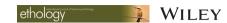
BEHAVIOURAL NOTES



"Urchin pinning": Behavioural observations reveal how hungry urchins actively prey upon their sea star predators

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Abstract

Green sea urchins (Strongylocentrotus droebachiensis) are dominant components of benthic ecosystems that form aggregations and can transform entire kelp forests into barren systems. While these urchins are known to unwittingly consume practically anything in their path while grazing, detailed descriptions of active predatory behaviour on known predators (i.e., predator-prey reversal) are undocumented. Here, we use laboratory observations to describe the behavioural tactics used by starved S. droebachiesis to actively attack and consume sea stars, Crossaster papposus-a known predator of S. droebachiensis. We observed urchins preying on three separate sea stars, with one being substantially consumed by urchins within 24 hr. Urchins exhibited a direct mode of attack on sea stars by individually mounting and consuming the tips of the arms. Interestingly, we did not observe any conflict between individual urchins for attacking the sea star despite there being ≈80 starving urchins in the tank (and only 10-12 arms on the sea stars). Some sea stars did not attempt to escape urchin predation at all, while others attempted to escape by fleeing and lifting arms on top of the urchins. Given that sensory perception in sea stars is largely derived from the arm tips, we suggest that urchins directly attack and consume many sea star arm tips in an attempt to "pin" sea stars before consuming them. As such, we term this predatory behaviour "urchin pinning." These observations ultimately provide the first detailed behavioural documentation of how urchins actively prey on a known predator and provide a basis for a wealth of future research.

KEYWORDS

benthic ecology, Echinodermata, feeding ecology, predator, prey reversal

1 | INTRODUCTION

Sea urchins are important components of many benthic marine ecosystems, as their impressive grazing ability can dictate the structure and function of entire biological communities (Hagen, 1995; Harrold & Pearse, 1987; Harrold & Reed, 1985; Lawrence, 1975). A prime example of this is the green sea urchin,

Strongylocentrotus droebachiensis. On both sides of the Atlantic Ocean, population outbreaks of *S. droebachiensis* can result in over-grazing on kelp, resulting in urchin barrens—areas devoid of kelp due to urchin grazing (Filbee-Dexter & Scheibling, 2014). As such, *S. droebachiensis* plays a considerable ecological role in kelp-associated ecosystems in temperate regions of the North Atlantic Ocean.

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Given the ability of S. droebachiensis to influence ecological communities, there is considerable interest in the biotic and abiotic factors that control their populations (Scheibling, 1996). Chief among these factors are disease and predation. Disease has been highlighted as a major control on S. droebachiensis populations, particularly in Atlantic Canada (Feehan & Scheibling, 2014). The role of predation, however, is thought to be less important in such systems (Scheibling, 1996) despite apparent vulnerability (Buitron, 2003) and the numerous predators of S. droebachiensis present in natural systems (Fagerli et al., 2014). One potential reason for this is that S. droebachiensis tend to gather in large aggregations which, while not elicited by predators (Rodriguez & Ojeda, 1998; Vadas et al., 1986), may be effective in avoiding predation (Johannesen et al., 2014). In such aggregations, these urchins are also notorious for consuming practically anything in their path, including members of their own species (Legault & Hunt, 2016) and man-made materials such as plastic flagging tape in both the laboratory and field (K. Legault, H. Hunt, pers. comm.).

Documentation of urchins consuming their predators also exist, representing an example of predator–prey reversal. For example, gut analysis and laboratory observations confirm that *S. droebachiensis* can consume multiple sea star species including *Asterias vulgaris*, *Solaster endeca* and *Crossaster papposus* (Himmelman & Steele, 1971; Scheibling & Hatcher, 2006). From these documentations, however, it is unclear if the urchins consumed live or dead sea stars. Furthermore, behavioural descriptions of how urchins are able to consume such predators—which are often far larger than even the largest urchins—are lacking. While one may be tempted to assume that large congregations of urchins are able to simply steamroll over predators that are caught in an aggregation, direct observations of predatory behaviour are necessary to truly understand how urchins are able to consume much larger animals that often prey upon them. Yet, such behavioural documentations remain scant.

Here, under laboratory conditions, we describe a novel behaviour whereby hungry green sea urchins actively attacked and consumed multiple sea stars, *Crossaster papposus* (a known predator of *S. drobachiensis*; Himmelman & Dutil, 1991; Gaymer et al., 2004; Dumont et al., 2007), in a predictive behavioural fashion which we term "urchin pinning."

2 | MATERIALS AND METHODS

Following an experiment measuring self-righting behaviour in *C. papposus* (collected from the Gullmar Fjord in western Sweden) at the Kristineberg Marine Research Centre (west coast of Sweden; 58.249700 °N, 11.445074 °E) in 2018, individual *C. papposus* were separated into different tanks for identification purposes so that individual sizes could be measured the following day. One of the individual sea stars (11 arms, 10.9 cm arm length, 0.3 kg) was placed in a 400-L tank with ≈ 80 green sea urchins from the Norwegian coast which had not been fed in more than two weeks. The water temperature and salinity in the tank (flow-through deep water taken from



FIGURE 1 Damage inflicted on sea star (*C. papposus*) by green sea urchins (*S. droebachiensis*) within 24 hr of the sea star being placed in a tank with ≈80 starving urchins [Colour figure can be viewed at wileyonlinelibrary.com]

30 m) were 11°C and 32.7, respectively. When the sea stars were retrieved for size measurements the following day, the sea star in the urchin tank was found under a pile of urchins. When we removed the urchins and retrieved the sea star, the arms were visibly and severely damaged (Figure 1), and there was no sea star tissue floating or on the bottom of the tank, suggesting that the urchins actively preyed upon the sea star.

To document how the urchins actually attacked and preyed on the sea star, two trials were conducted with two additional (uneaten) C. papposus individuals (hereafter C. papposus 1 and C. papposus 2). The two trials were conducted on separate but consecutive days (Trial 1: C. papposus 1, 31 July 2018; Trial 2: C. papposus 2, 01 August 2018). For each trial, sea stars were individually placed in the tank with C. droebachiensis and interactions were observed for C1 hr; photographs and videos of notable behaviours and interactions were taken at will (unfortunately, not continuously). Both trials were conducted in the same flow-through seawater tank as the original observation at temperature and salinity C11°C and 32, respectively.

3 | RESULTS

3.1 | Trial 1: C. papposus 1

Within 2 min of the sea star being placed in the tank, a single urchin approached the tip of one arm of the sea star, manoeuvered itself on top of the arm tip, and remained there (Figure 2a,b; Video S1; https://youtu.be/nBdlm_93MM4). Soon after, more urchins followed suit and after ≈10 min, three urchins had gathered on three

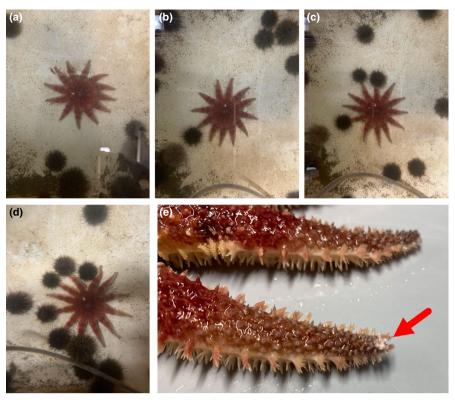


FIGURE 2 Sequence of urchins preying on a single sea star in (C. papposus 1; arm length = 10.9 cm). Individual urchins attack a single-arm tip and consume the arm from the outermost tip. (a) Sea star initially placed into tank. (b) First urchin attacks ≈2 min after the sea star was placed in the tank. (c) Three urchins attacked ≈5 min after sea star placed in tank; more urchins approaching. (d) After ≈30 min, 6/11 arms of sea star attacked. (e) Close up (taken after the sea star was removed from the tank) shows evidence of direct consumption, as the arm tip is damaged and the white, calcareous material is visible; no tissue was found in the tank [Colour figure can be viewed at wileyonlinelibrary.com]

separate arms of the sea star (Figure 2c; Video S2–S3; https://youtu.be/Ai4Yjrm8kH8, https://youtu.be/bk9dn6mOtvc), and after ≈1 hr, seven of the 12 arms were occupied by individual urchins (Figure 2d). The sea star was then removed from the tank to avoid further stress, and the tips of the arms were inspected for physical evidence of urchin feeding, which confirmed that the urchins were indeed eating the sea star (Figure 2e; no tissue found in tank). Surprisingly, the sea star did not attempt to flee during the urchin attacks.

During the interaction, not all urchin attacks on the sea star were sustained. To this extent, one urchin gave up after a single unsuccessful attempt at attacking an arm tip, while others made multiple attempts to mount the tips of multiple arms before giving up. Not all urchins that were unsuccessful on the first attempt gave up, however, and some urchins that were initially unsuccessful persisted and eventually succeeded.

3.2 | Trial 2: *C. papposus* 2

In contrast to *C. papposus* 1, *C. papposus* 2 was able to successfully escape and avoid urchin predation for the 1-hr period (Figure 3). Upon placing *C. papposus* 2 in the urchin tank, four urchins began to chase and attack (i.e., actively move towards and attempt to mount the arm tips of the sea star) the sea star within 3 min (Figure 3a). The urchins used the same predatory tactic as described in Trial 1: individual urchins attacking and "pinning" the tips of the arms. The sea star was then able to successfully escape the urchin attacks and fled towards the wall of the tank. Interestingly, the attacking urchins pursued the sea star as it fled (Figure 3b). The sea star proceeded

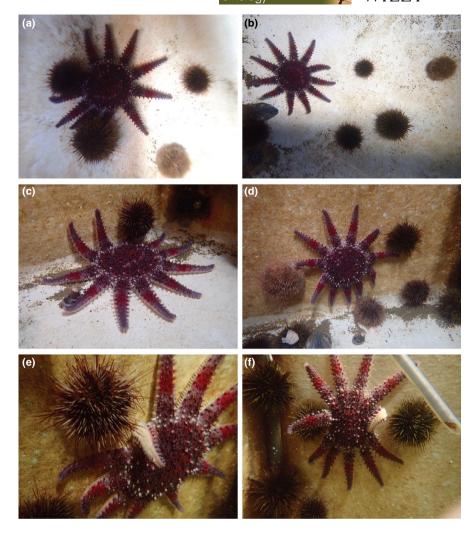
to climb the tank wall, where it was then attacked by a different urchin, and three more urchins attempted attacking the sea star on the wall (Figure 3c,d). To escape the urchin attacks, the sea star manoeuvered the arms that urchins were attacking laterally and/ or horizontally and placed the arms on top of the attacking urchins while it was fleeing the area (Figure 3e-f; Video S4; https://youtu.be/37ouN1ydc5o).

4 | DISCUSSION

Under laboratory conditions, we observed starved green sea urchins actively preying on a known predator. From this, we were able to describe a predictable predatory behaviour for the first time, whereby urchins individually attack and consume the tips of sea star arms (one urchin per arm). Given the known ecology of green sea urchins and documented cases of them having consumed sea star predators in the wild (including *C. papposus*), it seems probable that starved sea urchins invoke a behavioural predatory strategy to actively consume their predators.

In our observations, urchins were observed initially attacking the tips of the sea star's arms (multiple urchins pinning tips: https://youtu.be/bk9dn6mOtvc). The arm tips would be the first point of contact for an approaching sea urchin; however, the lack of urchin attempts to attack other areas of the sea star body suggest a directed method of attack. Initially, attacking the arm tips would likely be the most advantageous method for sea urchins, as the arm tips are small enough to fit inside the mouths of urchins and would thus increase the probability of urchins successfully consuming sea star tissue. The tips of sea star

FIGURE 3 Sequence of urchins attacking a sea star (C. papposus 2; arm length = 9.8 cm) and the sea star successfully escaping. (a) Two urchins attacking sea star arm tips; two others approaching. (b) Sea star escaped attacks in a. and fled; urchins pursued. (c) Sea star reached tank wall and was attacked by another urchin. (d) Sea star climbs wall to escape urchin predation, but multiple urchins continue attacking. (e-f) Sea star defensive behaviour: the sea stars manoeuver arms laterally and/or horizontally so that arms are on top of the attacking urchin and sea star flees [Colour figure can be viewed at wileyonlinelibrary. coml



arms are also known to play a crucial role in sensory perception (olfaction and light detection; Garm, 2017), and successfully attacking the arm tips would thus reduce a sea star's ability to make an informed escape. While larger sea stars may be stronger than urchins with respect to horizontal pull, it is unlikely that a sea star would be able to vertically lift arm tips (arm lifting response: https://youtu.be/37ouN1ydc5o) with multiple urchins. As such, we suggest that this combination of attacking many arms and consuming the tips results in urchins "pinning" the sea star to the benthos, and we thus term the urchins' predatory behaviour "urchin pinning." More direct experiments are needed to empirically test this explanation.

It is not entirely clear if our observations represent a true switch in urchin feeding mode (i.e., from grazer to predator) or if they represent a previously undescribed behavioural prey defence. From existing literature, it seems that our observations are more likely representative of predation rather than defence, as previous reports also describe active urchin predation on non-predatory echinoderms such as sand dollars, *Echinarachnius parma* (Himmelman & Steele, 1971; Scheibling & Hatcher, 2006). Furthermore, the damage invoked on the first sea star (i.e., Figure 1) suggests that the urchins actively preyed upon that sea star rather than attempted to thwart off a predator. Indeed, urchins that are able to switch feeding modes would be better equipped to survive periods in which preferred

foods are scarce (e.g., urchin barrens). Incorporating animal tissues into their diets can also provide nutritional benefits to urchins by enhancing the production of somatic and gonadal tissues (Knip & Scheibling, 2007; Meidel & Scheibling, 1998; Nestler & Harris, 1994). Ultimately, while attacking and consuming sea stars would provide an anti-predator function by default, it appears that our observations likely reflect a true shift in feeding mode from grazing to predation in *S. droebachiensis*.

In the initial instance where urchins grazed on the sea star (Figure 1), the urchins had not been fed for weeks. It is thus likely that hunger and the lack of preferred food (kelp) played a role in our observations such that urchins were more likely to attack a sea star under elevated hunger levels and decreased food availability. Indeed, elevated hunger levels can increase risky behaviours (Boutin, 2018) and can result in animals ingesting harmful food items (Crossley et al., 2018; Gilette et al., 2000). In addition, the tank in which these attacks occurred had an urchin:sea star ratio of ≈80:1. Given the size mismatch between an individual urchin and an individual adult sea star, it seems unlikely that urchins would successfully prey upon an adult sea star at a 1:1 ratio and it is proobable that urchins are bolder when in larger groups (as other aquatic invertebrates are; e.g., Wilson et al., 2012). Similar reversals between predator and prey based on density have been observed previously. For example, in

western South Africa, rock lobsters prey on mussels and whelks at Malgas Island, where the lobsters live alongside seaweed, mussels and whelks; however, when lobsters from Malgas Island were transferred to Marcus Island, an area dominated by a substantially larger whelk population and very few lobsters, the lobsters were actively preyed upon by whelks (Barkai & McQuaid, 1988). This context, coupled with urchin predation being an alternative feeding mode (i.e., the urchins are primarily grazers), suggests that an ecological trade off likely exists whereby urchins are able to weigh the relative benefits and risks of attacking a known predator. In situations where urchins are hungry and their preferred food is unavailable, and they are in large aggregations, they may initiate predatory activity on dangerous prey such as predatory sea stars.

If our observations do occur in nature, they may be most probable under situations in which urchins have been without food for days and other epifauna (including sea stars) are active, such as in urchin barrens (Filbee-Dexter & Scheibling, 2014). The extent to which urchins will engage predatory behaviour under such conditions, however, is unknown. If urchins are able to engage predatory feeding to sustain themselves in an urchin barren, it is thus possible that this switch in feeding made could temporarily stabilize this disturbed ecosystem state and delay the return of the ecosystem to its baseline conditions.

To our knowledge, these observations provide the first behavioural description of sea urchin predation on a sea star known to be a predator of the attacking urchins. From our observations, it is clear that groups of *S. droebachiensis* are capable of coordinated predatory behaviour to successfully attack and consume their own predators. Our observations not only document active S. droebachiensis predation on C. papposus, but also provide the basis for further research to better understand nuances of this predator-prey reversal system and the behaviours exhibited therein. Most notably, experiments testing whether or not directly attacking the arm tips result in reduced sea star escape capabilities are needed before our tentative explanation of "urchin pinning" may be accepted. For example, allowing urchins to eat or partially eat sea star arm tips and subsequently testing the sea star's ability to locate food could provide insight into whether or not the mode of urchin attack impairs sea star sensory perception. More detailed experimental studies quantifying the propensity of urchins of varying levels of hunger to attack and consume predatory and non-predatory sea stars, or other non-predators of comparable sizes, would lend insight into the nature of this behaviour as a true predatory feeding mode or a prey defence strategy. In such studies, attacking predators but not non-predators would indicate defence, whereas attacking both predators and non-predators would be indicative of predation. Alternatively, experiments could simply manipulate access to kelp and observe whether or not urchins elect to attack and consume sea stars in the presence of a preferred food source; if urchins avoid attacking sea stars in the presence of kelp, this would provide support for the "predator" hypothesis. Indeed, this latter approach could also lend insight into the underlying mechanism for our observations. For example, a group of urchins attacking a sea star in the presence of kelp would indicate a collective behaviour driven by urchin-sea star density mismatches (i.e., increased urchin boldness in

large aggregations). On the other hand, not attacking in the presence of kelp would indicate that the observed behaviour is metabolically driven. Ultimately, more detailed experiments are needed to understand the role of hunger, food availability and predator:prey density ratios to better understand the ecological contexts in which urchins switch feeding modes. Finally, urchin barrens that have persisted for days provide an optimal area to explore this potential predator-prey reversal in nature (Filbee-Dexter & Scheibling, 2014). Sampling urchin gut contents prior to and after the onset of an urchin barren could provide insight into whether or not urchins utilize a predatory feeding strategy to persist once the kelp is gone. This information could be useful for ecological modellers predicting the impacts of urchins on coastal systems, particularly when considering climate-driven range expansions off urchin species into new areas.

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CONFLICT OF INTEREST

We declare no conflict of interest.

AUTHOR CONTRIBUTION

JCC conducted and analysed observations (photography and videography) and wrote and revised the manuscript. SD provided access to animals. SD and FJ provided in-kind support for space and equipment and revised the manuscript.

ETHICAL APPROVAL

Ethical approval was not required for the species used in this experiment. Nonetheless, the study was strictly conducted under the premise of the three Rs of animal ethics.

DATA AVAILABILITY STATEMENT

All supplementary videos are provided in the online supplementary material accompanying this article and are freely accessible for public viewing on YouTube at: https://www.youtube.com/playlist?list=PL3XoyUPTmyZMiPCc3iP84VujJsAWT7e17

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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