

An empirical examination of consumer effects across twenty degrees of latitude

JAMES T. LAVENDER,^{1,4} KATHERINE A. DAFFORN,^{1,2} MELANIE J. BISHOP,^{2,3} AND EMMA L. JOHNSTON^{1,2}

¹*School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales, Australia*

²*Sydney Institute of Marine Science, Mosman, New South Wales, Australia*

³*Department of Biological Sciences, Macquarie University, Sydney, New South Wales, Australia*

Abstract. The strength and importance of consumer effects are predicted to increase toward low latitudes, but this hypothesis has rarely been tested using a spatially consistent methodology. In a consumer-exclusion experiment spanning twenty degrees of latitude along the east Australian coast, the magnitude of consumer effects on sub-tidal sessile assemblage composition was not greater at low than high latitudes. Across caged and control assemblages, Shannon's diversity, Pielou's evenness, and richness of functional groups decreased with increasing latitude, but the magnitude of consumer effects on these metrics did not display consistent latitudinal gradients. Instead, latitudinal gradients in consumer effects were apparent for individual functional groups. Solitary ascidians displayed the pattern consistent with predictions of greater direct effects of predators at low than high latitude. As consumers reduced the biomass of this and other competitive dominants, groups less prone to predation (e.g., hydroids, various groups of bryozoans) were able to take advantage of freed space in the presence of consumers and show increased abundances there. This large-scale empirical study demonstrates the complexity of species interactions, and the failure of assemblage-level metrics to adequately capture consumer effects over large spatial gradients.

Key words: *assemblages; biotic interactions hypothesis; consumers; interaction strength; latitudinal gradient; multivariate.*

INTRODUCTION

The biotic interactions hypothesis (BIH) has been used to explain a number of major ecological patterns, including that of increasing biological diversity with decreasing latitude (Willig et al. 2003). According to the hypothesis, abiotic processes regulate community composition at high latitudes, with biotic interactions becoming increasingly important toward low latitudes (Mittelbach et al. 2007). Although the hypothesis was originally put forward to explain patterns of speciation operating on evolutionary time scales, at ecological time scales, biotic interactions may also enhance diversity, for instance as a result of predators disrupting competitive dominance (Schemske et al. 2009). While biotic interactions are generally appreciated as ecologically important in determining biodiversity, the long-standing paradigm of increasing intensity and importance of biotic interactions with decreasing latitude requires empirical examination (Mittelbach et al. 2007, Schemske et al. 2009).

If biotic interactions are highly dependent on the prevailing biotic or abiotic conditions (Chamberlain et al. 2014), then variation in the strength of biotic interactions along a latitudinal gradient should have important consequences for assemblages containing members that

compete for shared resources. Predation and competition will interact to limit or enhance diversity, with the stronger of the forces determining outcomes for coexistence (Chesson and Kuang 2008). Early work on the relationships between abiotic and biotic stressors predicted consumers to exert their strongest influence on communities in low stress environments by reducing competition (Menge and Sutherland 1987). While consumers often reduce competitive intensity (e.g., growth, population sizes) in short-term studies (Gurevitch et al. 2000), theory and empirical evidence suggests consumers may have a positive, negative, or no effect on coexistence (i.e., diversity; Chase et al. 2002).

In a review of the available literature, Schemske et al. (2009) concluded that consumer effects are more important toward low latitudes. Consumers are more species rich and abundant (Floeter et al. 2005), and have a greater consumption rate (Coley and Barone 1996) and impact on prey populations (Freestone et al. 2011), at low than high latitudes. Similarly, prey display greater anti-consumer behavior in low than high climates (Díaz et al. 2013). However, recent studies of herbivory suggest this pattern of increasing biotic interactions with decreasing latitude may not be as common as previously implied (Coleman et al. 2006, Moles et al. 2011, Poore et al. 2012, Lim et al. 2015) and in a meta-analysis of benthic communities, consumer effects on aggregate prey abundance were greatest for low diversity prey communities while latitude was not an important predictor

Manuscript received 21 February 2017; revised 23 May 2017; accepted 1 June 2017. Corresponding Editor: Alan L. Shanks.

⁴E-mail: jlavender10@gmail.com

(Edwards et al. 2010). Few studies have directly tested whether the effects of consumers on assemblages decrease with latitude using a consistent experimental methodology (but see Freestone et al. 2011 for a recent exception), especially in the southern hemisphere (but see Kremer and da Rocha 2016).

Consumer–prey relationships operate within a complicated framework often involving interactions among multiple consumers and prey across a range of trophic levels (Polis and Strong 1996). Multiple co-occurring prey can have antagonistic effects, leading to increased susceptibility to consumers (Toscano et al. 2010). Conversely, multiple consumers can have additive or non-linear effects on a single prey (e.g., interference, intra-guild predation, and synergism; Schmitz 2007). On an ecological time scale, consumers may promote diversity by mediating the conditions for co-existence among competitors (Schemske et al. 2009). Early work on the relationship between abiotic and biotic stressors predicted consumers to exert their strongest influence on communities in low stress environments by reducing competition (Menge and Sutherland 1987). Biotic interactions generally shift from competitive to facilitative with increasing biotic, physical, or resource stress (He et al. 2013), with multiple stressors interacting to alter the shape of this relationship (le Roux and McGeoch 2010). Accordingly, on ecological time scales, latitudinal variation in consumer effects on population and community dynamics may depend on the susceptibility of taxa to consumers, as well as their competitive ability.

Studies of latitudinal gradients typically consider species-level interactions, and likewise the BIH is typically discussed at the species level. In communities where multiple species play a similar functional role, then alternative classification schemes may produce insightful ecological patterns. Taxa can be classified into functional groups based on how they respond to ecological inputs or how they affect ecosystem processes. For example, classification according to morphology is ecologically relevant in the context of space occupancy, competitive ability, and susceptibility to consumers (Karlson 1978, Watson and Barnes 2004) and coarse taxonomic classification can produce comparable ecological patterns to those occurring at finer resolutions (Fontaine et al. 2015). Morphology based functional groups are also a useful approach to assessing ecological performance in impacted environments (Segura et al. 2013). Furthermore, a coarse taxonomic approach facilitates meaningful comparisons of assemblages across large geographic ranges where the turnover of individual species is high, and helps overcome challenges related to poor taxonomic records and undescribed species.

Sub-tidal marine hard-substrata communities, such as those associated with rocky reefs, have long-served as model systems with which to investigate abiotic and biotic interactions (e.g., Menge and Sutherland 1987) as they support a great diversity of taxa and occur along vast swathes of every continental coastline. The primary

limiting resource of hard-substrata communities is space (Osman 1977), which is crucial for the acquisition of other resources. Here, a field experiment was performed along the east coast of Australia to assess how consumer impacts on sub-tidal marine hard-substrata assemblages vary with latitude. We predicted that with increasing latitude consumers would have a decreasing effect on the sessile assemblages and the covers of their constituent functional and taxonomic groups. We found local consumer effects were not consistently greater toward low latitudes, with idiosyncratic differences among the assemblage metrics and functional groups examined.

METHODS

The experiment was conducted in ten estuaries along the east coast of Australia, spanning a latitudinal gradient of 20°, from 16.5° S to 36.5° S (Appendix S1: Fig. S1a), and a gradient in average water temperature over the study period of 10°C (Appendix S1: Fig. S1b). Within each estuary, consumer manipulations were performed at a single study site, a marina containing floating pontoons, located within 11 km of the mouth of the estuary, with an average salinity >30 ppt, and which was protected from wave energy by a rocky breakwall or headland. The artificial substrates of marinas provided a standardized habitat that could be compared among sites across which natural rock types vary. Moreover, as urban infrastructure increasingly sprawls into marine environments (Glasby and Connell 1999, Bulleri and Chapman 2010) documenting biogeographic patterns in biodiversity on artificial structures is of growing interest and importance. At each site, caged, cage control and uncaged (control) substrata were deployed on two gray PVC panels (60 × 60 cm; Appendix S1: Fig. S2), suspended vertically at 1 m depth from floating pontoons, and separated horizontally by 6–12 m.

To each PVC panel, we attached nine lightly sanded black acrylic settlement plates (11 × 11 × 0.4 cm) that were randomly assigned among the three treatments, giving $n = 3$ per treatment for each panel, and $n = 6$ of each treatment across the two panels at each site. “Panel” was not included as a factor in the design as pilot studies demonstrated a lack of significant variation at this scale. Plates were attached to each panel using cable ties threaded through a 6 mm diameter hole in the center of the plates. Plates assigned to the caging treatment were enclosed with 15 × 15 mm plastic mesh, of dimensions 5 × 12 × 12 cm. Cages cut diagonally in half were used as cage controls and control plates remained free of mesh. The mesh size of the cages was large enough to avoid significant caging artifacts (Connell 2001), while small enough to exclude predatory fish, the dominant consumers at our study sites (Anderson and Connell 1999, Connell and Anderson 1999), as well as other common consumers of east Australian estuaries, including large molluscan grazers, *Octopus* spp., and blue swimmer (*Portunus pelagicus*) and mud (*Scylla*

serrata) crabs of the size that exerts greatest influence on benthic communities (Garside et al. 2015). Although the mesh size allowed passage of Blenniidae and Gobiidae, these are not normally predators on sessile epibiota (Connell and Anderson 1999), and so effects on sessile invertebrates may be limited to incidental disturbance by grazing activity (Christiansen et al. 2009). Furthermore, previous studies have found that natural densities of small invertebrate mesograzers (i.e., amphipods), that could enter cages, do not produce significant grazing impacts in east Australian estuaries (Poore et al. 2009; but see *Discussion*). Logistical limitations associated with the large spatial spread of the sampling sites prevented periodic cleaning of the cages, however caging artifacts were formally assessed in analyses (see *Results*).

Plates were left to develop assemblages for three months from August to November 2012 (Austral late winter–spring), which was sufficient to achieve mean cover of 80% (excluding overgrowth). All plates were deployed over a four-week period in a semi-haphazard order (to avoid latitudinal bias) with regard to study site, and retrieved in the same order to ensure similar submergence lengths. To retrieve samples, panels were removed from the water and promptly placed in separate containers (to capture and avoid between-sample mixing of the mobile epibiota associated with the sessile assemblages) and preserved in 10% formalin. Upon return to the laboratory, the mobile epibiota were separated from sessile assemblages by individually rinsing plates over a 1 mm sieve.

The cover of sessile organisms was quantified by overlaying an evenly spaced 1 cm grid spanning 10 × 10 cm on each plate. Taxa directly under a point were counted, with the center attachment point of plates excluded such that there were 99 points in total. Overgrowth/overlap among functional groups was relatively common. In cases of non-fatal overgrowth, a count was given to both taxa to best characterize the assemblages present. Accordingly, total cover could exceed 100% per plate. Taxa were identified to the lowest possible level and classified into functional groups according to their growth form (e.g., colonial or solitary, encrusting or non-encrusting), calcification, where this varied within a group (calcified or non-calcified) and broad taxonomic group. Study-wide, a total of 19 sessile functional groups occupied our experimental assemblages, including colonial or solitary ascidians (Class Ascidiacea), non-calcified or calcified stoloniferous bryozoans (Phylum Bryozoa), non-calcified or calcified arborescent bryozoans (Phylum Bryozoa), calcified encrusting bryozoans (Phylum Bryozoa), hydroids (Class Hydrozoa), barnacles (Order Sessilia), algae, ciliophora (Phylum Ciliophora), colonial or solitary calcified polychaetes (Suborder Serpulidae), non-calcified solitary polychaetes (Suborder Sabellida), encrusting or non-encrusting bivalves (Class Bivalvia), encrusting or non-encrusting sponges (Phylum Porifera) and foraminifera (Phylum

Foraminifera). Additional features of many sessile assemblages are muddy “tubes” constructed and occupied by certain species of otherwise mobile amphipods. These amphipod tubes can occupy significant space on hard substrates, and were accordingly considered part of the sessile functional group analysis in this study.

For two of the three replicate plates per treatment and panel ($n = 4$ for each treatment and site combination), mobile animals retained post-sieving were enumerated by coarse taxonomic group. The mobile fauna identified included peracarid crustaceans (Superorder Peracarida), Polychaeta, Nemertea, Platyhelminthes, Brachyura, Gastropoda, Ophiuroidea, terebellid polychaetes (Order Terebellida), or a mixed group of Dendrobranchiata, caridean crustaceans (Infraorder Caridea) or stenopodid crustaceans (Infraorder Stenopodidea). Two “cage” replicates (one from each panel) from Port Douglas and three “cage control” replicates from Port Macquarie were processed and analyzed.

Statistical analyses

In the event of increasing consumer effects toward lower latitudes, we expected that (1) statistical tests would reveal a significant latitude by consumer interaction and (2) post hoc tests for the significant interaction would reveal an increasing effects toward lower latitudes.

Multivariate measures of community composition in ecology based upon dissimilarity measures often fail to adequately describe the mean-variance relationship (Warton et al. 2012). Therefore, sessile assemblage composition (including algae) was analyzed in this study using a multivariate generalized linear model (MGLM) framework (Wang et al. 2012). The MGLM was fitted with the percent cover of functional groups as the response matrix, and latitude (continuous), consumer exclusion (categorical and fixed), and their interaction as the independent terms. For all analyses, control treatments were used as the reference level against which the effects of cage controls and caging were contrasted. A negative binomial distribution (log link) was used, based on examination of the residual vs. fitted plots. The probabilities of the test statistics (Wald value) for each independent term were calculated by pit-resampling using the `summary.manyglm` function in the `mvabund` package (Wang et al. 2015) in R studio version 3.1.2 (R Development Core Team 2014). Permutations were restricted by site (replicates from the same marina) to account for non-independence of samples collected from the same latitude. To further examine significant interactions, post-hoc MGLMs were performed at each sampled latitude, with counts of each functional group as the response matrix and consumer exclusion as the independent term, using a negative binomial distribution (log link). A model-based ordination procedure was used to visualize assemblage compositions using the `boral` package (Hui 2015) in R. As no caging artifacts were detected

(Appendix S1: Table S1), cage controls were excluded from ordination plots to permit easier visualization of the cage and control group differences.

Univariate analyses were conducted on Shannon's diversity (calculated as the exponential of the Shannon-Wiener index; Jost 2006), Pielou's evenness, richness, and total invertebrate cover (sum of all sessile functional groups per replicate, excluding algae), all calculated at a functional group level. These analyses used linear mixed models, with predictor variables of latitude (continuous), consumer treatment (categorical and fixed), their interaction, and a random factor of site, using the nlme package (Pinheiro et al. 2015) in R. Variances were allowed to differ among sites for evenness and total invertebrate cover, which improved model fits based on examination of the residuals. Bare space was analyzed using the same model design, but using a generalized linear mixed model with a negative binomial distribution (log link), using the lme4 package (Bates et al. 2015) in R. Univariate test statistics and associated probabilities for the cover of sessile functional groups that had on average >1% cover per replicate were extracted from the original multivariate assemblage composition model described above for further discussion. Similarly, univariate analyses of individual taxa of mobile invertebrates with an average abundance of >1 per replicate were obtained using an MGLM with a negative binomial distribution as described above. This framework for selecting variables from a multivariate data set for univariate analysis is considered preferable to SIMPER, which may bias selection of variables toward those with high variances as opposed to between-group effects (Warton et al. 2012). Test statistics differed among the univariate models based on the distribution used (Wald value for negative binomial and t value for normal distribution). To account for inflated likelihood of Type I errors given the large number of statistical tests performed in the study, a conservative P value cut-off of 0.01 was used throughout the study.

RESULTS

Assemblage composition

Control and cage control treatments did not differ in multivariate assemblage composition, indicating an absence of caging artifacts (Control/Cage control, $P = 0.630$; Control/Cage control \times Latitude, $P = 0.307$; Appendix S1: Table S1). Although consumer effects on sessile assemblage composition (as measured by the difference in assemblage composition between caged and control plates) varied among latitudes (Control/Cage \times Latitude interaction, $P = 0.001$; Appendix S1: Table S1), they did not follow the hypothesized trend of decreasing magnitude with increasing latitude (Appendix S1: Fig. S3). In post hoc analyses, control and cage treatments were significantly ($P < 0.01$) different at all locations except Townsville ($P = 0.09$; 19.26° S) and Tweed Heads ($P < 0.02$; 21.98° S).

Neither functional group diversity, calculated using Shannon diversity, Pielou's evenness, nor richness varied among latitudes, nor according to caging, cage controls, or their interacting effects (Fig. 1; Appendix S1: Table S2). Nevertheless, there was a non-significant trend for decreasing diversity, evenness, and richness with increasing latitude (Fig. 1; Appendix S1: Table S2).

Bare space, algae, and total invertebrate cover

No caging artifacts were found for bare space, algae or total invertebrate cover (Fig. 2b; Appendix S1: Table S3), allowing interpretation of differences between caged and control treatments as a consumer effect. Consumers shifted assemblages from invertebrate- to algae-dominated at high latitudes (Fig. 2a). Bare space displayed an interacting effect of consumer exclusion and latitude, with a shift from more bare space in caged than control treatments at the low latitudes to considerably more bare space in control than in caged treatments at high latitudes ($P < 0.001$, Fig. 2b (i); Appendix S1: Table S3). Although non-significant, algal cover displayed a trend for increasingly positive effects of consumers with increasing latitude (Fig. 2b (ii); Appendix S1: Table S3). Total invertebrate cover displayed an interacting effect of consumer treatment and latitude, which followed the opposite pattern to bare space ($P < 0.001$, Fig. 2b (iii); Appendix S1: Table S3). The consumer effect on total invertebrate cover was greater at higher than lower latitudes.

Univariate functional groups: strength of biotic interactions across latitude

Mixed relationships between consumers and latitude were observed, preventing broad generalizations across all of the examined groups with an average cover of >1% per replicate (Appendix S1: Table S4, Fig. S4). The main effects contrast (i.e., when latitude is zero) for caging artifacts were all non-significant for these functional groups with an average cover of >1% per replicate (Appendix S1: Table S4). Additionally, summary statistics of the fitted models indicated a lack of caging artifacts across all latitudes for these functional groups with an average cover of >1% per replicate (Appendix S1: Table S4).

Covers of colonial ascidians ($P = 0.001$), amphipod tubes ($P = 0.001$), calcified solitary polychaetes ($P = 0.001$), calcified arborescent bryozoans ($P = 0.001$), and solitary ascidians (non-significant trend, $P = 0.040$) displayed greater differences (on a natural logarithmic scale) between cage and control treatments at higher rather than lower latitudes (Appendix S1: Table S4, Fig. S4a–e; but see Discussion for interpretation of calcified arborescent bryozoan and solitary ascidian results). The negative effect of consumers on colonial ascidians and amphipod tubes increased with latitude. In contrast, the effect of consumers on cover of calcified solitary polychaetes was negative at low latitudes, but shifted to

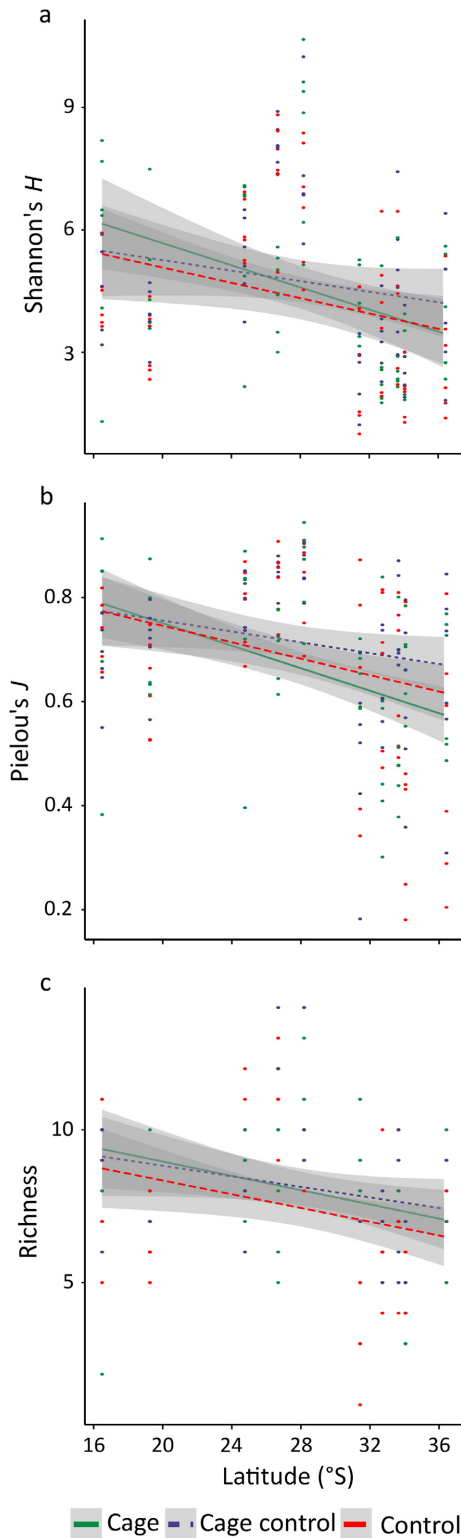


FIG. 1. Predicted functional group, (a) Shannon's diversity, (b) Pielou's evenness, and (c) richness, from generalized linear models as a function of latitude and consumer exclusion (see *Statistical analyses* for model details). Green solid line, cage; blue dotted line, cage control; red dashed line, control. Gray bands indicate standard errors of predictions. Dots represent measured values on individual replicate plates, colored according to treatment (green, cage; blue, cage control; red, control).

lower latitudes where cover of this group was greatest, with the effect of consumers switching to negative and of a greater magnitude toward higher latitudes. Solitary ascidian covers were also greatest at low latitudes ($P = 0.001$), where they were negatively affected by consumers, experiencing up to 30% lower cover when consumers were present.

Covers of hydroids ($P = 0.003$) displayed the greatest difference between cage and control treatments at lower latitudes at which they were most abundant, with cover greater in the presence of consumers than in caged treatments (Appendix S1: Table S4, Fig. S4f). Interactions between latitude and consumer exclusion were non-significant for the remaining functional groups. Cover of calcified encrusting bryozoans was greater in the presence than the absence of consumers ($P = 0.009$) and increased with decreasing latitude ($P = 0.001$; Appendix S1: Table S4, Fig. S4g). Barnacle cover increased with increasing latitude ($P = 0.001$), while non-calcified solitary polychaetes ($P = 0.001$), non-calcified stoloniferous bryozoans ($P = 0.001$), and non-calcified arborescent bryozoans ($P = 0.001$) showed the opposite pattern with cover increasing as latitude decreased (Appendix S1: Table S4, Fig. S4h–k), although no effects of consumers were observed for these functional groups (Appendix S1: Table S4). Cover of ciliophorans and encrusting sponges did not differ significantly with latitude or with caging (Appendix S1: Table S4, Fig. S4l, m).

Univariate mobile epibiota

No evidence of caging artifacts were detected for any of the mobile epibiota with an average abundance of >1 per replicate (Appendix S1: Table S5). Peracarida (hereafter peracarids) abundance shifted from a positive response to consumers at low latitudes to a negative effect, of greater magnitude, at high latitudes ($P = 0.001$; Appendix S1: Table S5, Fig. S5a). Polychaeta (hereafter polychaetes) abundances displayed similar patterns to peracarids, however the magnitude of the consumer effect at lower latitudes was greater ($P = 0.006$; Appendix S1: Table S5, Fig. S5b). No significant or clear patterns occurred for Nemertea (hereafter nemerteans) with respect to consumers (Appendix S1: Table S5, Fig. S5c).

positive as latitude increased. The cover of calcified arborescent bryozoans was relatively greater when exposed to consumers compared to caged treatments at

DISCUSSION

Experimental exclusion of consumers from sub-tidal marine hard-substrata assemblages did not produce the

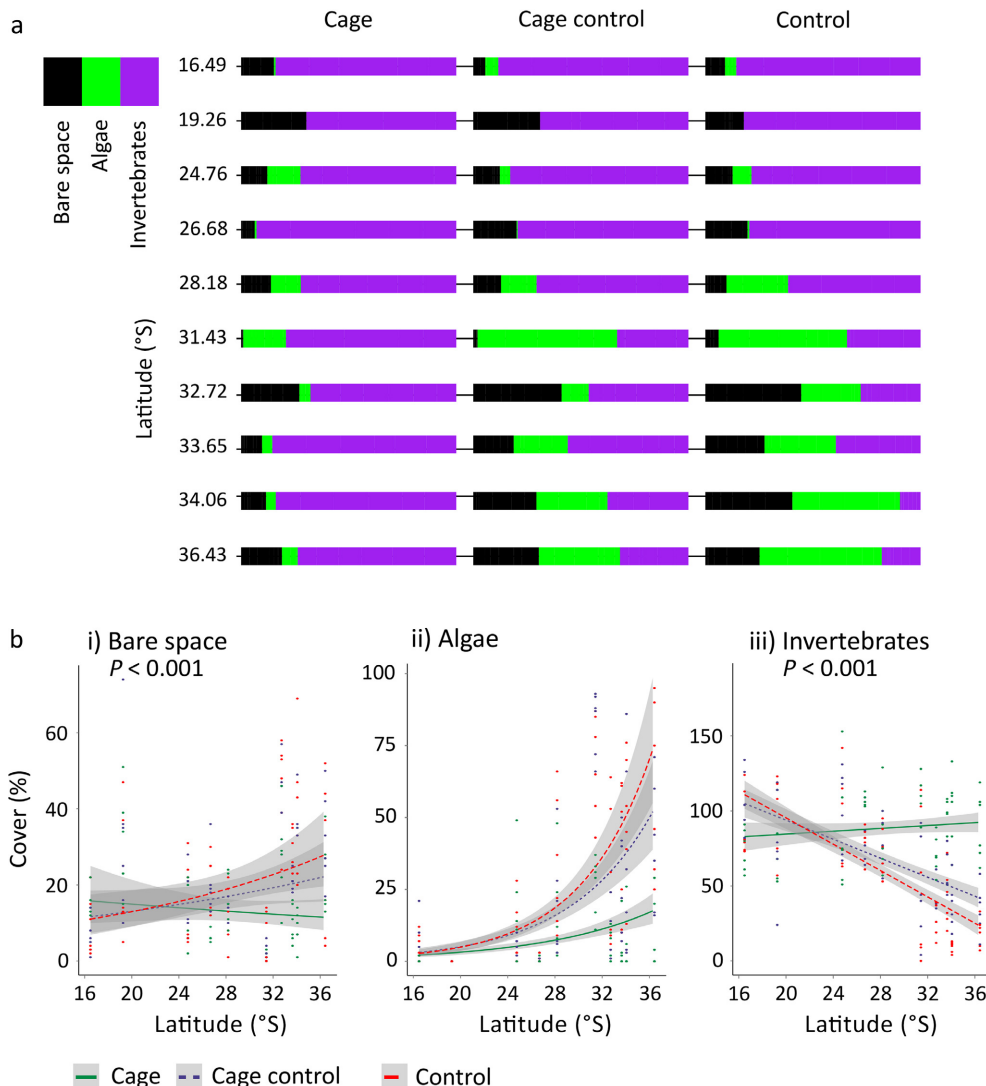


FIG. 2. (a) Proportionate cover of bare space, algae, and invertebrates for each consumer treatment across latitude. Black, bare space, green, algae; purple, invertebrates. (b) Latitudinal variation in (i) bare space, (ii) algae, and (iii) total invertebrate cover, as predicted from generalized linear models of cover as a function of latitude and consumer exclusion (see *Statistical analyses* for model details). Green solid line, cage; blue dotted line, cage control; red dashed line, control. Gray bands indicate standard errors of predictions. P values are given for variables with significant Control/Cage \times Latitude interactions. Dots represent measured values on individual replicate plates, colored according to treatment (green, cage; blue, cage control; red, control).

expected pattern of stronger consumer effects on assemblage-level assemblage composition at low as compared to high latitudes. Additionally, no interactive effects were observed among consumer exclusion treatments and latitude for functional group diversity, richness, or evenness. The lack of change in these coarse assemblage metrics hid latitudinal patterns observed in functional groups. Calcified arborescent bryozoans, solitary ascidians, and hydroids displayed the predicted pattern of increasing consumer effects with decreasing latitude (see *Univariate sessile functional groups and mobile epibiota: strength of biotic interactions across latitude* for interpretation of effect sizes on a natural logarithmic scale for calcified

arborescent bryozoans and solitary ascidians). By contrast, colonial ascidians, amphipod tubes, and calcified solitary polychaetes displayed an opposite pattern to that predicted by the BIH, whereby consumer effects appear greater toward higher latitudes.

Assemblage composition

Consumers had significant effects on prey assemblage composition at all latitudes sampled except Townsville and Tweed Heads, although the effects of consumers on assemblage-level metrics were spatially idiosyncratic and did not linearly increase with decreasing latitude. While

compositional differences between treatments at the majority of sites was observed in our study, there was no effect of consumers over three months on functional group diversity, richness, or evenness across latitude, unlike a previous study looking at species richness in the northern hemisphere (Freestone et al. 2011). In that study, Freestone et al. (2011) found little effect of consumers on sessile assemblage species richness at high latitudes, but at the lowest latitude, site richness was significantly greater in the absence of consumers compared to the presence of consumers. In contrast, in a southern hemisphere study spanning 24° of latitude in Brazil, species richness of sessile communities was generally unaffected by consumers at the two lowest latitude sites, although was greater in the presence of consumers at the highest latitude site (Kremer and da Rocha 2016). Latitudinal patterns in plant herbivory have been found to be stronger in the northern than southern hemisphere, and related to temperature on a global scale (Zhang et al. 2016).

After three months of development, the composition of sessile assemblages in this study was strongly influenced by consumers. However, it is uncertain how these sessile communities would develop if allowed to continue along their successional trajectories under varying conditions of consumer exposure. The composition of “early” successional communities is often in a transient state due to ongoing disturbance (such as caused by consumers; Fukami and Nakajima 2011). Sessile invertebrate assemblages may be particularly vulnerable to consumers at the early post-settlement stage (Lavender et al. 2014), in some instances exerting a strong influence on the successional dynamics of the community (Osman and Whitlatch 2004). Nevertheless, in other instances, early post-settlement predation has only weak effects on sessile communities (Sams and Keough 2007) or short-term consequences, with consumer effects at later stages of development more important for long-term composition (Vieira et al. 2012).

Bare space, algae, and total invertebrate cover

Bare space can arise in sessile communities as a consequence of consumers removing biomass, an inability of sessile organisms to fully utilize space due to low growth or recruitment, and/or the removal of organisms via other mechanisms (e.g., physical disturbance or natural sloughing off; Dayton 1971). Bare space and sessile invertebrate cover showed opposite patterns across latitude. Toward high latitudes, bare space was greater in control than caged treatments, while the reverse occurred for total cover of sessile invertebrates, suggesting sessile invertebrates as a combined group are increasingly negatively affected by consumers toward higher latitudes. In the lower latitudes, bare space was greater in the absence than the presence of consumers, perhaps because the release from top-down control allows organisms to reach such a large size that they slough off plates

or because functional groups that benefit from consumers have a greater ability to occupy space than those negatively affected by consumers.

Although not significant, turfing algae (small, predominantly filamentous algae) often dominated high latitude assemblages that were exposed to consumers. Predators may be targeting particular invertebrate groups (see *Univariate sessile functional groups and mobile epibiota: strength of biotic interactions across latitude*), releasing space that would otherwise be limiting and indirectly maintaining early successional turfing algae-dominated assemblages at higher latitudes. As our exclusion method does not discriminate between herbivores or predators, the results of this study also suggest that herbivore pressure toward higher latitudes is not sufficient to limit turfing algal cover. The increasing algal cover with latitude contrasts with previous work in natural rocky reef environments, from southern Queensland to southern New South Wales, Australia, where turfing algal cover decreased with increasing latitude (Connell and Irving 2008). Abiotic variables such as light are likely to be important for latitudinal gradients in turfing algae, indirectly influencing invertebrate cover. The vertical orientation and close proximity to the surface (1 m) provided well-lit conditions. However, during the sampling period of this study (August–November 2012), average day length (sunrise to sunset), was 12 h 13 min in the lowest latitude site Port Douglas and 12 h 25 min in the highest latitude site Bermagui, sourced from Geoscience Australia, and therefore day length is unlikely to have substantially contributed to the pronounced latitudinal gradient in algal cover (data available online).⁵

Univariate sessile functional groups and mobile epibiota: strength of biotic interactions across latitude

Variable directions and magnitudes of functional group responses to consumers along the study extent may reflect differential combinations of susceptibility to direct consumption and indirect consequences of an altered competitive environment. Alternatively, they may reflect a statistical artifact of variation in functional group cover. The magnitude of the difference between control and cage treatments on a natural logarithmic scale can be erroneous when either treatment is close to zero (Lajeunesse 2015). This would help explain the increasing magnitude of effect size with increasing latitudes within the studied latitudinal range for calcified arborescent bryozoans and solitary ascidians (non-significant trend), which on visual examination of the predicated covers to display a greater effect size of consumers toward lower latitudes.

For functional groups susceptible to consumers, we expected an increasing magnitude of response toward lower latitudes in accordance with the BIH. Previous work has demonstrated solitary ascidians are vulnerable

⁵ <http://www.ga.gov.au/geodesy/astro/sunrise.jsp>

to consumers (Lavender et al. 2014), and this group followed an expected pattern of greater effect of consumers toward low latitudes. Kremer and da Rocha (2016) also demonstrated predators negatively impacted introduced ascidians (colonial and solitary pooled) at three sites spanning 24° of latitude, providing a competitive release for groups such as barnacles. Similarly, ciliophora displayed a trend of a greater magnitude of decreasing cover in the presence of consumers toward low latitudes. However, contrary to predictions of the BIH our findings indicate the magnitude of negative consumer effects increased toward the high latitudes, for amphipod tubes and colonial ascidians.

The population-level responses can vary among taxa, being positively or negatively affected by consumers depending on how consumers alter the ratio of intra- to interspecific dynamics (Chase et al. 2002). Accordingly, a negative response to consumers may not be observed for all prey populations, with competitive release allowing some groups that are less prone to predation to capitalize on an increase in free space in the presence of consumers. Russ (1982) ranked the overgrowth ability of common encrusting groups of hard-substrata organisms, with colonial ascidians \geq sponges > bryozoans > barnacles, polychaetes, tube dwelling amphipods and hydroids. This may explain patterns from the current study where calcified solitary polychaetes and barnacles (non-significant trend) increasingly benefitted from consumers as latitude increased, potentially due to the reduced dominance of colonial ascidians. Many calcified solitary polychaetes and barnacles are early successional taxa (Dean 1981), which may be considered weak competitors according to the colonization–competition trade-off. For a number of groups, such as hydroids, calcified arborescent bryozoans and calcified encrusting bryozoans (a non-significant trend), we found that that the greater cover in treatments exposed to as opposed to protected from consumers increased in magnitude toward the low latitudes. The direction as well as the magnitude of consumer–prey interaction strengths may vary spatially as the abiotic and biotic conditions vary. For example, cover of non-calcified solitary polychaetes was negatively related to consumers in the higher latitudes, but positively related to consumers in the lower latitudes. The traditional classifications of the competitive abilities of marine sessile taxa may need revision (Hart et al. 2012).

Large consumers may indirectly affect sessile assemblages by altering the abundances of meso-predators, such as flatworms and whelks, which may potentially confound interpretations of large consumer effects (Lavender et al. 2014). However, this appears unlikely in our study, as mobile epibiota abundances were consistently low across consumer treatments in this study. Furthermore, previous research in Sydney Harbour has revealed that natural densities of mesograzers are insufficient to limit macroalgae or their epiphytes (Poore et al. 2009). In this study, the increasingly inflated amphipod

abundance, and hence grazing pressure, observed in the absence of large consumers toward high latitudes may have contributed to the trend of an increasingly negative effect of large consumer exclusion on algae toward high latitudes. Unsurprisingly, the peracarids followed a similar pattern to amphipod tubes of increasing numbers in caged relative to control treatments toward the high latitudes, while polychaete abundances increased in the presence of consumers toward lower latitudes. Large consumer effects on peracarids and polychaetes, and potentially other meso-predators that escaped during collection of plates (e.g., juvenile fish), may indirectly affect the sessile assemblages, highlighting the complex multi-trophic responses of natural communities to experimental manipulations.

Caveats

This study used marinas and acrylic settlement plates to “standardize” site and substrate characteristics across latitude, respectively, while still examining patterns under field conditions. However, site-specific idiosyncrasies among marinas may limit the ability to detect overall latitudinal patterns. Additionally, an unavoidable limitation of the current study was that fewer study sites were situated at low as compared to higher latitudes, such that generalization of consumer effects to other low latitude sites should be with caution.

Artificial structures differ from natural substrata in a number of features. For example, as compared to natural rocky reef, artificial structures are generally characterized by less topographical complexity and a vertical, as opposed to primarily horizontal, orientation (Bulleri and Chapman 2010). As a consequence, the assemblages found on artificial substrates often differ from those on natural rocky reefs (Connell and Glasby 1999), although the underlying mechanisms that cause their communities to differ require further examination (Bulleri and Chapman 2010). As global coastlines are becoming increasingly urbanized through the introduction of artificial structures (Glasby and Connell 1999, Bulleri and Chapman 2010), it is, however, important to understand the processes that structure communities on artificial structures.

Examination of functional groups in this study provides another perspective to the discussion of the BIH, with the findings of this study differing from predictions expected at the finer scale of species. Caution should be used in comparing results of coarser resolution studies with species level analysis. Functional level analysis used in this study may mask ecologically important trait differences between species within the assigned morphological groups, obscuring patterns at the species level. Where there is strong niche overlap, species richness may be high, but functional richness may be relatively low (Díaz and Cabido 2001). Aggregation of taxa to functional groups likely underestimates actual species richness and diversity, potentially making the analysis less

sensitive to differences between treatments. Nevertheless, the use of functional groups provides new insights into ecologically relevant biotic interactions across a large spatial gradient along which species composition varies greatly.

CONCLUSION

Consumer effects in natural systems are complex given the large number of interacting taxa both within and among trophic levels. Variable effects of consumers among functional groups may reflect differences in their susceptibility to consumption and their response to consumer-mediated alteration of the competitive environment. This study highlights the need to test hypotheses about large-scale spatial variation in consumer–prey interactions using a consistent methodology and multiple metrics of change, in settings where competitive interactions are allowed to occur. Understanding the ecological consequences of consumer–prey interactions is particularly relevant considering the global population decline of marine predators.

ACKNOWLEDGMENTS

The authors wish to thank the managers of the various marinas used in this study. Special thanks to S. Bracewell for assistance with fieldwork. This project was funded by an Australian Research Council Linkage Project (LP140100753) awarded to E. L. Johnston and partially supported by the University of New South Wales. J. T. Lavender was supported by an Australian Postgraduate Award. All authors contributed to the design of the study, J. T. Lavender performed the research (data collection and analyses) and wrote the first draft. All authors contributed significantly to the revisions of the drafts.

LITERATURE CITED

- Anderson, M. J., and S. D. Connell. 1999. Predation by fish on intertidal oysters. *Marine Ecology Progress Series* 187:203–211.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Bulleri, F., and M. G. Chapman. 2010. The introduction of coastal infrastructure as a driver of change in marine environments. *Journal of Applied Ecology* 47:26–35.
- Chamberlain, S. A., J. L. Bronstein, and J. A. Rudgers. 2014. How context dependent are species interactions? *Ecology Letters* 17:881–890.
- Chase, J. M., P. A. Abrams, J. P. Grover, S. Diehl, P. Chesson, R. D. Holt, S. A. Richards, R. M. Nisbet, and T. J. Case. 2002. The interaction between predation and competition: a review and synthesis. *Ecology Letters* 5:302–315.
- Chesson, P., and J. J. Kuang. 2008. The interaction between predation and competition. *Nature* 456:235–238.
- Christiansen, N. A., S. Ward, S. Harii, and I. R. Tibbetts. 2009. Grazing by a small fish affects the early stages of a post-settlement stony coral. *Coral Reefs* 28:47–51.
- Coleman, R. A., et al. 2006. A continental scale evaluation of the role of limpet grazing on rocky shores. *Oecologia* 147:556–564.
- Coley, P. D., and J. A. Barone. 1996. Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics* 27:305–335.
- Connell, S. D. 2001. Predatory fish do not always affect the early development of epibiotic assemblages. *Journal of Experimental Marine Biology and Ecology* 260:1–12.
- Connell, S. D., and M. J. Anderson. 1999. Predation by fish on assemblages of intertidal epibiota: effects of predator size and patch size. *Journal of Experimental Marine Biology and Ecology* 241:15–29.
- Connell, S. D., and T. M. Glasby. 1999. Do urban structures influence local abundance and diversity of subtidal epibiota? A case study from Sydney Harbour, Australia. *Marine Environmental Research* 47:373–387.
- Connell, S. D., and A. D. Irving. 2008. Integrating ecology with biogeography using landscape characteristics: a case study of subtidal habitat across continental Australia. *Journal of Biogeography* 35:1608–1621.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41:351–389.
- Dean, T. A. 1981. Structural aspects of sessile invertebrates as organizing forces in an estuarine fouling community. *Journal of Experimental Marine Biology and Ecology* 53:163–180.
- Díaz, S., and M. Cabido. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution* 16:646–655.
- Díaz, M., A. P. Møller, E. Flensted-Jensen, T. Grim, J. D. Ibáñez-Álamo, J. Jokimäki, G. Markó, and P. Tryjanowski. 2013. The geography of fear: a latitudinal gradient in anti-predator escape distances of birds across Europe. *PLoS ONE* 8:e64634.
- Edwards, K. F., K. M. Aquilino, R. J. Best, K. L. Sellheim, and J. J. Stachowicz. 2010. Prey diversity is associated with weaker consumer effects in a meta-analysis of benthic marine experiments. *Ecology Letters* 13:194–201.
- Floeter, S. R., M. D. Behrens, C. E. L. Ferreira, M. J. Paddock, and M. H. Horn. 2005. Geographical gradients of marine herbivorous fishes: patterns and processes. *Marine Biology* 147:1435–1447.
- Fontaine, A., R. Devillers, P. R. Peres-Neto, and L. E. Johnson. 2015. Delineating marine ecological units: a novel approach for deciding which taxonomic group to use and which taxonomic resolution to choose. *Diversity and Distributions* 21:1167–1180.
- Freestone, A. L., R. W. Osman, G. M. Ruiz, and M. E. Torchin. 2011. Stronger predation in the tropics shapes species richness patterns in marine communities. *Ecology* 92:983–993.
- Fukami, T., and M. Nakajima. 2011. Community assembly: alternative stable states or alternative transient states? *Ecology Letters* 14:973–984.
- Garside, C. J., M. A. Coleman, B. P. Kelaher, and M. J. Bishop. 2015. Putative predators of *Carcinus maenas* in eastern Australia. *Estuaries and Coasts* 38:1557–1568.
- Glasby, T. M., and S. D. Connell. 1999. Urban structures as marine habitats. *Ambio* 28:595–598.
- Gurevitch, J., J. A. Morrison, and L. V. Hedges. 2000. The interaction between competition and predation: a meta-analysis of field experiments. *American Naturalist* 155:435–453.
- Hart, S. P., J. R. Burgin, and D. J. Marshall. 2012. Revisiting competition in a classic model system using formal links between theory and data. *Ecology* 93:2015–2022.
- He, Q., M. D. Bertness, and A. H. Altieri. 2013. Global shifts towards positive species interactions with increasing environmental stress. *Ecology Letters* 16:695–706.
- Hui, F. K. C. 2015. boral: Bayesian Ordination and Regression AnaLysis. <https://CRAN.R-project.org/package=boral>
- Jost, L. 2006. Entropy and diversity. *Oikos* 113:363–375.

- Karlson, R. 1978. Predation and space utilization patterns in a marine epifaunal community. *Journal of Experimental Marine Biology and Ecology* 31:225–239.
- Kremer, L. P., and R. M. da Rocha. 2016. The biotic resistance role of fish predation in fouling communities. *Biological Invasions* 18:3223–3237.
- Lajeunesse, M. J. 2015. Bias and correction for the log response ratio in ecological meta-analysis. *Ecology* 96: 2056–2063.
- Lavender, J. T., K. A. Dafforn, and E. L. Johnston. 2014. Mesopredators: a confounding variable in consumer exclusion studies. *Journal of Experimental Marine Biology and Ecology* 456:26–33.
- le Roux, P. C., and M. A. McGeoch. 2010. Interaction intensity and importance along two stress gradients: adding shape to the stress-gradient hypothesis. *Oecologia* 162:733–745.
- Lim, J. Y., P. V. A. Fine, and G. G. Mittelbach. 2015. Assessing the latitudinal gradient in herbivory. *Global Ecology and Biogeography* 24:1106–1112.
- Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist* 130:730–757.
- Mittelbach, G. G., et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters* 10:315–331.
- Moles, A. T., S. P. Bonser, A. G. B. Poore, I. R. Wallis, and W. J. Foley. 2011. Assessing the evidence for latitudinal gradients in plant defence and herbivory. *Functional Ecology* 25: 380–388.
- Osman, R. W. 1977. The establishment and development of a marine epifaunal community. *Ecological Monographs* 47: 37–63.
- Osman, R. W., and R. B. Whitlatch. 2004. The control of the development of a marine benthic community by predation on recruits. *Journal of Experimental Marine Biology and Ecology* 311:117–145.
- Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar. 2015. nlme: linear and nonlinear mixed effects models. <https://CRAN.R-project.org/package=nlme>
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* 147:813–846.
- Poore, A. G. B., A. H. Campbell, and P. D. Steinberg. 2009. Natural densities of mesograzers fail to limit growth of macroalgae or their epiphytes in a temperate algal bed. *Journal of Ecology* 97:164–175.
- Poore, A. G. B., et al. 2012. Global patterns in the impact of marine herbivores on benthic primary producers. *Ecology Letters* 15:912–922.
- R Development Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Russ, G. R. 1982. Overgrowth in a marine epifaunal community: competitive hierarchies and competitive networks. *Oecologia* 53:12–19.
- Sams, M. A., and M. J. Keough. 2007. Predation during early post-settlement varies in importance for shaping marine sessile communities. *Marine Ecology Progress Series* 348:85–101.
- Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel, and K. Roy. 2009. Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology, Evolution, and Systematics* 40:245–269.
- Schmitz, O. J. 2007. Predator diversity and trophic interactions. *Ecology* 88:2415–2426.
- Segura, A. M., C. Kruk, D. Calliari, and H. Fort. 2013. Use of a morphology-based functional approach to model phytoplankton community succession in a shallow subtropical lake. *Freshwater Biology* 58:504–512.
- Toscano, B. J., F. J. Fodrie, S. L. Madsen, and S. P. Powers. 2010. Multiple prey effects: agonistic behaviors between prey species enhances consumption by their shared predator. *Journal of Experimental Marine Biology and Ecology* 385:59–65.
- Vieira, E. A., L. F. L. Duarte, and G. M. Dias. 2012. How the timing of predation affects composition and diversity of species in a marine sessile community? *Journal of Experimental Marine Biology and Ecology* 412:126–133.
- Wang, Y., U. Naumann, S. T. Wright, and D. I. Warton. 2012. mvabund – an R package for model-based analysis of multivariate abundance data. *Methods in Ecology and Evolution* 3:471–474.
- Wang, Y., U. Naumann, S. Wright, and D. Warton. 2015. mvabund: statistical methods for analysing multivariate abundance data. <https://CRAN.R-project.org/package=mvabund>
- Warton, D. I., S. T. Wright, and Y. Wang. 2012. Distance-based multivariate analyses confound location and dispersion effects. *Methods in Ecology and Evolution* 3:89–101.
- Watson, D. I., and D. K. A. Barnes. 2004. Quantifying assemblage distinctness with time: an example using temperate epibenthos. *Journal of Experimental Marine Biology and Ecology* 312:367–383.
- Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics* 34:273–309.
- Zhang, S., Y. Zhang, and K. Ma. 2016. Latitudinal variation in herbivory: hemispheric asymmetries and the role of climatic drivers. *Journal of Ecology* 104:1089–1095.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.1926/supinfo>