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NOTE

Intraspecific agonistic arm-fencing behavior in the Antarctic keystone sea star *Odontaster validus* influences prey acquisition

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ABSTRACT: The importance of intraspecific social behaviors in mediating foraging behaviors of marine invertebrate keystone predators has received little attention. In laboratory investigations employing time-lapse video, we observed that the keystone Antarctic sea star *Odontaster validus* displays frequent agonistic arm-fencing bouts with conspecifics when near prey (injured sea urchin). Arm-fencing bouts consisted of 2 individuals elevating the distal portion of an arm until positioned arm tip to arm tip. This was followed by intermittent or continuous arm to arm contact, carried out in attempts to place an arm onto the aboral (upper) surface of the opponent. Fifteen (79%) of the 19 bouts observed occurred near prey (mean ± 1 SE, 13 ± 1.6 cm distance to prey; n = 13). These bouts lasted 21.05 ± 2.53 min (n = 15). In all 5 bouts that involved a large individual (radius, R: distance from the tip of an arm to the center of the oral disk; 45 to 53 mm) competing with either a medium (R = 35 to 42 mm) or small (R = 25 to 32 mm) individual, the large sea star prevailed. The only exception occurred in 2 instances where a medium-sized sea star had settled onto prey and was subsequently challenged by a larger individual. Here, the outcomes were reversed in favor of the medium-sized individuals. These complex social behaviors mediating intraspecific competition for the acquisition of prey by a keystone predator are likely to have significant ramifications in terms of individual fitness, population structure, and community composition.

KEY WORDS: Keystone species · Agonism · Arm-fencing behavior · Predation · Sea star · *Odontaster validus*

INTRODUCTION

Keystone predators exert a disproportionate influence on the structure of communities relative to their abundance (Paine 1966, 1980, 1995). As such, factors that mediate their foraging behaviors may have far-reaching effects and are thus important to consider. In marine benthic communities, a classic example of a keystone predator is the temperate rocky intertidal sea star *Pisaster ochraceus* (Paine 1966). Known to consume primarily mussels (Feder 1959), the feeding activity of *P. ochraceus* prevents the monopolization of hard substrate by mussels, and this promotes increased habitat heterogeneity and higher species diversity. Palumbi & Freed (1988) demonstrated that *P. ochraceus* displays a form of agonistic intraspecific social behavior that increases dispersion among individuals when placed in high-density aggregations. This may result, in part, from pinching by pedicellaria, which is known to occur between individuals (Menge & Menge 1974). Accordingly, Palumbi & Freed (1988) concluded that social interactions that influence predation intensity by keystone species can have dramatic effects on prey diversity.

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A lesser known but equally important keystone predator is the Antarctic sea star *Odontaster validus.* This ubiquitous shallow-water species is omnivorous and exhibits a remarkable array of different types of feeding behaviors (Pearse 1965, 1969, Dearborn 1977, McClintock et al. 1988, reviewed by McClintock 1994). In a seminal field study, Dayton et al. (1974) found that *O. validus* serves as the keystone predator in the sponge-dominated Antarctic benthos by controlling populations of the large spongivorous sea star *Acodontaster conspicuus*. *O. validus* accomplishes this by inadvertently consuming the larvae and early juveniles of *A. conspicuus* through its filter and detrital feeding behaviors, as well as serving as a direct predator on adult sea stars.

Wobber (1975) first documented agonism in sea stars. In field studies, he reported *in situ* SCUBA observations of intraspecific encounters involving arm contact between 6 species of sea stars in Monterey Bay, California, USA. Additional behavioral studies with sea stars have documented interspecific escape and alarm responses (van Veldhuizen & Oakes 1981, McClintock et al. 2008) and interference competition for prey (Gaymer et al. 2002). With respect to intraspecific behavioral interactions, Wobber (1975) described in detail agonistic arm-fencing bouts in *Patiria miniata* and *Pycnopodia heliathoides.* These bouts generally occurred in the context of prey acquisition. Wobber (1975) speculated that selection should favor intraspecific bouts because the winner retains possession of the prey, grows larger, uses less energy in prey search, better survives when prey is scarce, and thus produces more progeny. Remarkably, since this initial study, other than descriptions of agonistic behavior in sea stars characterized by pedicellaria pinching (Sloan 1984), we know of no further published studies of intraspecific agonistic behaviors in sea stars and their potential implications.

We used time-lapse video under controlled laboratory conditions to examine intraspecific agonistic interactions between individuals of the common Antarctic keystone sea star *Odontaster validus* when presented with high quality prey.

MATERIALS AND METHODS

Adult individuals of the sea star *Odontaster validus* and the sea urchin *Sterechinus neumayeri* were collected, using SCUBA, from the benthos within 1 to 2 km of Palmer Station (5 to 30 m depth) located on Anvers Island (64.77° S, 64.05° W) on the central west coast of the Antarctic Peninsula in February and March 2007. Sea stars were held in a large holding tank for a period of several weeks and fed a maintenance diet of dried krill to standardize their nutritional condition. To investigate potential intraspecific behavioral interactions of *O. validus* in the presence of high quality prey, we used a time-lapse video camera (SONY Digital Recorder, Handycam, DCR-VX700) to film sea stars in a large circular laboratory tank. The camera was mounted approximately 3 m above the center of the seawater tank (1.8 m diameter and 0.76 m height, filled with seawater to a depth of 0.64 m, water volume 1629 l) such that the field of view encompassed the entire tank. The tank was equipped with fresh unfiltered seawater pumped directly from the sea at a rate of 2.5 l min^{-1} via a single hose inlet (ca. 2 cm hose diameter). Seawater drained from the tank at the air–water interface at the center of the tank via a standing vertical PVC drain pipe (10 cm diameter). Seawater temperature was essentially constant (approximately 2.0°C) over the course of the video time-lapse experiments. As sea stars were filmed over continuous 48 h periods and filming required constant lighted conditions, the fluorescent ceiling lights in the room remained on at all times. Individual sea stars were not fed during the experiments to ensure that they were all in a similar nutritional condition. Sea stars can remain in excellent nutritional condition over long periods of time in the absence of feeding (Jangoux 1982).

Experimental trials were initiated by placing 34 individuals of *Odontaster validus* collectively into a tight circle measuring approximately 30 cm in diameter on the bottom of 1 side of the circular tank. The 34 sea stars ranged in size (radius, R = distance from the tip of an arm to the center of the oral disc) from 25 to 53 mm. To evaluate the potential effect of body size on intraspecific interactions, we divided the 34 sea stars into 3 size categories: small (R = 25 to 32 mm; n = 6), medium (R = 35 to 42 mm; n = 17), and large (R = 45 to 53 mm; n = 11). Immediately following the introduction of the sea stars into the tank, we placed a large (60 to 66 mm diameter) fresh adult sea urchin *Sterechinus neumayeri* that had been cracked into 2 equal halves on the tank floor in the quadrant of the tank immediately opposite the quadrant with the sea stars. Thus, sea stars had to move approximately 1.5 m to reach the introduced prey, assuming they did so in a straight line. For each of the trials, the same 34 sea stars were used and the sea urchin prey was replaced with a freshly cracked individual. Time-lapse video was used to capture 0.2 s images each min over a 48 h period. Three replicate trials were conducted, with each beginning at approximately 08:00 to 09:00 h local time and ending 48 h later.

The time-lapse videos were viewed and analyzed on a PC using Windows Media Player software. We measured the time required for individuals to reach and contact each half urchin (n = 2 urchin halves per trial ×

3 trials = 6), and the numbers of *Odontaster validus* present within each of 4 designated quadrants on the bottom of the tank at the time that the first urchin-half was contacted by a sea star.

We then analyzed the time-lapse video to determine the number of sea stars displaying arm-fencing bouts with a conspecific during each 48 h trial as well as the quadrant of the tank in which bouts took place. Finally, we determined the size classes of sea stars (small, medium, or large) that participated in bouts and noted the outcomes of bouts with respect to the relative size classes of the 2 sea stars taking part.

The quadrant distribution of sea stars at the time the urchin was first contacted and the quadrant distribution of bouts were each compared to a uniform distribution using a chi-squared goodness-of-fit test.

RESULTS

Sea stars required a relatively long period of time (285 ± 58 min; n = 6) to locate and first make contact with prey. Moreover, analysis of the tank quadrant location of sea stars at the time at which prey was first contacted indicated that there were significantly ($p < 0.001$) more sea stars in the quadrant immediately adjacent to the initial starting quadrant than in the quadrant where the prey was located.

In total, 19 arm-fencing bouts were observed between pairs of *Odontaster validus* over the course of the three 48 h trials (6.3 ± 1.5 bouts per trial; mean ± 1 SE). Fifteen (79%) of these bouts occurred in the near vicinity of the prey (13 ± 1.6 cm from prey; mean ± 1 SE); 2 of the remaining 4 bouts occurred in the quadrant where sea stars were initially placed, and 1 additional bout occurred in each of the other 2 quadrants lacking the prey. Significantly ($p < 0.001$) more bouts were observed in the tank quadrant that contained the prey than in the quadrants lacking prey.

Arm-fencing bouts were characterized by both individuals raising the distal portion of an arm and directing it towards the raised arm of the other individual. Intermittent or continuous arm contact ('fencing') between the 2 individuals followed, with each individual attempting to place its arm over the arm and upper body surface of its competitor. When successful, this typically resulted in the 'loser' either retreating or allowing its competitor to move onto the urchin prey. Among the 15 arm-fencing bouts that occurred near the prey, 8 took place between large sea stars, and the remaining 7 took place between sea stars of different size classes. In 5 of these 7 bouts, large individuals that were in the near vicinity of the prey were involved in a bout with a medium or small individual. In all 5 of these bouts, the large sea stars won the bout (either remained on the prey or moved onto it, while the loser did not move onto the prey or retreated). In the remaining 2 bouts, a medium-sized individual had moved first onto the urchin prey and was then subsequently engaged in a bout with a larger individual. In both of these bouts, the medium-sized individual 'won,' retaining the prey that it had initially secured.

DISCUSSION

The potential role of intraspecific social interactions in influencing aspects of foraging in keystone predators has received little attention among marine invertebrates. This is probably due to several reasons. First, marine invertebrates are generally not considered to be capable of complex social interactions. This is particularly the case in the Echinodermata, where an oral nerve ring, radial nerves, and a nerve net comprise the totality of the nervous system. Second, the time scale of behavioral interactions is often out of phase with our own perception of time, and as such it is necessary to employ time-lapse video to both observe and to analyze prospective social behavioral interactions. Despite the current paucity of information, it is becoming apparent that theories of marine community structure and stability need to consider how social behaviors influence the trophic impacts of keystone predators.

The present study revealed that the keystone *Odontaster validus* exhibits a complex social behavior (agonistic arm-fencing behavior) in the presence of high quality prey that has important implications in terms of individual fitness and population structure, as well as prospective impacts on community composition. With respect to individual fitness, individuals that win arm bouts may be better able to capitalize on high quality food resources and thus ensure that more energy is available for metabolic needs, nutrient storage, and gamete production (Lawrence 1987). This may lower the investment in locating food resources or enhance the exploitation of higher quality foods (Wobber 1975). At the population and community level, it is possible that agonistic social interactions in the keystone predator *O. validus* impact the benthos in several ways. First, as losers of arm-fencing bouts often retreat, it is possible that agonistic behavioral interactions may decrease the density of *O. validus.* This could have important implications in population structure even if it occurs over relatively small spatial scales. The result would be similar to what Palumbi & Freed (1988) proposed for *Pisaster ochraceus*, where social aggression between aggregated individuals increases their rates of dispersal and thus decreases predation intensity.

In contrast to the keystone sea star *Pisaster ochraceus, Odontaster validus* also opportunistically aggregates on high quality prey (e.g. the sea star *Acodontaster conspicuus*, Dayton et al. 1974; injured sea urchins *Sterechinus neumayeri,* J. S. Pearse, J. B. McClintock pers. obs.) as well as on carrion (e.g. dead fish, J. B. McClintock pers. obs.). Here, if the prey is relatively small (e.g. injured sea urchin) and does not attract too many conspecifics, there is an opportunity for prey monopolization and agonistic bouts would be favored. If the food item is relatively large (e.g. dead fish, penguin, or seal) then such a large number of conspecifics may be attracted that agonistic bouts between individuals become futile, and rather than engage in bouts, sea stars simply pile onto the prey. Finally, as the natural diet of *O. validus* encompasses sponges, arm-fencing bouts between competing individuals could impact levels of spongivory and thus influence the structure of the sponge-dominated benthic communities of Antarctica (Dayton et al. 1974, McClintock et al. 2005).

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