Size-dependent interference competition between two sea star species demographically affected by wasting disease

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ABSTRACT: In systems where species interaction strengths change with body size, perturbations which result in size-selective mortality can potentially alter interactions by affecting not only population density, but also size structure. This study examined the size-dependency of interference competition between the sea stars *Pisaster ochraceus* and *Evasterias troschelii* using field surveys and behavioral experiments to better understand the indirect demographic effects of sea star wasting disease (SSWD) on competitive interactions. In Puget Sound, Washington, where these species utilize similar prey resources and intertidal habitat, SSWD has reduced population densities and body sizes similarly for both species. Interference behaviors were not apparent among stars <4 cm arm length, but among larger individuals, *Pisaster* was dominant. In the field, small stars were found in aggregations of conspecifics and heterospecifics more often than were large stars. In behavioral trials, small stars responded neutrally towards conspecifics and heterospecifics, but large *Evasterias* responded submissively towards large *Pisaster*. Additional observations suggested that aggressive use of pedicellariae by *Pisaster* was the mechanism for these avoidance behaviors. Although demonstration of limiting resources is required to conclude that competition occurs in the field, our results suggest that SSWD has decreased the intensity of potential competitive interactions between *Pisaster* and *Evasterias* by reducing not only population density, but also body size. Prior to SSWD and if/when *Pisaster* recovers, interference competition may allow *Pisaster* to dominate in preferred habitats. However, if *Pisaster* recovers more slowly than *Evasterias*, *Evasterias* may move into areas formerly dominated by *Pisaster*, and potentially fill *Pisaster*'s ecological role.

KEY WORDS: Interference competition · Size-structured interactions · Sea star wasting disease · *Pisaster ochraceus* · *Evasterias troschelii* · Puget Sound

INTRODUCTION

Species interaction strengths can change with body size due to changes in behavior and diet across ontogeny (Werner & Gilliam 1984, Gosselin & Qian 1997). As a result, perturbations which result in size-selective mortality, such as disease outbreaks, size-selective harvest, and climate change, can potentially alter species interactions and affect community structure (Fenberg & Roy 2008, Brose et al. 2012,

Eisenlord et al. 2016). For example, selective harvest of large limpets on rocky shores can affect the abundance of their avian predators, algal prey, and competing limpet species (Lindberg et al. 1998). Disease-induced mortality may also alter population size structure, but few studies have explored the resulting effects on species interactions. Pathogens and parasites are known to alter the strength and outcome of interactions through effects on fitness and behavior (Hatcher et al. 2006), but changes to population

demographics may be another, indirect means by which diseases can alter interactions.

In marine systems, sea stars are major predators that can have strong top-down impacts on their associated communities (Paine 1966, Menge et al. 1994, Robles et al. 2009) and compete with other sea star species for food (Menge 1972, Wobber 1975, Sloan 1984, Morissette & Himmelman 2000, Gaymer et al. 2002). The recent outbreak of sea star wasting disease (SSWD) on the Pacific coast of North America, which began in 2013–2014, has caused not only great declines in sea star density, but also altered the size structure of sea star populations (Eisenlord et al. 2016, Menge et al. 2016, Montecino-Latorre et al. 2016). In many areas, the abundance of juvenile and adult sea stars has declined, and some sites experienced a large influx of sea star recruits in 2015 (Menge et al. 2016). Understanding the relationship between body size and interaction strength is therefore relevant to understanding potential indirect effects of wasting disease on species interactions.

Although the effect of sea star body size on predatory interactions (Paine 1976, Sommer et al. 1999), and ontogenetic changes in sea star habitat use (Himmelman & Dutil 1991, Verling et al. 2003, Manzur et al. 2010, Bos et al. 2011, Rogers & Elliott 2013) have been well documented, the role of body size in competitive interactions has been less well explored. Competition between top predators such as sea stars has possible implications for predator distribution and coexistence, patterns of resource use, and community structure, as the presence of a competing species can trigger avoidance behaviors, changes in feeding behavior, and reductions in feeding rate (Menge & Menge 1974, Gaymer et al. 2002).

In this study, we examined the size-dependency of interference competition between *Pisaster ochraceus* and *Evasterias troschelii* (hereafter *Pisaster* and *Evasterias*), 2 common predatory sea star species that co-occur along the Pacific coast of North America. Both have experienced mortality from SSWD (Eisenlord et al. 2016, Menge et al. 2016, Montecino-Latorre et al. 2016); however, studies of SSWD have tended to focus primarily on *Pisaster*. Although there is regional variation in the habitat use and diet of *Pisaster* and *Evasterias* (Mauzey et al. 1968, Lambert 2001), we have observed the 2 species to be similarly abundant in intertidal and shallow subtidal habitats in our study region (south Puget Sound) to be of similar size, and to have similar diets primarily of mussels and barnacles (Rogers & Elliott 2013). While the diet and predatory influence of the keystone species *Pisaster* has been well studied (e.g. Feder 1959, Paine

1976), the ecologically comparable *Evasterias* has received relatively little attention, and its relationship with *Pisaster* is not as well known. *Pisaster* has shown changes in population size structure as a result of SSWD (Eisenlord et al. 2016), but whether SSWD has differentially affected the size and density of *Pisaster* and *Evasterias* is not known.

Pisaster has been reported to outcompete the smaller sea star *Leptasterias hexactis* for food in the San Juan Islands (Menge 1972), but the 2 are suspected to coexist by specializing on differently sized prey (Menge & Menge 1974). As a result, Menge (1972) predicted that coexistence between *Pisaster* and a similarly sized sea star such as *Evasterias* might not be possible. Indeed, prior to SSWD, the distribution of *Pisaster* and *Evasterias* in the field suggested that *Pisaster* may partially exclude *Evasterias* from habitats with higher quality food resources (Rogers & Elliott 2013). Interference competition (aggressive behavior) was the mechanism for *Pisaster*'s dominance over *L. hexactis* (Menge & Menge 1974); thus, our study focused primarily on interference as opposed to exploitative competition. Interference competition occurs when one organism physically prevents another from using a common resource. Exploitative competition occurs when one organism consumes resources at a faster rate than another, making them unavailable for the competitor.

We predicted that the mechanism for interference competition between *Pisaster* and *Evasterias* of different sizes would be differences in the use and morphology of pedicellariae (small, calcareous, claw-like structures on the aboral surface of many sea star species used in aggression and defense). *Pisaster* uses its pedicellariae to pinch *L. hexactis* (Menge & Menge 1974) and to defend itself against predatory species (Wobber 1975). There is also evidence that *Pisaster* body size may influence the effectiveness of defensive pedicellariae use against the predatory sea star *Solaster dawsoni* (Van Veldhuizen & Oakes 1981).

To examine the size-dependency of interference competition between *Pisaster* and *Evasterias* in the context of SSWD, we first documented changes in abundance and size distribution of *Pisaster* and *Evasterias* before and after SSWD in field surveys of fixed plots. We then studied interference interactions by (1) examining the proximity of *Pisaster* and *Evasterias* of different sizes to conspecifics and heterospecifics in the field, (2) experimentally quantifying behavioral interactions between *Pisaster* and *Evasterias* of different sizes, and (3) examining whether changes in pedicellaria morphology and activity could provide a mechanism for the observed behav-

iors. We predicted that *Pisaster* would be dominant to *Evasterias* and that interspecific interference behaviors would increase with increasing body size.

MATERIALS AND METHODS

Field surveys of sea star size and abundance

To document changes in the abundance and size distribution of *Pisaster* and *Evasterias*, we recorded the species and body size of all sea stars within fixed plots at 4 intertidal sites in South Puget Sound (Hyde Park, Pt. Defiance, Ruston Way, and Titlow) before SSWD (2013–2014) and after SSWD (2015–2017), searching under rocks and boulders during low tide (Rogers & Elliott 2013, Eisenlord et al. 2016). All sites were surveyed during April or May of each year from 2014 to 2017. During 2013 and 2014, surveys were done during additional months (December 2013; January, July, August 2014) in order to monitor the progression and onset of SSWD. For all sea stars, we used arm length (center of disk to tip of the arm) as our measure of body size, and we divided the sea stars into 3 sizes classes consistent with those used in previous studies (Menge et al. 2016, Eisenlord et al. 2016): recruit (0.5 to 4 cm arm length), juvenile (4 to 7 cm), and adult (7 to 25 cm). We used these size classes consistently throughout our study.

Field surveys of sea star proximity

To examine avoidance behavior of sea stars in the field, we surveyed the proximity of *Pisaster* and *Evasterias* of different size classes to other sea stars at 4 intertidal sites (Hyde Park, Pt. Defiance, Ruston Way, and Manchester State Park) during the summer (May to August) of 2014. Methods were the same as in the abundance and size distribution surveys, except we also photographed all sea stars. From the photographs, we recorded whether each individual was in close proximity to conspecifics and/or heterospecifics. A sea star was considered 'in close proximity' to another sea star if it was either touching or within 1 cm of another individual.

Behavioral interactions within different size classes

To quantify size-dependent interference competition, we examined interactions between sea stars of the same size class in several laboratory experiments.

All studies were performed during the summer months (May to August). For all experiments, *Pisaster* and *Evasterias* were collected from intertidal locations in south Puget Sound. Sea stars were separated by species in holding tanks, and not fed before use in experimental trials. Since we were interested primarily in the effect of size, rather than disease state, we only used individuals without symptoms of SSWD. We only examined interactions among individuals within each size class because competition (diet, habitat use) is expected to be greatest among similarly sized individuals. In line with this prediction, similarly sized sea stars were often found in similar habitats and microhabitats in our current and previous field surveys (Rogers & Elliott 2013).

Behavioral responses to contact

Prior to the SSWD outbreak, in 2009, we examined behavioral interactions between juvenile and adult *Pisaster* and *Evasterias* (recruits were rare at this time and not used). We placed individual sea stars in rectangular, plexiglass tanks with either 1 conspecific or 1 heterospecific of the same size class and filmed them using time lapse video for 2 to 4 h. Trials were conducted in a windowed room with natural light, but were shaded from direct sun. The video camcorder, which was positioned directly above the tank, recorded at intervals of either 0.5 s every 30 s (Sony DCR-DC120 NTSC), or 1 frame every 8 s (Sony DCR-HC42 NTSC).

We filled the experimental tank with fresh seawater immediately before adding the 2 sea stars, which were placed in the center of the tank, ~3 to 5 cm apart. Different sized experimental tanks were used depending on size class, as the tank needed to be large enough to allow the sea stars to move freely without contacting one another, but small enough to ensure a sufficient number of interactions would take place. We used a $100 \times 75 \times 30$ cm tank for large adults (14 to 25 cm), a $50 \times 40 \times 20$ cm tank for small adults (7 to 14 cm), and a $25 \times 20 \times 20$ cm tank for juveniles. Between trials, the tanks were emptied, wiped down with a paper towel, and rinsed with fresh seawater. For each species combination (heterospecific, *Evasterias–Evasterias*, and *Pisaster–Pisaster*), we performed 3 to 5 trials with juveniles and 6 to 10 trials with adults. Due to a limited number of specimens, particularly juvenile *Pisaster*, a minority of individuals used in conspecific trials were also used in heterospecific trials.

After the SSWD outbreak, in 2014, we repeated these trials using recruit and juvenile size classes

(adults were rare at this time and not used). We placed 4 sea stars of the same size class (all *Evasterias*, all *Pisaster*, or 2 *Evasterias* and 2 *Pisaster*) equidistant from one another in a circular container (28 cm diameter for juveniles and 16 cm diameter for recruits) filled with fresh seawater and filmed them for 30 min. Trials for juvenile sea stars were conducted in the field directly after collection under natural light but shaded from direct sun. Trials for recruits were conducted in a 12°C cold room under fluorescent lighting, and sea stars were held in a tank for a few days before trials were run. For each species combination, 6 or 7 trials were performed for each size class.

From the videos from both the 2009 and 2014 trials, we quantified the number of interactions (contacts) each sea star had with the other sea star(s) with which it was paired, and whether it responded submissively or neutrally in those interactions. Submissive responses were those in which the sea star clearly attempted to avoid contact with the other by retracting or curling away its arm and/or changing directions. Neutral responses were those in which the sea star made no attempt to avoid contact with the other sea star, and there was no discernible change in behavior after contact. We excluded 3 trials from 2009 in which <4 interactions occurred. The responses of conspecific sea stars in the same trial were averaged. Conspecific interactions in 2014 *Pisaster*–*Evasterias* trials were not included in the analysis. For each size class, we evaluated the effect of species and interaction type (conspecific or heterospecific) on the proportion of submissive responses using a binomial generalized linear model (logistic regression) with logit link function. The 2009 and 2014 trials were analyzed separately. All analyses were performed in R v.3.3.1 (R Core Team 2016).

Response of feeding *Evasterias* to contact with *Pisaster*

In 2009, we also examined the response of feeding *Evasterias* to contact with *Pisaster.* Individual *Evasterias* of juvenile and adult size (4 to 25 cm) were placed in a tank with a live, unattached mussel *Mytilus trossulus* ~2 to 4 cm in shell length. After centering itself over the mussel and hunching into the feeding position, the *Evasterias* was left to feed undisturbed for 10 min. After this initial feeding period, a size-matched *Pisaster* (n = 19) or *Evasterias* (n = 11) was placed on top of the feeding *Evasterias*. We recorded whether the feeding *Evasterias* remained stationary, moved away while maintaining possession of the mussel, or moved away and aban-

doned the mussel. *Evasterias* were not placed on top of feeding *Pisaster* because *Pisaster* did not feed readily on the mussels in the lab. The results were analyzed using a contingency table analysis.

Pedicellariae as a mechanism for competition

As a mechanism for the behavioral responses observed in our experiments, we examined the types, sizes, and use of pedicellariae by each sea star species. Pedicellariae are small, calcareous, claw-like structures found on the surface of many echinoderms (Campbell 1983). The types of pedicellariae we observed included crossed (the smallest, shaped like pliers), furcate (medium-sized, shaped like staple removers) and straight (the largest, shaped like alligator clamps).

Pedicellaria morphology

We collected recruit, juvenile, and adult (1 to 13 cm) *Pisaster* (n = 12) and *Evasterias* (n = 11) in 2014, fixed the specimens in buffered formalin, and stored them in 70% ethanol. We removed clumps of pedicellariae from the aboral surface of each specimen with forceps, dissolved the tissue with bleach, and visualized the isolated pedicellariae with a Hitachi S3400N variable pressure scanning electron microscope. For each specimen, we measured the lengths (base to tip) of 2 to 5 haphazardly selected pedicellariae of each of the 2 most common pedicellaria types (crossed and furcate), if present. We averaged the lengths of each pedicellaria type for each specimen. The effect of arm length and species on crossed pedicellaria length was analyzed using ANCOVA. The effect of arm length on furcate pedicellaria length in *Pisaster* was analyzed using linear regression.

For an additional 7 *Pisaster* specimens (recruits 1.3 to 3.1 cm arm length), we collected all pedicellariae present in a 3 × 3 mm subsample of the aboral surface, dissolved the tissue with bleach, and counted the number of each pedicellaria type. We calculated the proportion of each type out of the total number in the subsample, and used Spearman rank correlation to evaluate the relationship between arm length and the proportion of furcate pedicellariae.

Pedicellaria activity

To examine fine-scale changes in pedicellaria activity in response to contact with another sea star,
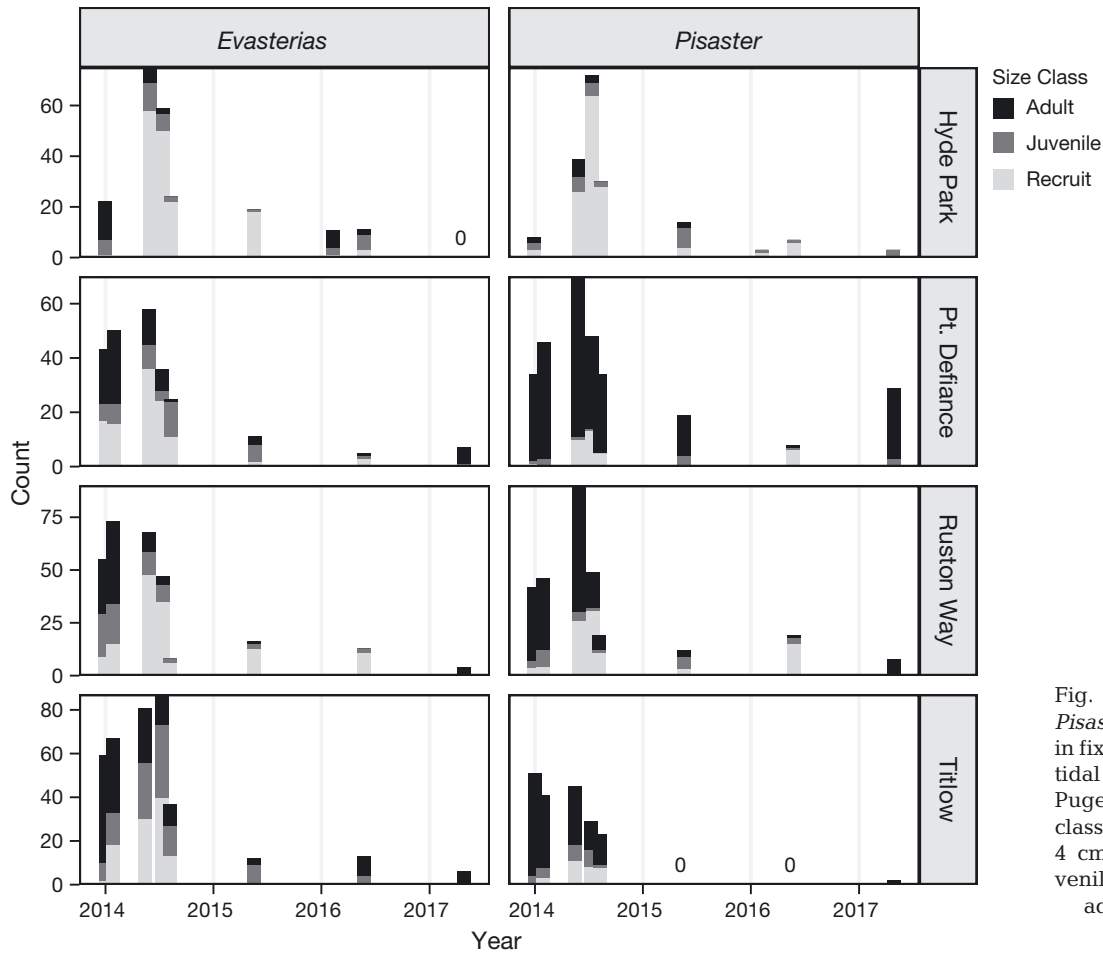
Fig. 1. Abundance of *Pisaster* and *Evasterias* in fixed plots at 4 intertidal sites in South Puget Sound, for 3 size classes: recruit (0.5 to 4 cm arm length), juvenile (4 to 7 cm), and adult (7 to 23 cm)

we placed a *Pisaster* or *Evasterias* on the aboral surface of a focal conspecific or heterospecific submerged in seawater and observed the aboral surface of the focal sea star using a dissecting microscope. We observed qualitative changes in pedicellaria activity, respiratory papulae contraction, arm movement, and locomotion. This work was conducted in 2009 using juvenile and adult sea stars.

RESULTS

Field surveys of sea star size and abundance

Both *Pisaster* and *Evasterias* showed similar declines in abundance after the onset of SSWD in South Puget Sound (Fig. 1). Over the course of 2014, the year of SSWD onset, most sites showed a decline in adult sea star abundance that coincided with a large pulse of recruitment. The recruitment pulse in 2014 was larger than annual recruitment pulses regularly observed in prior years (J. K. Elliott pers. obs.), and recruitment after 2014 was extremely low. In 2015

and 2016, spring sea star abundances were far below spring abundances in 2014, and populations of both species consisted primarily of recruit and juvenile sea stars. In 2017, overall abundances remained low; however, many populations consisted primarily of adults. It is not known whether the adults observed in 2017 were survivors of the initial outbreak, or whether they recruited during the pulse following the outbreak and took several years to reach adult size.

Field surveys of sea star proximity

Across the 4 sites for which we assessed the size and proximity of *Pisaster* and *Evasterias*, the proportion of sea stars in close proximity to a conspecific and/or heterospecific was lower for adult sea stars than for recruits (Fig. 2). Recruits of both species were often found in single- or multi-species aggregations under rocks in the field, and the majority (53%) of *Pisaster* recruits were found in close proximity to other *Pisaster* (Fig. 2). Larger sea stars, however, were more often found alone. While some adult
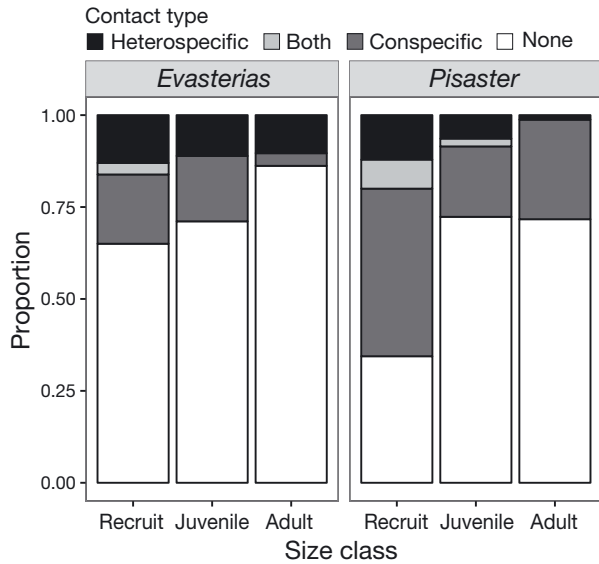
Fig. 2. Proportion of *Pisaster* and *Evasterias* in close proximity to conspecifics and heterospecifics in the field for 3 size classes: recruit (0.5 to 4 cm arm length), juvenile (4 to 7 cm), and adult (7 to 23 cm). Left to right, n = 223, 45, 29, 215, 47, 166

Pisaster were found in contact with other *Pisaster* in the field, few adult *Pisaster* (1%) were found in close proximity to *Evasterias*.

Behavioral interactions within different size classes

Behavioral responses to contact

For adult sea stars (2009 only), there was a significant interaction between species and interaction type (Table 1, Fig. 3a). *Pisaster* and *Evasterias* responded similarly to conspecifics (<10% of interactions were submissive on average), and *Pisaster* responded similarly to both conspecifics and heterospecifics. *Evasterias*, however, responded very submissively to *Pisaster*. For juvenile sea stars, there was a significant effect of species and interaction type on the proportion of submissive responses, but no interaction between species and interaction type (Table 1, Fig. 3a,b). This was consistent in both the 2009 and 2014 trials. Juveniles of both species responded more to heterospecifics than conspecifics. *Evasterias* responded more than *Pisaster* in both types of interactions, such that *Evasterias* responded submissively to *Pisaster* in over half of all interactions

on average. For sea stars in the recruit size class, there was no effect of species or interaction type on the proportion of submissive responses (Table 1, Fig. 3b). Neither species in the recruit size class exhibited a strong response to either conspecifics or heterospecifics.

Response of feeding *Evasterias* to contact with *Pisaster*

Feeding *Evasterias* were more likely to move away or abandon food if contacted by *Pisaster* than if contacted by another *Evasterias* (contingency table analysis, $\chi^2 = 15.7$, p < 0.001; Table 2). Movement of *Evasterias* away from *Pisaster* typically occurred very quickly (<60 s), and *Evasterias* only abandoned its food when contacted by *Pisaster*. *Evasterias* were most likely to remain stationary if contacted by a conspecific. For the range of sea star sizes used in these experiments (4 to 25 cm), there was no apparent effect of size on the behavioral response of *Evasterias*.

Pedicellariae as a mechanism for competition

Pedicellaria morphology

Evasterias possessed only crossed pedicellariae, whereas *Pisaster* possessed several pedicellariae types (crossed, furcate, and straight). Crossed pedicellaria length increased with increasing arm length (ANCOVA, arm length, $F_{1,19} = 22.9$, p < 0.001;

Table 1. Analysis of deviance results for the proportion of submissive responses in sea star behavioral trials (Type II Wald chi-squared tests). The effect of species (*Pisaster* or *Evasterias*) and interaction type (conspecific or heterospecific) were evaluated for each size class. *p < 0.05; **p < 0.001

| Trial year	Size class	Source	χ^2-value	p-value	Significance
2009	Adult	Species	88.36	<0.001	**
		Interaction type	99.64	<0.001	**
		Species × interaction type	6.516	0.011	*
	Juvenile	Species	31.77	<0.001	**
		Interaction type	24.00	<0.001	**
		Species × interaction type	0.89	0.346	
2014	Juvenile	Species	80.40	<0.001	**
		Interaction type	73.55	<0.001	**
		Species × interaction type	1.03	0.310	
	Recruit	Species	0.17	0.682	
		Interaction type	1.95	0.162	
		Species × interaction type	2.29	0.130	
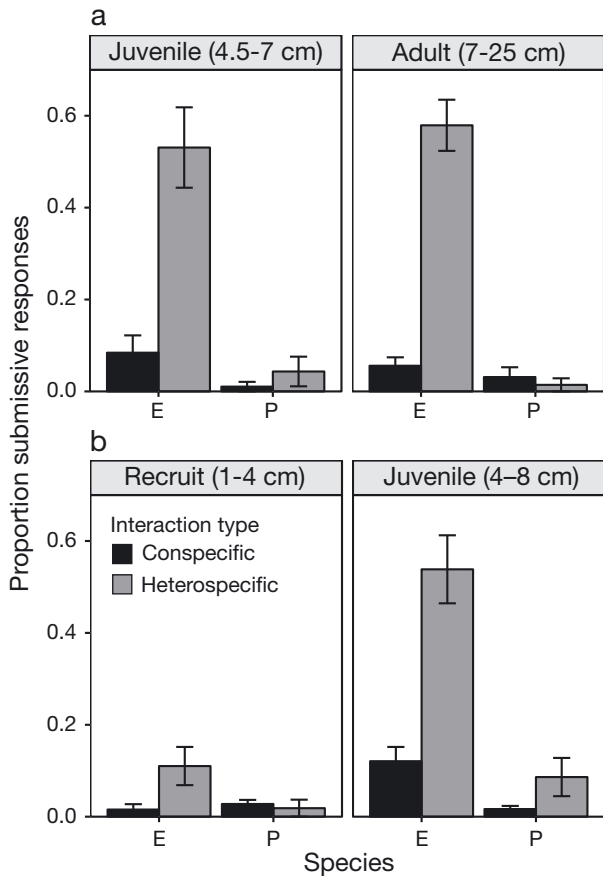
Fig. 3. Proportion submissive responses (mean ± 1 SE) of *Pisaster* (P) and *Evasterias* (E) as a function of size class and interaction type (response to conspecific or heterospecific) for (a) 2009 trials (n = 3 to 5 for juveniles, n = 6 to 10 for adults) and (b) 2014 trials (n = 6 to 7). Key in (b) applies to both panels

Table 2. Responses of feeding *Evasterias* to contact with a conspecific or *Pisaster*

Response of feeding *Evasterias*	Sea star placed on top	
	Evasterias	*Pisaster*
Remains stationary	9	2
Moves away	2	11
Moves away and abandons food	0	6

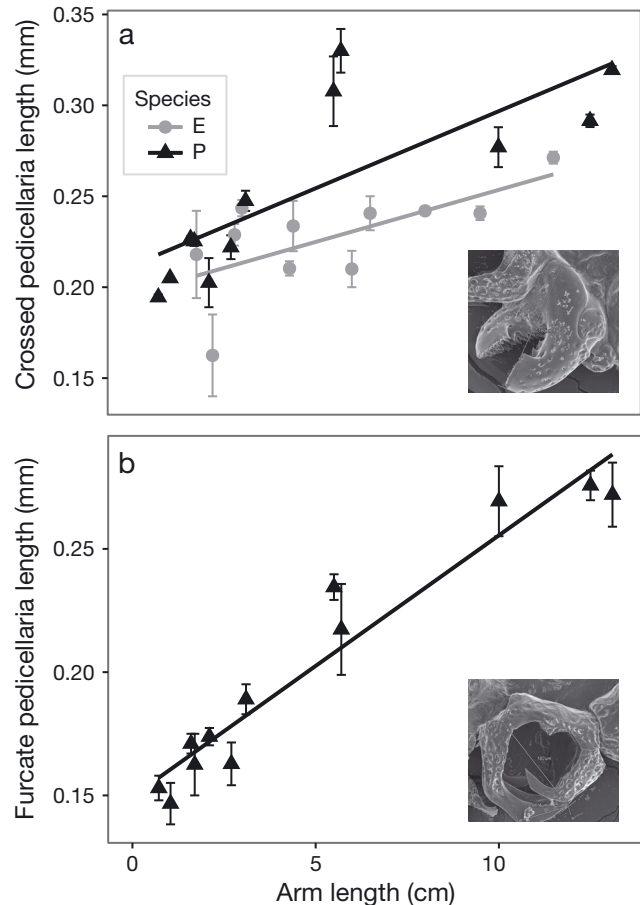

Fig. 4. (a) Relationship between arm length and crossed pedicellaria length (mean ± 1 SE) for *Pisaster* (P) *and Evasterias* (E). (b) Relationship between arm length and furcate pedicellaria length (mean ± 1 SE) for *Pisaster*. For each sea star, 2 to 5 pedicellariae were measured. Insets are scanning electron micrographs of crossed (a) and furcate (b) pedicellariae

Fig. 4a). This increase was similar for both species (species × arm length, $F_{1,19}$ = 0.67, p = 0.42). However, for a given arm length, *Pisaster* had longer crossed pedicellariae than *Evasterias* (species, $F_{1,19}$ = 6.83, p = 0.017). Furcate pedicellaria length in *Pisaster* also increased with increasing arm length (linear regression, $F_{1,10}$ = 137.7, p < 0.001, R^2 = 0.93; Fig. 4b). For *Pisaster* there was no relationship between the proportion of furcate pedicellariae and arm length (Spearman rank correlation, r = 0.56, n = 7, p = 0.19). On average, *Pisaster* possessed 76% (±5% SE) furcate, 16% (±3%) crossed, and 7% (±4%) straight pedicellariae.

Pedicellaria activity

In response to conspecifics, neither species activated pedicellariae. Generally, conspecific sea stars moved slowly away from one another, partially re-

tracting their respiratory papulae at points of contact. In response to heterospecifics, both species fully retracted their papulae, extended and gaped pedicellariae, and crawled away from the other sea star (Fig. 5). Papulae contraction and pedicellariae extension typically occurred within <60 s of initial contact. In *Evasterias*, this response typically occurred only at the points of contact with *Pisaster*. In *Pisaster* this
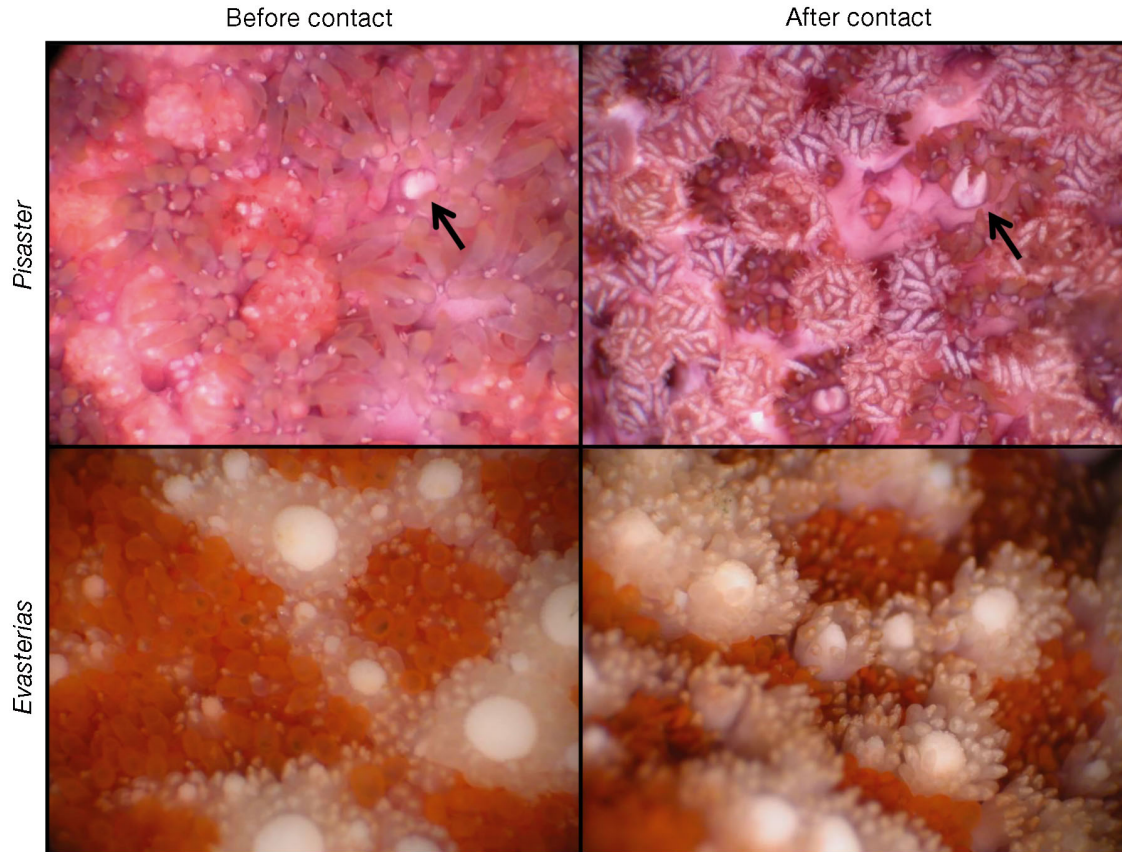
Fig. 5. Aboral surface of *Pisaster* (top panels) and *Evasterias* (bottom panels) before and after contact with a heterospecific (~4×
magnification). Images for *Pisaster* depict the same area (arrows point to a straight pedicellaria). Both species contracted papu-
lae and extended pedicellariae within 1 min of contact. Clusters of crossed and furcate pedicellariae are visible on *Pisaster* in
the top right image. *Evasterias* extended crossed pedicellariae arranged in clusters encircling the spines

response occurred over a greater area than that di-
rectly contacted by *Evasterias*, which often included
multiple arms, and on some occasions, the entire
body of the sea star. Frequently, clusters of pedicel-
lariae would detach from *Pisaster* and remain stuck
to the surface of *Evasterias* for several days.

DISCUSSION

Our study suggests that size-dependent interfer-
ence behaviors occur between the sea stars *Pisaster*
and *Evasterias*, and that SSWD, by reducing the rel-
ative abundance of adults and increasing the relative
abundance of recruits, may have indirectly reduced
the strength of interspecific competition. We found
little evidence of interference behaviors among re-
cruits (<4 cm arm length), but such behaviors were
apparent among larger individuals (juveniles and
adults), and *Pisaster* appeared to be dominant. In the
field, recruits were found in close proximity to con-

specifics and heterospecifics more often than larger
sea stars, and they did not exhibit strong submissive
responses towards conspecifics or heterospecifics in
behavioral trials. In contrast, larger individuals were
more often alone in the field, and larger *Evasterias*
responded submissively towards larger *Pisaster* in
behavioral trials (but not vice versa). In addition,
juvenile and adult *Evasterias* were more likely to
move away or abandon food if contacted by *Pisaster*
than by a conspecific. If limiting resources can be
demonstrated in the field, these behavioral results
suggest that interference competition could occur
between larger individuals of these species, domi-
nated by *Pisaster*.

In other rocky intertidal systems where one com-
petitor has experienced size-selective mortality (e.g.
size-selective harvesting of limpets and sea urchins),
increases in the abundance of competing species
have been observed, as well as a variety of indirect
effects on the intertidal community, including shared
algal prey and avian predators (Lindberg et al. 1998,

Guidetti et al. 2004). At our intertidal field sites in Puget Sound, however, both species have experienced similar declines in abundance and changes in size structure, and at present, increases in the relative abundance of *Evasterias*, the subordinate species, have not been observed. In the Salish Sea subtidal, there is some evidence that *Pisaster* has declined more than *Evasterias* in response to SSWD, although *Pisaster* is primarily an intertidal species with naturally low subtidal abundances (Montecino-Latorre et al. 2016). The immediate effects of SSWD on intertidal community structure may be primarily through the disease's effect on sea star abundance, the resulting decline in sea star predation pressure, and release from competition of non-asteroid predators such as whelks. However, competition among sea stars may become important if there are any asymmetries in recovery. If the recovery of *Pisaster* is slower than that of *Evasterias*, we might expect *Evasterias* to move into areas formerly dominated by *Pisaster*, and to potentially fill *Pisaster*'s ecological role. Prior to SSWD and if/when *Pisaster* recovers fully, interference competition may allow *Pisaster* to dominate in preferred habitats, as predicted by Menge & Menge (1974). Prior to SSWD, larger individuals of both species were found in habitats with more abundant food resources (rocky, piling, and dock habitats), and *Pisaster* tended to be more abundant than *Evasterias* in these habitats (Rogers & Elliott 2013). Competition could be one explanation for this pattern. *Evasterias* were also abundant at a minority of rocky intertidal sites where *Pisaster* were rare, such as Cattle Point on San Juan Island (T. L. Rogers & J. K. Elliott unpubl. data), which is suggestive of competitive exclusion.

Our results are consistent with a number of studies in other species, which have observed increases in interference interactions with increasing body size. Episodic recruitment may lead to high densities of juveniles subject to intense predation pressure, which may show reduced interference behaviors in early life history stages (Werner & Gilliam 1984). As individuals grow and compete for more limited shelter and food, they often become more aggressive, and density-dependent growth, mortality, and emigration rates become apparent. Examples can be seen in juvenile reef fish (Hixon & Jones 2005), crabs (Baeza et al. 2002, Moksnes 2004), and frog tadpoles (Werner 1994). Recruit and juvenile *Pisaster* and *Evasterias* are subject to intense predation pressure by gulls, and take shelter from predation under boulders and in crevices (Rogers & Elliott 2013). Sea star recruits living in these confined spaces appear to show reduced interference behaviors; however, exploitative competition may still occur.

Our work suggests aggressive use of pedicellariae by *Pisaster* is the mechanism for interference behaviors between *Pisaster* and *Evasterias*, and is what triggers the immediate, submissive responses of *Evasterias* to *Pisaster*. Similarly, *Leptasterias hexactis* reduced its feeding rate when subjected to pedicellaria aggression by *Pisaster* (Menge & Menge 1974). Although both *Pisaster* and *Evasterias* activated pedicellariae in response to heterospecifics, *Evasterias* possessed only the smallest pedicellaria type (crossed) and for a given arm length, had smaller crossed pedicellariae than *Pisaster*. This may explain the inability of *Evasterias* to alter the behavior of *Pisaster*. In contrast, *Pisaster*'s clusters of furcate pedicellariae, which detached onto the epidermis of *Evasterias*, may result in physical injury. The pedicellariae of both *Pisaster* and *Evasterias* became larger as they grew, which may explain why only larger *Pisaster* could elicit avoidance behaviors in *Evasterias*. The relevance of these responses to competition in the field remains to be tested. *Pisaster* (and other echinoderms) are known to use pedicellariae against potential predators (Wobber 1975, Dayton et al. 1977, Morissette & Himmelman 2000, McClintock et al. 2008), and although *Pisaster* and *Evasterias* do not prey on one another, it is possible that the pedicellariae response we observed could be a generalized anti-predator response towards heterospecifics, rather than a response to potential competitors.

The extent to which competition for limiting resources occurs in the field, its ultimate effects on growth and fitness, and the extent to which it is driven by exploitative versus interference competition remains to be tested through field (addition and removal) and laboratory experiments. Although there was no apparent inverse correlation between *Pisaster* and *Evasterias* density in the field at the site level (Rogers & Elliott 2013) as was seen for *Pisaster* and *L. hexactis* (Menge 1972), *Evasterias* may avoid areas occupied by *Pisaster* at the scale of individual prey items or aggregations, with ecological consequences, even if the species do not differ in abundance at the site level (Fancourt 2016). More importantly, however, the degree of dietary and habitat overlap between *Pisaster* and *Evasterias*, as well as between *Pisaster* and *L. hexactis* (which is likely a species complex; Foltz et al. 1996), is likely to be variable among locations and needs to be fully considered before definitive conclusions about competition can be made. For instance, *Evasterias* is also found

subtidally, where this species may have access to alternative prey resources (Young 1984). In addition, the abundance of sea stars relative to food resources is high in some habitats and low in others (Rogers & Elliott 2013), which may affect the relevance of competition. Moreover, if competition is relevant, the degree to which SSWD has affected competition via direct effects on population density versus indirect effects on size structure (interaction strength) is also in need of further research. It may be that reduced population density, which would reduce the probability of encounters between individuals and decrease shelter and/or food limitation, has a greater effect on competition than altered demographics.

In summary, we present the first known study of interactions between the sea stars *Pisaster* and *Evasterias*. We offer evidence that interference competitive behaviors occur among juvenile and adult sea stars, but not among recruits, and that among juveniles and adults, *Pisaster* is dominant and uses its pedicellariae to drive away *Evasterias*. SSWD has likely decreased potential competitive interactions between *Pisaster* and *Evasterias*, not only by decreasing population density, but also by reducing the sizes of individuals. In locations where the decline and/or recovery of sea stars from SSWD is asymmetric, competitive interactions (or lack thereof) may contribute to the resulting distribution and abundance of sea star species, and to their impact on the intertidal community. More broadly, size-selective mortality that results in a reduction of competition may help promote coexistence among competitors. Size-selective mortality that disproportionately affects one species may eliminate, reverse, or enhance competitive dominance relationships and affect species persistence.

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