The Pacific sand dollar *Dendraster excentricus*: A New Model to Explore Novelty in Neural Circuits

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Abstract

Decoding how neural circuitry functions and evolved is no small task, but studying how disparate nervous systems produce similar behaviors may offer unexpected insights. Cephalopods possess complex hierarchical nervous systems with a centralized brain adjacent to their decentralized nerve ring, cords, and ganglia of their arms, whereas echinoderms lack a centralized brain but have an independently evolved nerve ring with ganglia and radial nerves. Both groups possess numerous specialized appendages on "multi-arm" axes that serve analogous locomotor and sensory functions. This study focuses on how *Dendraster excentricus*, the Pacific sand dollar, can be used as a novel research model to investigate neural circuit evolution, given its unique secondary bilateral symmetry that is superimposed on the ancestral pentaradial structure observed in sea urchins. We used time-lapse videography in lab and field settings to generate behavioral ethograms of *D. excentricus* and initiated work using deep learning tools to analyze locomotion. These approaches, along with microCT and confocal imaging, will enable us to compare body movements and coordination of tube feet and spines across individuals. Initial findings are reported here. Specifically, our findings revealed distinct locomotor behaviors in *D. excentricus* that suggest directional control and spatial awareness, despite its decentralized neural anatomy. This research contributes to the understanding of how morphological and ecological divergence shape neural circuit functionality and provides a comparative framework for studying the evolution and function of nervous systems in marine invertebrates.

Introduction

Cephalopods are a well-established model of invertebrate intelligence, due to their large centralized brain and decentralized neural circuits within their arms, creating a dynamic feedback loop between sensory input and motor control. This distributed neural architecture allows for complex, adaptive behaviors such as object manipulation, camouflage, and problem-solving (Albertin & Katz, 2023). On the other hand, echinoderms lack a centralized brain altogether, relying instead on a nerve ring and radial nerve cords to coordinate movement (Freas & Cheng, 2022). Despite these distinct neuroanatomical differences, both groups possess specialized appendages that are analogous in function and structure. These consist of cephalopod suckers and echinoderm tube feet. They both provide support in locomotion, adhesion, and environmental interaction (Kier & Smith, 1990; Smith, 1937). This functional convergence, arising from entirely different evolutionary and developmental pathways, provides a unique opportunity to explore how distinct nervous systems have similar core algorithms and behavior.

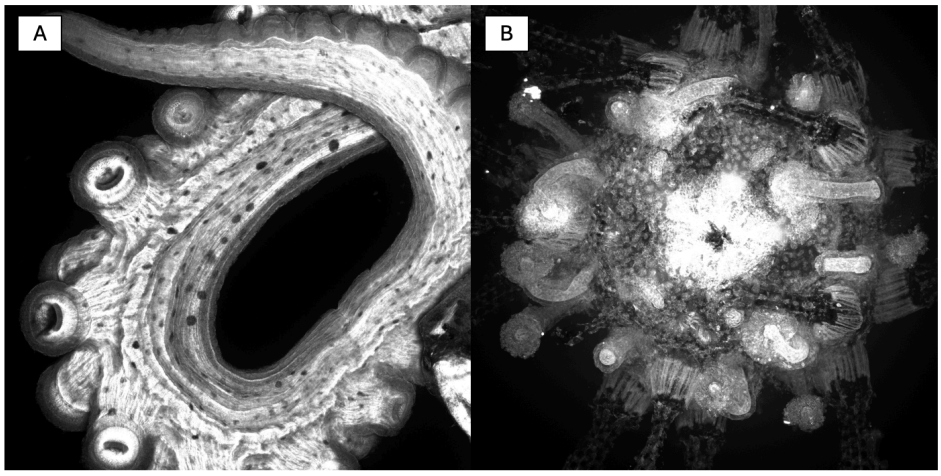

Figure 1. Comparative confocal microscopy of specialized appendages in a cephalopod and echinoderm. (A) Octopus arm tip featuring sucker structures. (B) Red sea urchin juvenile depicting developing tube feet.

Echinoderms evolved other unique features that make their neural circuitry intriguing. As a group, echinoderms share the defining feature of pentaradial symmetry in adulthood. Yet, species within the class Echinoidea diverge into two major morphological categories: regular and irregular urchins (Rozhnov, 2012). Regular echinoids, such as the red sea urchin (*M. franciscanus*), maintain a radially symmetrical, globular form optimized for movement in multiple directions. In contrast, irregular echinoids, including sand dollars, have evolved secondary bilateral symmetry superimposed on the ancestral pentaradial plan. This shift in body organization is associated with a flattened morphology, a defined anterior–posterior axis, and specialized locomotor and feeding strategies (Kerr & Kim, 1999). The shift is thought to have been driven by an evolutionary move to burrowing in sand habitats (Rozhnov, 2012). Comparing the anatomy and behavior of sea urchins to sand dollars will allow us to test how differences

in symmetry, morphology, and ecological niche influence movement patterns and the neural circuits that drive them.

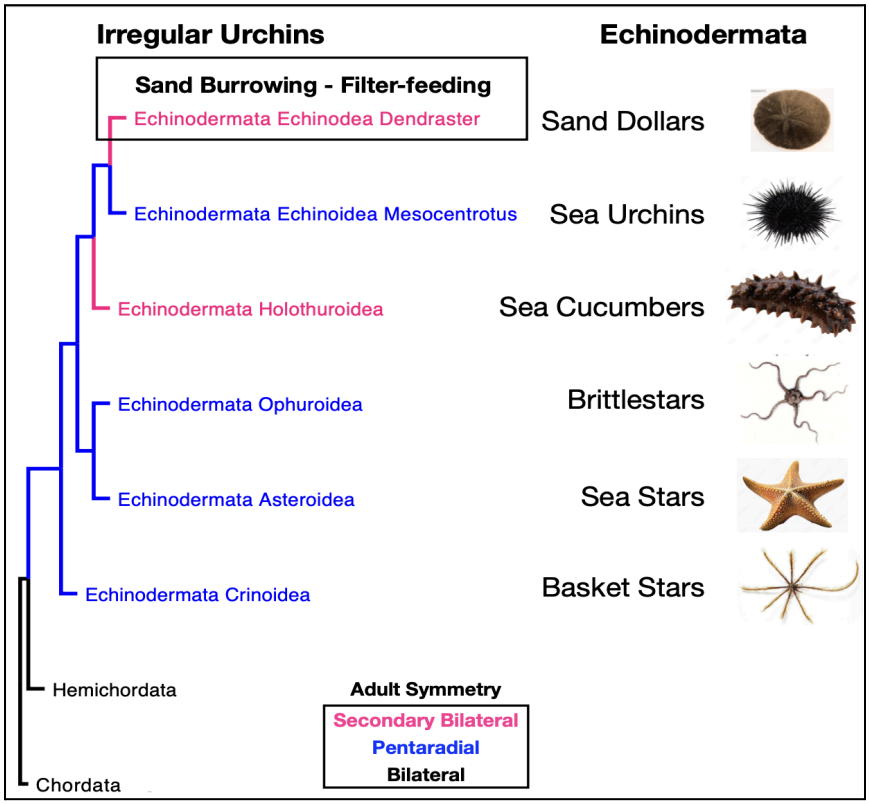

Figure 2. Phylogenetic tree illustrating the divergence of echinoderm classes and their morphological traits. Within Echinoidea, regular urchins such as *M. franciscanus* retain globular pentaradial symmetry, while irregular urchins like *D. excentricus* exhibit secondary bilateral symmetry.

The sand dollar we are specifically interested in is *Dendraster excentricus*, the Pacific sand dollar. Abundant along the Pacific coast, this animal is the ideal model organism for investigating evolutionary divergence, due to its clearly defined bilateral symmetry superimposed on a pentaradial foundation (Kerr & Kim, 1999). This feature has changed the biological algorithm these invertebrates utilize, giving them a different way of optimizing their locomotion for their preferred habitats. Fu-Shiang Chia (1969)

conducted an observational study on *D. excentricus* locomotion and feeding in Alki Point, Washington, where they discovered that these invertebrates primarily move using suckered tube feet, oral primary spines, and anterior marginal spines. These structures facilitate burrowing behaviors in a dominant forward pattern, which is a characteristic of sand dollars' adaptation to an endobenthic lifestyle. Chia also found that *D. excentricus* rotates its body before moving forward, due to the presence of a functional anterior-posterior axis, even in the absence of a morphologically distinct head. These behaviors raise underlying questions about the evolutionary origins of neural circuitry in bilateral echinoderms and how their complexity compares to that of other marine invertebrates.

Methods

Organism Collection

D. excentricus were collected from Crescent Beach on Orcas Island, San Juan Islands, WA, with more than 100 adult *D. excentricus* taken from the intertidal beds off Crescent Beach by Dr. Edsinger and others. Animals were maintained in flow tanks with sand in the back of Fernald lab spaces at Friday Harbor Laboratories. Juvenile *D. excentricus* were spawned by Meztli Mariscal Del Toro and Dr. Sophie George, who also raised and maintained specimens. For the comparative model, red sea urchins (*M.franciscanus*) were taken from the Fernald touch tank at the bottom of the stairs. Juvenile red sea urchins were borrowed from Jason Hodin's lab and we were given 50 organisms to do imaging of tube feet.

Imaging and Videography of Tube Feet and Spines Activity

A. Red Sea Urchin Tube Feet and Spines

Recently settled *M. franciscanus* juveniles were placed in a temperature-controlled stage at 10℃ under an inverted microscope. An iPhone 14 Pro Max and SkyFlow app was used to shoot video time-lapse of juveniles walking in a glass-bottom petri dish. Imaging sessions were ~2-4 hours. Urchin juveniles were also placed under compound and stereo microscopes to get top-down imaging of their body orientation and spines using the same temperature-controlled stage, with imaging durations of ~2-6 hours. Adult *M. franciscanus* taken from the Fernald floor tank and from Jason Hodin's lab were placed in a large glass aquarium with minimal saltwater and elevated above the benchtop on two styrofoam boxes. We then took iPhone video footage from under the tank, focused up at the urchin's oral surface to get walking and crawling behavior of the tube feet and spines. Two light bars were assembled against the sides of the tank to illuminate the bottom of these appendages evenly.

B. Sand Dollar Tube Feet and Spines

D. excentricus juveniles were recorded and imaged in the same orientation as the red sea urchin juveniles. Both compound and inverted microscope time-lapse data were taken at ~2-6 hours intervals but without use of a temperature-controlled stage. Adult *D. excentricus* were placed in a small glass aquarium, which was elevated above the benchtop on two styrofoam boxes and positioned against a window to take advantage of natural light. A swing-arm microscope was positioned beneath the tank to capture detailed views of the oral surface. An iLabCam iPhone holder was secured to the microscope using duct tape to record high-resolution still images and videos at normal

frame rates. At selected intervals, a tripod-mounted iPhone was positioned to record simultaneous zoomed-out video, providing broader behavioral context while maintaining the close-up imaging.

Confocal Experiment

A confocal fixation, labeling, and imaging was performed for both *D. excentricus* and *M. franciscanus* juveniles. Fixation used 4% paraformaldehyde in phosphate buffered saline (PBS) overnight to 1-week at 4℃ , rinsed, and stored in PBS. Labeling of general morphology used Potomac Gold NHS ester (gift Luke Lavis; 1:1000 PBS concentration overnight). Labeling f-actin to visualize muscle used phalloidin (Biotium 1:200 PBS concentration overnight). Samples were mounted on slides in PBS or 50% glycerol prior to imaging. Confocal microscopy was used to obtain high-resolution optical sections for detailed anatomical visualization.

MicroCT Imaging of D. excentricus

A quarter-sized *D. excentricus* specimen was fixed and infused with a high-density polyacrylamide gel to stabilize internal structures . The unlabeled specimen was scanned using micro-computed tomography (microCT), processed in Slicer software, and representative images were captured from the reconstructed 3D dataset.

Time-lapse Imaging of Arena Behavior

The initial experimental design to capture sand dollar movement in small arenas (built within outdoor tanks) involved tagging five *D. excentricus* using circular cut pieces

of masking tape in distinct colors, each representing a specific positional reference for later machine learning tracking. A red circle with a unique number served as the primary identifier for each sand dollar. Blue circles marked the right side (light blue for the bottom edge, dark blue for the top edge), while green circles marked the left side (light green for the bottom edge, dark green for the top edge). Tags were affixed to the aboral side using Krazy Glue, chosen for its generally low toxicity; a preliminary trial on a compromised individual confirmed the animal's recovery post-tagging. These individuals were placed in a square tank, similar to the final tank design but with poorer water flow, set up outdoors in a flow-through seawater system with sand filtered using a sieve. Behavior was monitored using the Skyflow time-lapse app at 10-second intervals. While this configuration did not achieve the desired conditions for the full experiment, the recorded videos were of sufficient quality to develop the ethogram used in the final study.

For the final experimental design, we set up one tank in the outdoor flow-through seawater tank spaces with sieved sand. We cleaned another seawater tank and removed all the sand from the bottom. Both tanks were separated into half-sized spaces using laminated sheets duct-taped together and taped to the sides of the tank walls. We rounded this shape to retain even flow. Bricks were also used to support the curve of the structure from behind the laminated sheets. A ladder and PVC pipes were set up with duct tape to create a solid foundation for the iPhone 14 Pro Max tripod. A tarp was hung on a line and draped over the tanks to shade the iPhone from glare on the time-lapse video shot in SkyFlow. It also helped protect tanks from external factors such as wind, birds, and debris. Ten sand dollars (*D. excentricus*) were tagged for machine learning purposes using triangle-shaped waterproof printing paper. The triangle shape indicated the

direction of the sand dollar's front end. We predesigned the tag size and added number identifiers within the triangles in Word. After printing and cutting out each triangle, Krazy Glue was used to attach tags to the posterior aboral surface of the sand dollar. This minimized the amount of damage inflicted on the sand dollars' spines and increased their range of motion. After tagging the ten individual *D. excentricus*, we added them to their tank. We started a time-lapse video every scheduled experiment day for 24-hour periods. These were shot using 4K resolution, one frame per 7.5 seconds for the start time and duration, along with putting the camera on wide view. This made the best quality video we could have for machine learning to analyze. When exporting our files, we used 2.5K resolution, 60 frame rate, and high quality.

Time-lapse of Field Behavior

To compare laboratory-elicited behavior with behavior in a natural habitat, field observations were conducted at Crescent Beach, Orcas Island, San Juan Islands, WA. During a low-tide period in a subtidal sand dollar bed, we constructed a stable underwater camera mount using PVC pipes, zip ties, and a clam shovel to anchor the structure in the sediment. A waterproof iPhone case was secured to the frame, and the iPhone was positioned to record continuous time-lapse video on SkyFlow at one frame per 7.5 seconds under natural current conditions. The video ran for three days. This setup was designed to withstand tidal flow while capturing the undisturbed behavior of the population.

Ethograms

Arena time-lapse videos were reviewed to identify and characterize distinct behavioral patterns. Observations were documented by taking detailed notes on the frequency, duration, and context of behaviors. Recurrent behaviors were grouped into categories, and standardized terminology was developed to describe each behavior unambiguously. These terms formed the basis of an ethogram, which served as a reference for subsequent behavioral annotation and analysis.

Machine Learning

Uploaded arena behavioral videos were used to train a DeepLabCut model by extracting frames at defined intervals and manually labeling anatomical landmarks. The labeled frames were incorporated into the training dataset to improve model tracking accuracy; however, further training and analysis were not completed due to technical issues regarding computational resources and time limitations.

Results

Imaging and Videography of Tube Feet and Spines Activity

A. Juvenile Observations

Under both inverted and compound microscopy, juvenile *M. franciscanus* and *D. excentricus* displayed strikingly similar behaviors in tube foot and spine activity. In both species, tube feet served as the primary structures for locomotion and orientation, with spines contributing to stability and fine-scale movement. Juveniles frequently extended tube feet vertically and laterally into the surrounding space, suggesting a role in environmental sensing as well as adhesion and locomotion. During locomotion, tube feet

appeared longer and more flexible than spines, anchoring and pulling the animal forward, while the spines provided resistance against the substrate and supported changes in posture. Interactions between juveniles were also mediated by tube foot contact, highlighting their sensory function.

B. Adult Observations

While our observations of adult *M. franciscanus* in the tank setup were limited due to time constraints, we noted behaviors consistent with those seen in juveniles. Tube feet continued to play a central role in locomotion, particularly in adhesion to surfaces, where they were used to pull the animal's body upward to climb tank walls or onto rocks. Spines contributed to faster and more efficient movement through the water, enabling adults to maneuver more dynamically than sand dollars and with a wider range of motion. Adult red urchins were capable of pivoting in multiple directions depending on environmental conditions, though few constraints were evident due to their climbing ability. As in juveniles, tube feet extended farther than spines and appeared to serve a prominent sensory role in addition to locomotion.

Adult *D. excentricus* exhibited coordinated and regionally modulated patterns of spine activity across the oral surface. Spine movements followed wave-like patterns that varied depending on body region. Along a distinct midline axis (red arrow, Figure 3), spines projected outward toward the edges of the body. In the central oral region, spines shifted inward toward the mouth (white arrows), facilitating particle transport and feeding. By contrast, spines along the lateral and posterior margins moved outward, away from the midline and toward the test edges. These bilateral and region-specific patterns

emphasize the ability of adult sand dollars to integrate locomotion, feeding, and environmental responses through finely tuned modulation of spines.

Spines appeared to drive most of the movement, while tube feet were observed mainly along the posterior and lateral edges. The tube feet extended outward but did not seem to contribute significantly to locomotion; instead, they appeared to function primarily as sensory appendages that aided in directional orientation. When the animal moved in a straight line, the inner spines closest to the mouth were largely inactive. Across the remainder of the oral surface, spine activity alternated in an every-other pattern, with adjacent groups of spines moving in opposite directions. This alternating organization produced the characteristic wave-like patterns of spine movement.

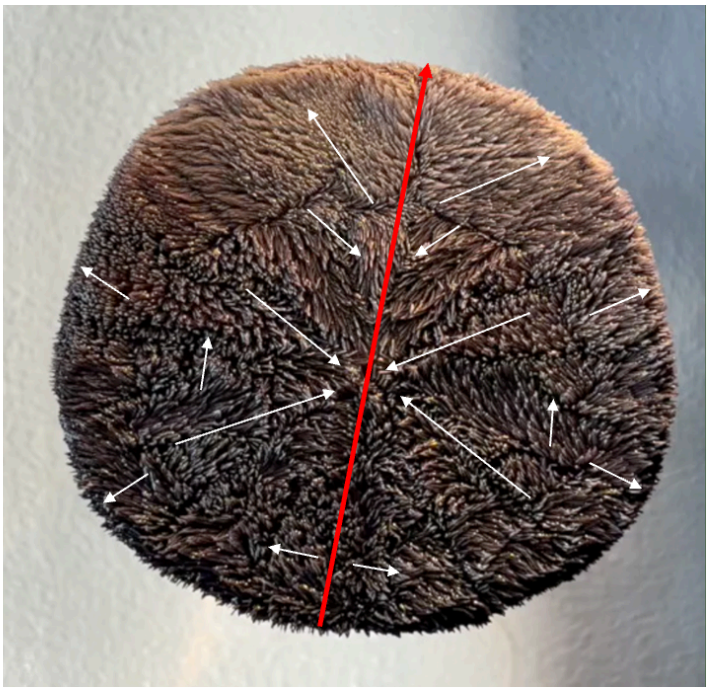

Figure 3. Spine movement dynamics on the oral surface of an adult sand dollar following KCl injection. A distinct midline axis (red arrow), oriented toward the functional anterior margin of the sand dollar, delineates directional differences in movement. In the central region, spines were observed moving inward toward the mouth (white arrows). In contrast, spines along the outer margins moved outward, away from

the midline axis, toward the edges of the animal. This figure only gives a general idea of the movements, but magnified, smaller subsections of these areas displayed modulated behavior as well.

MicroCT Scan of D. excentricus

The reconstructed 3D dataset, processed in Slicer software, revealed distinct skeletal features of the *D. excentricus* test. Clear radial patterns were visible across the test, along with the gonopores positioned near the petaloid regions on the aboral surface. On the oral surface, both the anus and mouth were well resolved. While the scan primarily captured calcified skeletal elements, some internal organization was apparent, and the position of Aristotle's lantern could be inferred from the surrounding skeletal framework, though fine internal soft-tissue structures were not fully resolved.

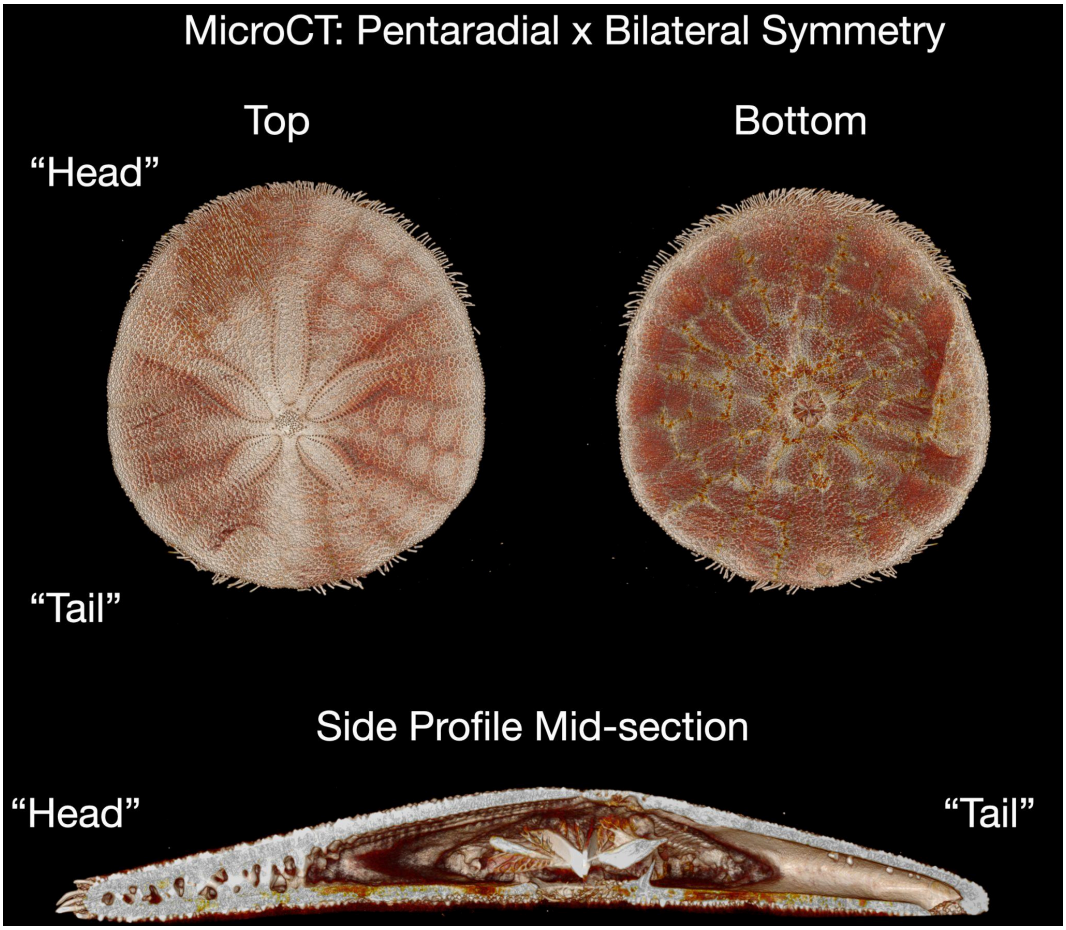

Figure 4. MicroCT reconstruction of *D. excentricus,* highlighting the coexistence of ancestral pentaradial symmetry and derived secondary bilateral symmetry. Dorsal (“top”) and ventral (“bottom”) views show the bilateral anterior (“head”) to posterior (“tail”) axis superimposed on the underlying pentaradial pattern. The mid-sagittal side profile reveals the internal morphology along this axis.

Time-lapse Imaging of Arena Behavior

Ten twenty-four hour high-quality time-lapse videos were obtained across both tank treatments (sand and no sand). In the no-sand tank, *D. excentricus* exhibited more sporadic and rapid locomotor patterns. Individuals frequently jolted forward in quick bursts of movement that were easily discernible at normal playback speed. Animals often climbed on top of one another and formed loose clumps, though they also dispersed to

explore the curved tank wall or the plastic sheet barrier. Encounters with obstacles such as bricks were typically led by the identified front end, after which individuals pivoted away while maintaining forward orientation. Turning behavior appeared less controlled than in sand; animals sometimes glided slightly in the opposite direction before successfully reorienting to continue forward movement.

In the sand tank, behavior was dominated by clumping and burrowing. Individuals consistently piled behind one another to form mounds, with the posterior ends raised and the anterior ends buried in the sand. These aggregations often persisted for extended periods, with all ten sand dollars occasionally clustering in a single corner of the tank. Overall locomotion was slower and more sedentary compared to the no-sand treatment, though animals displayed rapid bursts of activity when searching for new sand patches or conspecifics to burrow under. Turning movements in the sand tank appeared sharper and more controlled than in the no-sand condition, aided by partial burial and substrate anchoring. Together, these results highlight strong context-dependent behavioral differences: in the absence of sand, locomotion was faster and more erratic, whereas in the presence of sand, activity was reduced, with behaviors dominated by burrowing and clumping.

Behavior Title	**Definition**
Tight and Loose Spins	The subject performs rotational movements along its body axis, varying in speed and radius. *Tight spins:* Rapid rotations with a small turning radius.

	Loose spins: Slower, broader rotations with a larger turning radius. Movements may occur in either clockwise or counterclockwise directions.
Partial Burrow Resting	The subject remains motionless with the anterior (head) region buried in the sand while the rest of the body is exposed. This behavior persists for an extended period (e.g., several minutes in time-lapse or hours of real time) without active movement or locomotion.
Overlapping Locomotion	The subject moves actively across the substrate and physically contacts or traverses over other conspecifics (e.g., runs over or walks on top of other sand dollars) during active periods.
Clumping and Piling	Refers to the tendency of multiple individuals to aggregate in close physical contact, often stacking partially on top of one another. This behavior was most apparent in the sand treatment, where sand dollars frequently oriented head-first into the substrate while the posterior end remained elevated. Groups of individuals would align in series, forming mounds or layered clusters that sometimes encompassed the majority of animals in the tank.
Pivoting	The subject initiates a directional change or rotation (pivot) upon encountering a physical boundary, such as a wall or corner. Movement typically involves partial or full body rotation while maintaining contact with the surface.
Linear Direction	The subject moves in a relatively straight path with clear directional intent.
Lateral Edge Movement	Moving along the edge of an object with the oral side facing the object and inching across the side with the bottom sticking up and the top down in sand.

Figure 5. Ethogam consists of behaviors identified in both sand and no-sand tank setups. These were compared and refined using behaviors assessed from the original ethogram made from earlier tank designs and timelapses.

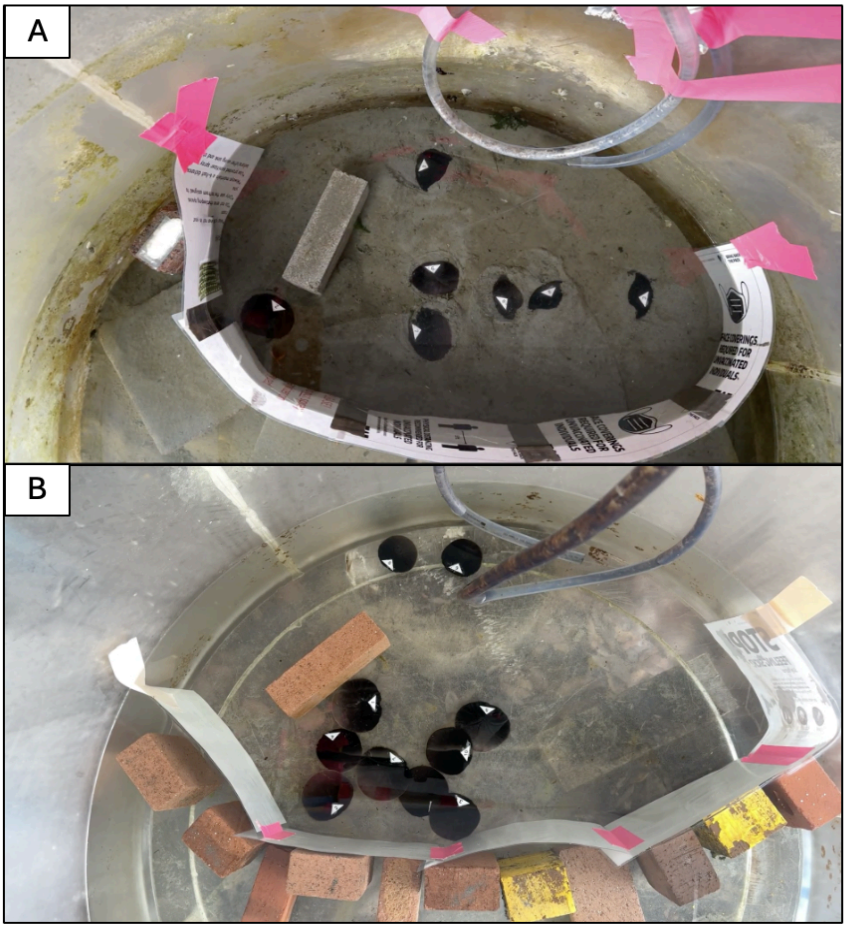

Figure 6. Final experimental tank setups. (A) Sand-filled tank with ten tagged D. excentricus individuals. (B) No-sand tank with ten tagged individuals. A brick obstacle was present in both setups.

Time-lapse of Field Behavior

At Crescent Beach, sand dollars showed behaviors very similar to those seen in the lab sand-tank setup. They moved forward with the top end leading and often gathered

into large clumps, stacking behind one another with the back ends raised above the sand. When the tide returned and water covered the bed, buried individuals emerged and began moving again, usually making small pivoting turns before orienting toward other sand dollars. Like in the lab, they often seemed to search for nearby individuals to burrow under or cluster with, forming stable groups.

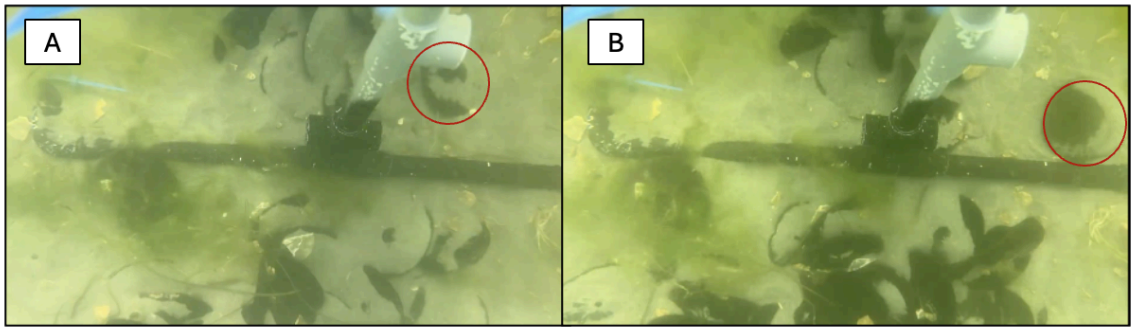

Figure 7. Field timelapse stills taken at Crescent Beach of *D. excentricus* bed. (A) Depicts burrowing clumps with individuals emerging from the sand. The red circle identifies an individual with their front end buried in sand. (B) Shows a similar still from the same video, seconds later, with individuals further exposed to water but still in clumped formation. Many sand dollars are pivoted upright with the lower end of the body sticking straight up. The circle around the same individual from (A) shows how the individual moved in a lateral line with the front end guiding their motion.

Machine Learning

Initial frame extraction and landmark labeling produced a workable training set, and the model began to recognize anatomical points with early accuracy. However, training could not be carried through to completion due to persistent GPU incompatibility and file handling issues. As a result, progress stalled at the preliminary stage, and no fully trained model or quantitative tracking data were generated.

Discussion

D. excentricus behavior varied noticeably between the sand and no-sand tank configurations. We believe that sand dollar behavior is strongly influenced by the substrate and how it impacts movement or activity. In the no-sand tank, *D. excentricus* displayed faster, sporadic movement in the time lapse video footage, possibly representing a stress response to unsuitable environmental conditions. Without sand, individuals were unable to bury the anterior region of their bodies, which is a typical feeding posture that allows water flow across the oral surface (Fu-Shiang, 1969). The stacking behavior on top of each other was potentially an attempt to replicate the piling patterns observed in the sand tank and field environment. This clumping and stacking behavior in itself was an interesting finding and that it stayed consistent in all settings. It possibly reflects that this is an innate behavior rather than an artifact of captivity. Potentially, the behavior may also serve ecological functions; the behavior might provide protection from predators by making the group appear as a larger, unified organism. It could also be used to reduce individual exposure to water flow or sediment disturbance, or perhaps in increased feeding efficiency by stabilizing the substrate. The persistence of these formations even in variable flow conditions at Crescent Beach supports the idea that clumping/piling is an adaptive, socially reinforced behavior in natural populations.

While we were able to observe piling behavior, clumping, quick locomotion, and others described in Figure 5, we were limited by our human-based ethograms and technical challenges encountered during DeepLabCut model training. Due to GPU and file compatibility issues, the model could not be fully trained, preventing automated tracking and quantitative analysis. Despite this, the potential applications of deep learning

tools in future echinoderm behavioral research remain significant. A fully functional model could provide a powerful means to visualize and quantify subtle algorithmic movement patterns that may be overlooked by human observations. Another application of machine learning we wanted to explore was DeepLabCut's capability to track individual spines or body regions across the oral surface which may have revealed fine-scale coordination and partial organization of locomotor circuits. Combining deep learning-based tracking with high-resolution imaging would open new opportunities to connect behavior with underlying neural and biomechanical control mechanisms.

Other than using machine learning to develop an understanding of the underlying neural circuitry in *D. excentricus*, studying the control mechanisms rooted in decentralized neural networks, possibly enhanced by mutable collagenous tissue (MCT), could be another tool to explore. Echinoderms are notable for lacking a centralized brain or prominent ganglia associated with cephalization (Crespi-Abril & Rubilar, 2023; Freas & Cheng, 2022). Their nervous system is a diffuse network organized into a central nervous system composed of a circumoral nerve ring and radial nerve cords that extend into the body sections (Díaz-Balzac & García-Arrarás, 2018). Yet in sand dollars, the coordinated motion of spines and the animal as a whole implies complex nervous organization that reflects their novel evolution of bilateral symmetry. Because sand dollars possess a decentralized neural control system, radial nerve coordination could potentially be inferred by looking at the sections of spine movement patterns depicted in our results, Figure 3. The spines movements, while coordinated by the nerve ring and/or local mechanical interactions, we propose here that the movements may also be modulated by mutable collagenous tissue (MCT), an unusual material unique to

echinoderms that possesses the ability to rapidly and reversibly change its stiffness (Mo et al., 2016). In previous studies on echinoderms, MCT has been linked to the changing of stiffness in the interfibrillar matrix, the material between the collagen fibrils, rather than altering the properties themselves. This rapid, neurally mediated control over tissue mechanics could be essential for quickly stabilizing the bilateral axis or adjusting the mechanical output of the spines during coordinated locomotion (Grabowsky, 1994; Mo et al., 2016).

Future work combining confocal imaging and transcriptomic approaches (RNAseq) could identify the specific neural or molecular pathways involved in generating movement in *D. excentricus*. For example, these approaches could support broader efforts to understand gene expression related to the *D. excentricus* nervous system, and can leverage deep bodies of knowledge in closely-related sea urchins, where for instance, the sea urchin genomes has revealed the genes required for synapse formation (Crespi-Abril & Rubilar, 2023). Overall, our findings highlight how *D. excentricus* integrates behavior, morphology, and neural organization to adapt within its environment and its potential for lab and field studies of behavior. New opportunities combining modern imaging and machine learning in *D. excentricus* can expand our understanding of the evolution of decentralized control in echinoderms and ultimately assess analogous systems and controls in echinoderms and cephalopods.

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