# DIFFERENCES IN DENSITY OF ABORAL TRIDENTATE PEDICELLARIAE OF *STRONGYLOCENTROTUS PURPURATUS*

# FROM TWO DIFFERENT SITES

by

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The purple urchin (Strongylocentrotus purpuratus) is a prominent grazer on the Oregon coast that has helped create and maintain urchin barrens by preventing the re-establishment and growth of new kelp. Urchins have 4 different types of pedicellariae on their tests: globiferous, tridentate, triphyllous, and ophicephalous (Coppard et al. 2012). Tridentate pedicellariae prevent the settling of any unwanted organisms on the urchin's test. With the notion that biodiversity and species richness is lower at jetties, it was hypothesized that urchins from a natural intertidal would have a higher number of pedicellariae due to having more organisms to fend off from settling. 100 urchins were collected, 50 from South cove, Cape Arago, and 50 from a jetty near OIMB. Urchins were taken into a lab and frozen in order to keep them intact before counting pedicellariae. A dissection scope was used to count aboral tridentate pedicellariae, and the diameter of each urchin was then measured and used to calculate the area of the urchin's aboral surface. Pedicellariae per mm<sup>2</sup> (ped/mm<sup>2</sup>) was generated for each urchin before being averaged out and plotted on a column graph with Standard Error (SE) being plotted as error bars. The average pedicellariae per mm<sup>2</sup> of urchins from South Cove was  $0.0309 \pm 0.001$  and the average of urchins from the OIMB jetty was  $0.0309 \pm 0.001$ . Potential future studies include looking at different types of pedicellariae with a similar question or how densities change between environment types.

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#### Introduction

Echinoderms are a diverse group of marine organisms that encompass the classes Crinoidea (feather stars), Asteroidea (sea stars), Holothuroidea (sea cucumbers), Ophiuroidea (brittle stars), and Echinoidea (sea urchins and sand dollars) (Telford et al. 2014). Sea urchins have a rounded calcium-based shell called a test and protruding from holes in the test are many spines or tube feet and while urchins have no eyes, they do have photoreceptor cells at the ends of their tube feet which allow urchins to have spatial vision and sense changes in light (Ullrich-Lüter et al. 2011). Sea urchins also have a specialized organ called an Aristotle's lantern, a complex set of muscles and 5 teeth that allow the urchin to graze and bore holes and dents into large rocks (Rahman & Arshad 2014). One of several species of urchin on the Oregon coast, and one that is known for its ability to overgraze when food is scarce, is the purple urchin or *Strongylocentrotus purpuratus* (Parnell et al. 2017). Found in shallow waters and in the intertidal, purple urchins have shorter spines than their red counterpart, *Mesocentrotus franciscanus*, and are prominent grazers in kelp forests (Rogers-Bennett & Okamoto 2020).

The reason why sea urchins have received increased research focus in the last few years is due to their habit of overgrazing and the emergence of urchin barrens (Dolinar & Edwards 2021). Starting in 2013, star wasting disease (SSWD) decimated populations of many sea star species on the US West coast (Menge et al. 2016). SSWD is a contagious threat that caused white lesions on the star's body, the loss of one or all its arms, and eventual death soon after (Miner et al. 2018). Though this disease was a problem in 2013, it got even worse in the period of 2014-2016 due to a catastrophic marine heat wave known since then as The Blob (Konar et al. 2019). SSWD was able to spread, causing higher rates of sea star mortality, with one of the affected species was the sunflower sea star (*Pycnopodia helianthoides*), an important predator in

kelp forests (Galloway et al. 2023). Though the sunflower star's population numbers were relatively small, the species contributed greatly to the biodiversity of kelp forests, as the stars kept certain species in check. A major predator of purple urchins is the sunflower sea star and, with sea star populations declining drastically due to SSWD, purple urchins were able to overgraze and completely eliminate a kelp forest's biodiversity, creating an urchin barren (Harvell & Lamb 2020).

Purple urchins, as well as other echinoids, have several kinds of pedicellariae. Pedicellariae are small, pincer-like appendages on stalks protruding from the test that are used in cleaning and defense against threats (Campbell 1983). The head of pedicellariae consists of multiple blades or valves. The four major types of pedicellariae that can be found on an urchin's test are seen in Figure 1. Figure 1 A-B are diagrams of globiferous pedicellariae, C is a diagram of tridentate pedicellariae, D is a diagram of ophicephalous pedicellariae, and E is a diagram of triphyllous pedicellariae (Harmer & Shipley 1922).

Globiferous pedicellariae are very specialized, their valves are tipped with teeth that pierce the skin of potential predators and inject them with venom to harm or deter them. Ophicephalous pedicellariae end with 3 valves that contain short blades. The valves of ophicephalous pedicellariae remain low and close to a test until stimulated, at which point they point towards, and converge upon, the threat and, if the inner surface of a valve is touched, close their jaws to hold on to the attacking organism. Triphyllous pedicellariae are the smallest of the four main types of pedicellariae; they have a long stalk with small blades on the valve. A unique behavior of triphyllous pedicellariae is that they are constantly opening and closing their valves, cleaning the surface of the urchin to prevent any bacteria from settling and growing. Tridentate pedicellariae are the largest variety and have three large valves with peripheral teeth. The valves

are held in a closed position until disturbed by mechanical stimuli, and they deter small invertebrates or invertebrate larvae from settling on the urchin as well as remove larger pieces of debris or matter (Coppard et al. 2012). Pedicellariae, coupled with other defense mechanisms like spines, help protect the urchin no matter what ecosystem or environment it resides in (Rahman & Arshad 2014).

Anthropogenic structures like jetties, sea walls, and other extensions of the coast are commonly constructed to function as breakwaters, preventing harsh wave action from harming docks and marinas as well as reducing erosion along the coastline (Burcharth 1994). Repeated exposure and submergence can lead to the development of intertidal communities on and around breakwaters. However, it is common for breakwater intertidal communities to have lower species diversity, richness, and evenness than natural rocky shore intertidal communities (Ravinesh & Bijukumar 2013). Because there might be different communities of other organisms and different environmental conditions at different sites and habitats, I investigated whether urchins from very different habitats differed in their number of tridentate pedicellariae. For example, at some habitats such as jetties, there might be different species of annelids, amphipods, larvae-producing bivalves, and other organisms that tridentate pedicellariae fend off around jetties.

If two different sites had different assemblages of intertidal organisms, with one site being a natural intertidal area and the other being a subtidal human created artificial structure like a jetty, the need for tridentate pedicellariae might not be the same, as one site should have a higher abundance of organisms that could settle on an urchin's test (Ravinesh & Bijukumar 2013). The jetty site of this study has a subtidal area with many boulders and, besides urchins, not that many other organisms. Taking that into account, urchins found at the natural site might have a different number of tridentate pedicellariae.

#### Methods

Urchins were collected from 2 sites: from a subtidal habitat (5-10 m deep) at a jetty near the Oregon Institute of Marine Biology on March 17<sup>th</sup>, 2023 and South cove, an intertidal area within Cape Arago state park on May 5<sup>th</sup>, 2023 (Figure 2).

To ensure that the urchins were collected in an unbiased way, urchins were collected systematically by only picking a few from any noticeable cluster of individuals and trying to collect those that were around the same size, between 55 and 70 millimeters.

Collected urchins were kept in a sea table until there was space in the freezer and were fed on a weekly basis. Individuals waiting to be frozen were fed either sea lettuce (*Ulva lactuca*) collected from nearby docks or pieces of bull kelp (*Nereocystis luetkeana*) found at South cove.

Urchins used for data collection were euthanized by being frozen, as observing structures as small and close to the test as pedicellariae is difficult if the urchin is alive. Euthanizing was necessary to count pedicellariae on urchins. All urchins collected were done so under the use of permits provided by OIMB or the Galloway Lab. Individual purple sea urchins produce millions of eggs each year across the entire Oregon coast, so removing 50 from 2 sites has a negligible effect on their population.

After being frozen for at least 3 hours, urchins were removed from the freezer and placed in a container of water under a stereo microscope/dissection microscope. Due to the differing size and height of urchins, with the smallest being 50.5 mm in diameter and 31.4 mm in height and the largest being 80.6 mm in diameter and 46 mm in height, different magnification settings were used as per needed for each individual. Defining the anus as the "center" and using it for a point of reference, tridentate pedicellariae were counted across multiple microscope fields of view. When counting, an urchin was thought of as a grid with 3 rows, dividing the urchin into

top (T), middle (M), and bottom portions (B). Each row contained 3 Fields of View (FOV), with the rightmost being field 1, the middle being field 2, and the leftmost being field 3. These FOV weren't randomly placed or chosen, they were planned out so that the entirety of the aboral surface could be observed.

Counting started in the center FOV, or M2 (middle section of the urchin, second field out of three), and consisted of counting every tridentate head, the part of the pedicellaria with the 3 valves, visible. Counting started in M2 due to the fact that the anus was a good landmark. Tallying the heads instead of the stalks was done to prevent any confusion with the stalks of tube feet. If the majority or entirety of a pedicellariae head was found in one FOV it was counted in that field, otherwise it would be counted in a different field (Figure 3). Movement between fields of vision was done by establishing a reference object, usually a partially out-of-frame spine, and moving the FOV until the observed object couldn't be seen. If the urchin shifted during counting, the FOV was moved back to M2, with the anus in the center of the FOV, and the same reference points were used to get back to the FOV being counted before the shift. Many off-center fields extended beyond the "edge" of the aboral surface, in this situation every pedicellariae head that was identifiable without changing the magnification or focus was counted. After counting all the pedicellariae in a FOV, it was checked over, counting every pedicellariae again, to make sure none were counted multiple times.

The diameter and height (in mm) of each urchin was then measured using calipers and the data were entered into an Excel spreadsheet. The summed pedicellariae counts and diameters of each individual were used to generate pedicellariae per mm<sup>2</sup> per individual sea urchin before being averaged and plotted on a bar graph, with the standard error (SE) being used to generate error bars (Figure 4). After plotting the data, a two-sample two-tailed t-test was performed to

assess whether the density of pedicellariae differed between the two sites before deriving a pvalue to assess statistical significance, where alpha = 0.05. The radius and pedicellariae density were also plotted on a scatterplot, including lines of best fit and R<sup>2</sup> values, before a Pearson correlation coefficient (r) was derived to assess the relationship between the size of an urchin and its pedicellariae density (Figure 5).

#### Results

The average pedicellariae per mm<sup>2</sup> of urchins from South Cove was  $0.0309 \pm 0.001$  (standard error) and the average density of pedicellariae of urchins from the OIMB jetty was  $0.0309 \pm 0.001$ , the values were not significantly different. (T-value = 0.9601, df = 49, p = 0.3416; Figure 4). The smallest urchin recorded had a diameter of 50.5 mm and a height of 31.4 mm while the largest recorded urchin had a diameter of 80.6 mm and a height of 46 mm.

The line of best fit for the Jetty data comparing urchin size and density of pedicellariae had the equation y = -0.0016x + 0.0803,  $R^2 = 0.318$ , r = -0.564, the line of best fit for the Intertidal data comparing urchin size and density of pedicellariae had the equation y = -0.0015x + 0.0772,  $R^2 = 0.476$ , r = -0.69 (Figure 5).

Both the jetty data and the intertidal data had low R<sup>2</sup> values and r values less than -0.5. The Pearson correlation coefficient, r, measures the direction and strength of the relationship between two variables, anything larger than 0.5 or less than -0.5 is generally considered to have a strong relationship (Kasuya 2019). The r values from both sites were less than -0.5, so there seems to be a strong negative correlation between the size of *Strongylocentrotus purpuratus* and the density of their tridentate pedicellariae, as the size of an urchin increases, the density decreases (Figure 5).

#### Discussion

Urchins found at South Cove and those at the OIMB jetty don't have different tridentate pedicellaria densities. The lack of significant difference indicates that I failed to reject the null hypothesis, which stated that there would not have been a difference in the density of tridentate pedicellariae of urchins collected from different sites. It's still possible that there could be a difference in pedicellariae between urchins raised in different environments, however, this study does not address that question: understanding how urchins would change between environment types would require sampling organisms from multiple sites of the same environment type, but this study only sampled from one of each. Moreover, the very similar means and standard errors in pedicellaria density between two very different sites provides fairly strong suggestive evidence that there are not likely to be differences in pedicellaria density among sites in general.

It's also possible that the difference in the abundance of tridentate-used species between the South cove and OIMB jetty habitats isn't what was expected. While studies like those performed by Ravinesh and Bijukumar (2013) show that the biodiversity and richness of species may be lower in artificial structures like jetties, other studies show different conclusions. A study in Hong Kong looking at assemblages on vertical seawalls showed that, while the percent coverage of the barnacle *Tetraclita squamosa* was higher on natural rocky shores, the anthropogenic structure hosted a greater coverage of the oyster *Saccostrea cucullate* and another barnacle species *Balanus amphitrite* while also hosting organisms that weren't found at the rocky shore sites, including 3 species of tube worms and the mussel *Perna viridus* (Nelson et al. 2009).

Another study focusing on the community of organisms on jetties was done in the Mediterranean where, although species richness and faunal abundance weren't significantly different on jetties, they did support species of algae, limpets, and the barnacle *Chthamalus* 

*stellatus* which weren't found on natural rocky shores (Bonnici et al. 2018). The intertidal assemblage can even change through the seasons, making one type of environment temporarily more diverse and plentiful when they're usually similar, as shown in a study done on the North coast of Taiwan (Li & Lee 2013). While the biodiversity of invertebrates may be lower at jetties in some cases, jetties may host multiple species that natural shores don't, and some of these exclusive species may need to be deterred by tridentate pedicellariae (Glasby & Connell 1999). For future studies, it's necessary to gain a deep understanding of the different species that can be found at either site, not just make assumptions based on general information.

There are several ways I would recommend future studies about the pedicellaria of urchins could improve upon the methods I used here. When calculating the area of the urchin's aboral surface, the equation for the area of a circle was used. This causes a problem: the area of the aboral surface is not flat, it's curved, meaning that the area calculations used for the pedicellariae per mm2 figures are not the actual values. The freezer used to euthanize and preserve urchins could only hold so many at a time, so while some urchins were being frozen, others could be found in the sea table being fed bits of algae or kelp found at the docks. This could have caused problems in data collection, as some urchins would be in better shape than others due to the amount they were fed before being frozen, which could have affected the ability to count pedicellariae, as unhealthy urchins had more clumps of hard-to-detangle tube feet and pedicellariae. Spines were another potential problem that could be dealt with in future studies, as they were capable of concealing or covering up shafts, heads, or even entire pedicellariae. The undersides of spines were checked frequently by either rotating the urchin to get a better topdown view or forcefully raising and lowering spines using teasers, however, it's still possible that some tridentate pedicellariae were missed. A possible solution would be to ensure many of

the spines were facing the same way. During the freezing process by having a foreign object come into contact with the urchin, a mechanical response could be triggered and it would converge/point many of its spines and tube feet towards the spot of contact, making the surface of the test easier to discern and analyze (Figure 6).

Though this study focused on intertidal and jetty habitats, it does open up possibilities on how urchins of the same species differ in other habitats, like urchin barrens. There are many ways for kelp forests to shift into barrens: abundance of predators, availability of algae, disease, and intense storms give urchins an opening to overgraze, preventing the reestablishment of the forest by preying on young pieces of kelp, and unless they get taken out by intense storms or disease, the barren will persist (Pearse 2006). While in barrens, urchins can be tough, surviving for years off pieces of drift algae, encrusting algae, salps, or slow-growing species that are resistant to grazers (Spindel et al. 2021). Urchin barrens are a unique opportunity to see if and how urchins raised in different environments are different on both an individual and populationlevel scale, and I believe that pedicellariae are a great possible subject of study (Tegner & Dayton 1981). Future studies could even focus on the densities of different pedicellariae: with the decline of the sunflower sea star, one of the purple urchin's main predators, maybe it's possible that the density of globiferous pedicellariae, which are mainly used to deter predators, would change over time (Rogers-Bennett & Okamoto 2020).

I was unable to find literature discussing the density or counts of pedicellariae regarding purple urchins. I was able to find one study that focused on the distribution of pedicellariae across the test of *Echinus esculentus*, finding that tridentate pedicellariae are most abundant on the aboral surface on the side of the urchin containing the madreporite. Though they didn't specifically measure the density of tridentate pedicellariae, the combined density of all

pedicellariae types was higher on the aboral surface (Ramsay & Campbell 1985). The novelty of this research is important, as pedicellariae are a very prominent part of an urchin's biology and further research into how they may change according to conditions has the potential to further our understanding of the plasticity and adaptability of sea urchins.

In conclusion, purple sea urchins collected from South cove and the OIMB jetty had no significant difference in the density of aboral tridentate pedicellariae. This could indicate that the urchins at different sites had no need for more/fewer pedicellariae or that the biodiversity and assemblage of organisms at either site wasn't completely realized and considered, though this is just one possible explanation out of many. By trying to further our understanding of *Strongylocentrotus purpuratus*, how it interacts with organisms around it and how it adapts to change, we can further our understanding of the biology and ecology of marine organisms as a whole.

## Figures



Figure 1: Visual representations of the 4 major types of pedicellariae

Illustrations made by Harmer and Shipley when describing the form and function of pedicellariae in *The Cambridge Natural History*. Globiferous pedicellariae (also called gemmiform) can be seen in A (closed), and B (open), tridentate pedicellariae (also called tridactyle) can be seen in C, ophicephalous pedicellariae can be seen in D, and triphyllous pedicellariae (also called trifoliate) can be seen in E (Harmer and Shipley 1922).



Figure 2: Aerial Satellite photos of (left to right) the OIMB jetty (43° 21' 16" N, 124° 20' 40" W), and South cove, Cape Arago (43° 18' 06" N, 124° 23' 58" W) obtained through Google Maps, red circles have been placed to indicate the spot of urchin collection.



Figure 3: The surface of an urchin's test

A photograph showing the surface of an urchin taken during data collection. Two example pedicellariae that would be counted are circled. If most of the head was within the FOV, it was counted.



Figure 4: Excel Column Graph showing the average pedicellariae density (pedicellariae/mm<sup>2</sup>) of the 50 urchins collected from each site.

Though the average density of tridentate pedicellariae is slightly higher in urchins from South cove  $(0.0309 \pm 0.001)$  than those from the OIMB jetty  $(0.0309 \pm 0.001)$ , the difference is not significant



Figure 5: Scatterplot graph showing the relationship between the radius of *Strongylocentrotus purpuratus* test (in mm) and the density of tridentate pedicellariae (pedicellariae/mm<sup>2</sup>).



Figure 6: Rough diagram showing possible solution to the problem of urchin spines concealing pedicellariae

## **Bibliography**

- Bonnici L, Borg JA, Evans J, Lanfranco S, Schembri PJ. 2018. Of Rocks and Hard Places: Comparing Biotic Assemblages on Concrete Jetties versus Natural Rock along a Microtidal Mediterranean Shore. Journal of Coastal Research 34:1136–1148. Coastal Education and Research Foundation.
- Burcharth HF. 1994. The Design Of Breakwaters. Pages 381–424 in Abbott MB, Price WA, editors. Coastal, Esturial And Harbour Engineers' Reference Book. Spon press, [London].
- Campbell AC. 1983. Form and Function of Pedicellariae. Page Echinoderm studies 1 (1983). CRC Press.
- Coppard SE, Kroh A, Smith AB. 2012. The evolution of pedicellariae in echinoids: an arms race against pests and parasites. Acta Zoologica **93**:125–148.
- Dolinar D, Edwards M. 2021, December. The metabolic depression and revival of purple urchins (Strongylocentrotus purpuratus) in response to macroalgal availability. Available from https://www.sciencedirect.com/science/article/pii/S0022098121001362?via%3Dihub (accessed May 23, 2023).
- Galloway A, Gravem S, Kobelt J, Heady W, Okamoto D, Sivitilli D, Saccomanno V, Hodin J, Whippo R. 2023, February 22. Sunflower sea star predation on urchins can facilitate kelp forest recovery | Proceedings of the Royal Society B: Biological Sciences. Available from https://royalsocietypublishing.org/doi/10.1098/rspb.2022.1897 (accessed May 23, 2023).
- Glasby T, Connell S. 1999. Urban structures as marine habitats. http://www.jstor.org/stable/4314964. ROYAL SWEDISH ACAD SCIENCES. Available from https://digital.library.adelaide.edu.au/dspace/handle/2440/12039 (accessed May 23, 2023).
- Harmer SF, Shipley SAE. 1922. The Cambridge Natural History. Macmillan and Company, limited.
- Harvell CD, Lamb JB. 2020. Disease outbreaks can threaten marine biodiversity. Page 0 in Behringer DC, Silliman BR, Lafferty KD, editors. Marine Disease Ecology. Oxford University Press. Available from https://doi.org/10.1093/oso/9780198821632.003.0008 (accessed May 12, 2023).
- Kasuya E. 2019. On the use of r and r squared in correlation and regression. Ecol. Res. **34**:235–236.

- Konar B, Mitchell TJ, Iken K, Coletti H, Dean T, Esler D, Lindeberg M, Pister B, Weitzman B. 2019. Wasting disease and static environmental variables drive sea star assemblages in the Northern Gulf of Alaska. Journal of Experimental Marine Biology and Ecology 520:151209.
- Li M-H, Lee T-H. 2013. Intertidal assemblages on artificial structures and natural rocky habitats on Taiwan's north coast. The Raffles bulletin of zoology **61**:331–342.
- Menge BA, Cerny-Chipman EB, Johnson A, Sullivan J, Gravem S, Chan F. 2016. Sea Star Wasting Disease in the Keystone Predator Pisaster ochraceus in Oregon: Insights into Differential Population Impacts, Recovery, Predation Rate, and Temperature Effects from Long-Term Research. PLoS ONE 11:1–28. Public Library of Science.
- Miner CM et al. 2018. Large-scale impacts of sea star wasting disease (SSWD) on intertidal sea stars and implications for recovery. PLOS ONE **13**:e0192870.
- Nelson L, Huang R, Chan B. 2009. Variations in intertidal assemblages and zonation Patterns between vertical artificial seawalls and natural rocky shores: a case study from Victoria Harbour, Hong Kong. Zoological Studies.
- Parnell PE, Fumo JT, Lennert-Cody CE, Schroeter SC, Dayton PK. 2017. Sea urchin behavior in a Southern California kelp forest: Food, fear, behavioral niches, and scaling up individual behavior. Journal of Shellfish Research 36:529–544. National Shellfisheries Association, Inc.
- Pearse JS. 2006. Ecological Role of Purple Sea Urchins. Science **314**:940–941. American Association for the Advancement of Science.
- Rahman M, Arshad A. 2014. Sea Urchins (Echinodermata: Echinoidea): Their Biology, Culture and Bioactive compounds. Page International Conference on Agricultural, Ecological and Medical Sciences (AEMS-2014) July 3-4, 2014 London (United Kingdom). International Institute of Chemical, Biological & Environmental Engineering. Available from http://iicbe.org/siteadmin/upload/8432C714075.pdf (accessed May 12, 2023).
- Ramsay E, Campbell A. 1985. An investigation of the distribution of pedicellariae in Echinus esculentus (L.). Page Echinodermata. CRC Press.
- Ravinesh R, Bijukumar A. 2013. Comparison of intertidal biodiversity associated with natural rocky shore and sea wall: A case study from the Kerala coast, India. IJMS Vol.42(2) [April 2013]. NISCAIR-CSIR, India. Available from http://nopr.niscpr.res.in/handle/123456789/16942 (accessed May 13, 2023).
- Rogers-Bennett L, Okamoto D. 2020. Chapter 32 Mesocentrotus franciscanus and Strongylocentrotus purpuratus. Pages 593–608 in Lawrence JM, editor. Developments in Aquaculture and Fisheries Science. Elsevier. Available from https://www.sciencedirect.com/science/article/pii/B9780128195703000329 (accessed May 23, 2023).

- Spindel N, Lee L, Okamoto D. 2021, July 8. Metabolic depression in sea urchin barrens associated with food deprivation. Available from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/ecy.3463?af=R (accessed May 23, 2023).
- Tegner MJ, Dayton PK. 1981. Population Structure, Recruitment and Mortality of Two Sea Urchins (Strongylocentrotus franciscanus and S. purpuratus) in a Kelp Forest. Marine Ecology Progress Series 5:255–268. Inter-Research Science Center.
- Telford MJ, Lowe CJ, Cameron CB, Ortega-Martinez O, Aronowicz J, Oliveri P, Copley RR. 2014. Phylogenomic analysis of echinoderm class relationships supports Asterozoa. Proceedings of the Royal Society B: Biological Sciences 281:20140479.
- Ullrich-Lüter EM, Dupont S, Arboleda E, Hausen H, Arnone MI. 2011. Unique system of photoreceptors in sea urchin tube feet. Proceedings of the National Academy of Sciences **108**:8367–8372.