

# Quantifying the Effects of Predator and Prey Body Size on Sea Star Feeding Behaviors

REBECCA A. GOODING AND CHRISTOPHER D. G. HARLEY\*

*Department of Zoology, University of British Columbia, 6270 University Blvd, Vancouver,  
British Columbia V6T1Z4 Canada*

**Abstract.** Body size plays a crucial role in determining the strength of species interactions, population dynamics, and community structure. We measured how changes in body size affect the trophic relationship between the sea star *Pisaster ochraceus* and its prey, the mussel *Mytilus trossulus*. We tested the effects of a wide range of predator and prey sizes on sea stars' prey-size preference, feeding rate, and prey tissue consumption. We found that preferred prey size increased with sea star size. *Pisaster* consumption rate (mussels consumed per day) and tissue intake rate (grams of tissue consumed per day) also increased with sea star size. *Pisaster* consumption rate, but not tissue intake rate, decreased with increasing mussel size. Juvenile sea stars preferred the most profitable prey sizes—that is, those that maximized tissue consumed per unit handling time. When adult sea stars were offered larger, more profitable mussels, tissue intake rates (grams per day) tended to increase, although this relationship was not statistically significant. Our results indicate that the *Pisaster-Mytilus* interaction depends on the sizes of both predator and prey, that predation rates are sensitive to even small changes in body size, and that shifts in size distributions may affect predator energetics and prey numbers differently depending on the factors that limit tissue consumption rates.

## Introduction

Body size is one of the fundamental drivers of an organism's biology, affecting everything from metabolism to behavior (Brown *et al.*, 2004). It is also a major determinant of the strength of species interactions (Emmerson and Raffaelli, 2004). Body size can affect predator feeding rates,

prey susceptibility, and the outcomes of competitive interactions (see review in Woodward *et al.*, 2005), as well as food web and community structure (Warren and Lawton, 1987; Jansson *et al.*, 2007; Heckmann *et al.*, 2012). As a result, any factor that alters body size will likely have cascading effects on populations and communities (*e.g.*, Springer *et al.*, 2003; Rudolf and Rasmussen, 2013).

Body size is influenced by a wide range of environmental and biological factors. Growth rates and adult body size often scale with temperature (Atkinson, 1995; Brown *et al.*, 2004), while physical stressors such as acute thermal stress and hydrodynamic disturbance can cause size-dependent mortality (Denny *et al.*, 1985; Peck *et al.*, 2009). At the population level, predation susceptibility, competitive interactions, and mate choice can all select for or against certain size classes (Menge, 1972; McClintock and Robnett 1986; Green, 1992). Anthropogenic activities also have both direct and indirect impacts on body size; these range from size-selective fisheries practices (Fenberg and Kaustuv, 2008) to climate- and ocean-acidification-induced changes in growth rates (*e.g.*, Drinkwater *et al.*, 2010; Kroeker *et al.*, 2014).

The direction and magnitude of natural and anthropogenic effects on body size are often species-specific (Brose *et al.*, 2012; Jochum *et al.*, 2012). As a result, any factor that differentially affects the relative body size of one or more interacting species could shift the nature of their interaction, with potential population and community consequences (Emmerson and Raffaelli, 2004; Aljetlawi *et al.*, 2004; Sanford *et al.*, 2014; Gaylord *et al.*, 2015). Gaining a quantitative understanding of how body size affects a given interaction would enable a more complete understanding of the role body size may play in structuring the community as a whole. This is especially important for interactions involving keystone species or ecosystem engineers, where body-size-driven changes to species interactions could drastically

Received 12 April 2013; accepted 21 April 2015.

\* To whom correspondence should be addressed. E-mail: harley@zoology.ubc.ca

alter community-level processes (Woodward *et al.*, 2005; Brose *et al.*, 2012; Rudolf and Rasmussen, 2013).

One interaction with known size-dependencies involves the sea star *Pisaster ochraceus*. This keystone predator is common on rocky shores from Alaska to Baja California (Morris *et al.*, 1980). *P. ochraceus* exerts strong impacts on the structure and diversity of mid-intertidal communities through predation on mussels, which are the dominant space holders and ecosystem engineers (Paine, 1966, 1974; Harley, 2011). Where predation by *P. ochraceus* is low, mussels occupy much of the available substratum, outcompeting other sessile macroorganisms for space but providing habitat for numerous species associated with mussel beds (Paine, 1974; Harley, 2011). In contrast, high *P. ochraceus* feeding rates keep mussel abundance in check, allowing other primary space holders to colonize the resulting open space (Paine 1966, 1974).

The size of sea stars and their prey has been shown to exhibit strong control over their interaction (Paine, 1976). *Pisaster ochraceus* exhibits a preference for mussels over other prey items (Landenberger, 1968) and for certain sizes of mussels (McClintock and Robnett, 1986). However, it is unclear whether this prey-size preference is due to physical limitations on the mussel sizes that can be consumed or is a cost-benefit decision that weighs handling time against tissue consumed. On wave-exposed shores, *P. ochraceus* is either unwilling or unable to physically consume the mussel *Mytilus californianus* beyond a shell length of 8–10 cm (Paine, 1976). However, even when offered mussels well below this apparent size-refuge, *P. ochraceus* prefers medium-sized *M. californianus* to larger and more energy-rich individuals, possibly due to energetic costs of dislodging larger individuals from the substratum to consume them (McClintock and Robnett, 1986).

On sheltered rocky shores, *M. californianus* is generally unavailable, and the *P. ochraceus* diet often includes a high proportion of *Mytilus trossulus* (Mauzey, 1966; Harley *et al.*, 2006). Unlike the congeneric *M. californianus*, upon which most of the past research has focused, adult *M. trossulus* seldom grow large enough to avoid predation by sea stars (Kozloff, 1996), nor do their relatively weak byssal thread attachments (Bell and Gosline, 1997) appear to pose a significant obstacle for *P. ochraceus* while feeding (R. Gooding, pers. obs.). Thus, *P. ochraceus*' prey-size preference and feeding behaviors on *M. trossulus* are probably driven primarily by the relative profitability (handling time versus tissue consumed; Krebs, 1980) of different mussel sizes.

Recent work suggests that future environmental change is likely to alter the growth of both *P. ochraceus* and *Mytilus* spp., making it even more important to understand how changing body sizes affect their interaction. Although some variables such as ocean warming may increase the growth rates of both sea stars and mussels (Sanford, 2002; Menge

*et al.*, 2008), the responses of these taxa to other factors such as ocean acidification may differ in magnitude and sign (Michaelidis *et al.*, 2005; Gooding *et al.*, 2009; Keppel *et al.*, 2015). Although these predictions involve growth rates rather than body size, altered growth rates could change the size-frequency distributions of some populations (Kirkpatrick, 1984; Havens and DeCosta, 1985).

In this study, we quantified *Pisaster ochraceus*' feeding behaviors across a range of body sizes of sea stars and their prey, the mussel *Mytilus trossulus*, to better understand how their interaction might be affected by changes in sea star or mussel size-frequency distributions (and therefore changes in the availability of particular prey sizes). Specifically, we predicted that (1) sea stars will consume smaller mussels more quickly and therefore consume more of them daily; (2) the balance between handling time and tissue gained will differ based on mussel size and will result in some mussel sizes being more profitable than others; (3) sea stars will preferentially consume particular mussel sizes, and their preferred prey size will increase with sea star size; (4) sea stars will prefer the prey size that provides the greatest tissue intake per unit of handling time and will consume the greatest amount of mussel tissue when feeding on their preferred prey size.

## Materials and Methods

### Animal collection and morphometrics

Specimens of the sea star *Pisaster ochraceus* Brandt, 1835, and the mussel *Mytilus trossulus* Gould, 1850, were collected at low tide from Jericho Beach (49.273°N, –123.188°W), which is a sheltered rocky shore habitat in Burrard Inlet near Vancouver, British Columbia, Canada. Sea stars were maintained submerged in a laboratory recirculating seawater system (13 °C, 28 psu salinity) for 1–3 months prior to any experiments; during this time sea stars were fed haphazardly sized mussels *ad libitum* about every 2 weeks. Juvenile *P. ochraceus* (arm length ~20–30 mm, wet mass 10–20 g) used for the experiments in Part II (below) were collected in November 2007, while juvenile and adult *P. ochraceus* (arm length ~35–155 mm, wet mass 20–400 g) used in Part I were collected in December 2010. Although no formal distinction was made between juvenile and adult sea stars in Part I, it should be noted that *P. ochraceus* reaches sexual maturity at about 100–150 g (Mauzey, 1966; Menge, 1974; Paine, 1976). A range of sizes of *M. trossulus* individuals were collected from Jericho Beach and maintained in a recirculating seawater system for 1–2 weeks prior to each set of experiments. New mussels and juvenile *P. ochraceus* were used for all experiments in Part II. We were unable to collect sufficient quantities of adult sea stars, so the same sea stars were used for both the feeding rate and prey-size preference experiments in Part I. However, sea stars were given 2 weeks to

recover between experiments and were arbitrarily re-assigned to treatments and containers. Additionally, prey-size preference was measured first in order to prevent effects of exposure to any one prey size during the feeding rate experiment. For all sizes of sea stars, a flexible tape was used to measure arm length to the nearest millimeter, from the mouth to the tip of the ray nearest to the madreporite.

The relationship between mussel size and tissue mass was quantified to allow calculations of *Pisaster ochraceus*' intake of prey tissue. *Mytilus trossulus* individuals ranging from 8 to 57 mm in shell length ( $n = 33$ ) were collected from Jericho Beach in December 2007 and kept in a recirculating seawater system for about 2 weeks prior to dissection. Each mussel was pried open (by cutting the adductor muscle) and excess water was drained from the mantle cavity. The mussel was then patted dry and weighed, the wet tissue was dissected out, and the empty shell was weighed again. The empty shell mass was subtracted from the total wet mass to obtain wet tissue mass. Mussel shell length was measured to the nearest 0.1 mm using vernier calipers. The relationship between mussel shell length and wet tissue mass was determined using a 2nd-order polynomial regression. There was a strong relationship between mussel shell length in millimeters and wet tissue mass in grams ( $R^2 = 0.99$ ;  $P < 0.001$ ), which was described by the following equation:

$$\text{Wet mussel tissue mass} = -2.889 + 0.1434 \\ \times \text{length} + 0.00309 \times (\text{length} - 32.52)^2$$

#### Part I: Sea star feeding behaviors with predator and prey size

To determine how the preferred size of prey scaled with sea star size, *Pisaster ochraceus* individuals across a range of sizes ( $n = 24$  sea stars, arm length 38 to 150 mm) were placed in separate plastic containers ( $28 \times 15 \times 11$  cm) with large holes to allow adequate water exchange with the seawater table (13 °C and 28 psu salinity). After a 48-h acclimation period without food, each sea star was given two mussels from each of six approximate size classes: shell length 10, 20, 30, 40, 50, and 60 mm ( $\pm 2$  mm;  $n = 12$  mussels in each container). Size classes were selected to span the range of mussel sizes available to sea stars in the field, while still keeping the number of treatments manageable. Sea stars were checked daily and empty mussel shells were removed and measured to the nearest 1 mm; they were then replaced by live mussels from the same size class. This was repeated for 9 days. The preferred mussel size for each sea star was calculated by taking the mean shell length of the mussels chosen by that individual.

To measure sea star feeding rate on different mussel sizes, sea stars were grouped into sets of three similarly sized individuals (8 sets total); each sea star in the set was

then housed separately and assigned one of three mussel size classes: 20 mm, 40 mm, or 55 mm ( $\pm 2$  mm). All sea stars were fed *ad libitum* on haphazardly sized mussels for 5 days prior to the experiment to standardize their hunger levels. Their arm length was then measured and they were placed in individual containers ( $28 \times 15 \times 11$  cm) and given six mussels from the appropriate prey size class. Empty mussel shells were removed and replaced with similarly sized live mussels daily. One of the smallest sea stars, which was assigned 55-mm mussels, did not feed during the experimental period and was therefore removed from the subsequent analyses. After 13 days, feeding rates for the remaining sea stars declined and the experiment was terminated.

Due to difficulties with getting mussels to remain attached to the substrate, especially smaller mussels that tended to move around the experimental containers, sea stars were fed unattached mussels. Although byssal thread attachment may contribute to handling costs of *P. ochraceus* fed *M. californianus* (McClintock and Robnett, 1986), sea stars in both the laboratory and the field often feed on *M. trossulus* without detaching them. This is especially common in juvenile sea stars, who orient their body against the side of the mussel shell, insert their stomach into the small gap between the valves where the byssus and foot emerge, and consume the entire mussel without detaching it from the substrate (R. Gooding, pers. obs.). Therefore, while it is possible that the lack of byssal attachment would reduce the amount of time required for a sea star to feed on a mussel, particularly for large, robustly attached mussel species living in exposed habitats (e.g., *M. californianus*), we do not feel that the absence of byssal attachment introduced undue bias in our experiments with *M. trossulus*.

#### Part II: Juvenile sea star feeding behaviors with prey size

To standardize hunger levels, juvenile sea stars (~25–30-mm arm length) were held without food for one week prior to experimentation, except for the feeding rate experiment for which they were fed mussels *ad libitum* for 3 days prior. During all experiments, sea stars were kept in the recirculating seawater table (13 °C and 28 psu) in small plastic containers ( $12 \times 12 \times 8.5$  cm) with mesh sides to allow adequate water flow. Sea star arm lengths (mean of all 5 arms) were measured at the beginning of each experiment. Mussels were sorted to within  $\pm 1$  mm of one of four size classes: 10 mm, 15 mm, 20 mm, and 25 mm shell length. These size classes were selected to be representative of the range of mussel sizes we had observed sea stars of this size consuming in the field.

The preferred prey size for juvenile sea stars was determined by giving sea stars ( $n = 13$  sea stars) two mussels from each of the four prey size classes, for a total of eight mussels per sea star. These mussels were placed haphazardly inside each experimental chamber to minimize any effects of proximity on sea star prey selections. A sea star

was assumed to have selected a mussel once it had initiated feeding (attachment of tube feet with mussel shell positioned against the sea star's mouth), at which point the remaining mussels were removed. Once the sea star had consumed the chosen mussel, the shell was removed and the sea star was provided with new mussels. This was repeated four times for each sea star over the course of 3 days.

To test sea stars' feeding rates on different mussel sizes, two sea stars were placed in each of 8 small plastic containers (described above). Mean arm length was measured to the nearest millimeter (mean  $\pm$  SD =  $25.2 \pm 2.0$  mm) at the beginning of the experiment. Each container was then randomly assigned to one of four prey size treatments, with two containers per treatment. Each container began with 20 mussels of the appropriate size class; this number of mussels was far more than what sea stars of this size can consume daily (R. Gooding, pers. obs.), thus ensuring that sea stars never ran out of mussels during the experiment. On the second day, empty mussel shells were removed and replaced with live mussels of the same size. Feeding rate was recorded for a total of 4 days, and mean daily per capita consumption rate (mussels consumed per day, per sea star) was calculated for each container. This was repeated in three separate trials, using fresh sea stars in each trial, for a total of six replicate containers for each prey size class.

The handling time required for each prey size class was determined by randomly assigning individual sea stars to be fed one of the four prey size classes. Handling time was defined as the time interval from when the sea star touched the mussel to the point when it released the empty mussel shell. It should be noted that most sea stars touched and then left the mussel two to four times before commencing feeding. These initial contacts were ignored, and handling time was recorded as the single, continuous contact period that included feeding. This allowed an estimate of the true handling time required for a given prey size, while eliminating time spent foraging or otherwise selecting prey. Sea stars sometimes hold onto prey shells even after they have finished eating, potentially leading us to overestimate handling time. However, small juvenile sea stars like those used in this experiment seemed to be less apt to do this; whenever we closely examined a juvenile sea star holding a mussel shell, its stomach was everted. Some sea stars did not feed during the 12-h period of the experiment and were subsequently removed from the analysis, resulting in unequal sample sizes ( $n = 4, 4, 3$ , and  $2$ ; for 10, 15, 20, and 25-mm mussels, respectively).

### Statistical analyses

For experiments from Part I, the relationship between prey-size preference and sea star size was analyzed using a linear regression. The effects of prey size and arm length on feeding rate and daily consumption of prey tissue were analyzed using separate ANCOVAs. Residual plots showed

that feeding rate and daily tissue consumption data increased in variance with sea star size; this was corrected with log-transformations of these response variables. The mussel size  $\times$  sea star size interaction term was nonsignificant ( $P > 0.3$ ) for both analyses, so it was removed.

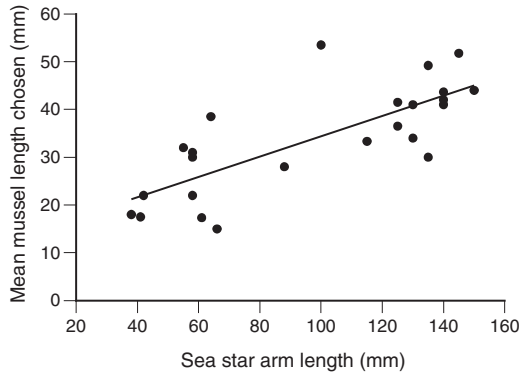
For experiments from Part II, we compared juvenile sea stars' preference for 10–15-mm versus 20–25-mm mussels with a chi-squared goodness of fit test; we pooled the four original prey size classes into two groups to increase the sample size and power of the statistical test since our original sample size was relatively small. The effects of prey size on handling time (minutes/mussel), profitability, mussels consumed per day, and mussel tissue consumed per day were analyzed with ANCOVAs, with sea star size as the covariate. Prey profitability was calculated by dividing the wet tissue mass of each mussel size class (estimated from the mussel length versus the mass equation determined above) by the corresponding handling time for that size class. Daily consumption of prey tissue for juvenile sea stars was calculated by multiplying the wet tissue mass of a mussel of a given size by the daily per capita feeding rate for that prey size. For mussel consumption rate and tissue consumption rate, data were log-transformed to meet the assumptions of the ANCOVA and to facilitate comparisons with the adult feeding data. For all ANCOVAs, initial tests were made to determine if the slopes of the lines for the response variable versus sea star size differed among prey size categories. Slopes did not differ (*i.e.*, the mussel size  $\times$  sea star size interaction was not significant) in any of the cases, and the interaction term was dropped from further consideration for all comparisons. All analyses were conducted using JMP 9.0.2 statistical software.

## Results

### Part I: Sea star feeding behaviors with predator and prey size

*Pisaster ochraceus*' preferred prey size increased with sea star arm length (Fig. 1; linear regression;  $F_{1,22} = 30.1$ ,  $P < 0.001$ ,  $R^2 = 0.578$ ). The daily feeding rate, expressed as mussels consumed per day, also increased with sea star size; however, as prey size increased, sea stars consumed fewer mussels (Fig. 2a; ANCOVA; arm length:  $F_{1,19} = 15.7$ ,  $P < 0.001$ ; mussel size:  $F_{2,19} = 33.5$ ,  $P < 0.001$ ). Sea stars ate significantly more small mussels than medium or large mussels (Tukey HSD;  $P < 0.05$ ). The amount of tissue consumed daily varied with sea star size (Fig. 2b), with larger sea stars consuming more tissue (ANCOVA; arm length:  $F_{1,19} = 17.6$ ,  $P < 0.001$ ). Daily tissue consumption tended to increase with increasing mussel size, although this effect was not statistically significant (ANCOVA; mussel size:  $F_{2,19} = 3.11$ ,  $P = 0.068$ ).





**Figure 1.** Patterns of prey-size preference across a range of *Pisaster ochraceus* sizes.

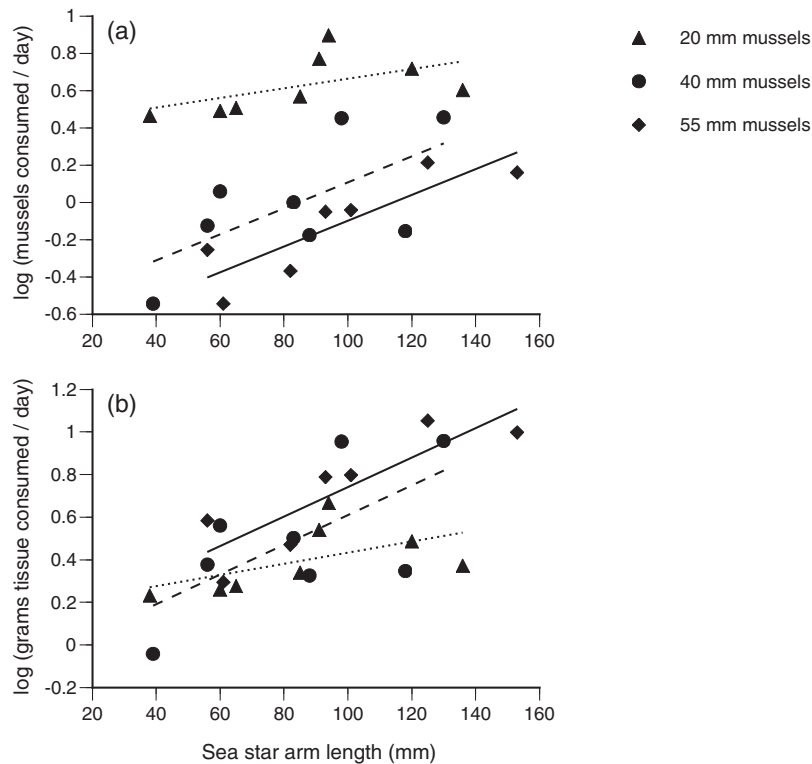
### Part II: Juvenile sea star feeding behaviors with prey size

Juvenile *Pisaster ochraceus* had a significantly greater preference for 20–25-mm mussels compared to 10–15-mm mussels (Fig. 3a; goodness of fit test:  $\chi^2 = 6.53$ ,  $df = 1$ ,  $P = 0.011$ ).

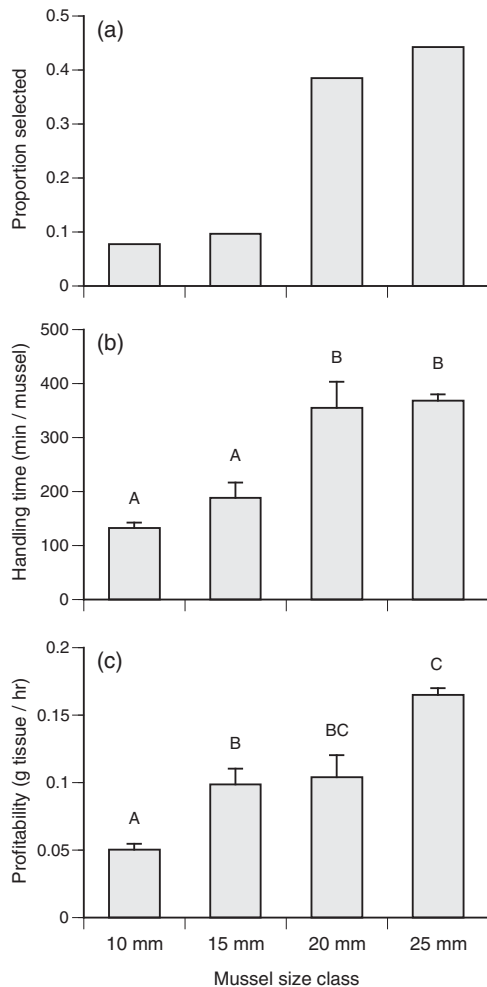
Handling time increased significantly with prey size for juvenile *P. ochraceus* (ANCOVA:  $F_{3,8} = 15.7$ ,  $P = 0.001$ ), but did not vary with sea star size (ANCOVA:  $F_{1,8} = 1.05$ ,

$P = 0.336$ ). Sea stars took significantly longer to consume 20- and 25-mm mussels than they did 10- and 15-mm ones (Fig. 3b). Profitability also varied with prey size but not sea star size (ANCOVA: prey size  $F_{3,8} = 13.4$ ,  $P = 0.002$ ; sea star size  $F_{1,8} = 1.17$ ,  $P = 0.312$ ). The largest size class of mussels provided more tissue per unit handling time than the two smallest size classes, and the 25, 20, and 15-mm mussels were all more profitable than 10-mm mussels (Fig. 3c).

The daily rate at which sea stars consumed mussels depended on both mussel size and sea star size (ANCOVA: mussel size  $F_{2,19} = 37.1$ ,  $P < 0.001$ ; sea star size  $F_{1,19} = 12.3$ ,  $P = 0.002$ ; Fig. 4a). Larger sea stars consumed more mussels, and sea stars tended to eat progressively fewer mussels with increasing prey size classes (Tukey HSD on mussels consumed by mussel size: 10 mm > 15 mm > 20 mm = 25 mm). When feeding was analyzed as the rate of food intake in grams per day, the higher biomass and profitability of larger mussels compensated for their longer handling time and the lower number of large mussels consumed. There was no effect of prey size on food intake rate (ANCOVA:  $F_{3,16} = 1.83$ ,  $P = 0.176$ ), although larger sea stars did consume more tissue per unit time (ANCOVA:  $F_{1,16} = 12.3$ ,  $P = 0.002$ ).



**Figure 2.** Adult *Pisaster ochraceus* feeding rates as a function of sea star and mussel (*Mytilus trossulus*) size: (a) mussel consumption rate, (b) mussel tissue consumption rate. Mussel size classes were 20 mm (triangles, dotted line), 40 mm (circles, dashed line), and 55 mm (diamonds, solid line). Note the log-scale on the y-axis.

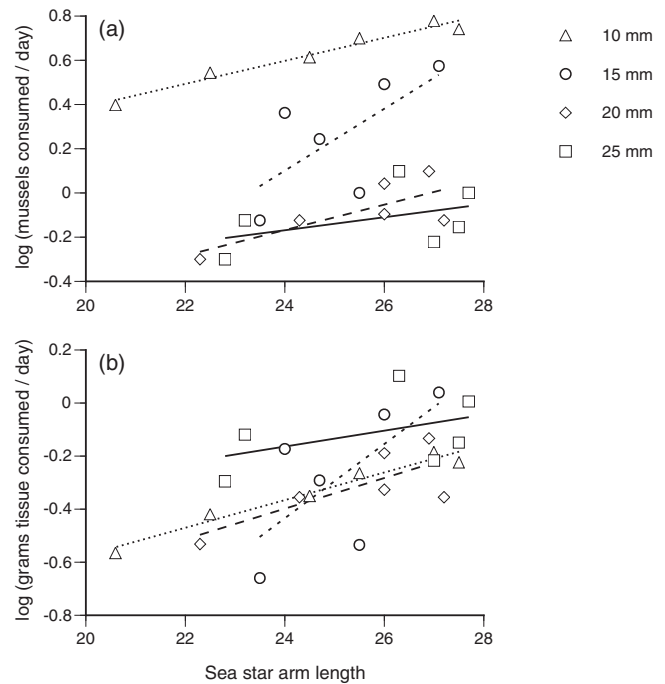


**Figure 3.** Juvenile *Pisaster ochraceus* feeding parameters as a function of prey size: (a) relative preference for different prey sizes, (b) mean handling time, (c) mean profitability. Relative preference was determined by pooling across sea stars and trials. Error bars represent  $\pm 1$  standard error of the mean. For (b) and (c), treatments that share a letter are not significantly different from one another (Tukey HSD).

## Discussion

Body size plays a prominent role in determining the strength of most predator-prey interactions (Brose *et al.*, 2012). Consequently, any factor that alters the relative sizes of two interacting species could have far-reaching implications for population dynamics and community functioning (Emmerson and Raffaelli, 2004; Jochum *et al.*, 2012). This is especially true for interactions involving species that have dominant effects on community structure, such as the predator-prey interaction between *Pisaster ochraceus* and its mussel prey (Paine, 1966).

Our findings support and expand upon past studies showing that *P. ochraceus*' feeding behaviors scale with the size of both the sea stars and the mussels (Paine, 1976). We found this pattern to be true across a wide range of sea star



**Figure 4.** Juvenile *Pisaster ochraceus* feeding rates as a function of sea star and mussel (*Mytilus trossulus*) size: (a) mussel consumption rate, (b) mussel tissue consumption rate. Mussel size classes were 10 mm (triangles, dotted line), 15 mm (circles, short-dashed line), 20 mm (diamonds, long-dashed line), and 25 mm (squares, solid line). Note the log-scale on the y-axis.

sizes including small juveniles, about which relatively little is known. In terms of the number of mussels consumed per day, the proportional effect of variation in prey size was consistent across sea star sizes. It is important to note, however, that this result was based on the analysis of log-transformed data, which implies that the effect of increasing predator size is multiplicative when plotted on an arithmetic axis. In other words, although the ratio of the daily consumption of large mussels alone to the daily consumption of small mussels alone was similar for all sea star sizes, the absolute difference in the number of mussels consumed may be considerably greater for larger sea stars. For example, a juvenile *P. ochraceus* with an arm length of 27 mm would consume about 4.9 more 10-mm than 25-mm mussels daily in no-choice trials (5.7 vs. 0.8 mussels per day, respectively), whereas a slightly smaller sea star, arm length 25 mm, would consume only about 2.9 more 10-mm than 25-mm mussels per day (3.5 vs. 0.6 mussels per day, respectively; see Fig. 4). Thus, small variations in *P. ochraceus* size may have large implications for the rate at which mussels are removed by these predators, especially when mussels are small.

It should be noted that mussels were not attached by byssus during our feeding experiments, which may have impacted handling time (McClintock and Robnett, 1986).

Although the potential effects of byssal attachment strength were not accounted for in our study, the weak attachment strength of *Mytilus trossulus* and the ability of even small *P. ochraceus* to consume *M. trossulus* individuals without detaching them from the substratum (R. Gooding, pers. obs.) suggest that the effects of byssal attachment may play a relatively minor role for this predator-prey pair in protected waters. Nevertheless, the fact that the importance of *M. trossulus* byssal thread attachment remains unquantified, along with other factors that inherently differ between laboratory and field conditions (e.g., duration of the feeding interactions, environmental variability, available search area), indicates that patterns of predation in the field are unlikely to exactly match patterns observed in these or indeed any laboratory-based experiments.

Juvenile sea stars preferred the largest prey sizes offered. These mussels required the longest handling times but also provided the most tissue per mussel, and the amount of tissue consumed per unit handling was maximized in larger mussels. The fact that sea stars preferred the most profitable prey in terms of energetic reward per unit time spent feeding was expected on the basis of optimal foraging theory (Pyke *et al.*, 1977).

We had also expected that *P. ochraceus* would take advantage of increased profitability to consume more mussel tissue per unit time when feeding on the most profitable prey sizes. This “energy maximizer” strategy (Schoener, 1971) is common in sea stars (e.g., Gaymer *et al.*, 2004, but see Tokeshi, 1989), and several traits of *P. ochraceus*—indeterminate growth where body size depends in large part on their energetic intake (Feder, 1956), positive correlations between size and reproductive output (Sanford and Menge, 2007), and negative correlations between size and risk of predation (Sewell and Watson, 1993)—all suggest that *P. ochraceus* should seek to consume as much prey tissue as possible. In our experiments, there were trends for *P. ochraceus* to maximize intake by consuming more tissue when offered more profitable mussel size classes, but tissue intake rate was not significantly related to profitability or prey size in either juvenile or adult sea stars.

Although it is possible that we simply lacked the statistical power to detect such differences, it is also possible that, for some physiological or behavioral reason, *P. ochraceus* does not consume as much tissue as predicted by theory. For example, digestion rate and stomach volume constrain the food intake of whelks (Burrows and Hughes, 1991) and fish (Hart and Gill, 1992), and may have limited intake in our experiments as well. However, *P. ochraceus* conducts much of its digestion externally while actively handling its prey (Feder, 1955), making it less likely that stomach volume would be a significant rate-limiting factor. Alternatively, *P. ochraceus*’ assimilation efficiency may decline sharply beyond a certain threshold of tissue consumption. Under this scenario, feeding activity would become less and less prof-

itable as tissue was consumed beyond a certain threshold (Barnier *et al.*, 1975; Vahl, 1984). Unfortunately, little is known about this aspect of *P. ochraceus*’ physiology, so it is difficult to judge its likelihood as a driving factor. A second, though not mutually exclusive, possibility is that *P. ochraceus* behaviorally minimizes its daily feeding time (see Hixon, 1982, for a description of “time minimizer” strategies). It could be that once *P. ochraceus* reaches a threshold of minimum or optimum daily energy intake, the potential costs of continued feeding outweigh the benefits. Actively feeding sea stars often assume a stationary, hunched position that leaves them only weakly attached to the substrate (Feder, 1955; Tokeshi, 1989). This may make them more vulnerable to dislodgement by waves (see Menge, 1974, for a discussion of decreased attachment area and increased dislodgement risk for brooding sea stars, which assume a posture analogous to feeding sea stars), or predation by gulls and otters. By preferentially selecting prey items that minimize the feeding time required to meet a particular energy intake requirement, as juvenile *P. ochraceus* did in our study, sea stars would also have more time for nonfeeding activities such as locomotion while seeking refuge from desiccation or thermal stress ahead of a falling tide. Similar trade-offs in foraging time *versus* nonfeeding activities have been found in whelks avoiding wave action (Burrows and Hughes, 1991), birds protecting their territories (Krebs, 1980), and squirrels avoiding predation (Lima *et al.*, 1985). Overall, given our small sample sizes and lack of information on mussel profitability in adult sea stars, the degree to which *P. ochraceus* acts as an energy maximizer, time minimizer, or something in between will require additional study.

### Summary and implications

Understanding which mechanisms dictate *Pisaster ochraceus*’ upper bound on daily tissue intake could be important in predicting how increased risk or altered prey size distributions might affect an individual sea star’s behavior and energetic intake. For example, if its tissue consumption rate is primarily dictated by behavioral choices, it may choose to spend less time feeding in the face of increased wave force or high aerial temperatures (Robles *et al.*, 1995; Pincebourde *et al.*, 2008), resulting in a lower net intake of prey tissue. However, if its tissue consumption is based primarily on a physiological limit, increased risk of physical harm may not be the first thing to cap its tissue intake. If digestion or other physiological rates are the limiting factor to prey intake, changing environmental temperatures could influence this limit (Brown *et al.*, 2004; Pincebourde *et al.*, 2008), potentially altering the number of mussels or amount of tissue an individual could consume daily (e.g., Sanford, 2002; Gooding *et al.*, 2009).

The strong effects of body size on the *Pisaster ochraceus*-*Mytilus trossulus* interaction make it likely that changes to body size will be a major contributor to the overall effect of environmental change on their community structure (see Brose *et al.*, 2012, for examples of this dynamic in other systems). We may be able to generate predictions regarding effects of environmental or anthropogenic change by combining our knowledge of how these factors directly affect body size with our understanding of how body size affects the predator-prey interaction. On a broader scale, our findings reinforce the importance of body size in predator-prey interactions and suggest that these factors could play a large role in determining organism, population, and community responses to environmental or anthropogenic change. Quantifying the interactions between species in appropriate levels of detail will continue to be an important component of our ongoing quest to understand and predict how spatial and temporal environmental variation will affect species and community functioning.

### Acknowledgments

We thank E. Tang, K. Lee, and J. R. Lim for assistance in the laboratory; T. Ingram and R. Kordas for helpful feedback; and R. "Purple Star" Lewis for motivation. This work was supported by a U.S. National Science Foundation Graduate Research Fellowship to R.A.G. and a Canadian Natural Sciences and Engineering Research Council Discovery Grant to C.D.G.H.

### Literature Cited

- Aljetlawi, A. A., E. Sparrevik, and K. Leonardsson. 2004. Prey-predator size-dependent response: derivation and rescaling to the real world. *J. Anim. Ecol.* **73**: 239–252.
- Atkinson, D. 1995. Effects of temperature on the size of aquatic ectotherms: exceptions to the general rule. *J. Therm. Biol.* **20**: 61–74.
- Barnier, G. W., M. V. Sheehan, and D. C. Williams. 1975. The production and secretion of digestive enzymes in the Purple Seastar *Pisaster ochraceus*. *Mar. Biol.* **29**: 261–266.
- Bell, E. C., and J. M. Gosline. 1997. Strategies for life in flow: tenacity, morphometry, and probability of dislodgement of two *Mytilus* species. *Mar. Ecol. Prog. Ser.* **159**: 197–208.
- Brose, U., J. A. Dunne, J. M. Montoya, O. L. Petchey, F. D. Schneider, and U. Jacob. 2012. Climate change in size-structured ecosystems. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **367**: 2903–2912.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* **85**: 1771–1789.
- Burrows, M., and R. N. Hughes. 1991. Optimal foraging decisions by dogwhelks, *Nucella lapillus* (L.): influences of mortality risk and rate-constrained digestion. *Funct. Ecol.* **5**: 461–475.
- Denny, M. W., T. L. Daniel, and M. Koehl. 1985. Mechanical limits to size in wave-swept organisms. *Ecol. Monogr.* **55**: 69–102.
- Drinkwater, K. F., G. Beaugrand, M. Kaeriyama, S. Kim, G. Ottersen, R. I. Perry, H.-O. Pörtner, J. J. Polovina, and A. Takasuka. 2010. On the processes linking climate to ecosystem changes. *J. Mar. Syst.* **79**: 374–388.
- Emmerson, M. C., and D. Raffaelli. 2004. Predator-prey body size, interaction strength and the stability of a real food web. *J. Anim. Ecol.* **73**: 399–409.
- Feder, H. M. 1955. On the methods used by the starfish *Pisaster ochraceus* in opening three types of bivalve molluscs. *Ecology* **36**: 764–767.
- Feder, H. M. 1956. Natural history studies on the starfish *Pisaster ochraceus* (Brandt, 1835) in the Monterey Bay area. Ph.D. dissertation, Stanford University.
- Fenberg, P. B., and R. Kaustuv. 2008. Ecological and evolutionary consequences of size-selective harvesting: how much do we know? *Mol. Ecol.* **17**: 209–220.
- Gaylord, B., K. J. Kroeker, J. M. Sunday, K. M. Anderson, J. P. Barry, N. E. Brown, S. D. Connell, S. Dupont, K. E. Fabricius, J. M. Hall-Spencer *et al.* 2015. Ocean acidification through the lens of ecological theory. *Ecology* **96**: 3–15.
- Gaymer, C. F., C. Dutil, and J. H. Himmelman. 2004. Prey selection and predatory impact of four major sea stars on a soft bottom subtidal community. *J. Exp. Mar. Biol. Ecol.* **313**: 353–374.
- Gooding, R. A., C. D. G. Harley, and E. Tang. 2009. Elevated water temperature and carbon dioxide concentration increase the growth of a keystone echinoderm. *Proc. Natl. Acad. Sci.* **106**: 9316–9321.
- Green, A. J. 1992. Positive allometry is likely with mate choice, competitive display and other functions. *Anim. Behav.* **43**: 170–172.
- Harley, C. D. G. 2011. Climate change, keystone predation, and biodiversity loss. *Science* **334**: 1124–1127.
- Harley, C. D. G., M. S. Pankey, J. P. Wares, R. K. Grosberg, and M. J. Wonham. 2006. Color polymorphism and genetic structure in the sea star *Pisaster ochraceus*. *Biol. Bull.* **211**: 248–262.
- Hart, P. J. B., and A. B. Gill. 1992. Constraints on prey size selection by the three-spined stickleback: energy requirements and the capacity and fullness of the gut. *J. Fish Biol.* **40**: 205–218.
- Havens, K., and J. DeCosta. 1985. The effect of acidification in enclosures on the biomass and population size structure of *Bosmina longirostris*. *Hydrobiologia* **122**: 153–158.
- Heckmann, L., B. Drossel, U. Brose, and C. Guill. 2012. Interactive effects of body-size structure and adaptive foraging on food-web stability. *Ecol. Lett.* **15**: 243–250.
- Hixon, M. A. 1982. Energy maximizers and time minimizers: theory and reality. *Am. Nat.* **119**: 596–599.
- Jansson, M., L. Persson, A. M. De Roos, R. I. Jones, and L. J. Tranvik. 2007. Terrestrial carbon and intraspecific size-variation shape lake ecosystems. *Trends Ecol. Evol.* **22**: 316–322.
- Jochum, M., F. D. Schneider, T. P. Crowe, U. Brose, and E. J. O’Gorman. 2012. Climate-induced changes in bottom-up and top-down processes independently alter a marine ecosystem. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **367**: 2962–2970.
- Keppel, E. A., R. A. Scrosati, and S. C. Courtenay. 2015. Interactive effects of ocean acidification and warming on subtidal mussels and sea stars from Atlantic Canada. *Mar. Biol. Res.* **11**: 337–348.
- Kirkpatrick, M. 1984. Demographic models based on size, not age, for organisms with indeterminate growth. *Ecology* **65**: 1874–1884.
- Kozloff, E. N. 1996. *Marine Invertebrates of the Pacific Northwest*. University of Washington Press, Seattle, WA.
- Krebs, J. R. 1980. Optimal foraging, predation risk and territory defence. *Ardea* **68**: 83–90.
- Kroeker, K. J., E. Sanford, B. M. Jellison, and B. Gaylord. 2014. Predicting the effects of ocean acidification on predator-prey interactions: a conceptual framework based on coastal molluscs. *Biol. Bull.* **226**: 211–222.
- Landenberger, D. E. 1968. Studies on selective feeding in the Pacific starfish *Pisaster* in Southern California. *Ecology* **49**: 1062–1075.
- Lima, S. L., T. J. Valone, and T. Caraco. 1985. Foraging-efficiency-predation-risk trade-off in the grey squirrel. *Anim. Behav.* **33**: 155–165.



- Mauzey, K. P. 1966.** Feeding behavior and reproductive cycles in *Pisaster ochraceus*. *Biol. Bull.* **131**: 127–144.
- McClintock, J. B., and T. J. Robnett. 1986.** Size selective predation by the asteroid *Pisaster ochraceus* on the bivalve *Mytilus californianus*: a cost-benefit analysis. *PSZNI Mar. Ecol.* **7**: 321–332.
- Menge, B. A. 1972.** Competition for food between two intertidal starfish species and its effect on body size and feeding. *Ecology* **53**: 635–644.
- Menge, B. A. 1974.** Effect of wave action and competition on brooding and reproductive effort in the sea star, *Leptasterias hexactis*. *Ecology* **55**: 84–93.
- Menge, B. A., F. Chan, and J. Lubchenco. 2008.** Response of a rocky intertidal ecosystem engineer and community dominant to climate change. *Ecol. Lett.* **11**: 151–162.
- Michaelidis, B., C. Ouzounis, A. Paleras, and H. O. Pörtner. 2005.** Effects of long-term moderate hypercapnia on acid–base balance and growth rate in marine mussels *Mytilus galloprovincialis*. *Mar. Ecol. Prog. Ser.* **293**: 109–118.
- Morris, R. H., D. P. Abbot, and E. C. Haderlie. 1980.** *Intertidal Invertebrates of California*. Stanford University Press, Stanford, CA.
- Paine, R. T. 1966.** Food web complexity and species diversity. *Am. Nat.* **100**: 65–75.
- Paine, R. T. 1974.** Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal prey. *Oecologia* **15**: 93–120.
- Paine, R. T. 1976.** Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology* **57**: 858–873.
- Peck, L. S., M. S. Clark, S. A. Morley, A. Massey, and H. Rossetti. 2009.** Animal temperature limits and ecological relevance: effects of size, activity and rates of change. *Funct. Ecol.* **23**: 248–256.
- Pincebourde, S., E. Sanford, and B. Helmuth. 2008.** Body temperature during low tide alters the feeding performance of a top intertidal predator. *Limnol. Oceanogr.* **53**: 1562–1573.
- Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977.** Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.* **52**: 137–154.
- Robles, C., R. Sherwood-Stephens, and M. Alvarado. 1995.** Responses of a key intertidal predator to varying recruitment of its prey. *Ecology* **76**: 565–579.
- Rudolf, V. H. W., and N. L. Rasmussen. 2013.** Ontogenetic functional diversity: size structure of a keystone predator drives functioning of a complex ecosystem. *Ecology* **94**: 1046–1056.
- Sanford, E. 2002.** The feeding, growth, and energetics of two rocky intertidal predators (*Pisaster ochraceus* and *Nucella canaliculata*) under water temperatures simulating episodic upwelling. *J. Exp. Mar. Biol. Ecol.* **273**: 199–218.
- Sanford, E., and B. A. Menge. 2007.** Reproductive output and consistency of source populations in the sea star *Pisaster ochraceus*. *Mar. Ecol. Prog. Ser.* **349**: 1–12.
- Sanford, E., B. Gaylord, A. Hettinger, E. A. Lenz, K. Meyer, and T. M. Hill. 2014.** Ocean acidification increases the vulnerability of native oysters to predation by invasive snails. *Proc. R. Soc. B.* **281**: 20132681.
- Schoener, T. W. 1971.** Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* **2**: 369–404.
- Sewell, M. A., and J. C. Watson. 1993.** A “source” for asteroid larvae? Recruitment of *Pisaster ochraceus*, *Pycnopodia helianthoides* and *Derasterias imbricata* in Nootka Sound, British Columbia. *Mar. Biol.* **117**: 387–398.
- Springer, A. M., J. A. Estes, G. B. van Vliet, T. M. Williams, D. F. Doak, E. M. Danner, K. A. Forney, and B. Pfister. 2003.** Sequential megafaunal collapse in the North Pacific Ocean: an ongoing legacy of industrial whaling? *Proc. Natl. Acad. Sci. USA* **100**: 12223–12228.
- Tokeshi, M. 1989.** Development of a foraging model for a field population of the South American sun-star *Heliaster helianthus*. *J. Anim. Ecol.* **58**: 189–206.
- Vahl, O. 1984.** The relationship between specific dynamic action (SDA) and growth in the common starfish, *Asterias rubens* L. *Oecologia* **61**: 122–125.
- Warren, P. H., and J. H. Lawton. 1987.** Invertebrate predator-prey body size relationships: an explanation for upper triangular food webs and patterns in food web structure? *Oecologia* **74**: 231–235.
- Woodward, G., B. Ebenman, M. C. Emmerson, J. M. Montoya, J. Olesen, A. Valido, and P. Warren. 2005.** Body size in ecological networks. *Trends Ecol. Evol.* **20**: 402–409.