

Title: Variation in body size drives spatial and temporal variation in lobster-urchin interaction strength

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ABSTRACT

Size-scaling relationships generated across huge variation in body mass from zooplankton to elephants offer critical insight into understanding similarities in species interactions across ecosystems. Yet to what extent ecologists can borrow from these relationships to effectively predict interactions between a single species pair remains poorly understood. Here, we combine experiments and long-term data to test how accurately published size-scaling relationships predict interactions between an economically and ecologically important predator-prey pair. We demonstrate that interaction strength is highly dependent on predator size, prey size, and prey density. We then used this relationship to predict plausible interaction strengths across ten years of data at five sites. Our analysis reveals that variation in body size accounts for up to 91% of the variation in interaction strength compared to density. However, predictions generated from even the closest size-scaling relationship from the literature underestimated the strength of interactions by a factor of 4.

I. 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, Rall et al. 2012, Uiterwaal and DeLong 2020). Despite the power of body size-scaling relationships across taxa, it is unclear how much can be borrowed from cross-taxa relationships to predict how strongly a given species pair interacts, and if these predictions might disentangle complexity in community ecology (e.g. Poisot et al. 2015). In this paper, we empirically test if general cross-taxonomic patterns relating interacting strength with predator and prey body size predict interaction strength in a focal predator-prey pair. Understanding if general body 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 behavior 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 (Werner and Gilliam 1984, De Roos et al. 2003, Barnes et al. 2010). 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 defenses such as spines (Laforsch and Tollrian 2004). Such changes in feeding behavior or defensive capacity as predators and prey grow through ontogeny introduces variation in interaction strength, where a

predator may have a strong interaction with a prey when the prey is small and a weak interaction when the prey grows larger. Consequently, even if different sites have exactly the same number of predator and prey individuals, changes in predator and prey size-frequency distributions may drive differences in the average interaction strength. For instance, sites with large predators and small prey could have stronger interactions while sites with large predators and small prey could have weaker interactions (Fig. 1). While previous work has focused on experimentally quantifying variation in interaction strength with predator and prey body size (Uiterwaal and DeLong 2020, Brose et al. 2017 *for review*), a next step in this field is to leverage the considerable theoretical and empirical evidence for the body size dependence of interactions to predict when and where predators drive the dynamics of prey populations.

A strong relationship between predator and prey body size and interaction strength across taxa could offer a means of predicting interactions for specific species pairs. Metanalyses show that across taxa larger predators tend to eat more than smaller predators, particularly when prey is abundant and smaller (Rall et al. 2012, Uiterwaal and DeLong 2020). The generality of these relationships suggests it may be possible to predict how strongly a given predator-prey pair interact by knowing only the size-frequency distributions of the predator and prey. However, two factors complicate this approach. First, there is substantial variation in the relationship between predator size, prey size, prey density, and interaction strength caused by covariates such as taxonomy (Rall et al. 2012), temperature (Englund et al. 2011), habitat dimensionality (Pawar et al. 2012, Barrios-O'Neill et al. 2016), and foraging mode (Barrios-O'Neill et al. 2019). Second, it is unclear whether general size-scaling relationships based on *interspecific* variation in body size are applicable to estimating interactions for a given species pair across *intraspecific*

variation in body size (White and Seymour 2003, Dell et al. 2011, Brose et al. 2017). To date, studies that focus on intraspecific variation in body size have typically found different relationships between body size and interaction strength than theoretical expectations or analyses of interspecific variation in body size (Wahlström et al. 2000, Aljetlawi et al. 2004, Uiterwaal et al. 2017). Yet, borrowing from general size-scaling relationships to naively predict interactions would be powerful (Andersen and Beyer 2015) considering the challenges and associated uncertainty in estimating interactions for species of management or conservation concern (Geary et al. 2020).

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 (Filbee-Dexter and Scheibling 2014, 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 and Caselle 2015). Yet, empirical evidence for urchin regulation by lobsters remains equivocal, with some studies pointing towards a strong top-down effect of lobsters (Lafferty 2004) and others suggesting that lobsters have only a weak impact on urchin populations (Guenther et al. 2012, Dunn and Hovel 2019, Malakhoff and Miller 2021). Previous work on California spiny lobster and other lobster species shows that larger lobster consume more and larger urchins (Tegner and Levin 1983, Ling et al. 2009), 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 intraspecific variation in lobster-urchin interactions. To test this hypothesis, we first ask, how does the body size and density of lobster and urchins vary across space and through time? We then ask, how does urchin size, lobster size, and urchin density alter consumption rates of urchins—a measure of interaction strength—in experimental mesocosms? We then combine our empirical estimates of urchin consumption rates with observational data to map spatiotemporal variation in interaction strength. Using these predictions, we disentangle the effects of lobster size, urchin size, and urchin density as drivers of variation in interaction strength. Finally, we ask how well do general size-scaling relationships from the literature predict lobster-urchin interaction strength across natural variation in body size and density?

II. METHODS

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 in the Santa Barbara Channel. Briefly, divers count the number of urchins greater than 20 mm in six quadrats

uniformly spaced along 40 m transects at each site (3-8 transects per site) (Santa Barbara Coastal LTER et al. 2021a). 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. 2021b). Divers count and estimate the carapace length to the nearest mm of all lobsters in 1200 m² plots centered around each transect (Santa Barbara Coastal LTER et al. 2021c).

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

To estimate how strongly lobster and urchin interact, we quantified the size-dependence of the lobster functional response. A predator's functional response determines how consumption rates change as a function of prey density. 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

$$C = \frac{\alpha N}{1 + \alpha h N} \quad \text{Eq. 1}$$

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

The metabolic theory of ecology (MTE) predicts that maximum consumption rates (i.e. $1/h$) scale with consumer body size at the same rate that metabolism scales with body size (Yodzis and Innes 1992, Brown et al. 2004). Therefore, handling time ($1/C_{\max}$) will decrease with

consumer body size according to a negative power law function ($h \propto m_c^{-\beta}$, where $\beta = 0.75$ based on MTE). 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:

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

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 and DeLong 2020, Table S1).

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 and Mittelbach 2006). Therefore, theory predicts that attack rates should increase according to power law functions of predator and prey size, according to

$$\alpha = \alpha_0 m_c^{\beta_{\alpha,c}} m_r^{\beta_{\alpha,r}} \quad Eq. 3$$

where α_0 is a constant, and $\beta_{\alpha,x}$ are scaling exponents (Rall et al. 2012, Uiterwaal and DeLong 2020, Table S1). Previous work suggests that attack rates increase and then decrease as a function of predator size for a given prey size (Wahlström et al. 2000, 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 1.2*). Therefore, we focus on the power-law scaling relationship (Eq. 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 placed a single lobster in an experimental arena, and fed each lobster one of three size classes of urchin at six different densities ($N = 2, 3, 5, 10, 16, 26$ 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 hours in 200 L foraging arenas. Prior to a trial, we fed lobsters *ad libitum* for 48 hours and then starved the predators for 48 hours. For more detail on the specifics of mesocosm experiments refer to *Supplement 2*.

To understand the relationship between a lobster's size, urchin density, and urchin size, we then estimated the parameters of the size-dependent functional response using a Bayesian hierarchical model. Specifically, we combined equations 1-3 and fit the resulting equation to 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 ($C_{i,j}$) followed a Poisson distribution such that

$$C_{i,j} \sim \text{Poisson}(\lambda_{i,j}) \quad \text{Eq. 4}$$

$$\lambda_{i,j} = \frac{\alpha_{i,j} N_i}{1 + \alpha_j h_j N_i}$$

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

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

where, α_j is the attack rate (d⁻¹ m⁻²), h_j is the handling time (d) of lobster j , and m_r was the average mass of the urchin size class that lobster j foraged on. We constructed informed priors on all β_x parameters, where β_x was normally distributed with a mean based on theoretical

predictions (Table S2). We assumed gamma distributions for the prior variances. We included a random effect of individual lobster ($\mu_{x,j}$) on the estimation of α and h , 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 burnin of 12,500 iterations and thinned the chains to retain every 3rd 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 and Gelman 1998). For more details on our modeling approach see *Supplement 1.3*.

How does lobster-urchin interaction strength vary across space and through time?

To generate plausible estimates for how strongly lobsters and urchins interact under natural conditions, we combined observational data on lobster size, urchin size, lobster density, and urchin density with our experimentally-parameterized functional response. We assumed that interactions were random at a site in a particular year, such that 1) any predator could interact with any prey and 2) predator-prey 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

$$IS_{i,j} = \frac{\alpha_0 m_c^{\beta_{\alpha,c}} m_r^{\beta_{\alpha,r}} NP}{1 + \alpha_0 m_c^{\beta_{\alpha,c}} m_r^{\beta_{\alpha,r}} h_0 m_c^{\beta_{h,c}} m_r^{\beta_{h,r}} N} \quad Eq. 5$$

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.

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 (Paine 1992, Berlow et al. 1999 and Novak et al. 2016 *for reviews*). Density may be a misleading metric of interaction strength, particularly for species that experience nonlinear, indeterminate growth, like many marine predators, where a single large individual may have the same mass as many smaller, younger individuals. Recent work highlights the importance of accounting for size-dependent consumption rates in estimating interaction strength (Andersen and Pedersen 2010, Atkins et al. 2015), yet how much of the variation in interaction strength between a predator-prey pair is due to variation in predator and prey body size relative to density remains unresolved.

To determine how much of the total variation in interaction strength was due to lobster and urchin body size relative to densities, we fixed body size across sites and years and simulated IS across variation in density. We then estimated the proportion of total variation due to body size as $1 - R^2$ of the correlation between the distribution of IS that incorporated both sources of

uncertainty and the distribution of *IS* when body size was fixed (see *Supplement 3.3* for further details).

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. Multi-species models—one tool used to determine management decisions in an ecosystem context—are highly sensitive to uncertainty in how strongly species interact (Hunsicker et al. 2011). The possibility of using body size and general size-scaling relationships to parameterize interaction coefficients in multispecies models is appealing considering the challenges of estimating interaction strength for many species of management concern. While there have been considerable advances in recent years in the implementation of size-structured models, these models often rely on theoretical estimates for how consumption changes with body size to make qualitative predictions for how disturbances, like harvest, impact communities (Blanchard et al. 2014, Persson et al. 2014). Testing how accurately general size-scaling relationships from the literature predict interaction between specific species could move size-structured food web models from qualitative predictions of general community phenomena to more quantitative predictions that guide management in data limited systems (e.g. Spence et al. 2021).

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 and 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 S1). All analyses were implemented in R 4.0.4 (R Core Team 2021).

III. RESULTS

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 – 6184.0 g (393.6 [88.8 – 897.8] g, \tilde{X} [95% CI] *unless otherwise specified*), while urchin mass was on average 39.2 [8.1 – 132.2] g (Fig. 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 (Fig. S1). Urchin density ranged from 0.75 – 32.2 ind. m⁻² (6.5 [0.8 – 27.8] ind. m⁻²), while the average lobster density was 0.03 [0.004 – 0.097] ind. m⁻².

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

The consumption rate of urchins by lobster increased with urchin density and lobster size, and decreased as urchin size increased (Fig. 2, Fig. S2). Only the largest lobsters regularly consumed the largest urchins, with the smaller 50% of lobsters only consuming < 1% of the large urchins offered. Alternatively, 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 (Fig. 3a, $\beta_{\alpha,c} = 0.025[-0.14 - 0.34]$, $\beta_{\alpha,r} = 0.080[-0.16 - 0.43]$). However, handling time decreased with lobster size and increased with urchin size (Fig. 3b, $\beta_{h,c} = -1.81[-2.38 - -1.24]$, $\beta_{h,r} = 1.29[1.03 - 1.61]$). Despite the inclusion of informative priors for the size-scaling exponents, the posterior estimates for the scaling exponents differed from first principle expectations. 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. $\beta_{h,r}$).

How does lobster-urchin interaction strength vary 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 relative interaction strength between lobsters and urchins varied considerably across narrow spatial and temporal scales ($0.014 [0.00020 - 0.061]$ ind. $\text{m}^{-2} \text{d}^{-1}$, Fig. 4). The variation in

interaction strength between sites ($\overline{CV}_{spatial} = 1.34 \pm 0.4, \bar{X} \pm 1 \text{ SD}$) was similar to the variation between years ($\overline{CV}_{temporal} = 1.25 \pm 0.1$).

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 predicted interaction strength across space and time, we tested how much of this variation could be attributed to differences in the body size versus the density of lobster and urchins. We found that body size accounted for the majority of the variation in plausible interaction strength (85-91%) compared to variation in density (Fig. 5a). In a hypothetical simulation, a 10-fold increase in lobster body size resulted in a ~250% increase in the median interaction strength, relative to only a 1.5% increase when the density of urchins increased 10-fold all else being equal (Fig. 5b). Communities characterized by large lobsters relative to urchin size and high urchin density displayed the highest interaction strength, while the interactions strength in communities with small lobsters relative to urchins and low urchin density approached zero (Fig. S4). Across all sites and years, lobster-urchin interactions were log-distributed with far more weak interactions than strong interactions (Fig. 5 a,c).

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 (Fig. S5, Spearman's rank order correlation test, $p < 0.001$). However,

published size-scaling relationships failed to estimate the magnitude of interactions between lobster and urchin. Even the closest prediction from the literature was 4.1 times less than the median interaction strength estimated by our experimental model (Fig. 5c). The precision of the predictions increased as the taxonomic specificity increased. The cross-taxa estimate performed the worst at predicting interaction strength, while the estimate for active marine crustacean predators performed the best.

IV. 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. Heterogeneity in predator and prey size distributions across space and through time caused 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 context dependency. Our findings demonstrate that natural and human-induced variation in body size in the field is 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.

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

In the lobster-urchin study system, 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 and 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 modeling work that highlights the importance of the 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 were effective predators of small urchins. Purple urchins display variable recruitment dynamics and 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 interactions.

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 is quantified by measuring the abundance of a focal species in the presence or absence of the interacting species (Wootton and 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 showed that up to 91% of the variation in plausible interaction strength can be attributed to variation in body size, highlighting 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.

Naïve predictions of interaction strength

423
424 Researchers are increasingly focused on implementing ecosystem-based approaches to
425 management (EBM), which seeks to examine the effects of human disturbances, such as harvest,
426 by accounting for species interactions, physical forces, social drivers, and economic
427 considerations (Long et al. 2015). One challenge to effective implementation of EBM is
428 uncertainty in the strength of species interactions, particularly when system specific data are
429 limited (Hunsicker et al. 2011). Previous work in food web ecology has utilized theoretical
430 scaling relationships to determine the structure and resilience of ecological networks (Brose et al.
431 2006, Petchey et al. 2008). Recently, applied ecologists have adapted a similar approach to
432 parameterize stage- or size structured models that assume general size-scaling relationships for
433 mortality, growth, and reproduction to understand the relative consequences of harvest on
434 populations (Andersen et al. 2009), communities (Claessen et al. 2009, Andersen et al. 2015), or
435 whole ecosystems (Fulton et al. 2011, Heymans et al. 2016). However, the assumption of general
436 size-scaling relationships may be violated in specific ecosystems (Reum et al. 2019, Spence et al.
437 2021). Our results support the assumption that qualitative predictions for when predators display
438 strong or weak interactions with their prey are resilient to inaccurate estimates of how
439 consumption varies with body size for particular species. However, our results suggest that
440 relying on general size-scaling relationships to parameterize models of a particular system will
441 likely fail to quantitatively predict the magnitude of trophic interactions. In other words, naïve
442 estimates of interaction strength may accurately predict the direction and rank order of
443 interaction strengths but not their magnitude. Failing to quantitatively estimate interactions is a
444 critical deficiency in predicting harvest quotas in an EBM framework.

The likely reason for the difference between our experimental estimates of interaction strength and estimates based on published size-scaling relationships are discrepancies between consumption-size relationships within species pairs compared to across species pairs (Brose et al. 2017). Previous metaanalyses typically relied on the average body size of a predator and its prey and the average parameters of the functional response to estimate how the functional response varies with body size (Rall et al. 2012, Uitterwaal and 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 (Wahlström et al. 2000, Aljetlawi et al. 2004, Uitterwaal 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.

Conclusion

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 demonstrated that variation in the body size of predator and prey, more so than variation in density, accounted for

most of the variation in how strongly lobster and urchin interact across narrow spatial and temporal scales. 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, Ripple et al. 2014, Robinson et al. 2017) through the interactive effects of harvest and warming temperatures (Baudron et al. 2014, Lindmark et al. 2018, Pauly and 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.

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V. FIGURES

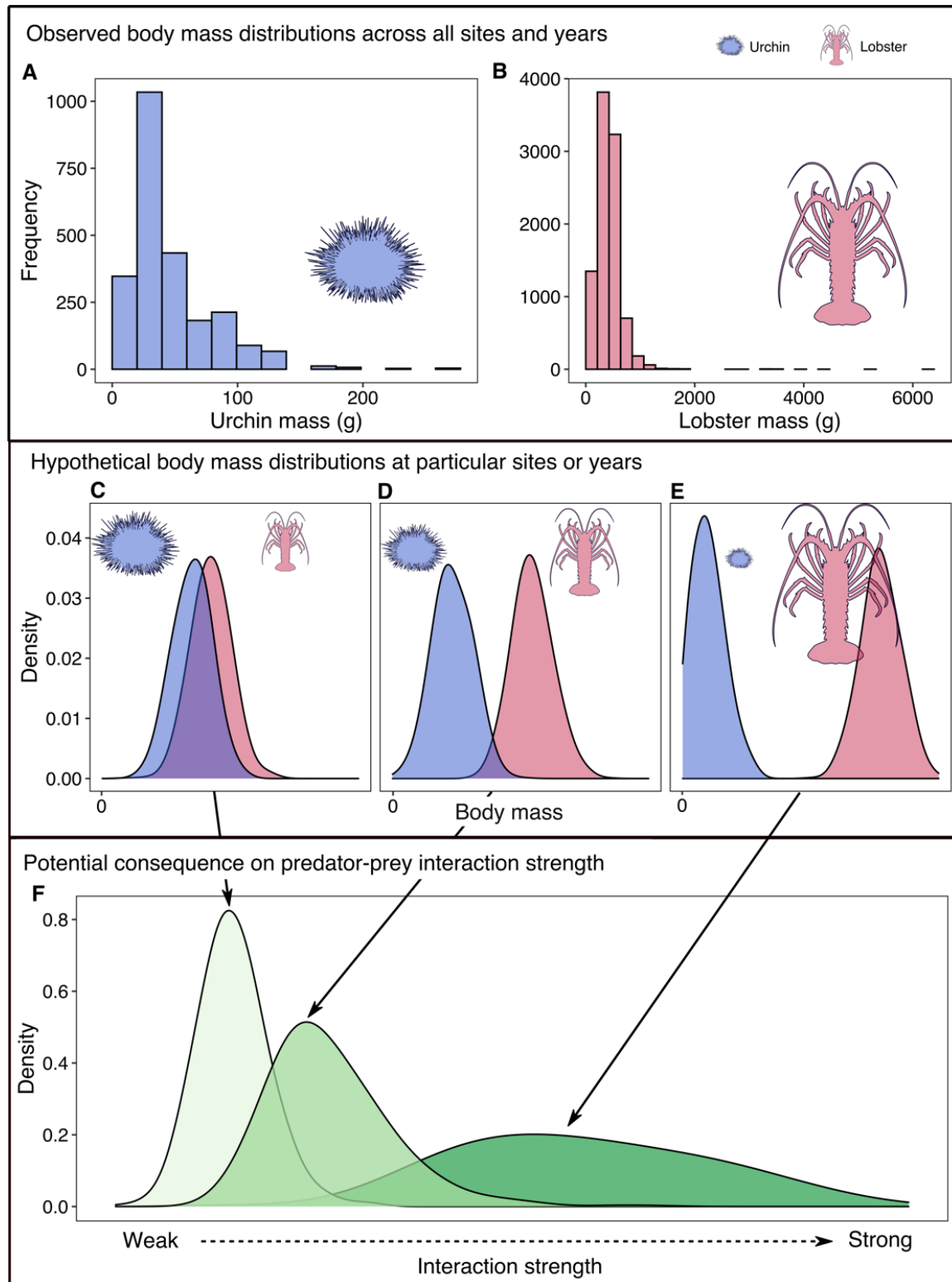
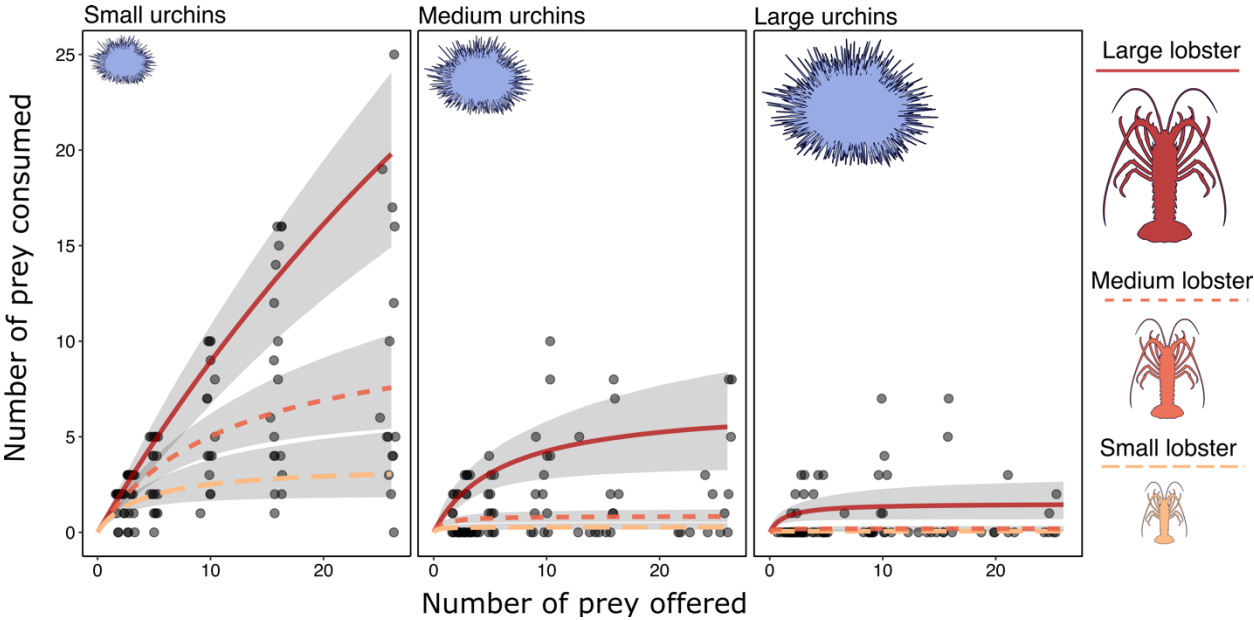


Figure 1.

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Figure 2.

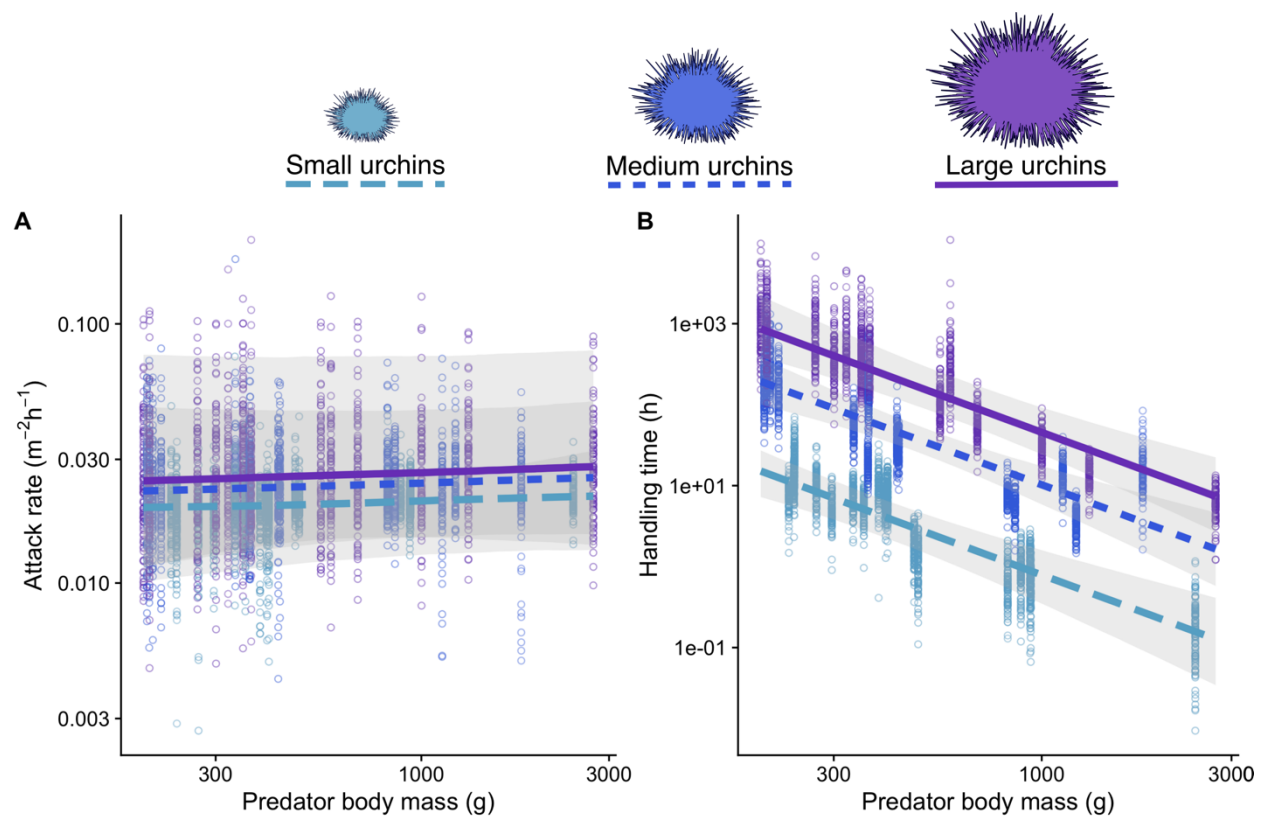
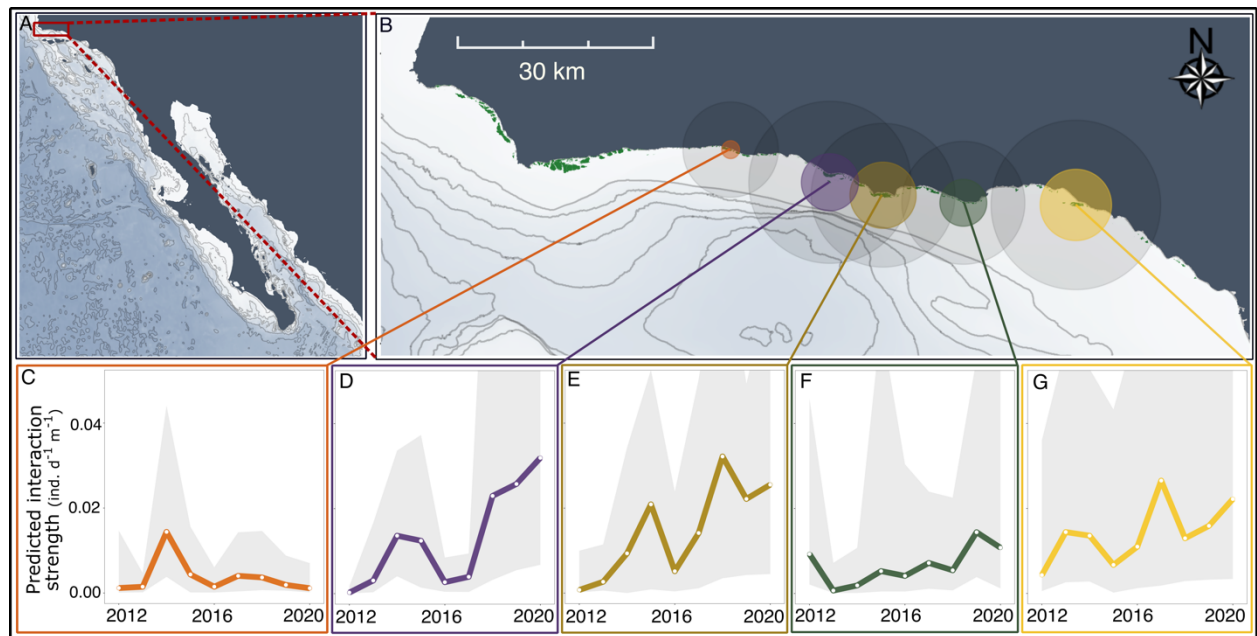


Figure 3.

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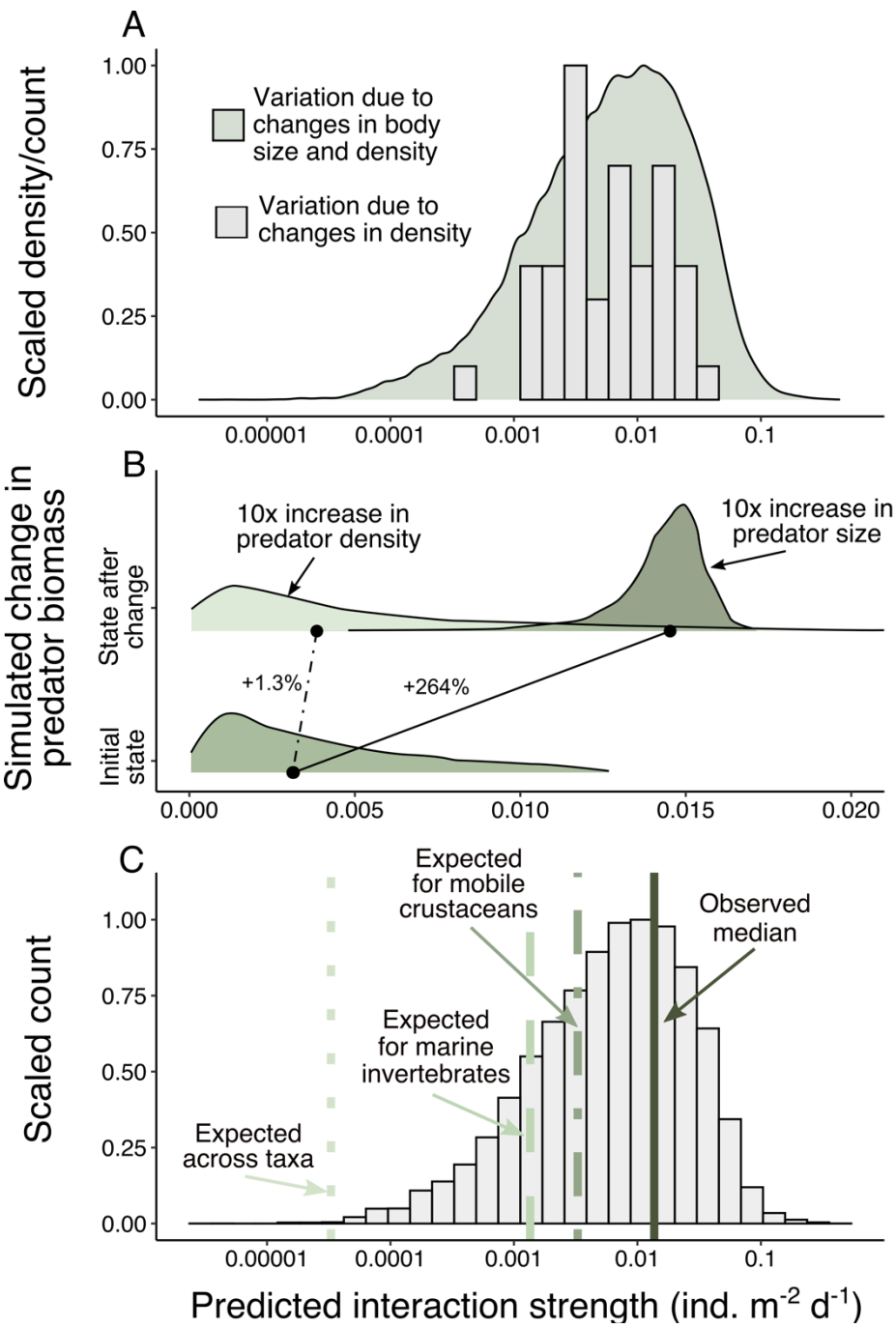
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Figure 4.

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Figure 5.

VI. Figure Captions

Figure 1. Observed body size distributions of a predator (*Panulirus interruptus* - lobster) (A) and their prey (*Strongylocentrotus purpuratus* - urchin) (B) across 5 sites monitored annually from 2012-2020. Different processes such as variation in recruitment, habitat suitability, or harvest can cause differences in the size of lobsters 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).

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 (\tilde{X} [95% CI]) from a Bayesian model for the body size dependent functional response. Prediction are 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 (\tilde{X} [95% CI]) for the body size scaling of each parameter according to power law functions of predator and prey mass (see *Methods* 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.

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 2012-2020 (A-B). Points and surrounding grayscale 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).

Figure 5. (A) Predicted interaction strengths between individual lobster predators (*Panulirus interruptus*) and their urchin prey (*Strongylocentrotus purpuratus*) across five sites and nine years of observational data. Variation in urchin and lobster body size accounted for 85-91% of the total variation in interactions, while variation in the density of lobsters and urchins accounted for the remainder. (B) A hypothetical simulation demonstrating the change in interaction strength for a 10-fold increase in urchin density compared to a 10-fold increase in lobster body mass assuming all else being equal. (C) Comparison of three estimates of the size-scaling of interaction strength from the literature with experimental predictions. Note the \log_{10} transformation on the x-axes in panels A and C.