

Variation in body size drives spatial and temporal variation in lobster–urchin interaction strength

Bartholomew P. DiFiore¹  | Adrian C. Stier^{1,2} 

¹Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California 93106, USA

²Marine Science Institute, University of California Santa Barbara, Santa Barbara, California 93116, USA

Correspondence

Bartholomew P. DiFiore
 Email: bdifiore@ucsb.edu

Funding information

California Sea Grant, University of California, San Diego, Grant/Award Number: R/OPCOAH-2; National Science Foundation, Grant/Award Number: NSF OCE 1831937; University of California

Handling Editor: Mariano Rodriguez-Cabal

Abstract

- How strongly predators and prey interact is both notoriously context dependent and difficult to measure. Yet across taxa, interaction strength is strongly related to predator size, prey size and prey density, suggesting that general cross-taxonomic relationships could be used to predict how strongly individual species interact.
- Here, we ask how accurately do general size-scaling relationships predict variation in interaction strength between specific species that vary in size and density across space and time?
- To address this question, we quantified the size and density dependence of the functional response of the California spiny lobster *Panulirus interruptus*, foraging on a key ecosystem engineer, the purple sea urchin *Strongylocentrotus purpuratus*, in experimental mesocosms. Based on these results, we then estimated variation in lobster–urchin interaction strength across five sites and 9 years of observational data. Finally, we compared our experimental estimates to predictions based on general size-scaling relationships from the literature.
- Our results reveal that predator and prey body size has the greatest effect on interaction strength when prey abundance is high. Due to consistently high urchin densities in the field, our simulations suggest that body size—relative to density—accounted for up to 87% of the spatio-temporal variation in interaction strength. However, general size-scaling relationships failed to predict the magnitude of interactions between lobster and urchin; even the best prediction from the literature was, on average, an order of magnitude (+18.7x) different than our experimental predictions.
- Harvest and climate change are driving reductions in the average body size of many marine species. Anticipating how reductions in body size will alter species interactions is critical to managing marine systems in an ecosystem context. Our results highlight the extent to which differences in size-frequency distributions can drive dramatic variation in the strength of interactions across narrow spatial and temporal scales. Furthermore, our work suggests that species-specific estimates for the scaling of interaction strength with body size, rather than general

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](#) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2023 The Authors. *Journal of Animal Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

size-scaling relationships, are necessary to quantitatively predict how reductions in body size will alter interaction strengths.

KEY WORDS

Bayesian statistics, functional response, interaction strength, kelp forest, lobster, sea urchin

1 | INTRODUCTION

The complexity and context dependency of species interactions has led numerous ecologists to argue that prediction in community ecology is impossible (Lawton, 1999). Yet, across species from widely different taxonomic groups there is considerable evidence for general patterns relating individual traits, like body size, to the strength of species interactions (Brown et al., 2004). For instance, recent syntheses of empirical work demonstrate that across taxa, how much predators consume at a given prey density—one measure of interaction strength (Berlow et al., 2004)—is strongly correlated with predator and prey size (Rall et al., 2012; Uiterwaal & DeLong, 2020). Yet despite the strength of general size-scaling relationships, it is unclear how accurately these relationships predict interactions between specific species, and if these predictions might disentangle complexity in community ecology (e.g. Poisot et al., 2015). In this paper, we present a case study testing if general cross-taxonomic patterns relating interaction strength with predator and prey body size predict how strongly a focal predator-prey pair interact. Understanding if general size-scaling relationships can be used to predict interactions between focal species would be powerful, particularly for species of management or conservation concern, whose large size, rarity or highly migratory behaviour make empirical estimates of interactions challenging (Geary et al., 2020).

Ontogenetic increases in body size can drive variation in the strength of interactions (Persson et al., 1998). As an individual predator grows, the amount, size and species of prey it consumes changes (Barnes et al., 2010; De Roos et al., 2003; Werner & Gilliam, 1984). Likewise, as an individual prey grows, its risk of predation can decrease as it outgrows a predator's gape (Urban, 2007), improves predator evasion (Martin et al., 2021) or develops defences such as spines (Laforsch & Tollrian, 2004). Such changes in feeding behaviour or defensive capacity as individual predators and prey grow through ontogeny can drive variation in interaction strength (Brose, 2010). This same phenomenon may extend to the scale of the community. Even if different communities have the same number of predator and prey individuals, differences in the distribution of biomass across size classes may cause differences in how strongly predator and prey interact across space or time. For instance, communities with larger predators and smaller prey could have stronger interactions, while communities with smaller predators and larger prey may have weaker interactions (Figure 1). A considerable body of prior work has quantified the effects of body size on consumption rates under controlled conditions (Brose et al., 2017; Uiterwaal & DeLong, 2020 for reviews). A next step in this field is to pair similar controlled experiments with observational data in order

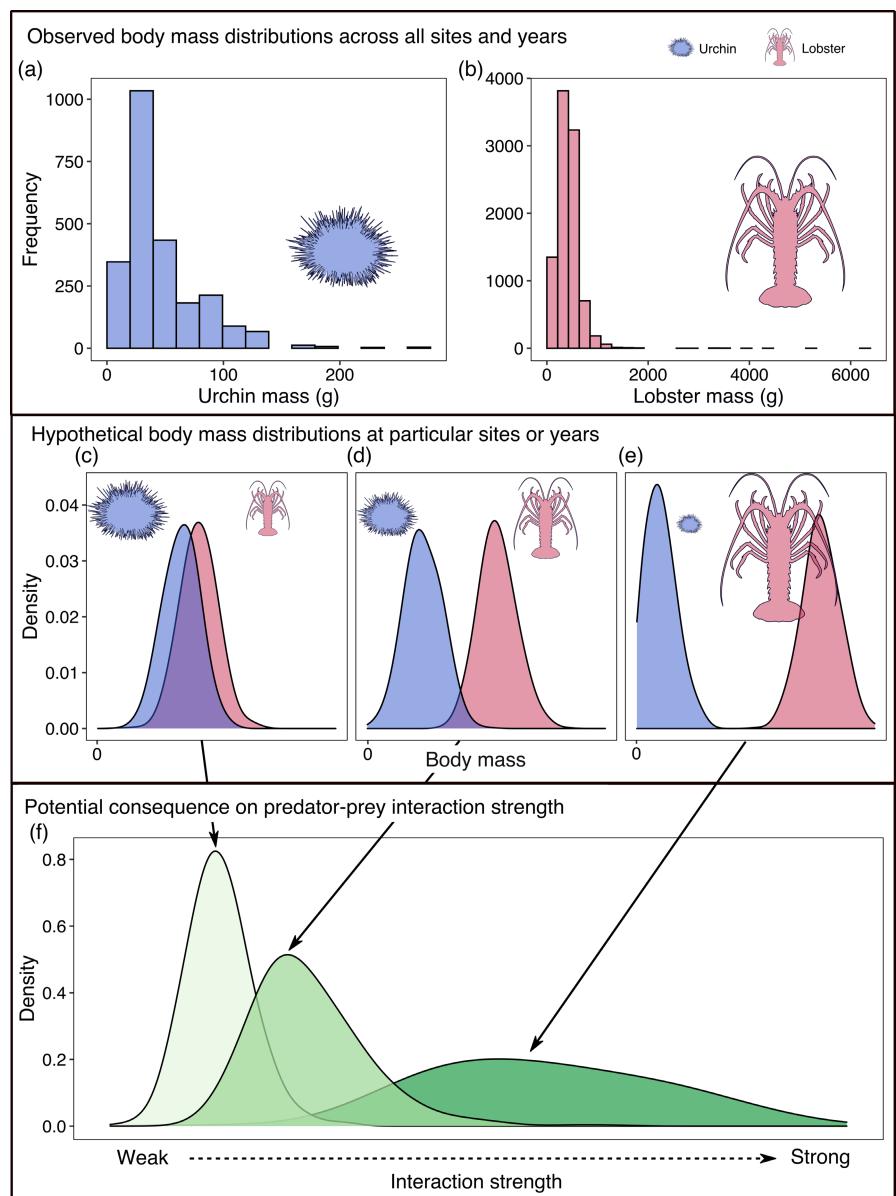
to understand how differences in the size structure of populations drives when and where predators interact strongly with their prey.

Across taxa, interaction strength tends to—on average—increase with predator size (Rall et al., 2012; Uiterwaal & DeLong, 2020), suggesting it may be possible to predict how strongly specific species interact knowing only the size and density of individuals. Indeed, previous work has widely relied on theoretical scaling exponents based on metabolic arguments (e.g. Brown et al., 2004) as a null expectation to estimate interaction strength (Berlow et al., 2009; Petchey et al., 2008; Yodzis & Innes, 1992). Adopting a similar approach based on empirical size-scaling relationships could offer a simple means of making quantitative predictions of interaction strength without in-depth experimentation. However, there is considerable noise around the mean trend in general size-scaling relationships due to differences in taxonomy (Rall et al., 2012), temperature (Englund et al., 2011), habitat dimensionality (Barrios-O'Neill et al., 2016; Pawar et al., 2012) and foraging mode (Barrios-O'Neill et al., 2019). Therefore, it is likely that for a given species pair, the relationship between body size and interaction strength differs from the mean trend across species. Yet understanding how far species pairs deviate from the mean trend will determine the utility of naively applying general size-scaling relationships.

Here, we explore the size dependence of interaction strength for two economically and ecologically important species: the California spiny lobster *Panulirus interruptus* (hereafter 'lobster')—a predator, and the purple sea urchin *Strongylocentrotus purpuratus* (hereafter 'urchin')—a prey. Understanding when and where lobster impact urchin populations is critical because increases in urchin abundance can drive communities to switch from kelp to urchin dominated states (Ling et al., 2015). Previous studies have shown that a high abundance of urchin predators can increase the resistance of kelp communities to urchin-driven phase shifts (Hamilton & Caselle, 2015). Yet, empirical evidence for urchin regulation by lobsters remains equivocal, with some studies finding a strong top-down effect (Lafferty, 2004) and others finding only a weak effect of lobsters (Dunn & Hovel, 2019; Guenther et al., 2012; Malakhoff & Miller, 2021). Previous work on California spiny lobster and other lobster species shows that larger lobster consume more and larger urchins (Ling et al., 2009; Tegner & Levin, 1983), yet the relative role of lobster size, urchin size and urchin density in driving interaction strength remains poorly understood.

In this manuscript, we test the hypothesis that general size-scaling relationships can be used to predict variation in lobster-urchin interactions. To test this hypothesis, we first quantified how the body size and density of lobster and urchins varied across space and through time. We then ask, how does urchin size, lobster size and urchin density alter consumption rates of urchins in

FIGURE 1 Observed body size distributions of a predator (*Panulirus interruptus*—lobster) (a) and their prey (*Strongylocentrotus purpuratus*—urchin) (b) across five sites monitored annually from 2012 to 2020. Different processes such as variation in recruitment, habitat suitability or harvest can cause differences in the size of predators, like lobster, relative to their prey independent of density (c–e). Theory predicts that larger predators will consume more total prey biomass than smaller predators, and that predators tend to consume more small than large prey. Such size-dependent foraging at the scale of the individual could result in large variation in interaction strength at the population-scale at different sites or years (f).



experimental mesocosms? By combining our empirical estimates of consumption rates with long-term observational data, we then disentangle the effects of lobster size, urchin size and urchin density on spatio-temporal variation in interaction strength. Finally, we address the question: how well do general size-scaling relationships predict interaction strength between a specific predator-prey pair across natural variation in body size and density?

2 | MATERIALS AND METHODS

2.1 | How do lobsters and urchins vary in body size and density across space and through time?

We used 9 years of spatially explicit observational data collected by the Santa Barbara coastal long-term ecological research program (SBC LTER) to explore how lobster and urchin density (ind.m^{-2}) and

body size varied across space and time. The SBC LTER collects annual data on the abundance and size distribution of lobsters and urchins at five sites. Briefly, divers count the number of urchins greater than 20 mm in six quadrats uniformly spaced along 40 m transects at each site (three to eight transects per site; Santa Barbara Coastal LTER et al., 2021b). Along a single transect, a diver estimates the test diameter of the first ~50 urchins to the nearest 0.5 cm (Santa Barbara Coastal LTER et al., 2021c). Divers count and estimate the carapace length to the nearest mm of all lobsters in 1200 m^2 plots centred around each transect (Santa Barbara Coastal LTER et al., 2021a).

2.2 | How does lobster predation on urchins vary with lobster size, urchin size and urchin density?

While there are numerous definitions of interaction strength in the literature, here we define interaction strength as a predator's

nonlinear functional response, which describes how consumption rates change as a function of prey density (Berlow et al., 2004 for review). Typically, consumption rates increase with prey density until predator satiation, at which point consumption becomes density independent (Jeschke et al., 2002). The initial increase in consumption approximates the rate that a predator searches space and finds new prey items (i.e. the attack rate), while the predator's maximum consumption rate is limited by the time it takes to manipulate and digest prey (i.e. the handling time) (Holling, 1959). Together, these relationships describe a type II functional response, such that

$$C = \frac{\alpha N}{1 + \alpha h N}, \quad (1)$$

where C is consumption rate, N is the initial density of prey, α is attack rate and h is handling time, or the inverse of a predator's maximum consumption rate ($1/C_{\max}$).

Theory predicts that maximum consumption rates (i.e. $1/h$) scale with consumer body size at the same rate that metabolism scales with body size (Brown et al., 2004; Yodzis & Innes, 1992). Therefore, handling time ($1/C_{\max}$) will decrease with consumer body size according to a negative power-law function ($h \propto m_c^{-\beta}$). A predator's handling time may also be a function of prey size. Larger prey can be more challenging to manipulate or digest resulting in longer handling times (Rall et al., 2012). Together, consumption rates at saturating prey densities are expected to vary according to:

$$\frac{1}{C_{\max}} = h = h_0 m_c^{\beta_{h,c}} m_r^{\beta_{h,r}}, \quad (2)$$

where m_c and m_r are predator and prey mass, respectively, h_0 is a constant, and $\beta_{h,c}$ and $\beta_{h,r}$ are scaling coefficients (Uiterwaal & DeLong, 2020).

Foraging theory and biomechanical arguments also provide expectations for how a predator's attack rate should vary with body size. Larger predators have higher mobility and larger prey are more easily detected (McGill & Mittelbach, 2006). Therefore, attack rates should increase according to power-law functions of predator and prey size, such that

$$\alpha = \alpha_0 m_c^{\beta_{a,c}} m_r^{\beta_{a,r}}, \quad (3)$$

where α_0 is a constant, and $\beta_{a,c}$ and $\beta_{a,r}$ are scaling exponents (Rall et al., 2012; Uiterwaal & DeLong, 2020). Previous work suggests that attack rates increase and then decrease as a function of predator size at a fixed prey size (Kalinkat et al., 2013; Uiterwaal et al., 2017). However, in preliminary analyses we found no evidence for a hump-shaped relationship between attack rates and size (see Supplement 1.1). Therefore, we focus on the power-law scaling relationship (Equation 3).

To determine the size dependence of the lobster functional response, we conducted a factorial experiment where we manipulated urchin density, urchin size and lobster size in mesocosms. The lobsters and urchins used in these experiments spanned the size range

of local populations surveyed by the SBC LTER. We collected all specimen with permission from the California Department of Fish and Wildlife (Scientific Research Permit #13746), and our study did not require ethical approval. We placed a single lobster in an experimental arena, and fed each lobster one of three size classes of urchin at six different densities ($N=2,3,5,10,16,26 \text{ ind.arena}^{-1}$). We selected urchin densities such that the highest density in experimental trials was representative of that in urchin-dominated areas (Rennick et al., 2022). We conducted all foraging trials for 48 h in 200 L arenas. Prior to a trial, we fed lobsters ad libitum for 48 h and then starved the predators for 48 h. For more detail on the specifics of mesocosm experiments refer to [Supplement 2](#).

We then estimated the parameters of the size-dependent functional response using a Bayesian hierarchical model. Specifically, we estimated the number of urchins eaten as a function of the number of urchins offered, lobster size (g), and urchin size (g). We assumed that the number of urchins consumed in trial i by lobster j (C_{ij}) followed a Poisson distribution such that

$$C_{ij} \sim \text{Poisson}(\lambda_{ij}), \quad (4)$$

$$\lambda_{ij} = \frac{\alpha_{ij} N_i}{1 + a_j h_j N_i},$$

$$\log(\alpha_j) = \log(\alpha_0) + \beta_{a,c} \log(m_{c,j}) + \beta_{a,r} \log(m_{r,j}) + \mu_{a,j},$$

$$\log(h_j) = \log(h_0) + \beta_{h,c} \log(m_{c,j}) + \beta_{h,r} \log(m_{r,j}) + \mu_{h,j},$$

where, α_j is the attack rate ($\text{day}^{-1} \text{m}^{-2}$) of lobster j , h_j is the handling time (d) of lobster j and m_j is the average mass of the urchin size class that lobster j foraged on. We constructed informed priors on all β parameters, where the β s were normally distributed with a mean based on theoretical predictions ([Table S1](#)). We assumed gamma distributions for the prior variances. We included a random effect of lobster individual on the estimation of α and h ($\mu_{a,j}, \mu_{h,j}$), assuming that errors between individuals were normally distributed with mean 0.

We implemented the model in Stan (Stan Development Team, 2022) which uses a Hamiltonian Monte Carlo procedure to estimate parameters. We ran three chains for 25,000 iterations with a burn-in of 12,500 iterations and thinned the chains to retain every third iteration. To diagnose model convergence, we visually assessed mixing of the model chains and confirmed using the Gelman–Rubin convergence diagnostic ($\hat{R} < 1.1$) (Brooks & Gelman, 1998). For more details on our modelling approach see [Supplement 1.2](#).

2.3 | How might lobster–urchin interaction strength have varied across space and through time?

To generate plausible estimates for how strongly lobsters and urchins interact under natural conditions, we combined the observational data with our experimentally parameterized functional response. We assumed that interactions were random at a site in

a particular year, such that (1) any lobster could interact with any urchin and (2) lobster and urchin density was homogenous across a site. Specifically, we resampled with replacement 1000 individual body masses from the size distributions of lobsters and urchins at each site/year and estimated the interaction strength (IS) between predator i and prey j as

$$IS_{ij} = \frac{\alpha_0 m_c^{\beta_{ac}} m_r^{\beta_{ar}} NP}{1 + \alpha_0 m_c^{\beta_{ac}} m_r^{\beta_{ar}} h_0 m_c^{\beta_{hc}} m_r^{\beta_{hr}} N}, \quad (5)$$

where N and P are the density of urchins and lobsters, respectively, averaged across transects at a site in a particular year, and m_x is the mass of lobster (c) and urchin (r) individuals in a particular draw from the size distribution. For simplicity, we set all parameters (α_0, h_0, β_x) as the median posterior estimate from the Bayesian model. Based on this procedure, IS represents a distribution of plausible interactions between lobster and urchin individuals at each site and year.

2.4 | Disentangling the effects of body size and density as drivers of variation in interaction strength

Many empirical studies of interaction strength focus on predator and prey density (Berlow et al., 1999; Novak et al., 2016 for reviews). However, estimating interaction strengths based on density alone may be inaccurate, particularly for species that experience nonlinear, indeterminate growth, like many marine species where a single large individual has the same mass as many smaller, younger individuals. Recent work highlights the importance of accounting for size-dependent consumption rates in estimating interaction strength (Atkins et al., 2015). But it is unclear how much of the variation in interaction strength would be missed by estimating interactions based solely on density.

To partition the amount of variation in interaction strength due to differences in body size versus density we used a simulation procedure. From Equation 5, it follows that there is an interaction between body size and density, such that at low urchin densities consumption rates will be determined by the size dependence of lobster attack rates, while at high urchin densities consumption rates will be determined by the size dependence of lobster handling times. To partition variance, we therefore compared the total variation in estimated interaction strengths accounting for variation in both density and body size to simulations where density varied at fixed values of lobster and urchin body size. We iterated this procedure across 625 different values of lobster size and urchin size such that sizes ranged from the maximum lobster mass and minimum urchin mass to the maximum urchin mass and minimum lobster mass. For each iteration, we estimated the proportion of variation due to differences in density as the correlation coefficient (R^2) of the simple linear regression between the estimated interaction strengths when both body size and density vary to the estimated interaction strengths when density varied at a fixed combination of body sizes. Considering the only sources of uncertainty in our estimates were body size and density,

we estimated the proportion of variation due to body size as $1 - R^2$ for each iteration and report the full range of values (see Supplement 3.3 for further details).

2.5 | How well can general size-scaling relationships predict species-specific interactions?

Resolving how accurately a given predator's consumption rate can be predicted from general size-scaling relationships and their covariates is at the crux of integrating our theoretical and experimental depth of knowledge about the size dependence of predator-prey interactions into ecosystem-based management practices. To determine how well general size-scaling relationships predict lobster-urchin interactions, we compared our experimental predictions with estimates from three published size-scaling relationships. Based on previous work demonstrating that both traits and taxonomy are important for predicting how strongly species interact (Rall et al., 2011), we hypothesized that size-scaling relationships from the literature would more precisely match our experimental predictions as they increased in taxonomic specificity. Therefore, we predicted how strongly lobsters and urchins interact based on a general cross-taxonomic estimate (Uiterwaal & DeLong, 2020), an estimate for marine invertebrates (Rall et al., 2012), and an estimate for active marine crustaceans foraging on static prey (Barrios-O'Neill et al., 2019; Table S2). Each of these previous analyses included covariates such as temperature, arena size or habitat dimensionality in their models of attack rates or handling times (Table S2). Therefore, we included these covariates when generating the predictions and fixed their values at the observed values in our mesocosm experiments (see Supplement 3.4 for more details). We converted the units of our observational variables (body size and density) into the units used in each previous study respectively, and then back converted all predicted values of interaction strength into urchins consumed per m^2 per day in order to compare with our experimental predictions. All analyses were implemented in R 4.0.4 (R Core Team, 2021).

3 | RESULTS

3.1 | Size-frequency distributions of lobsters relative to urchins varied widely in space and time

Lobster size ranged more than three orders of magnitude from 6.2 to 6184.0 g (393.6 [88.8–897.8] g, \bar{X} [95% CI] unless otherwise specified), while urchin mass was on average 39.2 [8.1–132.2] g (Figure 1a). The relative difference in body mass between lobsters and urchins changed from site to site and year to year with some sites at a particular time having relatively large lobsters and small urchins, while others had relatively small lobsters and large urchins (Figure S1). The average urchin density was 6.5 [0.8–27.8] ind. m^{-2} , while the average lobster density was 0.03 [0.004–0.097] ind. m^{-2} .

3.2 | Interaction strength between lobsters and urchins increased with urchin density and lobster size but decreased with urchin size

In mesocosm experiments, the consumption rate of urchins by lobster increased with urchin density and lobster size, and decreased as urchin size increased (Figure 2, Figure S2). Only the largest lobsters regularly consumed the largest urchins. For example, lobsters smaller than the median body size only consumed two individual large urchins across all feeding trials. However, all size classes of lobster consumed small urchins, and maximum consumption rates were highest for the largest lobsters preying on the smallest urchins. We found no evidence for variation in attack rates with lobster size or urchin size (Figure 3a, $\beta_{a,c}=0.050[-0.12$ to $0.41]$, $\beta_{a,r}=0.093[-0.15$ to $0.45]$). However, handling time decreased with lobster size and increased with urchin size (Figure 3b, $\beta_{h,c}=-1.61[-2.16$ to $-1.02]$, $\beta_{h,r}=1.30[1.03$ to $1.64]$). Despite the inclusion of informative priors, the posterior estimates for the scaling exponents differed from first principal expectations (Figure S3, Tables S1 and S3). Handling time decreased at a faster rate than expected with lobster size (e.g. $\beta_{h,c}$) and at a higher rate than expected with urchin size (e.g. $\beta_{h,r}$).

3.3 | How might lobster–urchin interaction strength have varied across space and through time?

By integrating our experimental model with long-term data on lobster and urchin body sizes and densities, we generated

plausible estimates for historic interaction strengths. We found that the inferred interaction strength between lobsters and urchins varied considerably across narrow spatial and temporal scales (0.01 [0.0004–0.08] $\text{ind.m}^{-2} \text{ day}^{-1}$, Figure 4). The variation in interaction strength between sites ($\text{CV}_{\text{spatial}}=1.21\pm 0.4$, $X\pm 1 \text{ SD}$) was similar to the variation between years ($\text{CV}_{\text{temporal}}=1.13\pm 0.1$).

3.4 | Variation in lobster–urchin interaction strength is caused by asymmetries in lobster and urchin body size rather than urchin density

Considering the extent of variation in inferred interaction strength across space and time, we tested how much of this variation could be attributed to differences in lobster–urchin body sizes versus densities. We found that body size accounted for the majority of the variation in inferred interaction strength (75%–87%) compared to variation in density (Figure 5a). To better understand the implication of body size accounting for the majority of variation, we generated a hypothetical community of lobster and urchins. We then used our experimental estimate of the size-dependent functional response to simulate a 10-fold increase in mean urchin density with no change in lobster or urchin size distributions relative to a 10-fold increase in mean lobster size with no change in the density of urchins or lobsters (Figure 5b). The increase in lobster body size resulted in a 230% increase in the median interaction strength, whereas the increase in urchin density resulted in only a 38% increase in interaction strength. In our estimates of interaction strength based on

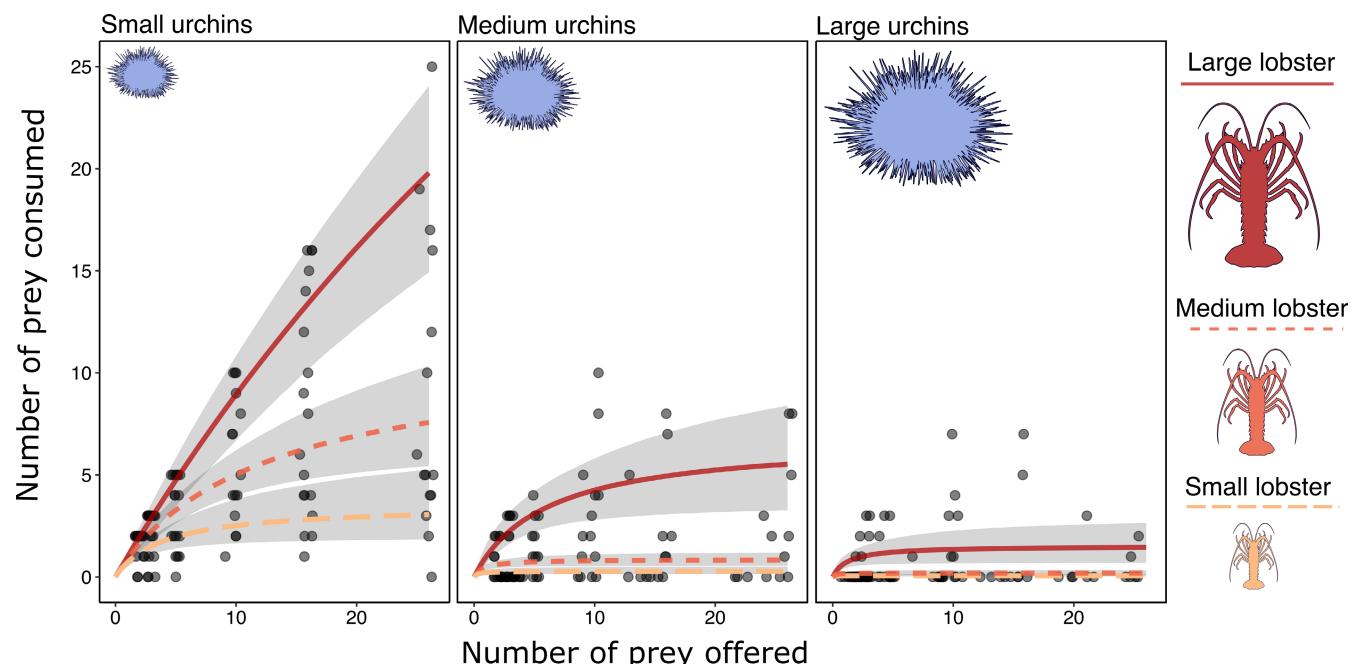


FIGURE 2 Purple sea urchin *Strongylocentrotus purpuratus* consumption rates by California spiny lobster *Panulirus interruptus* predators in mesocosm foraging trials. Individual lobsters ($n=45$) foraged on a single urchin class at six different urchin abundances. Lines are posterior predictions ($\bar{X} [95\% \text{ CI}]$) from a Bayesian model for the body size dependent functional response. Prediction is for hypothetical lobsters with body mass set to the 10th percentile, mean, and 90th percentile (e.g. small, medium, large) of the size distribution of lobster used in the experiment.

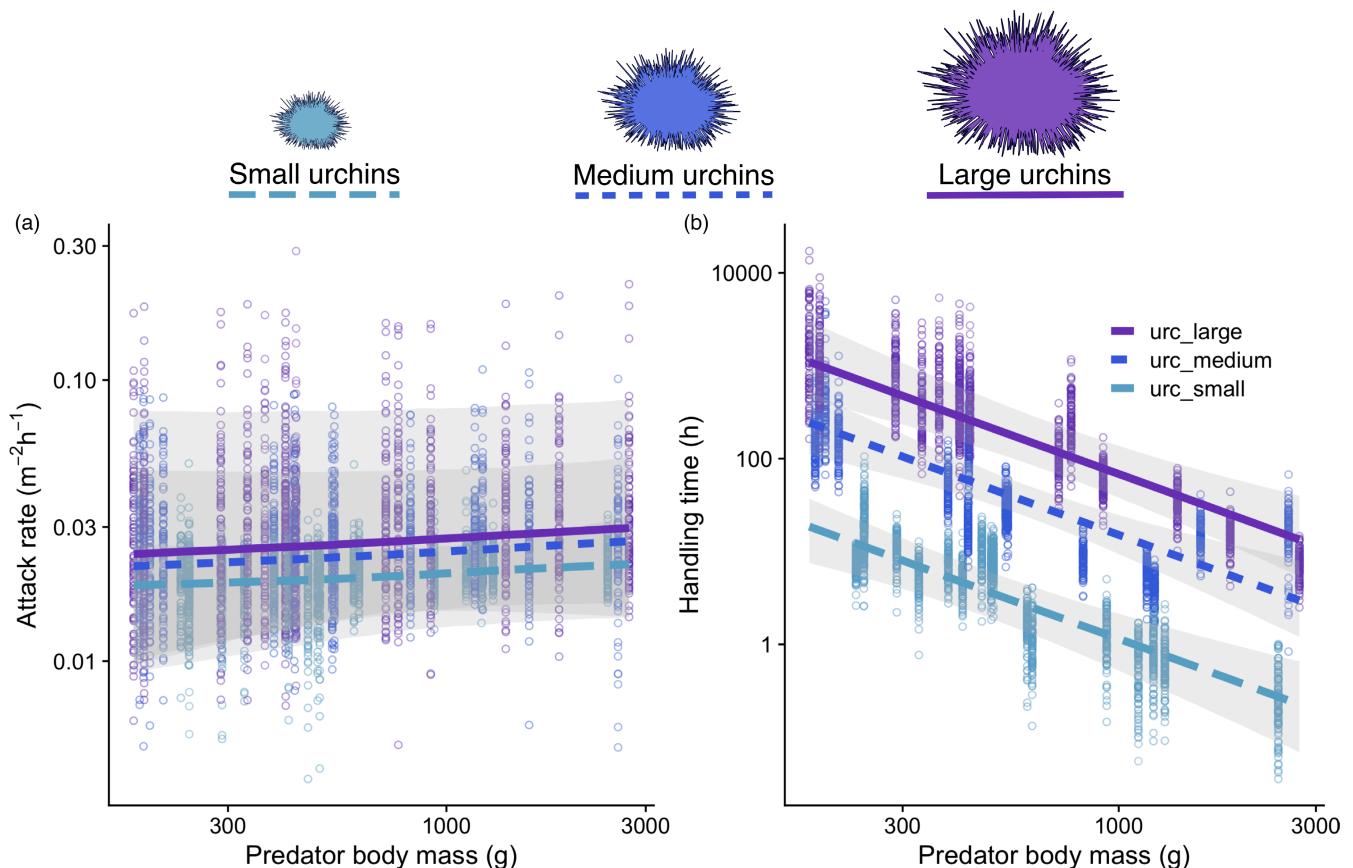


FIGURE 3 Body size scaling of the attack rate (a) and handling time (b) parameters of the functional response of California spiny lobster *Panulirus interruptus* foraging on purple urchins *Strongylocentrotus purpuratus*. Lines are posterior predictions (\bar{X} [95% CI]) for the body size scaling of each parameter according to power-law functions of predator and prey mass (see Section 2 for details). Data points are 100 sampled draws from the posterior distributions of α and h for each individual predator foraging on a particular prey size class using a Bayesian hierarchical model. Note the \log_{10} transformations of both axes.

the field data, communities characterized by large lobsters relative to urchin size and high urchin density displayed the highest interaction strength, while interaction strength in communities with small lobsters relative to urchins and low urchin density approached zero (Figure S4). Across all sites and years, lobster–urchin interactions were log-distributed with far more weak than strong interactions (Figure 5a,c).

3.5 | General size-scaling relationships failed to quantitatively predict lobster–urchin interactions

In general, size-scaling relationships from the literature provided similar rank order predictions for which sites or years displayed the strongest or the weakest interactions compared to our experimental estimates (Figure S5, Spearman's rank order correlation test, $p < 0.001$). However, published size-scaling relationships failed to estimate the magnitude of inferred interactions between lobster and urchin. The closest prediction from the literature to the average of our experimental prediction was for active crustacean predators foraging on static prey (Barrios-O'Neill et al., 2019). However, the average of this prediction was still 18.7 times greater than the interaction

strength estimated by our experimental model (Figure 5c, Figure S6). Furthermore, there was only a 15.6% overlap between the distribution of our experimental prediction and the distribution of the closest prediction from the literature. The precision of the predictions increased as the taxonomic specificity increased. The average of the cross-taxa estimate (Uiterwaal & DeLong, 2020) was five orders of magnitude lower than the experimental average, while the average estimate for marine invertebrates (Rall et al., 2012) was ~100 times less than the experimental average. The estimate for active marine crustacean predators performed the best.

4 | DISCUSSION

Understanding when and where predators will interact strongly with prey is critical to disentangling context dependency in trophic ecology, and can offer insight into the repercussions of disproportionate harvesting of species at the top of the food chain. Spatial and temporal heterogeneity in predator and prey size distributions driven by demographic variation (De Roos et al., 2003), spatially explicit size-structured harvest (Kay et al., 2012) and size-structured predation (Rudolf, 2008) may underlie much of the

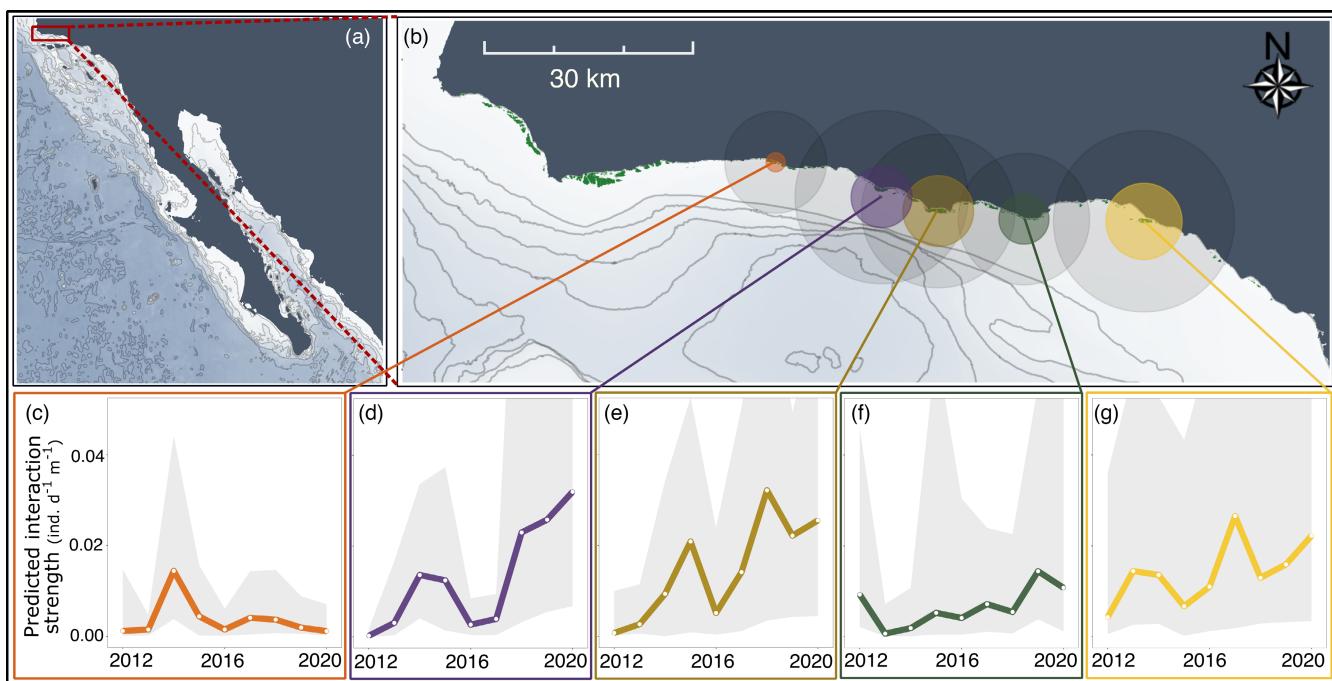


FIGURE 4 Predicted interaction strength between California spiny lobster *Panulirus interruptus* predators and purple sea urchin *Strongylocentrotus purpuratus* prey at five sites in the Santa Barbara Channel, USA from 2012 to 2020 (a, b). Points and surrounding greyscale circles represent the median and upper 95% CI of interaction strength simulated for historic observations of lobster and urchin size distributions and densities using a body size-dependent functional response parameterized from mesocosm foraging experiments. Inset plots (c–g) are the median interaction strength through time at each site. Green polygons along coastline are the historic extent of giant kelp forests estimated via satellite imagery (Santa Barbara Coastal LTER et al., 2022).

context dependency. Our findings demonstrate that body size is a strong determinant of lobster–urchin interactions in experimental trials and suggest that natural- and human-induced variation in body size in the field may be a powerful driver of interaction strength between lobsters and urchins. Our results provide insight into when and where we expect lobsters to play a dominant predatory role, and suggest that harvest-induced reductions in lobster size may have significant ecological consequences in kelp forest ecosystems.

4.1 | Body size drives variation in the role of lobsters in the kelp forest

The hypothesis that lobsters control urchin populations is contested, with some research finding evidence for predator-induced declines in urchins (Ling et al., 2009) and other research finding no evidence at all (Malakhoff & Miller, 2021). Our results suggest two scenarios when lobsters could potentially impact urchin populations, thereby potentially buffering macroalgae resources. We found that interaction strength is greatest when urchin density is high, lobsters are large, and urchins are small. In marine protected areas where lobsters are protected from fishing, lobster size and density are greater than in fished areas (Kay et al., 2012; Peters et al., 2019). With a relatively high density of large lobsters our results suggest that there could be substantial predation pressure on urchins, which is consistent

with recent modelling work that highlights the importance of size-selective predation on the recovery of kelp communities under different management strategies (Dunn et al., 2021). Alternatively, our foraging trials demonstrate that even small lobsters can be effective predators of small urchins. Purple urchins can recruit in large numbers to reefs if environmental and biological conditions allow (Okamoto et al., 2020). High densities of lobsters, even if small, may provide a bottleneck of mortality for small urchin recruits, effectively reducing the capacity of the urchin population to consume kelp (e.g. Rennick et al., 2022). However, strong interactions at one point in time could lead to weak interactions in the future as urchins grow large enough to experience reduced predation. Accounting for dynamic interactions between density and size structure can lead to counterintuitive predictions, such as increases in total prey biomass even when predator induced mortality increases (Schröder et al., 2009). Therefore, to understand the long-term dynamics of lobster–urchin interactions a critical next step is to explicitly model the dynamics of size-structured communities.

4.2 | Body size—Not density—Accounts for the majority of variation in interaction strength

Empirical research on predator–prey interactions has historically focused on estimating interaction strength based on species abundances (Novak et al., 2016). Typically, interaction strength

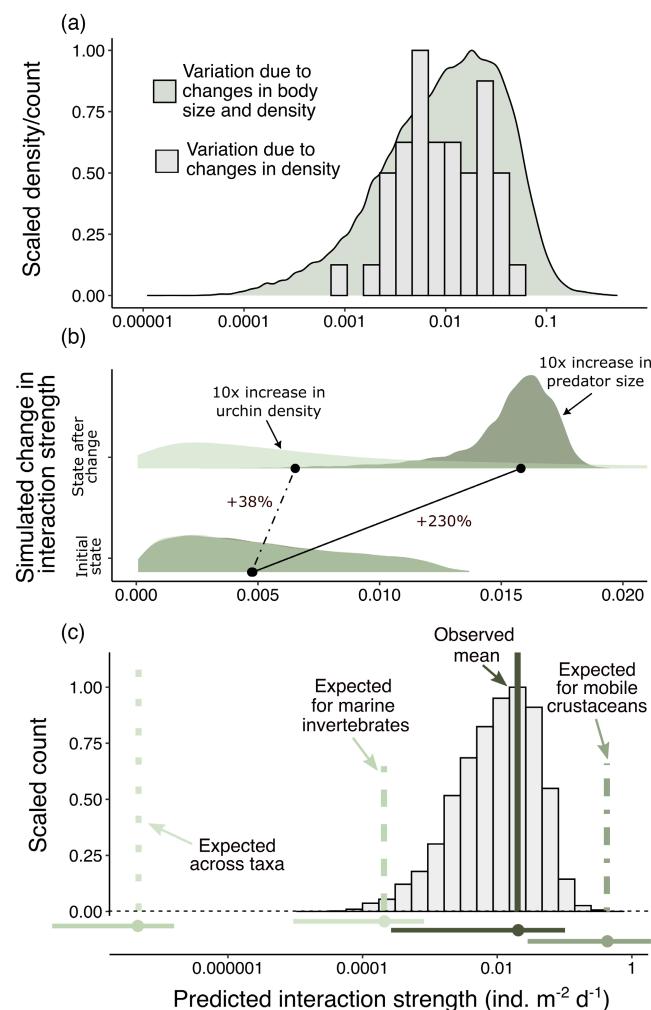


FIGURE 5 (a) Predicted interaction strengths between individual lobster predators *Panulirus interruptus* and their urchin prey *Strongylocentrotus purpuratus* across five sites and 9 years of observational data. Variation in urchin and lobster body size accounted for 82–89% of the total variation in interactions, while variation in density accounted for the remainder. (b) A hypothetical simulation demonstrating the change in interaction strength for a 10-fold increase in urchin density with no change in lobster size compared to a 10-fold increase in lobster body mass with no change in urchin density. In this simulation, interaction strength was estimated using the parameters from the experimental size-scaling relationship for lobster–urchin interactions. (c) Comparison of three estimates of the size scaling of interaction strength from the literature with experimental predictions. Points and intervals at the bottom are mean and 95% CIs of each distribution. Note the \log_{10} transformation on the x-axes in panels (a and c).

is quantified by measuring the abundance of a focal species in the presence or absence of the interacting species (Wootton & Emmerson, 2005). This abundance-based approach implicitly assumes that intraspecific variation in traits has little impact on how strongly populations interact. Yet, there is evidence that intraspecific variation in traits can overshadow interspecific effects (Des Roches et al., 2018). For example, recent work showed that accounting for size-specific differences in consumption rates using

theoretical size-scaling relationships (e.g. $m^{0.75}$) better predicts empirical interaction strength than density or biomass (Atkins et al., 2015).

Our study provides additional support for the critical role of accounting for intraspecific variation in body size in predicting interaction strength by demonstrating that lobster–urchin interactions are determined by their respective size distributions, more so than density. We attributed up to 89% of the variation in inferred interaction strength to variation in body size. One possible reason for this pattern is because lobster maximum consumption rates, not attack rates, were size dependent. As consumption becomes more density independent (e.g. approaches C_{\max}) it becomes more size dependent. Across our observational dataset, urchin densities were high relative to the average maximum consumption rates of lobster at a site. Thus, it was unlikely that lobsters were limited by urchin availability, but rather by lobsters' ability to handle prey—a parameter that is strongly size dependent. Therefore, we speculate that variation in predator and prey body size accounted for the majority of variation in interaction strength because at the observed urchin densities lobsters foraged in a size-dependent, rather than density-dependent, manner.

Together, our results highlight the extent to which focusing on species densities or biomass alone could lead to inaccurate estimates of interactions. Accounting for traits like body size could resolve long-standing debates on the role of predators in regulating prey populations (Poisot et al., 2015) and move debates from the static question of if predators impact prey dynamics, to when and where predators play a strong role in a community.

4.3 | Naïve predictions of interaction strength

Researchers are increasingly focused on implementing ecosystem-based approaches to management (EBM) that account for species interactions, physical forces, social drivers and economic considerations (Long et al., 2015). One challenge to effective implementation of EBM is uncertainty in the strength of species interactions, particularly when system-specific data are limited (Hunsicker et al., 2011). Previous work in food web ecology has utilized theoretical scaling relationships to determine the structure and resilience of ecological networks (Brose et al., 2006; Petchey et al., 2008). Recently, applied ecologists have adapted a similar approach to parameterize stage- or size-structured models, where they assume theoretical size-scaling exponents to estimate interaction strength along with other life-history parameters (Blanchard et al., 2017; see Reum et al., 2019, Spence et al., 2021 for exceptions). These models have led to conceptual advances in the consequences of harvest on populations (Andersen et al., 2009), communities (Andersen et al., 2015; Claessen et al., 2009) or whole ecosystems (Fulton et al., 2011; Heymans et al., 2016). Our results suggest that qualitative predictions for when predators display strong or weak interactions with their prey may be resilient to inaccurate estimates of how consumption varies with body size for particular species. However, our case

study on lobster–urchin interactions suggests that relying on general size-scaling relationships may fail to quantitatively predict the magnitude of trophic interactions between specific species. In other words, naïve estimates may accurately predict the direction and rank order of when and where predators interact strongly with prey but not the magnitude of these interactions. Failing to quantitatively estimate interactions is a critical deficiency in predicting harvest quotas in an EBM framework.

There are two likely reasons for the large discrepancy between our experimental estimates of interaction strength and estimates based on published size-scaling relationships. The first is that the relationship between body size and interaction strength is highly variable across different species and taxa (Rall et al., 2012; Uiterwaal & DeLong, 2020), or even among different functional groups in the marine benthos (Barrios-O'Neill et al., 2019). Here, we focused on the mean trend in the relationship between size and interaction strength from these studies to determine how much information could be borrowed to estimate the interaction strength of particular predator–prey pairs. However, the considerable variation around the mean is certainly a source of imprecision in using cross-species size-scaling relationships to estimate interactions for specific species.

The other likely reason our experimental estimates differed from estimates based on published size-scaling relationships is discrepancies between consumption-size relationships within species pairs compared to across species pairs (Brose et al., 2017). Previous metaanalyses used the average body size of a predator species and the average body size of its prey species to estimate how the functional response varies with body size (Rall et al., 2012; Uiterwaal & DeLong, 2020). However, body size varies among individuals, and consumption is a nonlinear function of body size. Therefore, the consumption rate of the average sized individual will poorly approximate the average consumption rate across variation in body size (Bolnick et al., 2011). While size-scaling relationships generated across the average body size of species may uncover general ecological patterns (White et al., 2019), our results add to a growing body of evidence that general relationships may have little bearing on how a particular predator's consumption rate on a prey changes with ontogenetic growth (Aljetlawi et al., 2004; Uiterwaal et al., 2017). Exploring if there are any general patterns in the consumption–body size relationship within species pairs could improve the utility of using body size to estimate ontogenetic variation in interaction strength in the absence of species-specific data.

5 | CONCLUSIONS

To sustainably harvest and conserve ecosystems, it is critical to predict how strongly predators interact with their prey—a challenging task considering the same species of predator can interact with its prey differently in different spatial or temporal contexts. Here, we used a simulation procedure to infer how strongly lobster and urchin may have interacted across narrow spatial and temporal scales. Our analysis suggests that variation in the body size of predator and prey,

more so than variation in density, accounted for the majority of variation in lobster–urchin interaction strength. Our results highlight the importance of accounting for body size when determining fine-scale variation in interaction strength, as two sites may have the same density of species, but species may interact strongly at one site and not at all at the other depending on variation in individual body size. For lobsters and urchins, species-specific estimates for how consumption changes with body size, rather than general size-scaling relationships, are necessary to sufficiently predict how changes in size drive changes in interaction strength.

Humans are driving reductions in the size of predators (Blanchard et al., 2005; Robinson et al., 2017) through the interactive effects of harvest and warming temperatures (Baudron et al., 2014; Lindmark et al., 2018; Pauly & Cheung, 2018). Such reductions in body size not only alter the economic and cultural value of the target population (Oke et al., 2020), but also lead to shifts in how strongly species interact in communities. Incorporating body size as a means of approximating how strongly species interact will improve ecologists' ability to predict when and where predators have strong effects on prey, a critical step in clarifying the context dependence of trophic interactions and understanding the repercussions of the ongoing losses of large predators.

AUTHOR CONTRIBUTIONS

Bartholomew P. DiFiore and Adrian C. Stier conceived the study. Bartholomew P. DiFiore collected and analysed the data, and wrote the first draft of the manuscript. Both authors contributed equally to revisions.

ACKNOWLEDGEMENTS

We thank Drs. Jameal Samhouri, Dan Reed, Holly Moeller, Ana Miller-ter Kuile and the Ocean Recoveries laboratory group for providing invaluable guidance on previous drafts of this manuscript. We also thank Drs. Erik Ward, Stephen Proulx and Dan Ovando for assistance in developing the Bayesian model. Joseph Curtis and many undergraduate researchers were integral to conducting the mesocosm experiment and maintaining the animals in captivity. Finally, the integration of experimental results with long-term data would not have been possible without the efforts of Clint Nelson, Li Kui and many others involved with the SBC LTER. This work was funded by an NSF Graduate Research Fellowship, a University of California Chancellor's award, the California Sea Grant Prop 84 grant program (R/OPCOAH-2) and the Santa Barbara Coastal Long-Term Ecological Research program (NSF OCE 1831937).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data used in this manuscript are available through the Environmental Data Initiative (EDI) and linked to the Santa Barbara Coastal long-term ecological research (SBC LTER) data catalogue. Lobster size and density data used in this manuscript can be found at

<https://doi.org/10.6073/PASTA/0BCDC7E8B22B8F2C1801085E8CA24D59> (Santa Barbara Coastal LTER et al., 2021a). For urchin size data see <https://doi.org/10.6073/PASTA/FD564DDDFE7B77FE9E4BD8417F166057> (Santa Barbara Coastal LTER et al., 2021b) and urchin density data see <https://doi.org/10.6073/pasta/f1cf070648d7654ada052835afb2cfe9> (Santa Barbara Coastal LTER et al., 2021c). Experimental results of the foraging trials can be found at <https://doi.org/10.6073/pasta/f3878aad622dfe9b05a7d0e75d39bddb> (Santa Barbara Coastal LTER et al., 2023). Code to source data files directly from EDI, analyse the data and generate figures is archived on Zenodo at <https://doi.org/10.5281/zenodo.7737746> (DiFiore & Stier, 2023).

ORCID

Bartholomew P. DiFiore  <https://orcid.org/0000-0002-9778-5371>
Adrian C. Stier  <https://orcid.org/0000-0002-4704-4145>

REFERENCES

- Aljetlawi, A. A., Sparrevik, E., & Leonardsson, K. (2004). Prey-predator size-dependent functional response: Derivation and rescaling to the real world. *Journal of Animal Ecology*, 73(2), 239–252. <https://doi.org/10.1111/j.0021-8790.2004.00800.x>
- Ander sen, K. H., Farnsworth, K. D., Pedersen, M., Gislason, H., & Beyer, J. E. (2009). How community ecology links natural mortality, growth, and production of fish populations. *ICES Journal of Marine Science*, 66(9), 1978–1984. <https://doi.org/10.1093/icesjms/fsp161>
- Ander sen, K. H., Jacobsen, N. S., & Farnsworth, K. D. (2015). The theoretical foundations for size spectrum models of fish communities. *Canadian Journal of Fisheries and Aquatic Sciences*, 73(4), 575–588. <https://doi.org/10.1139/cjfas-2015-0230>
- Atkins, R. L., Griffin, J. N., Angelini, C., O'Connor, M. I., & Silliman, B. R. (2015). Consumer-plant interaction strength: Importance of body size, density and metabolic biomass. *Oikos*, 124(10), 1274–1281. <https://doi.org/10.1111/oik.01966>
- Barnes, C., Maxwell, D., Reuman, D. C., & Jennings, S. (2010). Global patterns in predator-prey size relationships reveal size dependency of trophic transfer efficiency. *Ecology*, 91(1), 222–232. <https://doi.org/10.1890/08-2061.1>
- Barrios-O'Neill, D., Kelly, R., Dick, J. T. A., Ricciardi, A., MacIsaac, H. J., & Emmerson, M. C. (2016). On the context-dependent scaling of consumer feeding rates. *Ecology Letters*, 19(6), 668–678. <https://doi.org/10.1111/ele.12605>
- Barrios-O'Neill, D., Kelly, R., & Emmerson, M. C. (2019). Biomass encounter rates limit the size scaling of feeding interactions. *Ecology Letters*, 22(11), 1870–1878. <https://doi.org/10.1111/ele.13380>
- Baudron, A. R., Needle, C. L., Rijnsdorp, A. D., & Marshall, C. T. (2014). Warming temperatures and smaller body sizes: Synchronous changes in growth of North Sea fishes. *Global Change Biology*, 20(4), 1023–1031. <https://doi.org/10.1111/gcb.12514>
- Berlow, E. L., Dunne, J. A., Martinez, N. D., Stark, P. B., Williams, R. J., & Brose, U. (2009). Simple prediction of interaction strengths in complex food webs. *Proceedings of the National Academy of Sciences of the United States of America*, 106(1), 187–191. <https://doi.org/10.1073/pnas.0806823106>
- Berlow, E. L., Navarrete, S. A., Briggs, C. J., Power, M. E., & Menge, B. A. (1999). Quantifying variation in the strengths of species interactions. *Ecology*, 80(7), 2206–2224. [https://doi.org/10.1890/0012-9658\(1999\)080\[2206:QVITS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[2206:QVITS]2.0.CO;2)
- Berlow, E. L., Neutel, A.-M., Cohen, J. E., Ruiter, P. C. D., Ebenman, B., Emmerson, M., Fox, J. W., Jansen, V. A. A., Jones, J. I., Kokkoris, G. D., Logofet, D. O., McKane, A. J., Montoya, J. M., & Petchey, O. (2004). Interaction strengths in food webs: Issues and opportunities. *Journal of Animal Ecology*, 73(3), 585–598. <https://doi.org/10.1111/j.0021-8790.2004.00833.x>
- Blanchard, J. L., Henehan, R. F., Everett, J. D., Trebilco, R., & Richardson, A. J. (2017). From bacteria to whales: Using functional size spectra to model marine ecosystems. *Trends in Ecology & Evolution*, 32(3), 174–186. <https://doi.org/10.1016/j.tree.2016.12.003>
- Blanchard, J. L., Mills, C., Jennings, S., Fox, C. J., Rackham, B. D., Eastwood, P. D., & O'Brien, C. M. (2005). Distribution abundance relationships for North Sea Atlantic cod (*Gadus morhua*): Observation versus theory. *Canadian Journal of Fisheries and Aquatic Sciences*, 62(9), 2001–2009. <https://doi.org/10.1139/f05-109>
- Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., Rudolf, V. H. W., Schreiber, S. J., Urban, M. C., & Vasseur, D. A. (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, 26(4), 183–192. <https://doi.org/10.1016/j.tree.2011.01.009>
- Brooks, S. P., & Gelman, A. (1998). General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, 7(4), 434–455. <https://doi.org/10.1080/1061600.1998.10474787>
- Brose, U. (2010). Body-mass constraints on foraging behaviour determine population and food-web dynamics. *Functional Ecology*, 24(1), 28–34. <https://doi.org/10.1111/j.1365-2435.2009.01618.x>
- Brose, U., Blanchard, J. L., Eklöf, A., Galiana, N., Hartvig, M., Hirt, M. R., Kalinkat, G., Nordström, M. C., O'Gorman, E. J., Rall, B. C., Schneider, F. D., Thébaud, E., & Jacob, U. (2017). Predicting the consequences of species loss using size-structured biodiversity approaches. *Biological Reviews*, 92(2), 684–697. <https://doi.org/10.1111/brv.12250>
- Brose, U., Williams, R. J., & Martinez, N. D. (2006). Allometric scaling enhances stability in complex food webs. *Ecology Letters*, 9(11), 1228–1236. <https://doi.org/10.1111/j.1461-0248.2006.00978.x>
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85(7), 1771–1789. <https://doi.org/10.1890/03-9000>
- Claessen, D., de Vos, A. S., & de Roos, A. M. (2009). Bioenergetics, overcompensation, and the source-sink status of marine reserves. *Canadian Journal of Fisheries and Aquatic Sciences*, 66(7), 1059–1071. <https://doi.org/10.1139/F09-061>
- De Roos, A. M., Persson, L., & McCauley, E. (2003). The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. *Ecology Letters*, 6(5), 473–487. <https://doi.org/10.1046/j.1461-0248.2003.00458.x>
- Des Roches, S., Post, D. M., Turley, N. E., Bailey, J. K., Hendry, A. P., Kinnison, M. T., Schweitzer, J. A., & Palkovacs, E. P. (2018). The ecological importance of intraspecific variation. *Nature Ecology & Evolution*, 2(1), 57–64. <https://doi.org/10.1038/s41559-017-0402-5>
- DiFiore, B., & Stier, A. (2023). Data from: Variation in body size drives spatial and temporal variation in lobster-urchin interaction strength. *Zenodo Digital Repository*. <https://doi.org/10.5281/zenodo.7737746>
- Dunn, R. P., & Hovel, K. A. (2019). Experiments reveal limited top-down control of key herbivores in southern California kelp forests. *Ecology*, 100(3), e02625. <https://doi.org/10.1002/ecy.2625>
- Dunn, R. P., Samhouri, J. F., & Baskett, M. L. (2021). Transient dynamics during kelp forest recovery from fishing across multiple trophic levels. *Ecological Applications*, 31(6), e2367. <https://doi.org/10.1002/eap.2367>
- Englund, G., Öhlund, G., Hein, C. L., & Diehl, S. (2011). Temperature dependence of the functional response. *Ecology Letters*, 14(9), 914–921. <https://doi.org/10.1111/j.1461-0248.2011.01661.x>
- Fulton, E. A., Link, J. S., Kaplan, I. C., Savina-Rolland, M., Johnson, P., Ainsworth, C., Horne, P., Gorton, R., Gamble, R. J., Smith, A. D. M., & Smith, D. C. (2011). Lessons in modelling and management of marine ecosystems: The Atlantis experience. *Fish and Fisheries*, 12(2), 171–188. <https://doi.org/10.1111/j.1467-2979.2011.00412.x>

- Geary, W. L., Bode, M., Doherty, T. S., Fulton, E. A., Nimmo, D. G., Tulloch, A. I. T., Tulloch, V. J. D., & Ritchie, E. G. (2020). A guide to ecosystem models and their environmental applications. *Nature Ecology & Evolution*, 4(11), 1–13. <https://doi.org/10.1038/s41559-020-01298-8>
- Guenther, C. M., Lenihan, H. S., Grant, L. E., Lopez-Carr, D., & Reed, D. C. (2012). Trophic cascades induced by lobster fishing are not ubiquitous in Southern California kelp forests. *PLoS One*, 7(11), e49396. <https://doi.org/10.1371/journal.pone.0049396>
- Hamilton, S. L., & Caselle, J. E. (2015). Exploitation and recovery of a sea urchin predator has implications for the resilience of southern California kelp forests. *Proceedings of the Royal Society B: Biological Sciences*, 282(1799), 20141817. <https://doi.org/10.1098/rspb.2014.1817>
- Heymans, J. J., Coll, M., Link, J. S., Mackinson, S., Steenbeek, J., Walters, C., & Christensen, V. (2016). Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. *Ecological Modelling*, 331, 173–184. <https://doi.org/10.1016/j.ecolmodel.2015.12.007>
- Holling, C. S. (1959). Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, 91(7), 385–398. <https://doi.org/10.4039/Ent91385-7>
- Hunsicker, M. E., Ciannelli, L., Bailey, K. M., Buckel, J. A., White, J. W., Link, J. S., Essington, T. E., Gaichas, S., Anderson, T. W., Brodeur, R. D., Chan, K.-S., Chen, K., Englund, G., Frank, K. T., Freitas, V., Hixon, M. A., Hurst, T., Johnson, D. W., Kitchell, J. F., ... Zador, S. (2011). Functional responses and scaling in predator-prey interactions of marine fishes: Contemporary issues and emerging concepts. *Ecology Letters*, 14(12), 1288–1299. <https://doi.org/10.1111/j.1461-0248.2011.01696.x>
- Jeschke, J. M., Kopp, M., & Tollrian, R. (2002). Predator functional responses: Discriminating between handling and digesting prey. *Ecological Monographs*, 72(1), 95–112. [https://doi.org/10.1890/0012-9615\(2002\)072\[0095:PFRDBH\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2002)072[0095:PFRDBH]2.0.CO;2)
- Kalinkat, G., Schneider, F. D., Digel, C., Guill, C., Rall, B. C., & Brose, U. (2013). Body masses, functional responses and predator-prey stability. *Ecology Letters*, 16(9), 1126–1134. <https://doi.org/10.1111/ele.12147>
- Kay, M. C., Lenihan, H. S., Guenther, C. M., Wilson, J. R., Miller, C. J., & Shrout, S. W. (2012). Collaborative assessment of California spiny lobster population and fishery responses to a marine reserve network. *Ecological Applications*, 22(1), 322–335. <https://doi.org/10.1890/11-0155.1>
- Lafferty, K. D. (2004). Fishing for lobsters indirectly increases epidemics in sea urchins. *Ecological Applications*, 14(5), 1566–1573. <https://doi.org/10.1890/03-5088>
- Laforsch, C., & Tollrian, R. (2004). Inducible defenses in multipredator environments: Cyclomorphosis in *Daphnia Cucullata*. *Ecology*, 85(8), 2302–2311. <https://doi.org/10.1890/03-0286>
- Lawton, J. H. (1999). Are there general laws in ecology? *Oikos*, 84(2), 177–192. <https://doi.org/10.2307/3546712>
- Landmark, M., Huss, M., Ohlberger, J., & Gårdmark, A. (2018). Temperature-dependent body size effects determine population responses to climate warming. *Ecology Letters*, 21(2), 181–189. <https://doi.org/10.1111/ele.12880>
- Ling, S. D., Johnson, C. R., Frusher, S. D., & Ridgway, K. R. (2009). Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. *Proceedings of the National Academy of Sciences of the United States of America*, 106(52), 22341–22345. <https://doi.org/10.1073/pnas.0907529106>
- Ling, S. D., Scheibling, R. E., Rassweiler, A., Johnson, C. R., Shears, N., Connell, S. D., Salomon, A. K., Norderhaug, K. M., Pérez-Matus, A., Hernández, J. C., Clemente, S., Blamey, L. K., Hereu, B., Ballesteros, E., Sala, E., Garrabou, J., Cebrán, E., Zabala, M., Fujita, D., & Johnson, L. E. (2015). Global regime shift dynamics of catastrophic sea urchin overgrazing. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1659), 20130269. <https://doi.org/10.1098/rstb.2013.0269>
- Long, R. D., Charles, A., & Stephenson, R. L. (2015). Key principles of marine ecosystem-based management. *Marine Policy*, 57, 53–60. <https://doi.org/10.1016/j.marpol.2015.01.013>
- Malakhoff, K. D., & Miller, R. J. (2021). After 15 years, no evidence for trophic cascades in marine protected areas. *Proceedings of the Royal Society B: Biological Sciences*, 288(1945), 20203061. <https://doi.org/10.1098/rspb.2020.3061>
- Martin, B., Gil, M., Fahimipour, A., & Hein, A. (2021). Informational constraints on predator-prey interactions. *Oikos*, 2022(10), e08143. <https://doi.org/10.1111/oik.08143>
- McGill, B. J., & Mittelbach, G. G. (2006). An allometric vision and motion model to predict prey encounter rates. *Evolutionary Ecology Research*, 8, 691–701.
- Novak, M., Yeakel, J. D., Noble, A. E., Doak, D. F., Emmerson, M., Estes, J. A., Jacob, U., Tinker, M. T., & Wootton, J. T. (2016). Characterizing species interactions to understand press perturbations: What is the community matrix? *Annual Review of Ecology, Evolution, and Systematics*, 47(1), 409–432. <https://doi.org/10.1146/annurev-ecolsys-032416-010215>
- Okamoto, D. K., Schroeter, S. C., & Reed, D. C. (2020). Effects of ocean climate on spatiotemporal variation in sea urchin settlement and recruitment. *Limnology and Oceanography*, 65(9), 2076–2091. <https://doi.org/10.1002/lio.11440>
- Oke, K. B., Cunningham, C. J., Westley, P. A. H., Baskett, M. L., Carlson, S. M., Clark, J., Hendry, A. P., Karataev, V. A., Kendall, N. W., Kibebe, J., Kindsvater, H. K., Kobayashi, K. M., Lewis, B., Munch, S., Reynolds, J. D., Vick, G. K., & Palkovacs, E. P. (2020). Recent declines in salmon body size impact ecosystems and fisheries. *Nature Communications*, 11(1), 4155. <https://doi.org/10.1038/s41467-020-17726-z>
- Pauly, D., & Cheung, W. W. L. (2018). Sound physiological knowledge and principles in modeling shrinking of fishes under climate change. *Global Change Biology*, 24(1), e15–e26. <https://doi.org/10.1111/gcb.13831>
- Pawar, S., Dell, A. I., & Savage, V. M. (2012). Dimensionality of consumer search space drives trophic interaction strengths. *Nature*, 486(7404), 485–489. <https://doi.org/10.1038/nature11131>
- Persson, L., Leonardsson, K., de Roos, A. M., Gyllenberg, M., & Christensen, B. (1998). Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model. *Theoretical Population Biology*, 54(3), 270–293. <https://doi.org/10.1006/tpb.1998.1380>
- Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web structure. *Proceedings of the National Academy of Sciences of the United States of America*, 105(11), 4191–4196. <https://doi.org/10.1073/pnas.0710672105>
- Peters, J. R., Reed, D. C., & Burkepile, D. E. (2019). Climate and fishing drive regime shifts in consumer-mediated nutrient cycling in kelp forests. *Global Change Biology*, 25(9), 3179–3192. <https://doi.org/10.1111/gcb.14706>
- Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary through space and time. *Oikos*, 124(3), 243–251. <https://doi.org/10.1111/oik.01719>
- R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rall, B. C., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmüller, F., Vucic-Pestic, O., & Petchey, O. L. (2012). Universal temperature and body-mass scaling of feeding rates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1605), 2923–2934. <https://doi.org/10.1098/rstb.2012.0242>
- Rall, B. C., Kalinkat, G., Ott, D., Vucic-Pestic, O., & Brose, U. (2011). Taxonomic versus allometric constraints on non-linear interaction strengths. *Oikos*, 120(4), 483–492. <https://doi.org/10.1111/j.1600-0706.2010.18860.x>

- Rennick, M., DiFiore, B. P., Curtis, J., Reed, D. C., & Stier, A. C. (2022). Detrital supply suppresses deforestation to maintain healthy kelp forest ecosystems. *Ecology*, 103(5), e3673. <https://doi.org/10.1002/ecy.3673>
- Reum, J. C. P., Blanchard, J. L., Holsman, K. K., Aydin, K., & Punt, A. E. (2019). Species-specific ontogenetic diet shifts attenuate trophic cascades and lengthen food chains in exploited ecosystems. *Oikos*, 128(7), 1051–1064. <https://doi.org/10.1111/oik.05630>
- Robinson, J. P. W., Williams, I. D., Edwards, A. M., McPherson, J., Yeager, L., Vigliola, L., Brainard, R. E., & Baum, J. K. (2017). Fishing degrades size structure of coral reef fish communities. *Global Change Biology*, 23(3), 1009–1022. <https://doi.org/10.1111/gcb.13482>
- Rudolf, V. H. W. (2008). Consequences of size structure in the prey for predator-prey dynamics: The composite functional response. *Journal of Animal Ecology*, 77(3), 520–528. <https://doi.org/10.1111/j.1365-2656.2008.01368.x>
- Santa Barbara Coastal LTER, Bell, T. W., Cavanaugh, K. C., & Siegel, D. A. (2022). SBC LTER: Time series of quarterly NetCDF files of kelp biomass in the canopy from Landsat 5, 7 and 8, since 1984 (ongoing) [data set]. Environmental Data Initiative. <https://doi.org/10.6073/PASTA/3FF5E56EA13C55B474EE2DB6DD6B3DF>
- Santa Barbara Coastal LTER, DiFiore, B., & Stier, A. (2023). SBC LTER: Reef: The size-dependent functional response of lobster foraging on purple urchin ver 1. Environmental Data Initiative. <https://doi.org/10.6073/pasta/f3878aad622dfe9b05a7d0e75d39bdbb>
- Santa Barbara Coastal LTER, Reed, D. C., & Miller, R. J. (2021a). SBC LTER: Reef: Abundance, size and fishing effort for California spiny lobster (*Panulirus interruptus*), ongoing since 2012 [data set]. Environmental Data Initiative. <https://doi.org/10.6073/PASTA/0BCDC7E8B22B8F2C1801085E8CA24D59>
- Santa Barbara Coastal LTER, Reed, D. C., & Miller, R. J. (2021b). SBC LTER: Reef: Annual time series of biomass for kelp forest species, ongoing since 2000 [data set]. Environmental Data Initiative. <https://doi.org/10.6073/PASTA/F1CF070648D7654ADA052835AFB2CFE9>
- Santa Barbara Coastal LTER, Reed, D. C., & Miller, R. J. (2021c). SBC LTER: Reef: Long-term experiment: Kelp removal: Urchin size frequency distribution [data set]. Environmental Data Initiative. <https://doi.org/10.6073/PASTA/FD564DDDDE7B77FE9E4BD8417F166057>
- Schröder, A., Persson, L., & de Roos, A. M. (2009). Culling experiments demonstrate size-class specific biomass increases with mortality. *Proceedings of the National Academy of Sciences of the United States of America*, 106(8), 2671–2676. <https://doi.org/10.1073/pnas.0808279106>
- Spence, M. A., Thorpe, R. B., Blackwell, P. G., Scott, F., Southwell, R., & Blanchard, J. L. (2021). Quantifying uncertainty and dynamical changes in multi-species fishing mortality rates, catches and biomass by combining state-space and size-based multi-species models. *Fish and Fisheries*, 22(4), 667–681. <https://doi.org/10.1111/faf.12543>
- Stan Development Team. (2022). Stan modeling language users guide and reference manual (2.29). <https://mc-stan.org>
- Tegner, M. J., & Levin, L. A. (1983). Spiny lobsters and sea urchins: Analysis of a predator-prey interaction. *Journal of Experimental Marine Biology and Ecology*, 73(2), 125–150. [https://doi.org/10.1016/0022-0981\(83\)90079-5](https://doi.org/10.1016/0022-0981(83)90079-5)
- Uiterwaal, S. F., & DeLong, J. P. (2020). Functional responses are maximized at intermediate temperatures. *Ecology*, 101(4), e02975. <https://doi.org/10.1002/ecy.2975>
- Uiterwaal, S. F., Mares, C., & DeLong, J. P. (2017). Body size, body size ratio, and prey type influence the functional response of damselfly nymphs. *Oecologia*, 185(3), 339–346. <https://doi.org/10.1007/s00442-017-3963-8>
- Urban, M. C. (2007). The growth-predation risk trade-off under a growing gape-limited predation threat. *Ecology*, 88(10), 2587–2597. <https://doi.org/10.1890/06-1946.1>
- Werner, E. E., & Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics*, 15(1), 393–425. <https://doi.org/10.1146/annurev.es.15.110184.002141>
- White, C. R., Marshall, D. J., Alton, L. A., Arnold, P. A., Beaman, J. E., Bywater, C. L., Condon, C., Crispin, T. S., Janetzki, A., Pirtle, E., Winwood-Smith, H. S., Angilletta, M. J., Chenoweth, S. F., Franklin, C. E., Halsey, L. G., Kearney, M. R., Portugal, S. J., & Ortiz-Barrientos, D. (2019). The origin and maintenance of metabolic allometry in animals. *Nature Ecology & Evolution*, 3(4), 598–603. <https://doi.org/10.1038/s41559-019-0839-9>
- Wootton, J. T., & Emmerson, M. (2005). Measurement of interaction strength in nature. *Annual Review of Ecology, Evolution, and Systematics*, 36(1), 419–444. <https://doi.org/10.1146/annurev.ecolsys.36.091704.175535>
- Yodzis, P., & Innes, S. (1992). Body size and consumer-resource dynamics. *The American Naturalist*, 139(6), 1151–1175. <https://doi.org/10.1086/285380>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Summary of prior distributions used to model the body-size dependence of the lobster functional response.

Table S2. Summary of the final model structure, units, and fixed values of covariates used to predict interaction strength based on relationships from the literature.

Table S3. Summary of equations and parameter estimates for the size-scaling of the functional response based on theoretical and empirical sources.

Figure S1. Change in the predator (California spiny lobster) to prey (purple urchin) body mass ratio between sites and years. The mean and variance of the predator:prey ratio varies between sites and years. The predator:prey ratio was estimated by resampling from the size distributions of predators and prey with replacement. The y-axis is \log_{10} transformed for visualization purposes.

Figure S2. The functional responses of individual lobster predators foraging on urchin prey in mesocosms. Lines are median predictions ($\pm 95\%$ CI) from a Bayesian hierarchical model that estimated the number of urchins consumed as a function of lobster body size, prey body size, and prey density. Panels are arranged in descending order of lobster body size within a particular prey size class.

Figure S3. Comparison of posterior and prior predictive distributions for population level parameters from a Bayesian hierarchical model. Priors are informed based on theoretical predictions (see Table S2 for details on each prior).

Figure S4. The median rate of urchins consumed per lobster predator (e.g. per predator interaction strength) as a function of the median predator:prey body mass ratio (top) and urchin density (bottom). Each point represents a site in a particular year. Sites or times with large lobster, small urchins, and high urchin density were estimated to have the strongest interactions.

Figure S5. Rank order of interaction strength estimated via experimentation and three different predictions from the literature for the size-scaling of consumption rates. Site-year combinations are arranged in decreasing order according to the experimental prediction.

Figure S6. Median and 95% CI's of simulated predictions for interaction

strength based on our experimental estimates and estimates of the size-scaling of interaction strength from the literature. UD (Uiterwaal and DeLong 2020), Rall et al. (2012), BO (Barrios-O'Neill et al. 2019), and Experimental match the predictions reported in the main text. However, UD w/uncertainty and Exp. w/uncertainty incorporate uncertainty in the regression coefficients. For experimental estimates, we sampled from the posterior distribution of each parameter, such that each draw in the simulation paired a unique lobster body size, urchin body size, and parameter set. Uiterwaal and Delong report mean \pm SE of the regression parameters. To incorporate uncertainty, we sampled from a uniform distribution, where the bounds were

defined by the 95% CI's of the mean of each parameter. Rall et al. (2012) and Barrios-O'Neill et al. (2019) do not report confidence intervals on their parameter estimates.

How to cite this article: DiFiore, B. P., & Stier, A. C. (2023).

Variation in body size drives spatial and temporal variation in lobster-urchin interaction strength. *Journal of Animal Ecology*, 00, 1–14. <https://doi.org/10.1111/1365-2656.13918>

Variation in body size drives spatial and temporal variation in lobster–urchin interaction strength

Bartholomew P. DiFiore¹, Adrian C. Stier^{1,2}

¹ Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California 93106 USA

²Marine Science Institute, University of California Santa Barbara, Santa Barbara, California 93116, USA

Correspondence e-mail: bdifiore@ucsb.edu

1. Modeling

1.1. Alternative forms for the size-scaling of attack rates

Previous work has shown that attack rates of predators tend to increase with predator body size to a maximum before declining (e.g. a hump shaped relationship) (Aljetlawi et al., 2004; Barrios-O’Neill et al., 2016; Kalinkat et al., 2013; McCoy et al., 2011; Uiterwaal et al., 2017; Vucic-Pestic et al., 2010; Wahlström et al., 2000). We initially explored the data to determine the relationship between attack rate, predator body size, and prey body size. To estimate the parameters of the functional response for each predator (e.g. α and h), we fit a modified version of the Bayesian model described in the main text. Specifically, we fit a type II functional response (Eq. 1) to each individual predator, where α and h for each individual were drawn from prior distributions for the prey size class that the individual was fed nested within the overall population of lobsters. We assumed that the number of prey consumed in trial i (C_i) was binomially distributed given the number of prey offered (N_i) and the proportion of prey consumed (P_i). Thus,

$$C_i \sim \text{Binomial}(N_i, P_i) \quad (\text{Eq. 1})$$

$$P_i = \frac{1}{\alpha_{j,k}^{-1} + h_{j,k} N_i}$$

where, $\alpha_{j,k}$ is the attack rate of lobster j (1,2,...46) in treatment k (1,2,3), and $h_{j,k}$ is the handling time of lobster j in treatment k . The model results provided predictions for the functional response for the overall population of lobsters, the subpopulations of lobsters that foraged on each prey size class, and each individual lobster without assuming any *a priori* relationship between α , h , predator size and prey size.

We then modeled the posterior median estimate of α for each lobster as a function of lobster and urchin body size. Following metanalyses conducted across taxa (Rall et al. 2012, Uiterwaal and Delong et al. 2020), we fit the following equation to the data using multiple linear regression:

$$\log(\alpha_j) = \log(\alpha_0) + \beta_{\alpha,c} \log(m_{c,j}) + \beta_{\alpha,r} \log(m_{r,j}) \quad (\text{Eq. 2})$$

We expected that if α followed a unimodal function of predator mass at a fixed prey mass, then the residuals of the regression would display a hump shaped pattern (*see Barrios-O'Neill et al. 2016 for a similar approach*). However, we found no evidence for a pattern in the residuals. To confirm, we included a polynomial term in the regression equation for predator mass, but AIC comparison suggested that the inclusion of the polynomial term did not improve model fit.

We also tested to see if the size-scaling of α and h was dependent on predator size alone, prey size alone, both predator and prey size, or the ratio of predator and prey size. The best fit models for both parameters based on AIC-comparison were models that included both predator and prey size with independent scaling exponents. Uiterwaal and Delong (2020) found a similar lack of support for body mass ratio-dependence relative to independent effects of predator and prey size.

1.2. Model details

Previous studies that examined allometric scaling of the functional response have either fit the functional response and then explored allometric relationships among the parameters sequentially (e.g. Barrios-O'Neill 2016) or fit the allometric functional response in a single step (e.g. McCoy et al. 2011, Kalinkat et al. 2013). A recent simulation analysis suggests that the most accurate and precise method of fitting the functional response is to fit the multivariate response surface directly (Uszko et al., 2020), which also reduces complications in propagating uncertainty between multiple models. Following our preliminary analysis (*see Supplement 1.1*), we choose to adopt the approach of Uszko et al. (2020) and fit the size-dependent functional response directly to the data using a Bayesian hierarchical approach.

Specifically, we assumed that α and h for each lobster predator was determined by the lobster's mass and the mass of the urchin size class that it was preying on, where error in α and h between individuals was normally distributed. How many urchins a lobster consumed was dependent on urchin density according to a type II functional response, were the number of urchins eaten followed a Poisson distribution. The model sought to estimate the probability of the parameters given the data and the prior distribution.

Hierarchical, nonlinear models can be fit in a maximum likelihood framework (Bolker, 2008; Oddi et al., 2019). However, we chose to utilize Bayesian approaches because they allow for the incorporation of prior information, and offer a more direct means of estimating and interpreting parameter uncertainty in hierarchical models (Bolker, 2008; Ellison, 2004). Considering the widespread adoption of $\frac{3}{4}$ scaling of consumption based on metabolic theory (Brown et al., 2004), a Bayesian approach allowed us to include informative prior distributions based on theoretical constants (Table S2).

Table S1. Summary of prior distributions used to model the body-size dependence of the lobster functional response.

Parameter	Prior
<i>Population-level</i>	
$\log(\alpha_0)$	$normal(0, \sigma)$

$\beta_{\alpha,c}$	<i>normal</i> (0.75, σ)
$\beta_{\alpha,r}$	<i>normal</i> (0.5, σ)
$\log(\alpha_0)$	<i>normal</i> (0, σ)
$\beta_{h,c}$	<i>normal</i> (-0.75, σ)
$\beta_{h,r}$	<i>normal</i> (0.5, σ)
<i>Individual-level</i>	
$\mu_{\alpha,j}$	<i>normal</i> (0, σ^*)
$\mu_{\alpha,j}$	<i>normal</i> (0, σ^*)
<i>Variances</i>	
σ	<i>gamma</i> (1,1)
σ^*	<i>gamma</i> (2,1)

Traditional functional response experiments account for prey depletion using Rodger's random predator equation (Real, 1977). However, we did not account for prey depletion in our analysis because, to our knowledge, there is no practical way to implement Rodger's random predator equation with hierarchical structure (McCoy et al., 2011).

2. Mesocosm experiments

To determine the size-dependence of the lobster functional response, we conducted a response-surface experiment where we manipulated prey density, prey size, and predator size. Trained divers collected lobsters and urchins from kelp forests in the Santa Barbara Channel.

Experimental lobsters ranged in size from 53 – 160 mm carapace length (n = 45). Each lobster was weighed to the nearest gram (range: 196 - 2736 g; see Jerde et al. 2019 for methods). We classified urchins into three size bins (1.0-2.9, 3.0-4.9, 5.0-7.0 cm test diameter; *small*, *medium*, and *large*, respectively). For subsequent analyses, we used the center of each urchin size class to estimate urchin mass according to published test-diameter to length relationships (3.3, 23.9, 76.7 g; Reed et al. 2016). Lobster and urchin sizes used in experiments spanned the range of variation in body size for natural populations based on the observational data (lobsters: 421.3 [88.8 – 897.8] g, urchins: 46.6 [8.1 – 132.2], \bar{X} [95% CI]). Urchins were only collected from sites with kelp present because gonad weight is lower in urchins from barrens and barren urchins are less palatable to predators (Eurich et al., 2014).

In order to determine the relationship between consumption rates, body size, and prey density, we sought to estimate the functional response of each individual lobster. Therefore, we conducted foraging trials in which an individual predator foraged on a single size class of prey at each experimental prey density (n = 6). We assigned predators to size bins (n = 4), and then randomly assigned each predator a prey size class treatment (n = 3), to ensure even replication across the response surface.

We conducted all foraging trials in 400 L laboratory mesocosms with a continuous flow of ambient seawater at \sim 7 L min⁻¹. Each mesocosm was divided into two foraging arenas by a permeable plastic barrier. We haphazardly assigned predators to foraging arenas, where they remained for the duration of the experiment. Each arena contained a half-round PVC shelter, and

three bricks. The area of each mesocosm was 0.52 m². Following capture, we allowed each predator at least three weeks to acclimate to the mesocosms, during which we fed them a mixed diet of urchins and mussels (*Mytilus californianus* or *Mytilus galloprovincialis*) and confirmed that each individual foraged on at least one urchin. Prey were maintained in separate mesocosms, and fed giant kelp fronds and stipes (*Macrocystis pyrifera*) for > 1 week.

To initiate a trial, predators were fed mussels *ad libidum* for 48 hours, followed by a 48-hour starvation period. At the start of the trial, we added a given number of urchins within the predators' assigned prey size class to each arena. Lobsters are nocturnal predators and typically remained sheltered when prey were added to the tanks during the afternoon. We saw no evidence of immediate predation, and urchins moved about the tank freely until nightfall. We allowed predators to forage on prey for 48 hours, after which we counted each remaining prey item to estimate the number of urchins consumed by an individual lobster. No predator consumed all prey in trials with the highest prey density. We conducted trials in consecutive weeks, where predators were randomly assigned a new prey density each week. During the experimental period, ambient water temperatures in the flow-through system were on average $16.1^\circ \pm 1.8$ C ($\bar{X} \pm 1$ SD).

We found evidence of non-predation related urchin mortality during trials. When consuming urchins, lobsters pry their prey from the substrate and crack the test at the vent. By inspecting each urchin for evidence of damage to the test near the vent we discriminated between urchins that died due to predation or natural mortality. We subtracted the number of urchins that experienced non-predation mortality from the total number of urchins available.

3. Simulation

3.1. Estimating predator:prey ratio for observational data

To determine the extent to which lobster and urchin body size varied between sites, we estimated the predator:prey body size ratio for each site in each year. To do this we resampled 1000 draws with replacement from the size-distribution of lobster and urchin at each site/year, and calculated the ratio of individual lobster mass to urchin mass. We then plotted the distributions of lobster:urchin size ratios as a function of site and year (see Fig. S1).

3.2. Simulating plausible distributions of lobster-urchin consumption rates based on observational data

Lobster-urchin interactions are only one feeding link in the complex food web dynamics of the kelp forest (Morton et al., 2021; Tegner & Levin, 1983). Lobsters are opportunistic predators and urchins are preyed upon by other consumers (e.g. *Semicossyphus pulcher*; Hamilton and Caselle 2015). Therefore, we were only interested in estimating consumption rates that accounted for body size variation *relative* to consumption rates that ignore body size. Indeed, estimated consumption rates at any time point are likely different than actual urchin consumption. However, in the absence of spatiotemporal species-specific data on urchin consumption rates,

our predictions offer a means of exploring the consequences of body size on estimated variation in consumer-resource interactions.

3.3. Partitioning variance between density and body size

Considering the extent of variation in interaction strength between lobsters and urchins, we sought to partition the amount of variation caused by differences in lobster and urchin density between sites/years and the amount of variation driven by differences in the size-distributions of lobsters and urchins. The size-dependent functional response in our experiment depends on the interactive effects of lobster size, urchin size, and urchin density (see Eq. 5 in main text). For example, at a particular body size of lobster and urchin, the interaction strength will depend on the density of urchins. Our experimental data suggests that lobster attack rates are largely invariant with lobster size or urchin size ($\beta_{\alpha,c}, \beta_{\alpha,r} \approx 0$). This means that lobster and urchin body size will have a greater impact on *IS* when the urchin density is high, compared to when urchin density is low, because at low urchin density predators are constrained by their ability to find new prey (e.g. attack rate, α), which is invariant with body size. Therefore, to partition the variation in interaction strength between body size and density, we fixed the body size of lobster and urchin at different values and estimated interaction strength across variation in density.

Specifically, we selected 625 different values of lobster size and urchin size such that sizes ranged from the max lobster mass and minimum urchin mass to the max urchin mass and minimum lobster mass. We then estimated the distribution of *IS* assuming only variation in lobster and urchin density for each combination of fixed lobster and urchin size. Finally, we used simple linear regression to estimate the proportion of variance explained (R^2) by the predictions where only density varied, relative to the predictions based on joint variation in body size and density. We reported the full range of resulting $1-R^2$ values to estimate the proportion of variance explained by body size.

3.4. Predicting interaction strengths based on previous relationships in the literature

We conducted a non-systematic search of the literature to find estimates for the size-scaling of the functional response. For empirical estimates, we relied on Rall et al. (2012), Barrios-O'Neill et al. (2019), and a recent metanalysis (Uiterwaal & DeLong, 2020) which represents the largest compilation of functional response data available to date. For the complete data source to Uiterwaal and DeLong (2020), please refer to the FoRAGE database (Uiterwaal et al., 2022).

Each of the three papers we used to generate predictions utilized other covariates to model parameters of the functional response. Barring interactions in these models, the scaling-coefficients on the body mass of resource and consumer should not be affected by the covariates. However, the intercepts will not be directly comparable unless we accounted for the covariates. Therefore, for each manuscript we included the covariates from their models and fixed the values of those covariates at the observed value in our mesocosm trials.

Table S2. Summary of the final model structure, units, and fixed values of covariates used to predict interaction strength based on relationships from the literature.

Uiterwaal and DeLong 2020	
Final models	
α	$\ln(\alpha) = \alpha_0 + \beta_{c,\alpha} \ln(m_c) + \beta_{r,\alpha} \ln(m_r) + \beta_T T + \beta_{T^2} T^2 + \beta_A \ln(A) + **$
h	$\ln(h) = h_0 + \beta_{c,h} \ln(m_c) + \beta_{r,h} \ln(m_r) + \beta_T T + \beta_{T^2} T^2 + \beta_A \ln(A) + \beta_D D + **$
Units and fixed values	
$m = \text{mg}$; density = ind. Cm^{-2} ; time = days; $T = 16.1^\circ\text{C}$; $A = 5.206 \times 10^4 \text{ cm}^2$; $D = 2$ (e.g. 2-D)	
** Uiterwaal and Delong include random effects based on taxonomy. However, we focused only on the population level effect (e.g. across taxa). Therefore, we did not include random effect shifts to the intercept.	
Rall et al. 2012	
Final models	
α	$\ln(\alpha) = \alpha_0 + \beta_{c,\alpha} \ln(m_c) + \beta_{r,\alpha} \ln(m_r) + \beta_T \frac{T - T_0}{kTT_0}$
h	$\ln(h) = h_0 + \beta_{c,h} \ln(m_c) + \beta_{r,h} \ln(m_r) + \beta_T \frac{T - T_0}{kTT_0}$
Units and fixed values	
$m = \text{mg}$; density = ind. m^{-2} ; time = seconds; $T = 289.25 \text{ }^\circ\text{K}$; $T_0 = 293.15 \text{ }^\circ\text{K}$; $k = 8.61733326 * 10^{-5} \text{ eV K}^{-1}$	
Barrios-O'Neill et al. 2019***	
Final models	
α	$\ln(\alpha) = N(\alpha_{0,j} + \beta_{c,\alpha} \ln(m_c) + \beta_{r,\alpha} \ln(m_r) + \beta_T \ln(T) + \beta_{m_r \times T} \ln(m_r) \ln(T) + \beta_{ACstat} I_{ACstat} + \beta_{filt} I_{filt}, \sigma)$ $\alpha_{0,j} = N(\mu_{\alpha 0}, \sigma_{\alpha 0,j}), \text{for Taxa } j = 1, \dots, J$ where $I_{ACstat} = 1$ and $I_{filt} = 0$
C_{max}	$\ln(C_{max}) = N(C_{0,j} + \beta_{c,h} \ln(m_c) + \beta_{r,h} \ln(m_r) + \beta_T \ln(T) + \beta_{m_c \times T} \ln(m_c) \ln(T) + \beta_{ACstat} I_{ACstat} + \beta_{filt} I_{filt}, \sigma)$ $C_{0,j} = N(\mu_{c0}, \sigma_{c0,j}), \text{for Taxa } j = 1, \dots, J$ Where $I_{ACstat} = 1$ and $I_{filt} = 0$
Units and fixed values	
$m = \text{g}$; density = ind. m^{-2} ; time = days; $T = 16.1^\circ\text{C}$	
*** Barrios-O'Neill et al. (2019) included both a categorical fixed effect for encounter strategy and a random effect of taxonomy. We were interested in active predators foraging on static prey (I_{ACstat}) and crustacean predators. Therefore, we estimated the intercept for both models as	
$I = \mu_x + \beta_{ACstat} + X_{crustacean}$ where x, X is either $\alpha_0 C_0$ and I is the final intercept used in the simulation	

Table S3. Summary of equations and parameter estimates for the size-scaling of the functional response based on theoretical and empirical sources.

Source	$\ln(\alpha_0)$	$\beta_{\alpha,c}$	$\beta_{\alpha,r}$	β_T	β_{T^2}	β_A	$\ln(h_0)$	$\beta_{h,c}$	$\beta_{h,r}$	β_T	β_{T^2}	β_A	β_D	Taxonomic scale
First principles	--	0.58 - 0.92 ¹	0.33 - 0.66 ¹	--	--	--	--	-0.66 to -1 ²	0-1 ³	--	--	--	--	Theoretical
Uiterwaal and DeLong 2020	-8.45 ± 1.05	0.05 ± 0.03	-0.0005 ± 0.02	0.10 ± 0.03	- 0.003 ± 0.001	0.98 ± 0.05	0.83 +- 0.85	-0.25 ± 0.03	0.34 +- 0.02	-0.24 ± 0.04	0.005 ± 0.001	-0.01 ± 0.03	-0.64 ± 0.19	Cross taxa; general estimate
Rall et al. 2012	-21.23	0.85	0.09	0.42	--	--	10.38	-0.76	0.76	-0.30	--	--	--	Marine invertebrates
Barrios-O'Neil 2019	-8.08 + -1.07 + 0 ⁴	0.58	0.59	1.84	--	--	-6.07 ⁵ + 0.55 + 0.48	1.44 ⁵	0.27 ⁵	1.78 ⁵	--	--	--	Active crustaceans that forage on static resources

¹ McGill and Mittlebach 2006; ² Brown et al. 2004, Glazier 2010; ³ Rall et al. 2012, Jescke et al. 2002
⁴ Barrios-O'Neill et al. (2019) report that all random effects on attack rate intersect the group level effect and don't report the random effects therefore we assume they are zero.
⁵ Barrios-O'Neill et al. (2019) fit maximum consumption rates (C_{max}). We converted to handling times when generating predictions.

4. Supplemental Figures

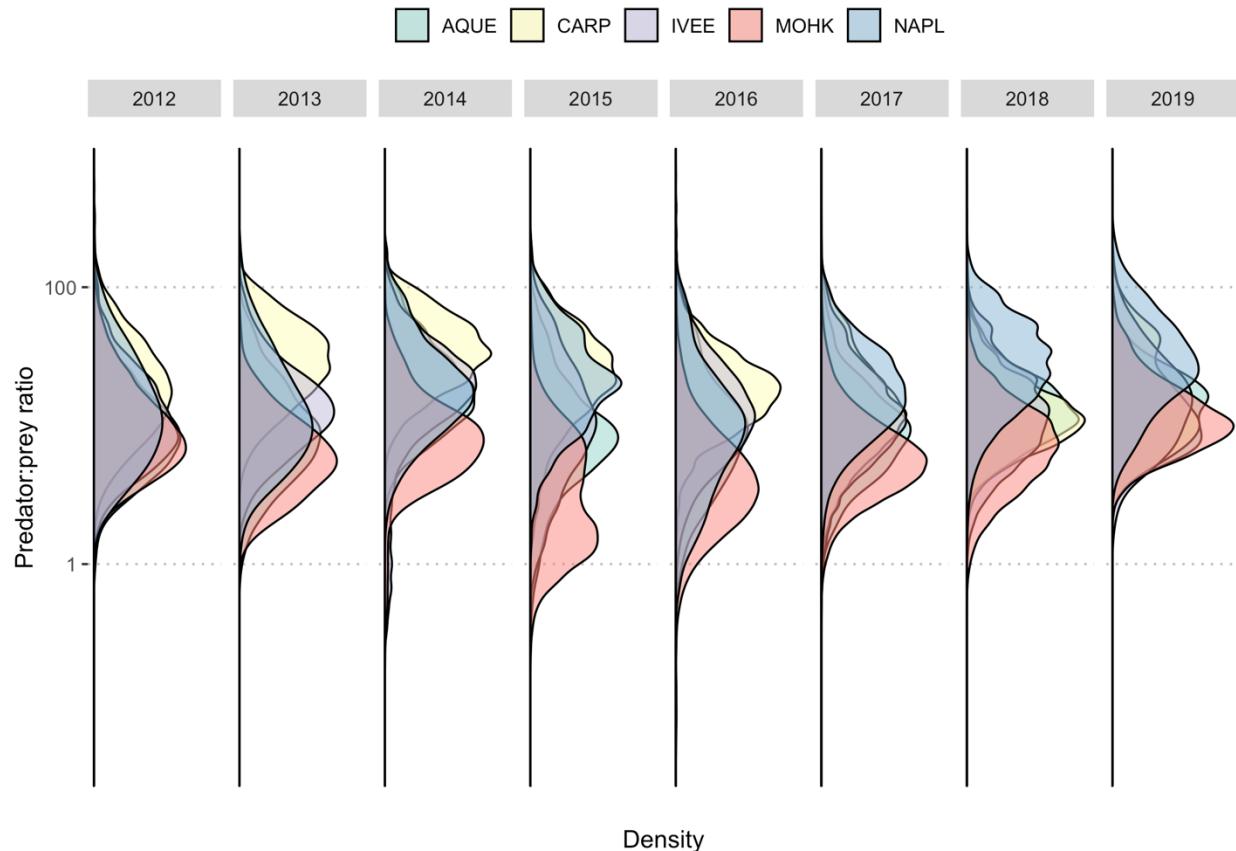


Figure S1. Change in the predator (California spiny lobster) to prey (purple urchin) body mass ratio between sites and years. The mean and variance of the predator:prey ratio varies between sites and years. The predator:prey ratio was estimated by resampling from the size distributions of predators and prey with replacement. The y-axis is \log_{10} transformed for visualization purposes.

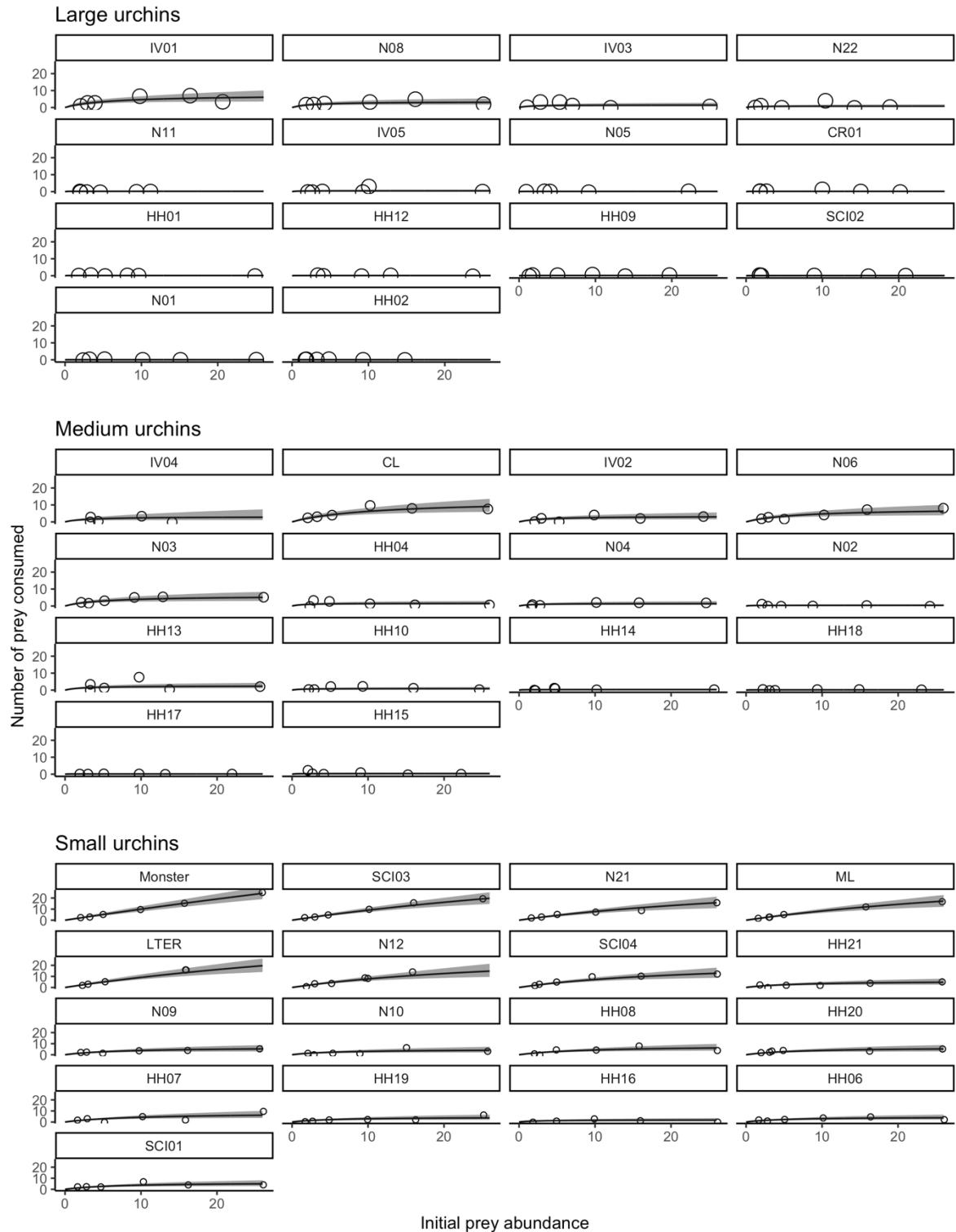


Figure S2. The functional responses of individual lobster predators foraging on urchin prey in mesocosms. Lines are median predictions ($\pm 95\%$ CI) from a Bayesian hierarchical model that estimated the number of urchins consumed as a function of lobster body size, prey body size, and prey density. Panels are arranged in descending order of lobster body size within a particular prey size class.

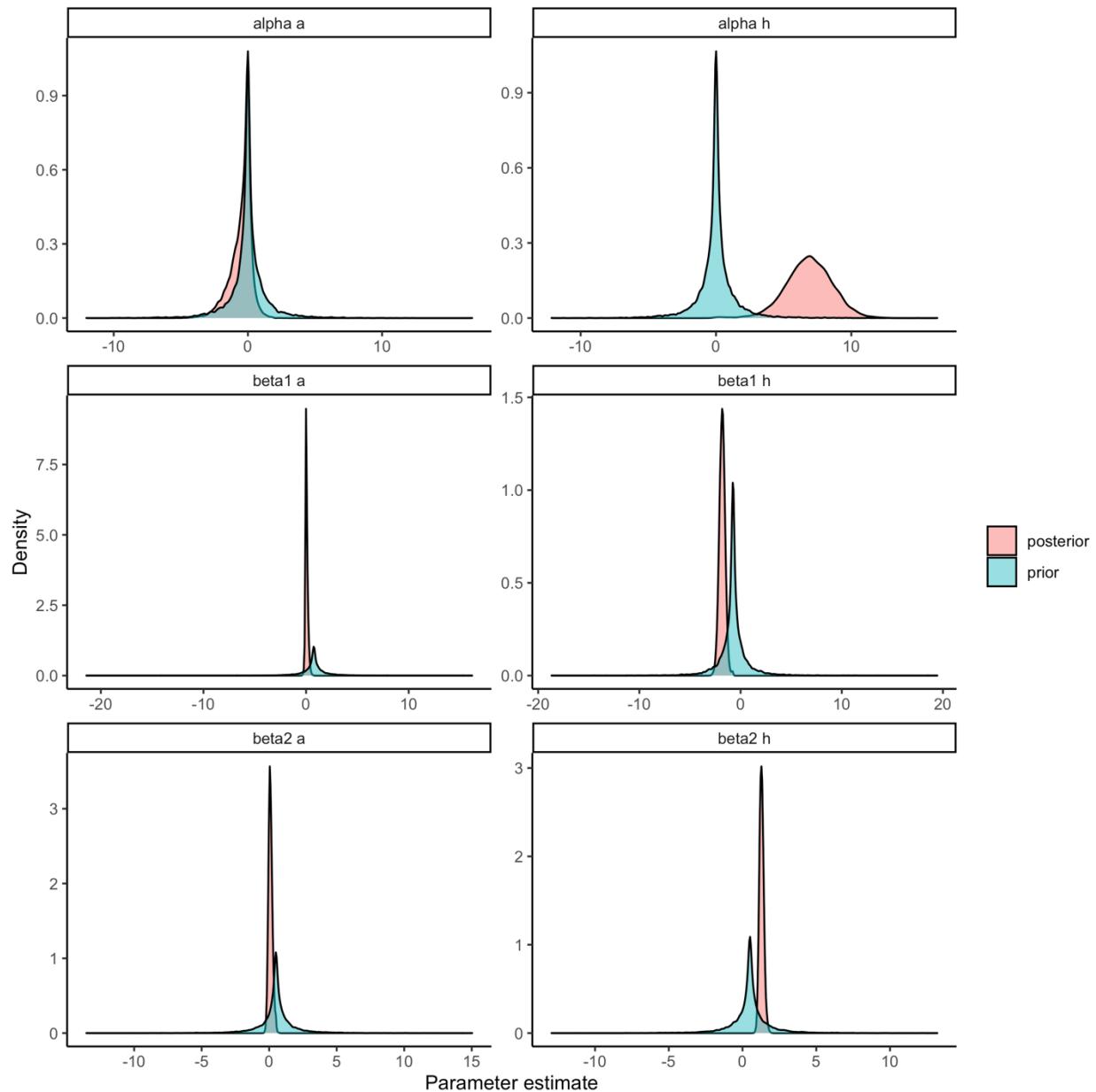
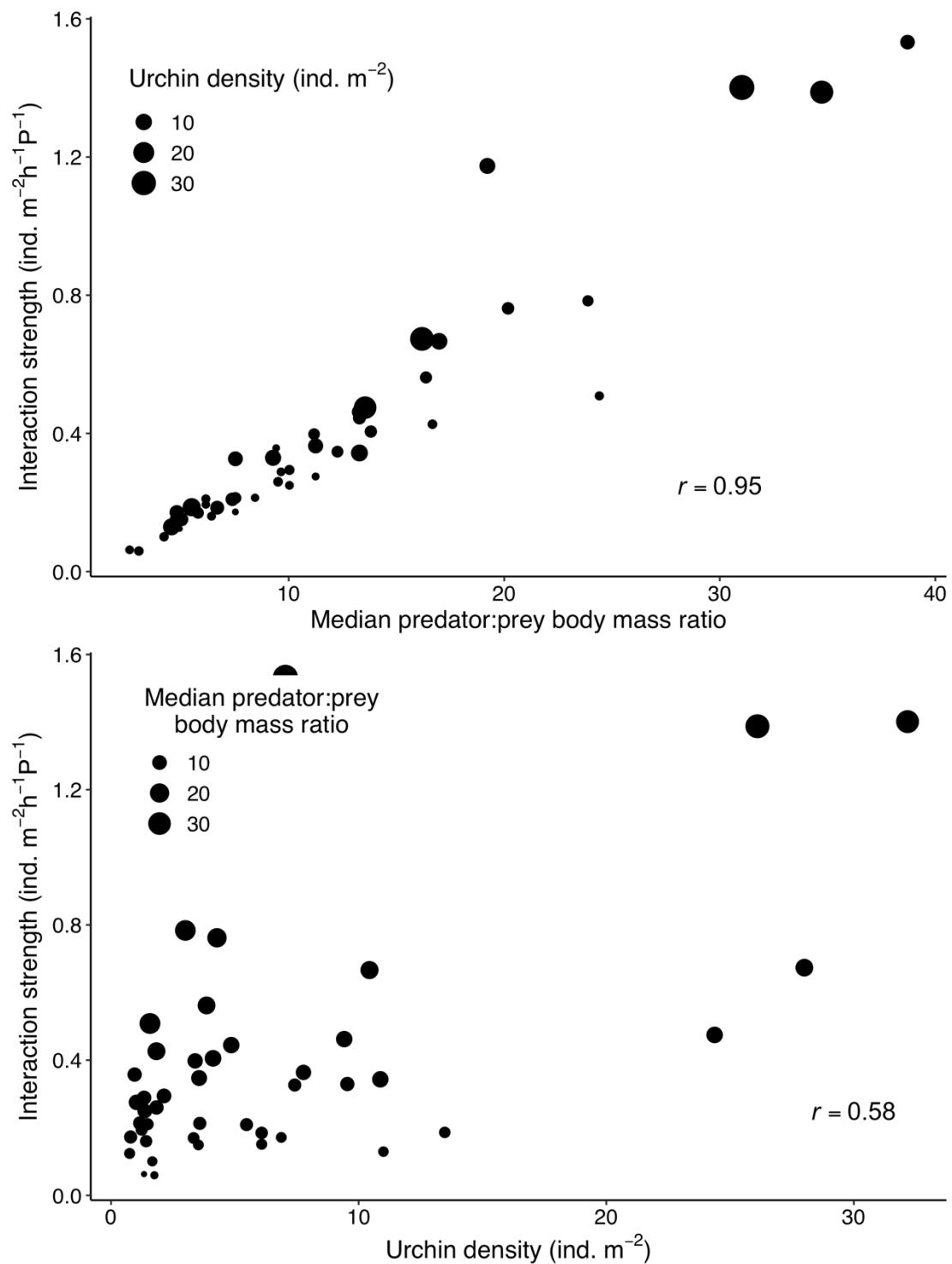


Figure S3. Comparison of posterior and prior predictive distributions for population level parameters from a Bayesian hierarchical model. Priors are informed based on theoretical predictions (see Table S2 for details on each prior).



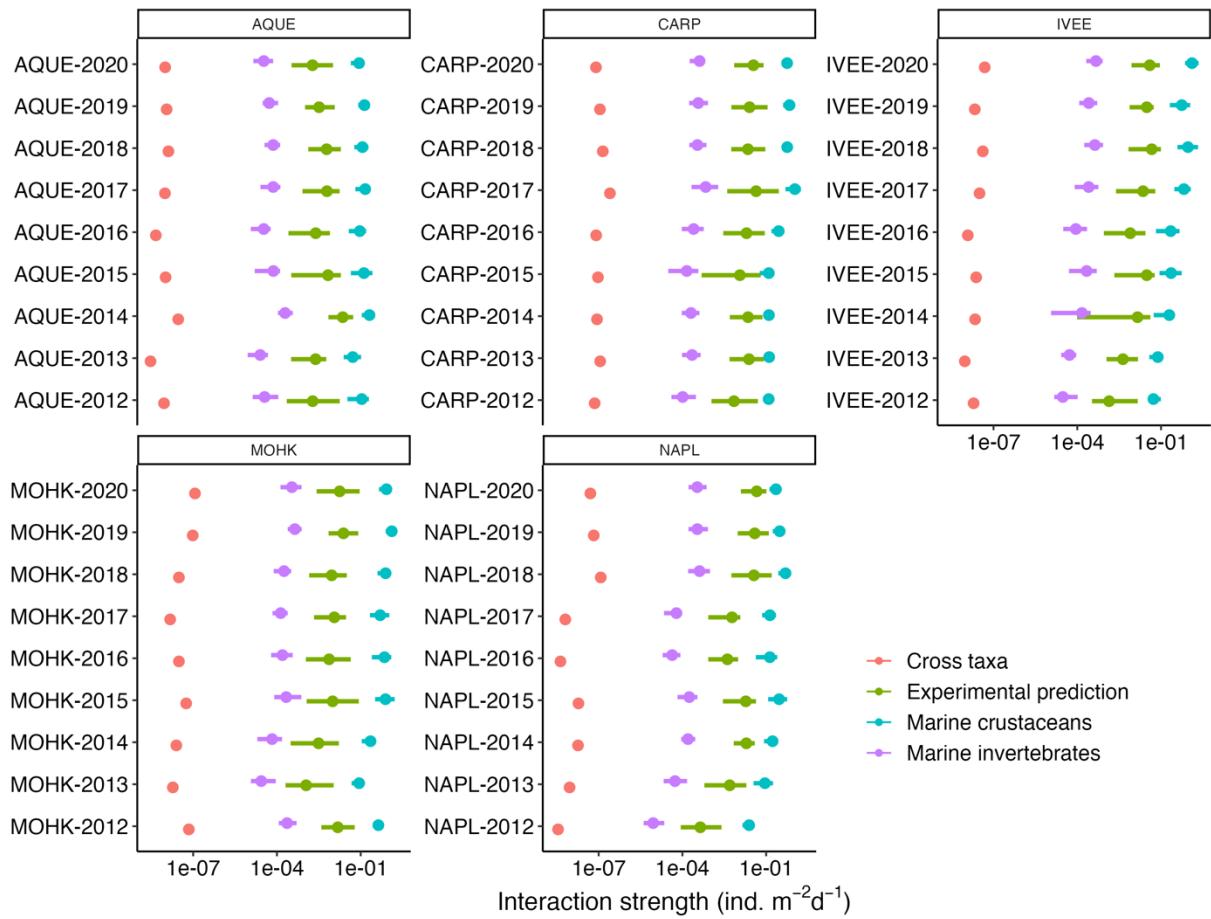


Figure S5. Rank order of interaction strength estimated via experimentation and three different predictions from the literature for the size-scaling of consumption rates. Site-year combinations are arranged in decreasing order according to the experimental prediction.

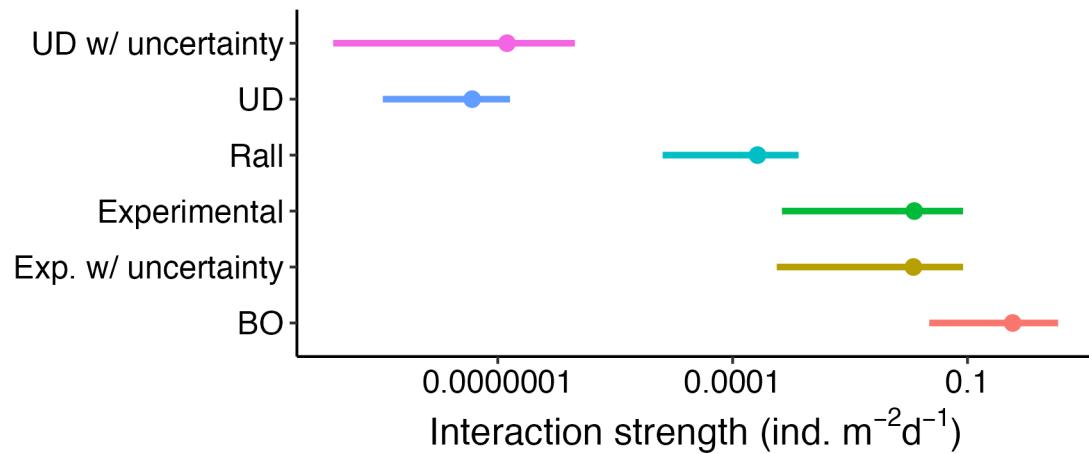


Figure S6. Median and 95% CI's of simulated predictions for interaction strength based on our experimental estimates and estimates of the size-scaling of interaction strength from the literature. UD (Uiterwaal and DeLong 2020), Rall et al. (2012), BO (Barrios-O'Neill et al. 2019), and Experimental match the predictions reported in the main text. However, UD w/ uncertainty and Exp. w/ uncertainty incorporate uncertainty in the regression coefficients. For experimental estimates, we sampled from the posterior distribution of each parameter, such that each draw in the simulation paired a unique lobster body size, urchin body size, and parameter set. Uiterwaal and Delong report mean \pm SE of the regression parameters. To incorporate uncertainty, we sampled from a uniform distribution, where the bounds were defined by the 95% CI's of the mean of each parameter. Rall et al. (2012) and Barrios-O'Neill et al. (2019) do not report confidence intervals on their parameter estimates.

5. References

- Aljetlawi, A. A., Sparrevik, E., & Leonardsson, K. (2004). Prey–predator size-dependent functional response: Derivation and rescaling to the real world. *Journal of Animal Ecology*, 73(2), 239–252. <https://doi.org/10.1111/j.0021-8790.2004.00800.x>
- Barrios-O'Neill, D., Kelly, R., Dick, J. T. A., Ricciardi, A., MacIsaac, H. J., & Emmerson, M. C. (2016). On the context-dependent scaling of consumer feeding rates. *Ecology Letters*, 19(6), 668–678. <https://doi.org/10.1111/ele.12605>
- Bolker, B. M. (2008). *Ecological models and data in R*. Princeton University Press.
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85(7), 1771–1789. <https://doi.org/10.1890/03-9000>
- Ellison, A. M. (2004). Bayesian inference in ecology. *Ecology Letters*, 7(6), 509–520. <https://doi.org/10.1111/j.1461-0248.2004.00603.x>
- Eurich, J., Selden, R., & Warner, R. (2014). California spiny lobster preference for urchins from kelp forests: Implications for urchin barren persistence. *Marine Ecology Progress Series*, 498, 217–225. <https://doi.org/10.3354/meps10643>
- Hamilton, S. L., & Caselle, J. E. (2015). Exploitation and recovery of a sea urchin predator has implications for the resilience of southern California kelp forests. *Proceedings of the Royal Society of London B: Biological Sciences*, 282(1799), 20141817. <https://doi.org/10.1098/rspb.2014.1817>
- Jerde, C. L., Kraskura, K., Eliason, E. J., Csik, S. R., Stier, A. C., & Taper, M. L. (2019). Strong Evidence for an Intraspecific Metabolic Scaling Coefficient Near 0.89 in Fish. *Frontiers in Physiology*, 10. <https://doi.org/10.3389/fphys.2019.01166>

Supporting Information

- Kalinkat, G., Schneider, F. D., Digel, C., Guill, C., Rall, B. C., & Brose, U. (2013). Body masses, functional responses and predator–prey stability. *Ecology Letters*, 16(9), 1126–1134. <https://doi.org/10.1111/ele.12147>
- McCoy, M. W., Bolker, B. M., Warkentin, K. M., & Vonesh, J. R. (2011). Predicting Predation through Prey Ontogeny Using Size-Dependent Functional Response Models. *The American Naturalist*, 177(6), 752–766. <https://doi.org/10.1086/659950>
- Morton, D. N., Antonino, C. Y., Broughton, F. J., Dykman, L. N., Kuris, A. M., & Lafferty, K. D. (2021). A food web including parasites for kelp forests of the Santa Barbara Channel, California. *Scientific Data*, 8(1), 99. <https://doi.org/10.1038/s41597-021-00880-4>
- Oddi, F. J., Miguez, F. E., Ghermandi, L., Bianchi, L. O., & Garibaldi, L. A. (2019). A nonlinear mixed-effects modeling approach for ecological data: Using temporal dynamics of vegetation moisture as an example. *Ecology and Evolution*, 9(18), 10225–10240. <https://doi.org/10.1002/ece3.5543>
- Rall, B. C., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmüller, F., Vucic-Pestic, O., & Petchey, O. L. (2012). Universal temperature and body-mass scaling of feeding rates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1605), 2923–2934. <https://doi.org/10.1098/rstb.2012.0242>
- Real, L. A. (1977). The Kinetics of Functional Response. *The American Naturalist*, 111(978), 289–300.
- Reed, D. C., Nelson, J. C., Harrer, S. L., & Miller, R. J. (2016). Estimating biomass of benthic kelp forest invertebrates from body size and percent cover data. *Marine Biology*, 163(5), 101. <https://doi.org/10.1007/s00227-016-2879-x>

Supporting Information

- Tegner, M. J., & Levin, L. A. (1983). Spiny lobsters and sea urchins: Analysis of a predator-prey interaction. *Journal of Experimental Marine Biology and Ecology*, 73(2), 125–150.
[https://doi.org/10.1016/0022-0981\(83\)90079-5](https://doi.org/10.1016/0022-0981(83)90079-5)
- Uiterwaal, S. F., & DeLong, J. P. (2020). Functional responses are maximized at intermediate temperatures. *Ecology*, 101(4). <https://doi.org/10.1002/ecy.2975>
- Uiterwaal, S. F., Lagerstrom, I. T., Lyon, S. R., & DeLong, J. P. (2022). FoRAGE database: A compilation of functional responses for consumers and parasitoids. *Ecology*, 103(7), e3706. <https://doi.org/10.1002/ecy.3706>
- Uiterwaal, S. F., Mares, C., & DeLong, J. P. (2017). Body size, body size ratio, and prey type influence the functional response of damselfly nymphs. *Oecologia*, 185(3), 339–346.
<https://doi.org/10.1007/s00442-017-3963-8>
- Uszko, W., Diehl, S., & Wickman, J. (2020). Fitting functional response surfaces to data: A best practice guide. *Ecosphere*, 11(4), e03051. <https://doi.org/10.1002/ecs2.3051>
- Vucic-Pestic, O., Rall, B. C., Kalinkat, G., & Brose, U. (2010). Allometric functional response model: Body masses constrain interaction strengths. *Journal of Animal Ecology*, 79(1), 249–256. <https://doi.org/10.1111/j.1365-2656.2009.01622.x>
- Wahlström, E., Persson, L., Diehl, S., & Byström, P. (2000). Size-dependent foraging efficiency, cannibalism and zooplankton community structure. *Oecologia*, 123(1), 138–148.
<https://doi.org/10.1007/s004420050999>