LETTER

Organismal traits are more important than environment for species interactions in the intertidal zone

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Abstract

Species interactions come in a variety of forms, from weak to strong, and negative or positive, each with unique consequences for local community structure. However, interactions depend on several biotic, abiotic and scale-dependent variables that make their magnitude and direction difficult to predict. Here, we quantify the relative impacts of multiple factors on species interactions for a diverse array of intertidal organisms, using our own experiments across a range of environments in New Zealand and North America. Interaction strengths are related to organism body size and trophic level, but are relatively insensitive to environmental conditions associated with tidal height. Although species at higher trophic levels exert stronger per-capita effects on other taxa, their population-level impacts are equivalent to basal trophic groups. This indicates that interaction intensity is largely based on requirements for resources, such as food or space, that follow allometric scaling rules. These results demonstrate the potential to predict interactivity based on simple criteria without detailed information on particular species or communities.

Keywords

INTRODUCTION

Many environmental, organismal and scale-dependent variables dictate the nature of species interactions in communities. Predicting the relative influences of these factors is a primary goal of theoretical and empirical research. However, due to the logistical challenge of quantifying interactions in diverse communities, most studies focus on only one explanatory variable or a few species, in a single place, for short times. Few studies make community-wide assessments of the multiple factors driving interactivity in combination, and consequently we do not know how interactions are contingent on biotic and abiotic context. There is a clear need in ecology and conservation for research that examines this context dependency, and how it evolves over space and time (Berlow *et al.* 2004; Wootton & Emmerson 2005; Agrawal *et al.* 2007).

An understanding of the functional basis of species interactions would allow researchers to focus on the characteristics of species that are most important for predicting community dynamics. Body size may be a valuable species trait

because it is scaled to trophic interaction strength in empirical and model food webs (Emmerson & Raffaelli 2004; Berlow *et al.* 2009), and correlated with several allometric properties including metabolism, home range, abundance and trophic status across a wide range of ecosystems (Woodward *et al.* 2005). Larger, more mobile, or abundant species have greater potential to interact with other populations and thus may exert stronger community-wide effects (Duffy 2003). Large predators, for example, often have strong effects that can cascade through communities to lower trophic levels (Shurin *et al.* 2002). Community assembly may select for certain combinations of species, particularly those with weak interactions that can stabilize cyclic or chaotic population dynamics (McCann *et al.* 1998). This could lead to predictable associations between diversity and the strength of links in interaction webs based on organismal traits (Kokkoris *et al.* 2002).

Species interactivity may be further governed by environmental factors or the scope of the experiment. Across gradients in environmental stress, negative interactions often dominate under less stressful conditions whereas positive interactions are thought to be more prevalent under stressful

regimes (Bertness & Callaway 1994). A recent meta-analysis of 11 alpine plant removal experiments, for example, observed a shift from competitive to facilitative interactions with increasing temperature and wind stress along an elevation gradient (Callaway *et al.* 2002). However, other studies examining this relationship at multiple sites or times often find that it depends on the geographic scale, coexisting taxa and experimental duration (Bertness & Shumway 1993; Greenlee & Callaway 1996; Pennings *et al.* 2003), which indicates a need for further research on the environmental control of species interactions across habitats and regions varying in physical stress (Brooker *et al.* 2008). The temporal scale of resolution or the experimental duration may bias measurements of interaction strengths since, theoretically, indirect effects unfold more slowly as they are transmitted along chains of direct interactions (Yodzis 1988). At broad temporal and spatial scales, interactions may be weaker due to segregation of species. Larger study areas typically include more heterogeneous habitats and greater species richness, in part because coexistence is possible at larger scales as spatial niche segregation weakens interactions that would otherwise lead to exclusion (Grace & Wetzel 1981). Despite much research on each of these factors, their relative impacts on species interactivity are largely unknown.

Our goal here is to identify the features of organisms, communities and environments that influence interaction direction and magnitude across widely separated ecosystems. In this synthesis, we test the relative importance of diversity, environmental stress, spatio-temporal scale and species traits (factors relating to body size and trophic type) as determinants of species interactions amongst all taxa in intertidal communities. We use a data set of our own empirically derived community-wide interaction coefficients, based on specific responses to the removal of dominant algal and invertebrate taxa on intertidal reefs in the northern (Oregon and British Columbia) and southern (New Zealand) Pacific Ocean. Experiments vary in intertidal elevation, the sizes of manipulated plots, and the types and numbers of species present, but are identical in the ways that species are manipulated and the responses are measured.

MATERIAL AND METHODS

Field techniques

Data from 30 of our own independent field experiments were used to quantify the sign and strength of species interactions. The experiments were performed on wave-exposed rocky intertidal reefs along the South Island of New Zealand and the West Coast of North America at various times between 2002 and 2008 (dates and additional metadata given in Table S1). Each experiment consisted of three to five replicate 'removal' and unmanipulated control plots of equal size, ranging from 0.024 to 1.25 m^2, at the same tidal elevation (Fig. 1). A single focal species was eliminated from the removal plots and continually excluded
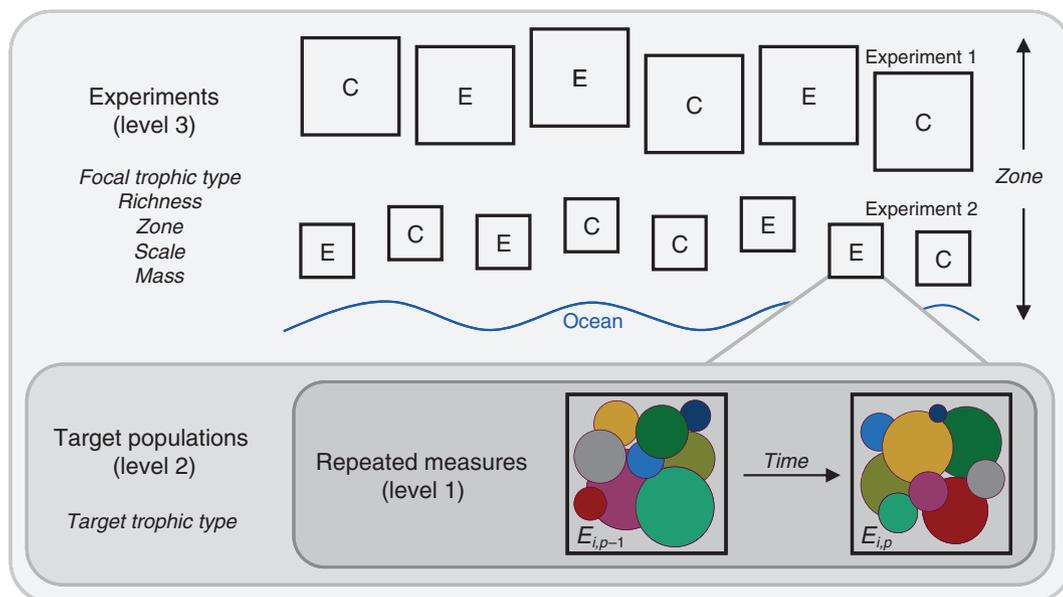

Figure 1 A schematic depicting the layout of two of the 30 experiments described in Table S1. Each experiment consisted of replicate control (C) and experimental 'removal' (E) plots, of the same size, in one intertidal zone, at one of eight sites. The abundances of all target taxa ($E_{i,p}$ in Eqn. 1) were measured at varying time intervals over the duration of the experiment. The data were analysed at three levels of organization: repeated measures (level 1), target populations (level 2) and experiments or 'communities' (level 3). Seven factors hypothesized to impact interaction sign and strength (italicized) were included as predictors at one of the three levels of the analyses.

for the duration of the study (see Lilley & Schiel 2006 for further descriptions of the experimental protocol used at all sites). We selected the largest and most dominant algae and invertebrates as focal species. Their densities (individuals m^{-2}) were monitored throughout the experiment by searching the control and removal plots thoroughly during daytime low tides, at intervals corresponding with the scheduled maintenance of the removal treatments. Body mass of the focal species was measured by removing and weighing every focal individual present in equally sized quadrats interspersed amongst the study plots. In each removal and control plot, we also measured the abundances of all associated, non-manipulated target species. Individuals of mobile organisms were enumerated and abundances of sessile taxa were quantified by visually estimating percent coverage of the entire plot in the field. One experiment, in a structurally complex intertidal mussel habitat in New Zealand, required destructive sampling to measure the abundances of organisms within the mussel bed. A 10 cm diameter PVC pipe was used to collect three 'cores' from the 2.0 m^2 removal and control plots, from which densities of the target taxa were quantified in the laboratory. In every experiment, abundances of the target populations were monitored at varying intervals, typically every 3–6 months, for up to 3 years after the experiment was initiated.

Interaction metric

The effect of a focal species on a target taxon was calculated using the log ratio of the response in density of the target species in a removal treatment unit relative to an untreated control plot (Osenberg *et al.* 1997; Wootton 1997). The Dynamic Index interaction coefficient,

$$\mathrm{DI}_{ij,p} = \ln \frac{C_{i,p}/C_{i,p-1}}{E_{i,p}/E_{i,p-1}} \div (\Delta t \cdot Y) \qquad (1)$$

gives the per-capita impact of the focal species j on the population trajectory of target species i at monitoring period p, when $C_{i,p}$ is the abundance of the target organism in the presence of the focal species and $E_{i,p}$ is its abundance in the absence of the focal species. The time between sample periods, Δt, is expressed in days. Density of the focal species in the control plot, Y, is an average of repeated estimates taken between monitoring periods p and $p-1$. The value of Y is expressed in individuals per square metre to facilitate comparisons amongst plots varying in size. Because it is a log ratio, $\mathrm{DI}_{ij,p}$ cannot be calculated with abundance values of zero. In such cases, one individual per square meter is added to all E and C values (Wootton 1997).

One advantage of the Dynamic Index is that it is distributed around zero (Berlow *et al.* 1999); species whose abundances decline in the absence of the focal species,

relative to the control, will have positive interaction coefficients, while those that increase will have negative coefficients. Another benefit of this metric is that it does not require communities to be at equilibrium, however, its accuracy is greatest when the abundances of the target taxa are close to their initial conditions (Berlow *et al.* 1999). Thus, since target populations have different growth rates and lifespans, the time between monitoring periods (Δt) should be short enough to measure small changes in the abundance of populations with fast growth or turnover. However, sampling rates must also be long enough or repeated over time scales that can capture changes in the seasonal, slow-growing and long-lived populations. Using these criteria, we chose to monitor experiments every 3–6 months ($\overline{\Delta t} = 140$ days), where possible, for at least 1 year. We also include $C_{i,p-1}$ and $E_{i,p-1}$ in Eqn. 1 to account for spatial variation in the initial abundances of target taxa. These terms eliminate the inaccuracy of $\mathrm{DI}_{ij,p}$, as it is often used (Berlow *et al.* 1999), caused by the assumption that no differences exist in starting abundances between treatments. Note that 'initial' here refers to the previous monitoring period ($p-1$), instead of the start of the experiment. This step-by-step calculation minimizes the error in $\mathrm{DI}_{ij,p}$ caused by large changes in target abundances over time. This approach requires the simplifying assumption that the effect of a focal species is directly related to its density. Although nonlinear species interactions do occur, models using linear coefficients can predict the outcomes of experimental perturbations and often outperform models using nonlinear functions form in intertidal communities (Wootton 1997; Novak in press).

Data were bootstrapped to produce every combination of control and removal plots within each experiment, and $\mathrm{DI}_{ij,p}$ values were calculated for all the target taxa present in each pair of plots (cf. Paine 1992). A total of 87 275 pairwise species interactions were estimated. The mean interaction coefficient for each focal and target taxon pair, $\overline{\mathrm{DI}}_{ij,p}$, was then computed by averaging across the combinations of control and removal plots for each monitoring period within each experiment to produce 3397 separate interaction estimates, which were then analysed for associations with biological and environmental variables.

Interaction sign

In the first of two analyses, we tested the hypothesis that the sign (negative or positive) of each pairwise interaction between a focal and target taxon was related to the trophic identity of the target and focal taxa, body size of the focal species, plot size, species richness, shore height and duration of the experiment. To quantify interaction sign, we reduced the $\overline{\mathrm{DI}}_{ij,p}$ coefficients into binary positive or negative responses. A logistic multilevel regression was used to model the change in interaction sign across three nested

hierarchical levels: repeated measures (level 1; $n = 3397$), target populations (level 2; $n = 1287$), and experiments or 'communities' (level 3; $n = 30$; see Fig. 1). A logit link function was used to express interaction sign as the probability of being positive.

Multilevel models use nested regression equations to partition the variance in a response across hierarchical levels of organization. These models are adept at accounting for the statistical interdependencies of observations within levels, such as repeated measurements of target populations from the same experimental units (Blackwell *et al.* 2006; McMahon & Diez 2007). This is because the errors at each level are modelled around the varying intercepts and slopes of the independent groups. These intercepts and slopes are then treated as responses in the regression at the next level. The assumptions of normality and homogenous variance are assessed at each level by visually examining the data and residuals. There is currently no consensus on the appropriateness of F-statistics for multilevel models, so P-values are generated using Markov Chain Monte Carlo methods (Bolker *et al.* 2008). In this study, model parameters and P-values were computed using the nlme and lme4 packages for R (R Development Core Team 2008).

Seven factors hypothesized to affect interaction sign were included as predictors at the appropriate level of the model: Time (level 1), Target (level 2), Focal, Richness, Zone, Scale and Mass (level 3). Time refers to the sampling date in julian days. Target and Focal represent the trophic types (producer, suspension feeder, herbivore, carnivore or omnivore) of the responding and manipulated populations, respectively. In the intertidal zone, carnivores consume suspension feeders and herbivores, which in turn feed on primary producers, so that the trophic types span a range of trophic levels. Richness is the average number of species observed in an experiment across all sampling times and therefore represents the species richness of the community in which the experiment was placed. These values are chosen for simplicity as analyses using jacknifed estimates of experiment-level richness (Heltshe & Forrester 1983) give qualitatively similar results. Zone is an ordered factor with three levels (low, middle and high), used as a proxy for the degree of environmental stress. In the intertidal zone, there is a clear gradient in heat and desiccation stress across zones (Bertness & Leonard 1997), much like the elevation gradient in alpine ecosystems (Callaway *et al.* 2002). Scale represents the plot size, and ranges from 0.024 to 1.25 m^2. Finally, Mass is the average log-transformed body mass of the focal species excluded in the removal experiments. Numerical predictors were centred by subtracting the mean value so that the model tested for differences under average conditions (Pinheiro & Bates 2000). The model also included tests for Target × Richness, Target × Stress, Target × Scale, Target × Mass and Target × Focal cross-level interactions.

Interaction strength

Next, we assessed whether variation in the strengths of the species interactions could be attributed to the seven factors also hypothesized to impact interaction sign (Time, Target, Focal, Richness, Zone, Scale and Mass, described earlier). Interaction strength was computed as the absolute value of the interaction coefficient, $\overline{DI}_{ij,p}$. Otherwise, strong positive and negative interactions on both sides of zero could have been averaged to give an overall weak community-wide effect (Dodds & Nelson 2006). As such, interaction strength was always a positive value. A linear multilevel model was used with the same hierarchical structure and predictors described before for interaction sign and shown in Fig. 1. Response values were log-transformed to meet assumptions of normality. We assessed the benefit of including an autoregressive order-one correlation to account for the inherent correlation between sample times (Pinheiro & Bates 2000), but it did not improve the model fit.

RESULTS

Interaction sign

Communities are characterized by a balanced proportion of positive and negative interactions (Fig. 2) regardless of the biotic or abiotic context (Table 1A and Table S2A). None of the seven predictors examined in this study can explain differences in the interaction sign at the level of the
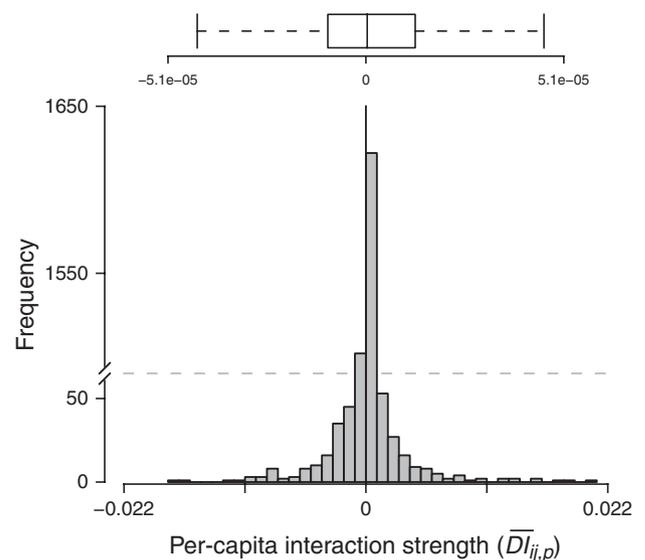

Figure 2 The distribution of interaction coefficients ($\overline{DI}_{ij,p}$) with many weak and few strong, and a balanced proportion of negative and positive effects ($n = 3397$). Note the break in the y-axis. The upper plot shows the median, first and third quartiles (box), and 1.5 interquartile range (whiskers) of the $\overline{DI}_{ij,p}$ values on a finer scale.

Table 1 Results of the multilevel models testing the effects of factors on the sign (A) and strength (B) of species interactions

	d.f.	SS	MS	*P*-value
A				
Factor				
Time	1	0.032	0.032	0.747
Target Trophic Type	4	3.229	0.807	0.415
Zone	1	0.085	0.085	0.371
Scale	1	1.870	1.870	0.638
Richness	1	0.841	0.841	0.712
Body Size	1	0.014	0.014	0.898
Focal Trophic Type	3	2.826	0.942	0.910
Target Trophic Type × Zone	4	5.947	1.487	0.497
Target Trophic Type × Scale	4	1.709	0.427	0.181
Target Trophic Type × Richness	4	3.742	0.936	0.096
Target Trophic Type × Body Size	4	4.939	1.235	0.068
Target Trophic Type × Focal Trophic Type	12	8.934	0.745	0.445
Random effect				Variance
Target population intercept				0.206
Target population slope				~ 0
Experiment intercept				0.013
Experiment slope				~ 0
Residual				1.00
B				
Factor				
Time	1	1.726	1.726	0.881
Target Trophic Type	4	135.8	33.95	< 0.001
Zone	1	136.0	136.0	0.272
Scale	1	3.534	3.534	0.329
Richness	1	59.15	59.15	0.990
Body Size	1	262.2	262.2	< 0.001
Focal Trophic Type	3	303.1	101.0	< 0.001
Target Trophic Type × Zone	4	19.11	4.777	0.809
Target Trophic Type × Scale	4	37.87	9.468	0.452
Target Trophic Type × Richness	4	4.526	1.131	0.627
Target Trophic Type × Body Size	4	12.92	3.230	0.202
Target Trophic Type × Focal Trophic Type	12	47.03	3.920	0.133
Random effect				Variance
Target population intercept				0.634
Target population slope				~ 0
Experiment intercept				1.08
Experiment slope				~ 0
Residual				1.65

communities, target populations or repeated measures through time (all $P > 0.05$). Environmental stress, for example, is unrelated to interaction sign across all community members (Zone $P = 0.371$) and trophic types (Target Trophic Type × Zone interaction $P = 0.497$). Remaining interactive effects of predictors at the experiment and target population levels are also insignificant (all $P > 0.05$), although omnivores have a weak tendency to engage in more positive interactions with larger focal species (Table S2A). Randomly varying intercepts by target populations account for more of the variation in the proportion of positive and negative $\overline{DI}_{ij,p}$ values than any other random effect (Table 1A). Random intercepts by experiments and the target- and experiment-level slopes provide little added benefit to the model, with variance components all near zero.

Interaction strength

Species interactions are predominantly weak, with strengths near zero. Relatively few effects are stronger than 5.0×10^{-5} $|\overline{DI}_{ij,p}|$ (Fig. 2). Interaction strength is directly related to the body size ($P < 0.001$) and trophic type (Target $P < 0.001$,
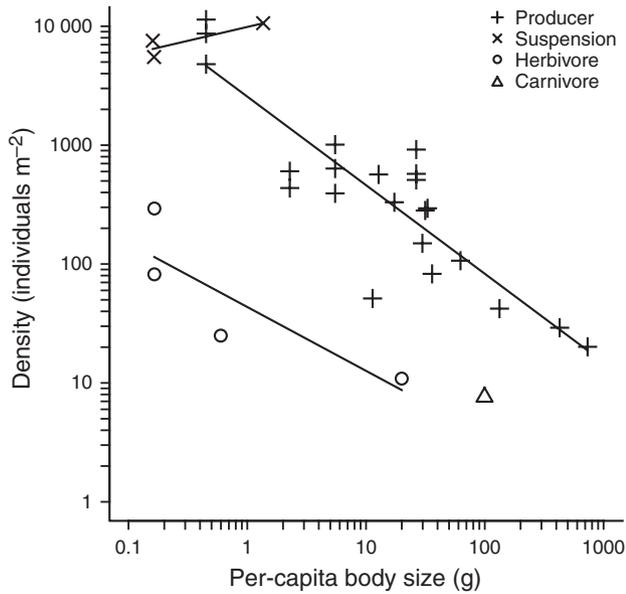
Figure 3 The density of a focal species (individuals m^{-2}) is inversely related to its body size (g) across the 30 experiments in this study. The symbols represent different trophic types. The lines show trends for producers [ln(y) = −0.745·ln(x) + 7.85], suspension feeders [ln(y) = 0.233·ln(x) + 9.20] and herbivores [ln(y) = −0.534·ln(x) + 3.72].

Focal $P < 0.001$) of an organism (Table 1B). Body sizes of the focal species are also inversely related to their density (Fig. 3). As Fig. 4 shows, the differences in $|\overline{DI}_{ij,p}|$ associated with focal species body size are greater than the differences in $|\overline{DI}_{ij,p}|$ amongst focal trophic types across the focal species we tested. A 17 g increase above the average log-transformed body size (9.9 g) is associated with a change of 0.79 in log-transformed interaction strength across the experiments (Table S2B). Focal trophic types, meanwhile, vary between 0.12 and 4.0 in $\ln|\overline{DI}_{ij,p}|$. Herbivores and the carnivore *Pisaster ochraceus* have stronger effects than producers ($P < 0.001$ and $P = 0.001$, respectively), which have slightly weaker impacts than the suspension-feeding barnacles and mussels, though this difference is not significant ($P = 0.842$; Table S2B). As Fig. 5b shows, on a per-population basis ($|\overline{DI}_{ij,p} \cdot Y|$), focal species varying in trophic type have indistinguishable effects ($F_{3,26} = 1.239$, $P = 0.316$). Community wide, the per-population and per-capita effects of focal species are not correlated ($n = 30$, $\rho = -0.073$, $P = 0.702$). Target trophic types (the small symbols in Figs. 4 and 5) differ by 0.24–0.64 $\ln|\overline{DI}_{ij,p}|$ from producers (the base contrast), and explain a significant portion of the variation within experiments ($P < 0.001$; Table 1B). This is because target herbivores show stronger responses to removals than producers, carnivores and omnivores, which are themselves more affected than suspension feeders (Table S2B). It is important to note, however, that the significant differences amongst target trophic types are slight compared to the overall variation in $\ln|\overline{DI}_{ij,p}|$, and several times smaller than the differences in per-capita interaction strength amongst focal trophic types (Table S2B). These patterns are independent of the species
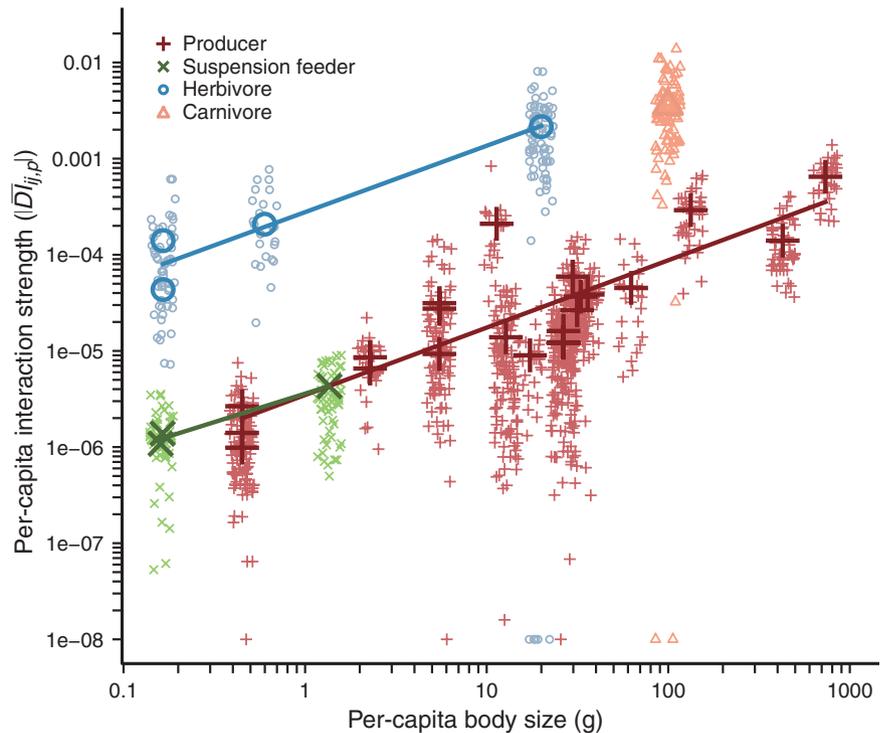

Figure 4 The relationship between focal species body size and per-capita interaction strength. The small points symbolize the average strength of an interaction between a focal species and a target population across all sampling times (the target population level). The large points represent the average effect of a focal species across all target taxa (experiment-level data). Colours and symbols indicate the trophic type of the focal species. Lines are fit using least-squares regression for each trophic group, through experiment-level results [producers: ln(y) = 0.701·ln(x) − 12.6, suspension feeders: ln(y) = 0.592·ln(x) − 12.5, herbivores: ln(y) = 0.690·ln(x) − 8.19].
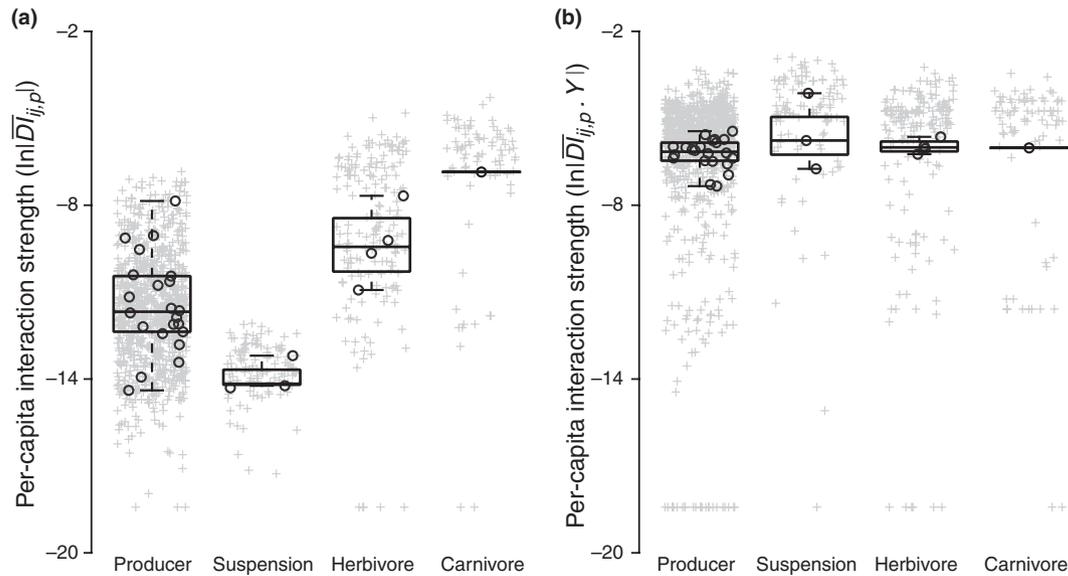
Figure 5 The strength of per-capita (a) and population-level (b) effects of focal species grouped by trophic type. Producers and suspension feeders have weaker per-capita impacts than herbivores and the carnivore *Pisaster ochraceus*, but effects at the population level are equivalent across trophic groups.

type being removed, as indicated by the non-significant Target × Focal Trophic Type interaction ($P = 0.133$; Table 1B). Interaction strength is unaffected by the temporal ($P = 0.881$) and spatial ($P = 0.329$) scale of the experiment, richness of the study plots ($P = 0.990$) and environmental conditions along a gradient in tidal height ($P = 0.272$; Table 1B). Experiment-level random intercepts account for 32% of the total variation. Substantially less variance in interaction strength (19%) is accounted for by the random intercepts by target populations. The random slopes at neither level improve the fit of the model (*c.* 0; Table 1B).

DISCUSSION

Our synthesis of 30 intertidal species removal experiments indicates that traits of organisms play a dominant role in determining the strength, but not the sign, of interactions amongst organisms. Positive and negative interactions are equally prevalent in all cases, regardless of tidal height, temporal or spatial scale of the experiment, species richness of the community or the types of species examined. The first of these observations is most surprising as it suggests that the increase in facilitative interactions with environmental stress occurs in some taxa but is not a general feature of interactions across all members of the community. Individual producers and suspension feeders exert weaker per-capita impacts on communities than herbivores and the single carnivore tested. However, since these smaller organisms with lower trophic positions are more numerically abundant, their population-level effects are equivalent

to other trophic types. Population density declines with increasing body size, offsetting the increase in per-capita interaction strength, to yield a more consistent population-level impact on other community members across a range of sizes. This suggests that the impact of an intertidal organism on a population with which it co-occurs is predictable based on a few easily measured traits such as size and trophic type, and is relatively less dependent on environmental context.

Body size

Large taxa have stronger per-capita effects than small-bodied species (Fig. 4), suggesting that interactivity reflects allometric species traits such as abundance, feeding ecology and range size (Woodward *et al.* 2005; Wootton & Emmerson 2005). Measured here as body mass, size spans four orders of magnitude from barnacles (< 1 g) to one of the world's largest algal species, *Durvillaea antarctica* (< 1 kg intertidally; Table S1). Other studies have shown that body size predicts per-capita feeding rates (Hillebrand *et al.* 2009) and therefore the strength of trophic interactions in food webs (Emmerson & Raffaelli 2004; Berlow *et al.* 2009). Our results indicate that body size is also the best predictor of the strength of non-trophic interactions, which are often powerful positive and negative forces in communities. Some of the strongest per-capita interactions measured here were non-trophic impacts of the habitat-engineering producer *D. antarctica*. An individual *D. antarctica* excludes many understory species when its fronds are whipped against the substrate by waves, but also provides habitat for dozens of

macroinvertebrate grazers in its large holdfast (Santelices *et al.* 1980). Sessile species like *D. antarctica* that can reach lengths of 10 m often interact with organisms over scales greater than the home ranges of their associated mobile invertebrate consumers. Interestingly, although the two species are separated biogeographically, one sessile *D. antarctica* physically impacts an area comparable to the typical foraging range of the predatory sea star *P. ochraceus* (Robles *et al.* 1995). Body size serves as the best measure of the potential for mobile and sessile species of all trophic types to engage in direct trophic and non-trophic interactions that result in strong community-wide effects.

Trophic type

Even after accounting for body size, there is a trend towards stronger per-capita effects of focal species at higher trophic levels (Fig. 4). This result is due to significantly stronger impacts of the mobile herbivores and the one carnivore we tested (*P. ochraceus*) relative to the sessile suspension feeders and producers (Fig. 5a; Table S2B). The clear distinction between the mobile and sessile trophic types suggests that the per-capita effect of a consumer may be related more to how it captures its prey than the identity or attributes of the prey. Other studies have demonstrated that the great mobility of *P. ochraceus* affords it exceptionally strong impacts on community dynamics (Menge *et al.* 1994), and therefore it may not be a representative intertidal carnivore. However, our decision to remove only large, dominant focal species probably resulted in disproportionately strong interactions across all trophic types. A previous study on the effects of the focal species *Katharina tunicata*, for example, concluded that this herbivore plays a 'pivotal role' in communities, partly because of its large size and abundance (Duggins & Dethier 1985). This bias does not restrict comparisons between the experiments, but limits our ability to generalize to the smaller or rarer community members. Further empirical investigation is required to assess whether their per-capita effects also scale with body size and trophic type.

The sign of an interaction is unpredictable based on organismal traits such as trophic group or body size (Table 1A). For instance, consumers are equally likely to benefit or suffer from interactions with producer species. This result emphasizes the importance of trophic and non-trophic interactions (Jones *et al.* 1997). In our experiments, for example, removing the barnacle *Balanus glandula* allowed us to detect its direct positive effects on the grazing snail *Littorina* spp., for which it creates habitat (Harley 2006). Meanwhile, through inhibition of grazing by limpets, *B. glandula* also has indirect positive effects on many macroalgae (Farrell 1991), but direct negative effects on species such as *Chthamalus dalli*, which it out-competes for space (Dayton

1971). Paine (1992) likewise found that intertidal herbivores have negative and positive effects on the alga *Alaria marginata*, by consuming it directly or preferring its competitors. Ultimately, through the complex assortment of interaction types, positive responses are balanced by an equal number of negative responses in communities and the sign of the outcome is unpredictable based strictly on trophic type.

One unique aspect of this study is that it examines all the pairwise interactions between a focal species and every target population that constitutes a community. Studies quantifying interaction coefficients in the intertidal zone typically focus on select pairs of species (e.g. Navarrete & Menge 1996; Wootton 1997). We expand on these studies with a community-wide approach that offers additional insights into the large within-community variation in the responses of the target populations. A small, but significant, portion of this variation in $|\overline{DI}_{ij,p}|$ is explained by the trophic type of the target organism (Table 1B). Remaining variation at the target population level may be due to unmeasured properties of the target organisms such as their body size. This theory is supported by food web studies measuring interactions as the contribution of species to the diets of others, which are finding that the ratio of predator:prey body sizes is related to the strength of the predators' per-capita effect. In the Ythan Estuary, for example, the predator:prey body size ratio predicts the impacts of individual crabs and shrimp on four species of prey in an intertidal food web (Emmerson & Raffaelli 2004). It is unclear whether the focal:target body size ratio can also accurately predict interaction strengths in communities with strong non-trophic effects. We hope that future community-wide studies using data on body sizes will be able to test this hypothesis.

Per-capita vs. population effects

On a per-capita basis, mobile consumers exert stronger effects on populations than do producers and suspension feeders (Fig. 5a); however, population-level effects are equivalent across organisms of different sizes or trophic types (Fig. 5b). The per-capita effects of the one predator and four herbivores are large because their numerical densities are low compared to the suspension feeders and producers (Fig. 3). This pattern of lower abundance with higher trophic levels and body sizes is common in many ecosystems (Woodward *et al.* 2005). The inverse scaling relationships between body size and both population abundance and individual mass-specific metabolic rates led Damuth (1987) to propose that population energy use is invariant, as the increasing metabolism of larger taxa is offset by their lower abundance (but see Marquet *et al.* 1995). Our results suggest an interesting corollary: although species' impacts on other community members span many

orders of magnitude and increase with size and trophic position on an individual basis, they are relatively uniform at the population level, varying by one order of magnitude. Per-population interactions are much more consistent than per-capita effects, and unrelated to organismal size or trophic type.

Variation in per-capita and per-population estimates of interaction strength is frequently used to identify 'keystone' species with disproportionately large impacts relative to their abundance. Navarrete & Menge (1996), for example, show that the rate of mussel consumption by the keystone predator *P. ochraceus* is several times greater than that of *Nucella emarginata*, on both a per-capita and per-population basis. They also observe, as we do in this study, that the variation in the per-capita impacts of the two species is orders of magnitude greater than the variation in the population-level estimates. Together, the results indicate that the per-capita 'keystone' impact of *P. ochraceus* can be attributed largely to factors related to its size, trophic status and mobility. After discounting these traits that covary with density, the per-population effects of *P. ochraceus* are similar to those of species with weaker per-capita effects on other community members.

These results have important implications for ecology and conservation. First, they indicate that easily measurable ecological traits of individuals such as body size can be used to predict the strength of their per-capita impact. Interaction intensity may be an emergent property of metabolic rate, reflecting the ability of species to monopolize resources including food or space. Second, they guide predictions of the secondary consequences of invasions and extinctions of populations in ecosystems. Large species with high trophic positions are rarer and therefore more vulnerable to extinction (Duffy 2003). If the population-level effects of taxa of different trophic types are indistinguishable, as our results suggest, then the removal of a consumer population is likely to have a community-wide effect comparable to the extinction a dominant low-trophic 'foundation' species. Species introductions may follow equivalent rules. One study by Levin *et al.* (2002) found that invasions by an alga and suspension-feeding bryozoan had commensurate community-wide impacts. As in our deletion experiments, the introduced focal populations had many weak and few strong effects that were evenly positive and negative.

Environmental stress

The harshness of the environment can determine trophic structure and shift certain species interactions from more negative to positive in communities from the low to high intertidal (Menge & Sutherland 1987; Bertness & Leonard 1997). However, we find no evidence for a coordinated community-wide shift (Table 1A), nor do the strengths of

interactions vary across habitats along an environmental stress gradient (Table 1B). This may be due to variability in the responses of species to environmental stressors and the range of interaction types present in diverse assemblages. Communities represent collections of taxa existing within a niche defined by their tolerance limits. Thus, a high intertidal alga that provides shade, for example, will facilitate organisms living at their upper thermal limits (Bruno *et al.* 2003). However, other species will be inhibited by the same modification, or by corresponding reductions in light availability or water flow, and will respond negatively. Taxa from a single trophic group that are engaged in similar types of interactions might be expected to show consistent responses to stressors that are not apparent in other groups of organisms. In fact, most evidence for an environmental stress–species interaction relationship has come from single trophic level studies on plant–plant interactions (Brooker *et al.* 2008). However, our results show that the signs of interactions of all trophic groups are invariant across the stress gradient (Table 1A). Facilitative interactions in general do not become more prevalent across a gradient of increasing heat stress in the rocky intertidal.

There may be other explanations for why facilitation does not generally increase with stress. Our analyses examine whether factors such as environmental stress affect the trend in the sign of the interactions over time. In such time series, the sign of an interaction between a pair of species is rarely constant, and often even alternates directions. This temporal variability may originate from several biotic and abiotic factors. Environmental fluctuations at daily (Foster 2002) to annual (Greenlee & Callaway 1996) time scales can reverse the direction of species interactions. Indirect interactions and ontogenic shifts may also switch interaction signs (Yodzis 1988; Miriti 2006). Our data integrate across these sources of variability and show that over long terms the direction of an interaction cannot be explained by any of the seven factors we tested at the population and community levels.

Species richness

In this study of assemblages with up to 62 taxa, richness is unrelated to interaction sign and strength. However, the prevalence of weak links (Fig. 2) may be obscuring patterns between richness and stronger associations at the community level, since weak interactions, close to zero, tend to be more variable and therefore difficult to predict (Berlow 1999). To address the possibility that richness and the six other explanatory variables predict the magnitude and direction of a subset of the strongest effects, we repeated the two analyses described earlier, using the sign or strength of the strongest 50% of the pairwise interactions from each sampling period ($\overline{\text{DI}}_{ij,p}$) as the response. The results of the

analyses were qualitatively identical to those reported using all pairwise interactions between the focal and target species (Table 1). The sign of even the strongest half of the effects is independent of species richness and the other easily measured attributes of assemblages and organisms. However, the results also suggest that simpler experiments, using less speciose habitats or subsets of the strongest interactors, instead of the full suite of species, can provide valid insight into the causes of variation in per-capita interaction strength.

Temporal and spatial scales

The strength of our experimental approach is that it is tractable, but a limitation is that direct and indirect effects cannot be distinguished. Theory holds that indirect interactions are slower to manifest and can have large effects (Yodzis 1988), hence interaction strength should increase over time. However, we find no consistent change in per-capita interaction magnitude or direction over time (Table 1), suggesting either that indirect effects are not slower to propagate, or that indirect interactions are similar in strength and sign to direct ones (see also Menge 1997). Empirical research that estimates direct effects independently of indirect ones (e.g. Schmitz 1997) will provide further insight into the associations between the separate and combined measures and serve as a more direct test of many theoretical predictions.

We also find no impact of the size of the experimental unit on the sign or strength of species interactions (Table 1). The plot sizes in our study are not large enough to encompass the variety of habitats necessary to generate spatial segregation that would reduce community-wide per-capita interaction strengths. It does not appear that our study, or previous intertidal experiments on species interactions spanning these local scales and time periods, are dramatically biased by artifacts arising from spatial and temporal extent.

CONCLUSION

The variability and context dependency of species interactions presents one of the greatest challenges to predictions of ecosystem dynamics in response to perturbations (Agrawal *et al.* 2007). Our results highlight important points about the factors regulating the sign and magnitude of interactions. First, per-capita interaction strength increases with size and trophic position, but is relatively insensitive to environmental conditions, such as tidal height or the species richness of the community. This shows that measurable features of organisms provide a more reliable indication of their per-capita impact on other species than the degree of stress by the environment in which they are found.

Although mobile consumers exert stronger impacts on other species at the individual level, population-level effects are equivalent across trophic groups. This suggests that interaction intensity arises out of use of resources such as food or space that show similar allometric relationships. These patterns are a promising sign of future prospects for models of community dynamics rooted in the functional traits of organisms without the need for detailed information on the particulars of the local environment.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 The 30 experiments conducted as part of this study.
Table S2 Parameter estimates from the multilevel models used to test the effects of factors on the sign (A) and strength (B) of species interactions.

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