Reports

Ecology, 99(1), 2018, pp. 29–35

Latitude, temperature, and habitat complexity predict predation pressure in eelgrass beds across the Northern Hemisphere

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Abstract. Latitudinal gradients in species interactions are widely cited as potential causes or consequences of global patterns of biodiversity. However, mechanistic studies documenting changes in interactions across broad geographic ranges are limited. We surveyed predation intensity on common prey (live amphipods and gastropods) in communities of eelgrass (*Zostera marina*) at 48 sites across its Northern Hemisphere range, encompassing over 37° of latitude and four continental coastlines. Predation on amphipods declined with latitude on all coasts but declined more strongly along western ocean margins where temperature gradients are steeper. Whereas in situ water temperature at the time of the experiments was uncorrelated with predation, mean annual temperature strongly positively predicted predation, suggesting a more complex mechanism than simply increased metabolic activity at the time of predation. This large-scale biogeographic pattern was modified by local habitat characteristics; predation declined with higher shoot density both among and within sites. Predation rates on gastropods, by contrast, were uniformly low and varied little among sites. The high replication and geographic extent of our study not only provides additional evidence to support biogeographic variation in predation intensity, but also insight into the mechanisms that relate temperature and biogeographic gradients in species interactions.

Key words: *biogeography; latitude; mesograzer; predation; seagrass; species interactions; temperature;* Zostera.

Manuscript received 15 May 2017; revised 23 August 2017; accepted 30 August 2017. Corresponding Editor: Hannah L. Buckley.

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Introduction

Predation pressure is greater at lower than at higher latitudes for many taxa, from fishes to marine invertebrates, ants, and birds (Vermeij 1987, Schemske et al. 2009, Freestone and Osman 2011). Declines in the strength of predation and other interactions with latitude have been implicated as either a cause or a consequence of latitudinal gradients in biodiversity (Dobzhansky 1950). However, despite a long history of investigation, the extent to which these gradients represent a monotonic decline with latitude vs. a categorical difference between higher and lower latitudes remains unresolved because most studies rely on extreme differences between tropical and extra-tropical or temperate regions (Novotny et al. 2006, Pennings et al. 2009, Freestone et al. 2011). Many factors covary between high and low latitudes, and most studies offer relatively sparse geographic coverage of intermediate latitudes (but see Harper and Peck 2016, Roslin et al. 2017). Thus, it can be difficult to infer the underlying causes of ecological variation correlated with latitude and whether they result from discrete differences between environments or from factors that change continuously with latitude.

While numerous processes may drive latitudinal gradients in species interactions, perhaps the most fundamental is temperature, which generally declines with latitude and affects metabolic rates, demography, and ecological and evolutionary processes (Sanford 2002, Edwards et al. 2010, O'Connor et al. 2011, Manyak-Davis et al. 2013, Dell et al. 2014, Schluter 2016). While a wealth of data is available on biogeographic patterns in population abundance, traits, and diversity, standardized comparisons of communities and species interactions are much more rare. Geographic variation in predation strength may be an important driver of community assembly and evolutionary adaptation, but testing this requires rigorous quantification of species interactions across wide latitudinal gradients (Moles and Ollerton 2016). Thus, understanding the drivers of predation risk at multiple scales remains an important challenge for understanding variability in the strength of biotic interactions.

Eelgrass (*Zostera marina*) is a key foundation species in estuaries and coastal seas across the northern hemisphere (30° to 67° latitude), and thus provides a unique opportunity to test latitudinal gradients in ecological processes within communities of a single habitat-forming species, minimizing potential confounding factors in prior biogeographic studies. Like other seagrasses, eelgrass provides many important functions and services in coastal ecosystems, forming complex, productive habitats for abundant and diverse organisms (Cullen-Unsworth et al. 2014, Duffy et al. 2013) as well as model systems for testing community interactions across spatial scales (Nelson 1980, Orth et al. 1984, Virnstein et al. 1984, Heck and Wilson 1987, Heck and Crowder 1991). Small invertebrate mesograzers are key trophic links in these communities, and often act as mutualists, facilitating seagrasses via selective grazing of their algal competitors (Valentine and Duffy 2006, Duffy et al. 2015). Thus, understanding and predicting global drivers of top-down pressure on these epifauna may have strong implications for seagrass ecology.

To quantify and mechanistically explore variation in predation pressure on seagrass epifauna with latitude, we used a comparative-experimental approach of standardized field surveys and predation assays in 48 eelgrass communities across the species' range. We measured predation pressure on the two major types of common seagrass-associated mesograzers (amphipods and gastropods) across latitudinal gradients, and explored the potential role of local and global environmental factors on predation. These taxa represent two distinct functional groups (amphipods are generally more mobile and less defended than their shelled gastropod counterparts), and may respond differently to predation, with consequences for the strength of top-down control (Östman et al. 2016).

Methods

To assess biogeographic patterns in predation in *Zostera marina* habitats, in the summer of 2014 we conducted a series of assays of epifaunal predation within 48 eelgrass beds across the Northern Hemisphere (see Appendix S1). All eelgrass beds were in shallow water (0–3 m water depth at low tide), and were typically monospecific *Zostera marina*. We measured the intensity of predation on two live, locally abundant, mesograzer species (one species in the Order Amphipoda, one shelled species in the Class Gastropoda) by tethering one individual of each species within each of 20 1-m^2 plots per site and recording presence or absence of these prey after 24 h. We also quantified habitat structure (plant biomass, shoot density, morphology), and characteristics of the epifaunal community (abundance, species richness, body sizes) within each plot using standardized methods (see Environmental surveys, below). Most sites were surveyed in mid-summer; exact sampling times were based on local site logistics and known system dynamics to target peak productivity.

Predation assays

Locally collected live prey were tethered and deployed within each experimental plot for 24 h to quantify predation intensity. We glued individual prey to a 10 cm piece of braided fishing line (diameter 0.13 mm; Berkley Fireline(TM), Spirit Lake, Iowa) tied to a stake (Appendix S1: Fig. S1). One prey stake per individual prey (a replicate) was deployed adjacent to a live *Zostera marina* shoot within field plots. While the species tethered at each location varied (Appendix S1: Table S1), individuals within and across sites were similar in size (10.7 ± 4.6 mm [mean ± SD] for 773 amphipods and 6.5 ± 3.4 mm for 711 gastropods measured from field deployments), were commonly found in surveys and are known to be eaten by local mesopredators. All stakes were retrieved after 24 h and prey were scored as present or absent. Partially consumed prey were considered eaten; molted prey were removed from the analysis. To test whether missing prey might result from failure of the glue binding the prey to the tether, we held a subset of 5–10 prey per site in a flow-through mesocosm, bucket of seawater, or predator exclusion field cage for 24 h. Water flow did not vary appreciably among sites (see Duffy et al. 2015) and no prey detached from tethers in the control trials; thus all missing prey were assumed to be due to predation. Missing stakes were rare and were not included in the analysis.

Environmental surveys

In conjunction with the predation assays, we also surveyed characteristics of the eelgrass community and recorded in situ temperature and salinity measurements. We quantified seagrass shoot density within each plot by counting all shoots per 1-m^2 plot for sites with low seagrass density (less than 50 shoots/plot), or all shoots within a haphazardly placed smaller quadrat (314 cm^2) for sites with higher seagrass density. We assessed seagrass biomass from two cores (20 cm diameter, 20 cm deep) per plot. Cores were cleaned of sediment, separated into belowground (root, rhizome) and aboveground (shoot, leaf) tissues, and dried in an oven at 60°C until there was no change in mass. We collected a 3-cm length from one healthy inner leaf from each of five randomly distributed *Zostera marina* shoots per plot and processed these samples for tissue nitrogen as a proxy for site-level nutrient status (Burkholder et al. 2007) using a CHN analyzer (Thermo Fisher Scientific, Waltham, Massachusetts, USA). We also removed and sorted to species all macroalgae from each plot, and dried these to constant mass. We collected epifauna from *Zostera marina* shoots in the center of each plot by placing a fine mesh bag over the seagrass and cutting it at the sediment surface (see Reynolds et al. 2014). Epifauna were preserved (in 70% ethanol or frozen), identified to lowest taxonomic resolution, and counted. We determined size class (a proxy for body size) for all specimens using a series of stacking sieves (Edgar 1990). To sample potential predators of seagrass-associated epifauna, we deployed Gee-style minnow traps for 24 h at 13 of our study sites and determined catch-per-unit-effort (CPUE, Appendix S1: Table S1). In addition to water temperature measured during field work at each site, we retrieved estimates of annual mean sea surface temperature (SST) from the surrounding region provided by NASA and made available in the Bio-ORACLE data set (Tyberghein et al. 2012; 9.6-km^2 resolution, 2002–2009). We used the raster package in R (R Core Team 2016) to extract the annual mean temperature and temperature range from all cells within 10 km of each site, and averaged these estimates to generate site-level predictors.

Analyses

We tested the influence of latitude and environmental drivers on predation intensity on amphipods using two sets of generalized linear models at (1) the broad site scale and (2) local scale (up to 20 plots per site) in R. Due to the consistently low predation rates on gastropods (see *Results*), we constructed models only to predict predation on amphipods, which were sufficiently abundant to tether at 42 of our sites.

We first modeled amphipod predation at a given site ($N = 42$ sites) as a matrix of total successes (prey missing) and failures (prey remaining) with a quasibinomial error distribution and logit link using the lme4 package. This allowed us to weight by sample size per site and to address overdispersion of the data. The following models were constructed a priori using site-level means of environmental variables and compared to predict predation pressure on tethered prey: biogeography (latitude, ocean, and ocean margin; models 1–5), abiotic environment (in situ temperature, salinity, and leaf percent nitrogen as a proxy for site-level eutrophication; model 6), temperature regime (regional mean annual water temperature and temperature range; models 7–9), animal community (mobile crustacean density and median body size; model 10), biodiversity (richness of total or crustacean mobile epifauna; models 11–12), and habitat complexity (seagrass aboveground biomass, density, and canopy height, and biomass of macroalgae; model 13). Based on findings from the hypothesis-driven model set, we then constructed two composite models with shoot density and either the interaction of latitude and ocean margin (model 14), or mean annual water temperature (model 15). Salinity and seagrass biomass correlated strongly with latitude and moderately with mean annual temperature, and were thus removed from the composite model set. We compared models using quasi Akaike information criteria corrected for sample size (qAIC$_c$) values, calculated using the bbmle package in R. A second, plot-level analysis used each individual plot as a replicate in a hierarchical mixed model on the plot-level binomial data with site as a random factor to compare the role of local community and habitat characteristics on predation intensity. Data were transformed as necessary to meet model assumptions. The limited predator trap sampling (Appendix S1: Table S1) precluded the formal inclusion of secondary consumers in our broader statistical analyses and correlations between predation and CPUEs were evaluated separately.

RESULTS

We found a strong biogeographic signal in predation intensity on amphipods across 42 seagrass beds in the Northern Hemisphere, with predation declining monotonically with latitude from 100% consumption at the southernmost sites to ~20% in the north (Fig. 1a). Few gastropods were consumed at most sites (14% ± 16% loss [mean ± SD]) relative to amphipods (68% ± 35% loss; Fig. 1b). Predation on amphipods did not correlate with predation on gastropods (hierarchical binomial mixed model with plot nested within site, $P = 0.232$) due largely to a lack of variation in predation in gastropods among sites. Although predation on amphipods declined with latitude along all four coasts, it declined more sharply along western ocean basin margins (Fig. 1c), potentially reflecting steeper thermal gradients along those coasts. Indeed, mean annual water temperature best predicted predation intensity on amphipods (Table 1, Fig. 1d). Characteristics of the mobile epifaunal community did not predict predation on amphipods, nor did ambient water temperature at the time the assays were conducted (Table 1). Predation on amphipods decreased with increasing seagrass shoot density (Fig. 1e), and the model that best described our data included both shoot density and mean annual temperature (model 15). The across-site results were consistent with those at the plot-scale where shoot density also correlated with reduced odds of predation (Table 2). Unlike many of the other variables, shoot density was uncorrelated with latitude ($F_{1,40} = 2.616$, $P = 0.1136$, $R^2 = 0.61$). While total secondary consumer species richness was generally low, the CPUE of fishes (Pearson's $r = 0.42$), but not invertebrates (Pearson's $r < 0.01$), positively correlated with predation intensity on amphipods (Appendix S1: Table S1).

DISCUSSION

Using a comparative-experimental approach within the habitat formed by a single species of seagrass (*Zostera marina*) across its range, we found a strong latitudinal signal in the intensity of predation on epifaunal amphipods (Fig. 1, Table 1). Latitudinal gradients in species' abundances and diversity are a general and consistent pattern across many communities (e.g., Dobzhansky 1950, Pianka 1966, Hillebrand 2004). Limited data suggest that species interactions increase in intensity at low compared to high latitudes, but whether this trend is a contributor to the diversity gradient, a consequence of it, or simply driven by the same environmental variables is poorly understood (Schemske et al. 2009). Here, we found a latitudinal signal in predation intensity on a vulnerable prey type (amphipods) compared to an armored prey (gastropods) that was likely driven by biogeographic variation in temperature regime and habitat structure.

Predation on amphipods followed a strong latitudinal cline with high predation at low latitudes on both coasts, but a sharper decline with latitude on western compared to eastern ocean margins (Fig. 1c). This correlated with annual mean temperature, whereby thermal gradients are generally steeper on western than eastern ocean margins due to western boundary currents, which move warm

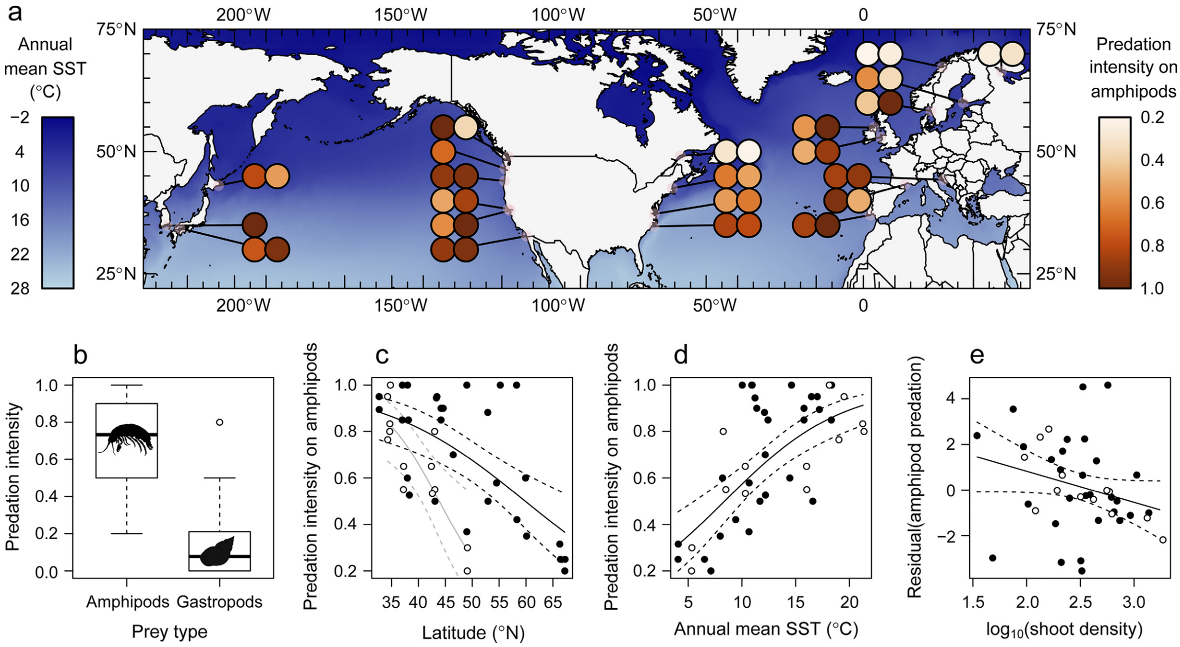

FIG. 1. (a) Map of field sites and predation intensity on amphipods from distributed experimental field assays at 42 sites across the Northern Hemisphere with mean annual sea surface water temperature (SST). Adjacent circles represent sites in close geographic proximity. Warmer colors (closer to red) indicate greater predation intensity. (b) Median predation intensity across sites was greater on amphipod compared to gastropod prey. (c) Predation on amphipods declines more steeply with latitude along western (open symbols, grey lines) than eastern (solid symbols, black lines) ocean margins and (d) increases with annual mean water temperature. (e) Predation on amphipods was negatively correlated with seagrass shoot density after accounting for effects of mean annual temperature. Regressions (solid lines) and 95% confidence intervals (dashed line) are fit from model 15, Table 1.

Table 1. Comparisons of candidate quasibinomial (logit link) models estimating components of site-level variation in predation intensity on amphipods across the Northern Hemisphere. SST = sea surface temperature

						Predictors																		
Site-level models	df	Pseudo R^2	qAIC$_c$	delta qAIC$_c$	Weight	Latitude	Margin	Ocean	Latitude × Margin	Latitude × Ocean	Italicize In situ temperature	Italicize In situ salinity	Leaf % nitrogen	Abbreviate as: Annual mean SST	Annual mean SST range	Annual mean SST ×range	Log crustacean density	Median gammarid size	Log epifaunal richness	Crustacean richness	Log seagrass biomass	Log macroalgae biomass	Log shoot density	Log canopy height
1. Biogeography	2	0.31	85.40	10.59	0.00	**−0.73**																		
2. Biogeography	4	0.43	81.80	6.99	0.02	**−0.97**	**−1.14**	0.08																
3. Biogeography	4	0.46	79.55	4.75	0.06	**−0.88**	**−1.50**		−0.90															
4. Biogeography	5	0.46	82.24	7.43	0.02	**−0.86**	**−1.48**	0.09	−0.90															
5. Biogeography	6	0.46	85.13	10.32	0.00	**−0.86**	**−1.49**	0.09	−0.91	0.02														
6. Abiotic environment	4	0.32	89.52	14.71	0.00						0.23	**0.62**	−0.19											
7. Temperature regime	2	0.41	77.88	3.07	0.14									**0.92**										
8. Temperature regime	2	0.04	105.10	30.28	0.00										−0.27									
9. Temperature regime	4	0.45	80.34	5.52	0.04									**0.99**	−0.19	−0.29								
10. Community	3	0.02	109.01	34.19	0.00												0.20	0.00						
11. Total biodiversity	2	0.04	105.47	30.65	0.00														0.25					
12. Biodiversity	2	0.07	103.13	28.31	0.00															*0.34*				
13. Seagrass habitat	5	0.25	96.63	21.81	0.00																**0.73**	−0.09	**−0.95**	*−0.68*
14. Composite I	5	0.49	79.48	4.67	0.06	**−0.77**	**−1.41**		−1.00														*−0.31*	
15. Composite II	3	0.49	74.81	0.00	0.65									**0.85**									**−0.41**	

Notes: Boldface and italic numbers are statistically significant regression coefficients (bold, $P < 0.05$; italic $0.10 > P > 0.05$). Coefficients for continuous variables are standardized. Based on comparing quasi Akaike information criteria corrected for sample size (qAIC$_c$) values, the composite II (Model 15) best describes the data.

tropical waters offshore as they flow poleward and deliver it to the higher latitudes of eastern margins. The importance of ocean circulation and latitude-driven effects of temperature is supported by our modeling results, where the strongest model predicting the strength of predation included mean annual water temperature (Table 1, Fig. 1d). Although a difference in the slope of the predation effect with latitude varied across continental coastlines, statistical confidence in the interaction between latitude and ocean margin was marginal ($P < 0.10$), possibly due to non-linear relationships between latitude and temperature regime and/or our comparatively more limited geographic sampling on western margins.

Table 2. Hierarchical mixed binomial model of local (plot-scale) variation in predation intensity on amphipods with site as a random term.

Predictors	Coefficient	Pr (>|z|)	CI (2.5, 97.5%)
log(crustacean density)	0.203	0.271	−0.167, 0.569
log(seagrass biomass)	0.284	0.072	−0.031, 0.598
log(macroalgae biomass)	0.087	0.667	−0.315, 0.508
log(shoot density)	−0.737	<0.001	−1.118, −0.371
log(canopy height)	−0.054	0.807	−0.487, 0.393

Note: Marginal $R^2 = 0.112$, conditional $R^2 = 0.403$. $N = 42$ sites and 809 plots.

Our results suggest that temperature, or factors related to temperature, may drive increased predation on seagrass epifauna. The failure of ambient water temperature at the time of sampling to explain this variation suggests that the relationship is not simply a direct metabolic correlate, but instead may be related to variation in plant (habitat), epifauna, or consumer assemblage characteristics influenced by the long-term temperature regime. In addition to the influence of regional temperature, we found that increasing shoot density decreased predation on amphipods both across and within sites (Tables 1 and 2, Fig. 1e), likely because increasing shoot density can reduce detection and capture of mobile prey by active fish and crab predators (Lannin and Hovel 2011, Carroll et al. 2015, Hovel et al. 2016; but see Mattila et al. 2008). Shoot density was independent of both latitude and mean annual water temperature, and thus may be a useful predictor of predation intensity on amphipods at both broad (site) and fine (plot) scales. In contrast, plant biomass negatively correlated with latitude, suggesting that its greater potential to serve as prey refuge in low-latitude sites was not strong enough to overcome a latitudinal signal of predation pressure. Thus, a clear prediction of predation intensity at a particular site requires understanding the combined influence of multiple biogeographic (latitude, temperature) and local (shoot density) drivers.

Whereas rates of predation on amphipods were generally high and varied with latitude, temperature, and shoot density, predation on similarly sized gastropods was consistently very low (Fig. 1b). Similarly, a meta-analysis of experiments in North Atlantic seagrass and seaweed systems concluded that crustacean populations respond more strongly to predation than gastropods do and that cascading top-down effects are primarily mediated through crustacean grazers (Östman et al. 2016). The higher predation we observed on amphipods vs. gastropods may arise, in part, due to a preponderance of browsing fish and fewer crushing crustacean predators in temperate to boreal grass beds. Indeed, surveys of secondary consumer abundance at 13 of our sites found over 6.5 times more fish than invertebrate consumers. Additionally, reduced prey value of gastropods vs. amphipods, or more rapid consumption by vertebrate than invertebrate predators, may mean that our standardized 24 h deployment interval was insufficient to capture variability in lower predation rates on gastropods. As a corollary, temperate seagrass beds may provide sufficient refuge to gastropods as to obscure a more general effect of latitudinal variation in predation found in our and other studies. However, the greater abundance of crushing fish predators in the tropics may restore a latitudinal gradient in predation on gastropods across a broader range of habitats (Palmer 1979).

In summary, we find consistent latitudinal declines in predation on a common type of crustacean across four coasts and two oceans, with variation in predation closely linked to annual mean temperature. These strong global gradients in predation pressure can nevertheless be modified by local habitat factors (e.g., shoot density), demonstrating that large sample sizes across continuous environmental and biological variation are needed to adequately capture drivers of latitudinal gradients in ecological patterns and processes. Although we avoided working in degraded seagrass beds, anthropogenic stressors in these habitats (including overfishing, eutrophication, and habitat destruction) are known to strongly influence ecological linkages and should be accounted for when making biogeographic comparisons that inform conservation and management. Because our sites are within temperate communities based on the same foundation species (*Zostera marina*) and with similar food web structure (eelgrass and microalgae, invertebrate mesograzers, fish, and invertebrate predators), our results are less influenced by the biological differences in comparisons between temperate and tropical systems. Thus we suggest that the latitudinal gradient in predation is likely robust, and determined more by thermally associated community differences than metabolically influenced direct effects of temperature. Whether this mechanistic connection is robust awaits intensive studies like ours, conducted in a range of other systems.

ACKNOWLEDGMENTS

This research is supported by NSF BIO-OCE grant 1336206, 1336741, and 1336905 (to J. E. Duffy, J. J. Stachowicz, K. A. Hovel), and in-kind support from author institutions. We thank the numerous staff and students, particularly our “ZENterns,” who assisted with this research (www.ZENscience.org). Contribution no. 3708 of the Virginia Institute of Marine Science, College of William and Mary.

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