffin et al. 2009). Grazers were collected from the low to mid shore at a site next to the laboratory, which is typical of local rocky shores, and were acclimatized outdoors in flowing seawater at ambient temperature for a week prior to the start of the experiment. Monoculture densities were chosen to reflect natural densities within rock pools at the collection site (*Patella*, 9.5 ± 2.5 individuals/m²; *Littorina*, 13.5 ± 3.4 individuals/m²; *Gibbula*, 19.3 ± 3.5 individuals/m² [mean \pm SE]), with the density of *Patella* reduced to ensure a more comparable initial total biomass among treatment levels (monocultures, *Patella*, 1.26 ± 0.04 g shell-free dry biomass; *Littorina*, 1.55 ± 0.04 g; *Gibbula* 1.01 ± 0.01 g; polyculture, 1.29 ± 0.03 g).

To manipulate “wave action,” water was delivered to mesocosms via either (1) individual hoses supplying water at a rate of ~ 1.5 L/minute (range 1.1–2.4 L/minute) from a height of 5 cm, simulating a low disturbance regime, or (2) weighted overhead dump buckets that emptied their contents every ~ 1 minute (range 36–93 s) from a height of 0.7 m, simulating increased wave action. Each dump bucket delivered a total water volume of ~ 4 L per rotation, shared across either two or three mesocosms. Plaster dissolution rates were used to quantify differences in “water motion” between the two wave action treatments (Porter et al. 2000). Plaster spheres (~ 5 cm diameter) were cast using molds, dried at 70°C for 24 hours, and weighed to the nearest 0.01 g. Individual spheres were screwed onto blocks and placed at the bottom of a random subset of mesocosms within each wave action treatment ($n = 6$). To enable comparison with natural rock pools under moderate wave exposure, six additional spheres were screwed to the substratum within separate pools (~ 20 cm deep) on the same shore from which grazers were collected. Plaster spheres were collected after 48 hours, dried, and reweighed to calculate mass lost per hour. Plaster dissolution rates for enhanced wave action (0.36 ± 0.02 g/h [mean \pm SE]), which did not differ significantly from those recorded in natural rock pools (0.33 ± 0.01 g/h), were greater than those observed under low wave action (0.17 ± 0.01 g/h; one-way ANOVA, $MS = 0.06$, $F_{2,15} = 50.85$, $P < 0.001$). It should be noted that our simulated wave action cannot be expected to recreate the complex patterns of water flow generated by tides and wave action on rocky shores (e.g., Gaylord 1999). It does appear, however, that the magnitude of hydrodynamic disturbance in the en-

hanced wave action treatment is comparable to that experienced by rock pools on a moderately exposed shore under typical conditions, at least in terms of the aspects of water motion that regulate the thickness of diffusive boundary layers (Porter et al. 2000).

Elevated temperatures were achieved using aquarium heaters (Elite Submersible 300 W, Hagen Inc., USA). Temperature was monitored weekly throughout the experiment using a digital aquarium thermometer (Marina Aqua-Minder; Rolf C. Hagen, Montreal, Quebec, Canada), sampling the center of each mesocosm after gentle mixing to disrupt any thermal stratification. The mean temperature over the course of the experiment was approximately 2°C greater in elevated temperature mesocosms ($9.43^\circ \pm 0.06^\circ\text{C}$ [mean \pm SE]) compared to ambient levels ($7.41^\circ \pm 0.01^\circ\text{C}$), in line with the predicted increase in sea surface temperature by 2080 in the Irish Sea (Hulme et al. 2002). Data loggers (iButton thermochron DS1922L, Maxim Integrated Products, San Jose, California, USA) were used to record temperature every 15 minutes throughout the experiment in a random subset of mesocosms within each temperature treatment ($n = 4$ mesocosms). The average daily temperature range ($0.70^\circ \pm 0.06^\circ\text{C}$ overall) did not differ significantly between ambient and elevated temperature mesocosms (one-way ANOVA, $MS = 0.07$, $F_{1,6} = 2.85$, $P = 0.143$). Thus, experimental temperatures were within the range experienced by intertidal rock pools in the northwest UK during February and March (~ 0.5 – 13°C ; Morris and Taylor 1983). While our outdoor mesocosms incorporated greater environmental variability than studies conducted under controlled laboratory conditions, diurnal temperature fluctuations in natural rock pools are often substantially larger as a result of tidal emersion and solar heating, particularly during summer months (Morris and Taylor 1983).

Each mesocosm was stocked with a consistent wet biomass of three locally common macroalgal species: *Fucus vesiculosus* (90 g), *Palmaria palmata* (25 g), and *Ulva lactuca* (7 g). Algal biomasses were representative of their relative abundances on local shores (Vye et al., *in press*). Macroalgae were cleaned of epiphytes and mobile fauna and dried of excess water prior to weighing, and then secured in a random order to three positions on a plastic mesh inlay in each mesocosm, prior to the addition of grazers. At the end of the experiment, macroalgae were reweighed after removing epiphytes and excess water. Pieces of algae that had broken off or become detached, but were retained within mesocosms, were included in the measurements.

Microalgal biomass was quantified at the beginning and the end of the experiment by measuring total chlorophyll *a* concentration using a benthic fluorometer (BenthosTorch; bbe Moldaenke GmbH, Schwentinental, Germany [Aberle et al. 2006]) on a natural slate tile ($10 \times 10 \times 1$ cm) attached to the mesh inlay within each mesocosm. An average reading for each tile was calculated from three haphazardly spaced measure-

ments. There was no difference in total chlorophyll *a* concentration among microalgal settlement tiles allocated to different treatments at the start of the experiment (ANOVA; $P > 0.05$ for all terms).

Grazers were measured and shell-free dry biomasses were calculated using length–mass relationships established using an additional 50 individuals of each species collected from the same shore prior to the experiment. In conjunction with values obtained at the beginning, these relationships were used to estimate the mean total shell-free dry biomass of grazers in each mesocosm.

Data analysis

The difference between final and initial biomass (biomass accumulation) was calculated for both microalgae and macroalgae (all species combined). For mesocosms containing grazers, the dynamic interaction strength (Laska and Wootton 1998) between grazers and both microalgae and macroalgae (all species combined) was calculated as

$$a_{ij} = \frac{\ln(B_i^{+j}/\bar{B}_i^{-j})}{\bar{B}_j \times t} \quad (1)$$

where B_i^{+j} is the final biomass of the algal resource *i* (either microalgae or macroalgae) in the presence of grazer assemblage *j* (monocultures or polyculture); \bar{B}_i^{-j} is the mean final biomass of the algal resource *i* in the absence of grazers within the respective combination of wave action and temperature; \bar{B}_j is the mean total shell-free dry biomass of the grazer assemblage *j*; and *t* represents time. Explicit quantification of species interaction strengths and how they vary across relevant environmental contexts is critical for enhancing the predictive power of ecological studies (Agrawal et al. 2007). Interaction strength data were range standardized, by subtracting the minimum value from each observed value and dividing by the range, to account for the presence of negative values and enable transformation prior to analysis.

ANOVA was used to examine the effects of experimental treatments on biomass accumulation and interaction strengths, separately for microalgae and macroalgae. Models incorporated all possible individual and interactive combinations of wave action (fixed, two levels), temperature (fixed, two levels) and grazer diversity (fixed, five levels). For analyses involving biomass, a priori planned contrasts were also performed to detect differences between (1) no grazers vs. all other grazer treatments (grazer presence contrast) and (2) grazer monocultures vs. the polyculture (species richness contrast; Hypothesis 1b), enabling us to test for non-transgressive overyielding, i.e., the performance of the polyculture exceeding that of the mean performance of its component species in monoculture (Fridley 2001, Blake and Duffy 2012). Where a significant interaction between grazer diversity and either wave action or temperature was identified, a separate ANOVA, including planned contrasts, was then performed for each level

of the respective environmental factor. Prior to analysis, normality and homoscedasticity were assessed using Shapiro-Wilk and Cochran's tests, respectively. To correct non-normality, microalgal biomass data were square-root-transformed and interaction strength data were squared. Student-Newman-Keuls (SNK) tests were used to make post hoc comparisons among levels of significant terms.

To investigate further the effects of grazer diversity on algal biomass, we calculated the stringent overyielding criterion, D_{\max} , a positive value of which is an unambiguous indication of transgressive overyielding, i.e., the performance of a polyculture exceeding that of the best-performing component monoculture (Loreau 1998). Thus, calculating this value aids the evaluation of potential mechanisms underlying diversity effects (e.g., Bracken et al. 2011). For all mesocosms containing grazers, we expressed microalgal and macroalgal biomass accumulation as the difference from the mean of the no-grazer treatment within the relevant combination of wave action and temperature (relative biomass accumulation). Then, for each polyculture mesocosm, we calculated the overyielding criterion as

$$D_{\max} = \frac{(P - M_{\max})}{M_{\max}} \quad (2)$$

where *P* is the performance (the inverse of relative biomass accumulation standardized by mean total grazer biomass) of the polyculture and M_{\max} is the average performance of the best-performing monoculture within the respective treatment combination.

Permutational multivariate analysis of variance (PERMANOVA; Anderson 2001, McArdle and Anderson 2001) was used to test for effects of experimental treatments on final macroalgal assemblage structure, based on the same model structure as the ANOVAs and including the planned contrasts for grazer presence and species richness. Although algal assemblages comprised only three taxa, changes in competitive interactions among algal species (Harley et al. 2012) may result in nonindependent responses to treatments, which would violate the assumptions of traditional univariate procedures (Anderson 2001). Multivariate tests involved 9999 permutations of residuals under the reduced model and were based on Bray-Curtis dissimilarities. Post hoc pairwise *t* tests were carried out to reveal differences between levels of significant terms, and the relative contributions of individual macroalgal species to differences among treatment groups were determined using similarity of percentages analyses (SIMPER; Clarke 1993). For all multivariate analyses, macroalgal biomass data were $\log_{10}(x + 1)$ -transformed to reduce the influence of *Fucus*, the dominant species by biomass (Clarke and Warwick 2001). All analyses were performed in R (version 3.0.1; R Development Core Team 2013), except for PERMANOVAs, which were carried out using the PERMANOVA+ add-on in PRIMER (version 6.1.13; PRIMER-E, Plymouth, UK).

RESULTS

Microalgal and macroalgal biomass

Microalgal biomass was affected by grazer presence, identity, and species richness (Fig. 1a, b; Table 1a). Total microalgal biomass was lower in the presence of grazers (grazer presence contrast, Table 1a), and was reduced more strongly by the *Littorina* and *Gibbula* monocultures compared to the *Patella* monoculture (SNK tests, Fig. 1a inset). The effect of the grazer polyculture on microalgal biomass was greater than that of the mean of all monocultures (species richness contrast, Table 1a) but not the best-performing monoculture, i.e., *Littorina* (D_{\max} across all polycultures = -0.09 ± 0.07 [mean \pm SE]). Regardless of grazer diversity, enhanced wave action promoted the accumulation of microalgal biomass, whereas increased temperature had no effect (Fig. 1a, b; Table 1a).

The influence of grazer diversity on total macroalgal biomass was determined by wave action (Fig. 1c, d; Table 1b). With low wave action, there was no effect of grazer diversity (MS = 8.00, $F_{4,80} = 0.12$, $P = 0.973$), but when wave action was enhanced, biomass was affected by both grazer identity and species richness (see Appendix A for further details). In terms of grazer identity, there was a difference between the *Patella* monoculture, in which there was a tendency toward greater total macroalgal biomass than in the absence of grazers, and the *Littorina* monoculture, which significantly reduced biomass relative to the controls (SNK tests, Fig. 1d). Furthermore, with enhanced wave action, the grazer polyculture reduced total macroalgal biomass to a greater extent than that of both the average of the monocultures (Fig. 1d; species richness contrast, Appendix A) and the *Littorina* monoculture (D_{\max} , enhanced wave action, 0.15 ± 0.12 ; low wave action, -0.13 ± 0.10).

Macroalgal assemblage structure

Macroalgal assemblage structure was affected by grazer identity, in addition to the interaction between wave action and temperature (Table 1c). A comparative decrease in the biomass of *Ulva* in both the grazer polyculture and, to a greater extent, the *Littorina* monoculture appeared to drive the shift in assemblage structure (SIMPER, $\bar{\delta} > 49.6\%$, where $\bar{\delta}$ is the contribution of a species to the average dissimilarity between groups) in these two grazer diversity treatments relative to the other three (Appendices B and C). The *Littorina* monoculture differed to the polyculture owing primarily to a reduced biomass of *Ulva* ($\bar{\delta} = 64.4\%$) and *Palmaria* ($\bar{\delta} = 20.3\%$), along with a greater *Fucus* biomass (Appendix C), yet there was no overall effect of grazer species richness on assemblage structure (species richness contrast, Table 1c). Elevated temperature affected macroalgal assemblage structure under enhanced wave action only (PERMANOVA post hoc tests; low wave action $t = 0.32$, $P = 0.889$; enhanced wave

action $t = 2.54$, $P = 0.002$), via a reduction in the biomass of *Ulva* ($\bar{\delta} = 54.1\%$) and a reversal of the growth of *Palmaria* ($\bar{\delta} = 29.0\%$; Appendix C).

Grazer–algal interaction strengths

Interactions between grazers and microalgae were consistently negative, and differed according to grazer identity, being stronger for *Littorina* and *Gibbula* than for *Patella* (Table 2a; see also Appendix D). Conversely, interactions of grazers with macroalgae were either negative or positive, and depended on the interaction of wave action separately with temperature and grazer diversity (Fig. 2; Table 2b). When there was low wave action, elevated temperature caused an overall shift in grazer–macroalgal interaction strength from negative to positive but there was no effect of grazer diversity (Fig. 2a inset). With enhanced wave action, although post hoc tests were inconclusive, the overall positive interaction strength involving *Patella* differed from the negative interaction strengths involving *Littorina* and the grazer polyculture (Fig. 2b). The polyculture interaction strength was also more negative than that of the *Gibbula* monoculture (Fig. 2b).

DISCUSSION

Shifts in the composition and diversity of biotic assemblages, together with the intensification of multiple abiotic stressors, are predicted to have profound effects on the functioning of coastal marine ecosystems (Harley et al. 2006, Hawkins et al. 2009). This study is the first to test the combined effects of increased hydrodynamic disturbance and ocean warming on the role of consumer diversity in ecosystems. Our findings demonstrate that increased wave action may exacerbate the effect of changing grazer diversity on algal biomass. Further, we have shown that wave action can interact with warming to drive shifts in algal assemblage structure and that it may disrupt warming-induced positive interactions between grazers and algae. Overall, these results highlight the potential for complex, interactive impacts of multiple abiotic and biotic stressors on natural communities, which may lead to unpredictable responses of ecosystems to environmental change.

We found a pervasive influence of grazer species identity, dominated by the periwinkle *Littorina littorea*, on all measured responses of algal assemblages, highlighting the apparent prevalence of idiosyncratic consumer effects in marine ecosystems (e.g., Emmerson et al. 2001, O'Connor and Crowe 2005, Griffin et al. 2010). Differentiation among grazer species in terms of traits related to resource capture (Hawkins et al. 1989) may account for such consumer identity effects in conjunction with variation in species-specific densities (Griffin et al. 2010). While the relative roles of consumers within natural ecosystems may be predicted from their functional traits, the effects of grazers on producers also depend largely on the traits of producers (Poore et al. 2012). In our study, for example, the effects of consumer

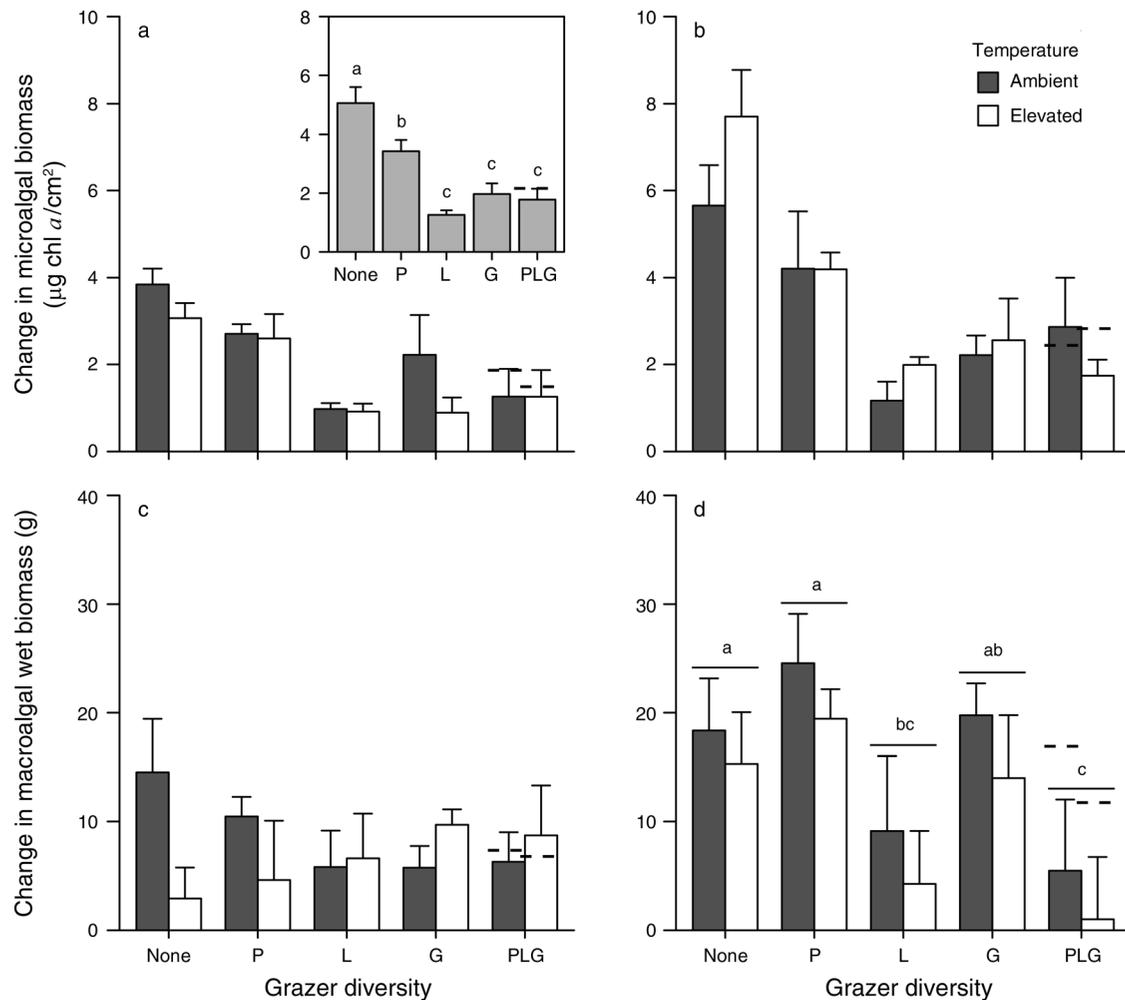


FIG. 1. Change in total (a, b) microalgal and (c, d) macroalgal biomass (mean + SE) for different levels of temperature and grazer diversity (none, no grazers; P, L, and G, monocultures of *Patella*, *Littorina*, and *Gibbula*, respectively; PLG, polyculture containing all three species) under (a, c) low and (b, d) enhanced wave action. The inset shows mean microalgal values for grazer diversity pooled across levels of wave action and temperature. Groups labeled by the same lowercase letter are not significantly different ($P > 0.05$; SNK tests). Dashed lines indicate expected values for polycultures derived from monoculture means, weighted according to average total grazer dry biomass.

TABLE 1. ANOVAs and PERMANOVA testing the effects of wave action, temperature, and grazer diversity (including planned contrasts for grazer presence and species richness) on the change in total biomass for (a) microalgae and (b) macroalgae, and (c) macroalgal assemblage structure.

Source of variation	df	a) Microalgal biomass			b) Macroalgal biomass			c) Macroalgal assemblage structure		
		MS	F	P	MS	F	P	MS	Pseudo F	P
Wave action, W	1	4.48	19.69	<0.001	781.20	7.98	0.006	29.96	4.62	0.007
Temperature, T	1	0.002	0.01	0.935	281.90	2.88	0.094	18.47	2.85	0.053
Grazer diversity, Gr	4	4.42	19.43	<0.001	346.68	3.54	0.010	47.70	7.35	<0.001
Grazer presence	1	1.99	8.75	0.004	149.21	1.53	0.220	20.41	2.54	0.073
Species richness	1	3.35	14.75	<0.001	506.05	5.17	0.026	7.59	0.85	0.440
W × T	1	0.58	2.53	0.116	42.38	0.43	0.512	18.55	2.86	0.049
W × Gr	4	0.14	0.61	0.656	276.91	2.83	0.030	6.44	0.99	0.459
T × Gr	4	0.13	0.58	0.680	42.06	0.43	0.787	3.80	0.59	0.814
W × T × Gr	4	0.15	0.64	0.638	67.05	0.69	0.604	6.36	0.98	0.461
Residual	80	0.23			97.84			6.49		

TABLE 2. ANOVAs testing the effects of wave action, temperature and grazer diversity on dynamic interaction strengths between grazers and (a) microalgae and (b) macroalgae.

Source of variation	df	a) Microalgae			b) Macroalgae		
		MS	F	P	MS	F	P
Wave action, W	1	0.04	0.84	0.362	0.02	0.61	0.438
Temperature, T	1	0.01	0.21	0.648	0.29	7.98	0.006
Grazer diversity, Gr	3	0.26	5.44	0.002	0.12	3.37	0.024
W × T	1	0.01	0.25	0.618	0.48	13.36	0.001
W × Gr	3	0.01	0.19	0.901	0.11	3.20	0.029
T × Gr	3	0.03	0.53	0.665	0.02	0.60	0.621
W × T × Gr	3	0.03	0.68	0.568	0.01	0.35	0.787
Residual	64	0.05			0.04		

identity on macroalgal assemblages appeared to be driven by the strong interaction between *L. littorea* and *Ulva lactuca*, reflecting the strong preference of this grazer for palatable ephemeral green algal species over perennial brown and red species (Norton et al. 1990). The topshell *Gibbula umbilicalis*, which feeds largely on microalgae and filamentous macroalgae, is frequently encountered on leathery macrophytes, although it is most likely to be feeding on epiphytes (Steneck and Watling 1982). In contrast, the limpet *Patella vulgata* is a generalist that grazes predominantly on microbial films, which may harbor macroalgal sporelings (Hawkins and Hartnoll 1983, Hawkins et al. 1989). Whereas *P. vulgata* regulates establishment of macroalgae on emergent substrata on European rocky shores (Hawkins and Hartnoll 1983), it has less of an effect on mature macroalgae (but see Davies et al. 2007). Further, the relatively weak effects of *P. vulgata* in the current study may relate to the unsuitability of rock pool habitats for this species (Firth and Crowe 2010) and reduced grazing activity under nontidal conditions (Hawkins and Hartnoll 1983).

As predicted, biomass accumulation of both microalgae and macroalgae decreased with increasing con-

sumer species richness (cf. Bruno et al. 2008, Blake and Duffy 2012). Importantly, however, the effect of grazer species richness on macroalgal biomass emerged only when wave action was enhanced. Moreover, under these conditions, the fact that the grazing performance of the polyculture exceeded that of the *Littorina littorea* monoculture is indicative of a complementarity effect (Loreau 1998), which can involve two types of mechanism. First, differentiation among species in terms of feeding mode may provide the basis for resource partitioning, thus enabling greater total resource use by the more species rich polyculture compared to monocultures (Loreau and Hector 2001). This trait differentiation must be combined with sufficient environmental heterogeneity to allow the expression of complementary resource use. For example, using these same three species, Griffin et al. (2009) showed that the effect of grazer richness on algae manifested itself only on spatially heterogeneous substrata. In our study, wave action may have enhanced environmental heterogeneity in other terms (i.e., water flow), which perhaps led to the redistribution of grazers, resulting in greater spatial complementarity.

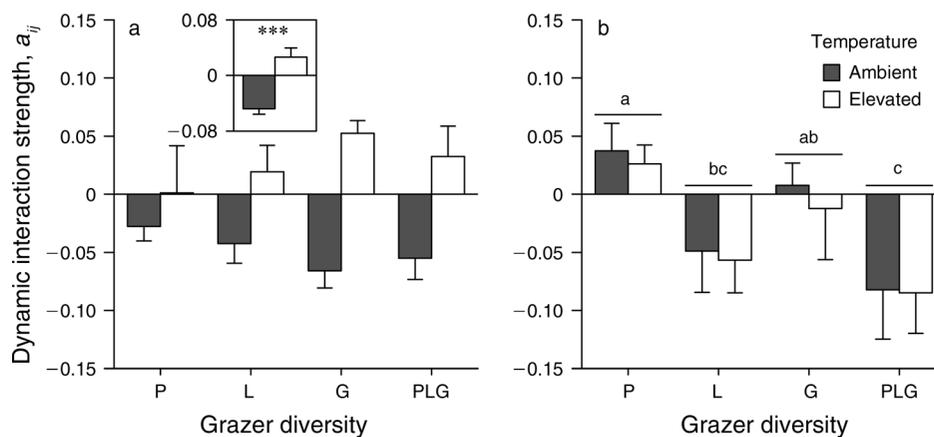


FIG. 2. Interaction strengths (mean \pm SE; see Eq. 1) between grazers and macroalgae (all species combined) for different levels of temperature and grazer diversity (see description in Fig. 1) under (a) low and (b) enhanced wave action. Groups labeled with the same letter are not significantly different ($P > 0.05$; SNK tests). The inset shows mean values for different temperatures, pooled across levels of grazer diversity, within low wave action only.

*** $P < 0.001$; SNK tests.

The second type of mechanism underlying species complementarity involves facilitative interspecific interactions among consumers in polyculture, which may enhance the performance of particular species (Cardinale et al. 2002). For example, *Gibbula umbilicalis* exerts minimal grazing impact on *Fucus vesiculosus* in isolation, but its effect on the algae may be greater on areas grazed previously by other species (Steneck and Watling 1982, Viejo and Arrontes 1992). If increased wave action altered the spatial distribution of grazers so that such facilitative interactions became stronger or more frequent, this could also explain why the effects of grazer diversity were dependent on wave action. Further experimentation is necessary to separate the relative effects of grazer species in polyculture compared to monoculture and to clarify the contributions of different mechanisms to the observed patterns. In particular, the effect of wave action on the spatial distribution and feeding behavior of grazer species would be revealing. Overall, however, our results highlight that physical disturbance regimes may be critical in modifying biodiversity–ecosystem functioning relationships (Cardinale and Palmer 2002). While we found that the role of consumer diversity was insensitive to temperature, recent studies have reported either interactive (Eklöf et al. 2012) or independent (Blake and Duffy 2012) effects of warming and grazer diversity on primary producer assemblages in coastal marine ecosystems. Such contrasting results highlight the complexity of responses of multi-trophic systems to abiotic and biotic change, and emphasize the need to assess the relative importance of biodiversity across a range of contexts.

Independently of grazer diversity, both wave action and temperature affected algal assemblages, with wave action appearing to have a greater overall influence than elevated temperature on measured ecosystem responses. The positive effects of enhanced wave action on algal biomass accumulation may be attributable to increased nutrient uptake via reduction in the diffusion boundary layer overlying algal surfaces (Hepburn et al. 2007), in agreement with the relatively high rates of dissolution of plaster spheres observed in this treatment (Porter et al. 2000). Other potential mechanisms include the resuspension of overlying detrital matter or dislodgement of competing epiphytes (Kersen et al. 2011), or improved water–air gas exchange. The disruption of grazer foraging by increased hydrodynamic disturbance (Nielsen 2001) is an unlikely explanation, given that wave action did not modify grazer–algal interaction strengths. Although the magnitude of experimental warming was small compared to diurnal and seasonal ranges experienced by temperate rock pools (Morris and Taylor 1983), temperature contributed to a significant shift in macroalgal assemblage structure over a relatively short timescale. With enhanced wave action, warming appeared to promote the growth of *F. vesiculosus* at the expense of the other macroalgal species, which may reflect interspecific differences in physiological responses

and changes in competitive interactions within the assemblage (Harley et al. 2012). For example, the positive response of furoid canopy algae to elevated temperatures may have been facilitated by the dislodgement of epiphytes under enhanced wave action, which then led to increased shading and increased competition with the other algal species. Regardless of mechanisms, these results suggest that the influence of warming on the structure of coastal algal assemblages will be complicated further by shifts in the nearshore hydrodynamic regime.

A key finding was the reversal of grazer–macroalgal interactions from negative to positive (i.e., facilitative) in response to elevated temperature, an effect which disappeared under enhanced wave action. Grazers may facilitate macroalgal growth either by removing fouling epiphytes or by increasing the concentration of available nutrients (Guidone et al. 2012). The context-dependency of facilitation in our study may be explained by the more pronounced effect of grazers on nutrient concentrations at elevated temperatures (Werner and Matthiessen 2013) or the greater potential for grazing to alleviate the growth-inhibiting effects of heavier epiphytic loads that develop under conditions of reduced wave action and warming (Kersen et al. 2011). The apparent disruptive effect of wave action on warming-induced positive species interactions is another means by which altered environmental conditions can modify the effects of consumer diversity change. While the importance of facilitation in structuring communities still requires greater attention (Bulleri 2009), our results illustrate the benefit of considering interspecific interaction strengths, and how they may change with context, when determining the consequences of altered consumer diversity within multi-trophic food webs (Duffy 2002).

In conclusion, our findings support expectations that changes in consumer diversity, as is predicted for rocky shores in many parts of the world, combined with increased hydrodynamic disturbance and ocean warming, have large implications for the dynamics of coastal benthic ecosystems (Hawkins et al. 2009), within which both microalgal and macroalgal assemblages play critical roles (Bracken and Williams 2013, Golléty and Crowe 2013). As with all experimental manipulations, there are certain caveats to consider when attempting to extend the results of this study to natural coastal systems. Our wave manipulation could not mimic the complex flow regimes generated by wave action on rocky intertidal substrata (Gaylord 1999), even though the hydrodynamic disturbance was arguably of comparable overall magnitude to that experienced by a moderately exposed shore under typical conditions. Combined with the modifying influence of the tidal cycle on flow regimes, this would result in far greater variability of community responses than can be detected in such an experimental setting. Additionally, owing to logistical restrictions on the number of treatments and the study duration, it is not clear how our findings would

vary across the full range of environmental conditions throughout the year. Despite this, our findings provide new insight into the importance of changes in consumer diversity for ecosystem processes under conditions that are relevant to predicted environmental change over the coming decades. Although complementary field research may be required to enhance the precise relevance and predictability of our findings, studies conducted under relatively constrained conditions are likely to underestimate the consequences of changing biodiversity in real-world ecosystems (Duffy 2009). Overall, when evaluating the consequences of species loss against a background of global environmental change, studies should aim to clarify the relative importance of different environmental variables in regulating multiple ecosystem processes, while identifying stressors that have the potential to modify the effects of biodiversity change.

ACKNOWLEDGMENTS

We are grateful to S. J. Hawkins, J. D. R. Houghton, and two anonymous reviewers for providing comments on earlier drafts of this paper. We thank B. Fantana, H. Hetjens, P. Johnston, V. McCreedy, D. McElroy, B. McNamara, H. van Rein, and S. Vye for their assistance with experimental work. L. Kregting gave valuable advice on characterizing hydrodynamic regimes in coastal systems. This study was completed as part of a PhD studentship funded by the Department for Employment and Learning Northern Ireland.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–D are available online: <http://dx.doi.org/10.1890/14-0577.1.sm>

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