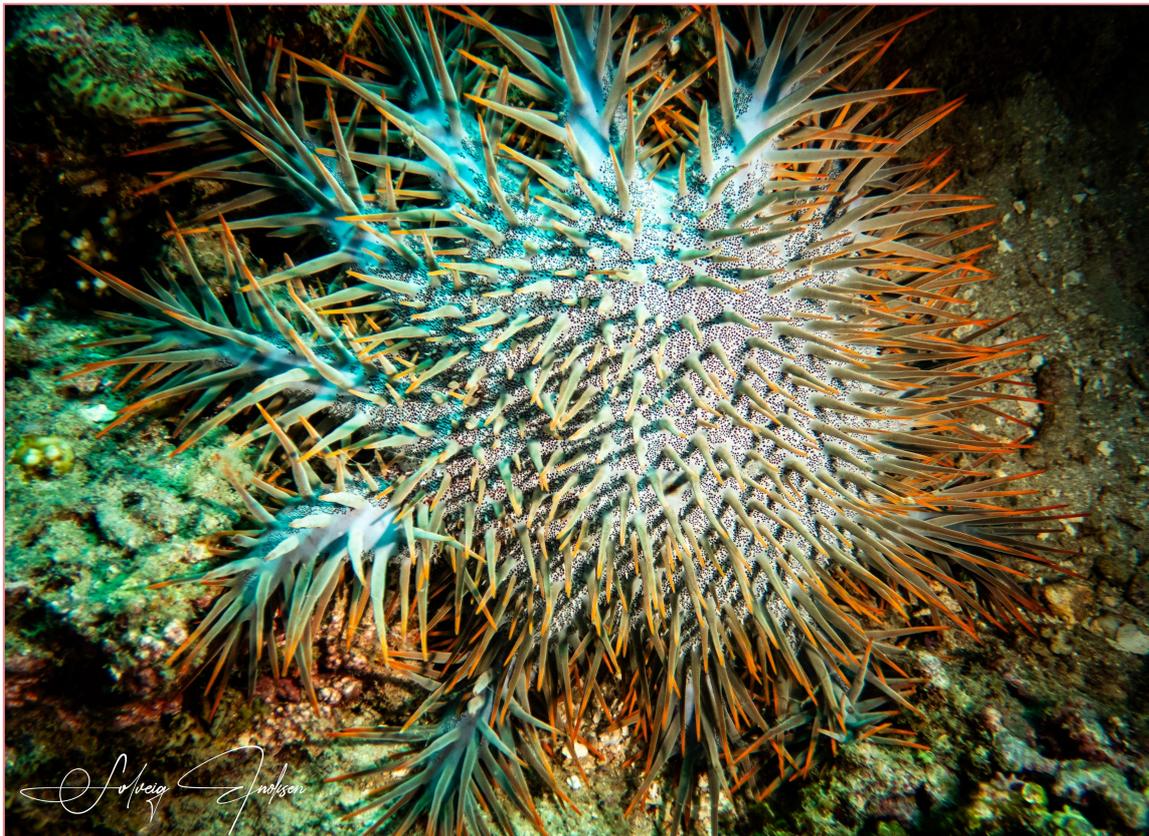


Student: Malou Poulsen – rbj795
Supervisor: Anders Lydik Garm



Nocturnal visual orientation in Crown-of-Thorns starfish (*Acanthaster planci*).

An experimental assessment of nocturnal orientation under varying light illuminations.



Photograph taken by Solveig Enoksen, a fellow volunteer at Marine Conservation Philippines.

9th of January 2026

Table of Contents

ABSTRACT	5
INTRODUCTION	6
GENERAL STARFISH BIOLOGY AND ECOLOGY	6
THE CORALLIVORE CROWN-OF-THORNS STARFISH, <i>ACANTHASTER PLANCI</i>	8
<i>Diel activity patterns and nocturnality in A. planci</i>	9
THE SENSORY BIOLOGY OF ASTEROIDEA, WITH FOCUS ON <i>A. PLANCI</i>	10
<i>Mechanoreception</i>	10
<i>Chemotaxis</i>	11
<i>Phototaxis</i>	12
RESEARCH GAPS IN THE NOCTURNAL BEHAVIOUR OF <i>A. PLANCI</i>	16
<i>The possible role of lunar illumination in nocturnal navigation</i>	16
<i>Compound eyes in deep-sea starfish</i>	16
RESEARCH AIMS	17
HYPOTHESIS	17
METHODOLOGY	18
EXPERIMENT LOCATION	18
STUDY SPECIES	19
LIGHT CONDITIONS	20
EXPERIMENTAL DESIGN	20
<i>Experimental manipulations</i>	21
DATA COLLECTION AND ANALYSIS	24
RESULTS	24
ORIENTATION PATTERNS	25
DIRECTIONAL ORIENTATION	26
THE LUNAR ILLUMINATIONS' EFFECT ON ORIENTATION ACCURACY	27
THE INFLUENCE OF RHEOTAXIS ON NAVIGATION	28
DISCUSSION	29
DAYTIME ORIENTATION	29
THE ROLE OF VISION IN NOCTURNAL NAVIGATION	30
LUNAR ILLUMINATION AND ORIENTATION ACCURACY	31
ECOLOGICAL AND THEORETICAL IMPLICATIONS	31
METHODOLOGICAL CONSIDERATIONS	31

FUTURE RESEARCH RECOMMENDATIONS	32
CONCLUSIONS.....	32
ACKNOWLEDGEMENTS	33
REFERENCE LIST	34
APPENDIXES	41
APPENDIX A: INDIVIDUAL TRAJECTORIES.	41
APPENDIX B: EXPERIMENTAL DATA	44

Abstract

Crown-of-Thorns starfish (*Acanthaster planci* species complex) are important corallivores whose feeding activity influences coral reef ecosystems, particularly during population outbreaks. Although this species complex is often described as nocturnal, little is known about how individuals navigate reef habitats at night or whether vision contributes to orientation under low-light conditions. This study experimentally investigated whether *Acanthaster* cf. *solaris* can visually orient towards reef structures at night and whether lunar illumination and ocular input influence this behaviour. Individuals were placed a fixed distance from an isolated reef structure, and their movement trajectories were recorded under new moon, full moon, and daylight conditions. Additional trials were conducted using eye-ablated individuals to assess the role of vision. Circular statistical analyses revealed that intact starfish oriented non-randomly toward the reef under both new moon and full moon conditions, whereas daytime trials and blinded trials showed random movement patterns. No significant difference in orientation accuracy was detected between lunar phases. These findings demonstrate that *A. cf. solaris* relies on visual input for nocturnal navigation and can orient toward reef structures under low light intensities. This result suggests that the visual system of *A. cf. solaris* is adapted for low-light environments and highlights the importance of nocturnal vision in foraging behaviour in this species.

Introduction

General starfish biology and ecology

Starfish (Asteroidea) are marine invertebrates within the phylum Echinodermata. This phylum includes starfish (Asteroidea), sea urchins and sand dollars (Echinoidea), brittle stars (Ophiuroidea), sea cucumbers (Holothuroidea) and feather stars and sea lilies (Crinoidea) (Brusca R. C., 2016). Asteroids are characterized by radial symmetry, a calcareous endoskeleton, and a water vascular system. This class is distributed across all major ocean basins, being strictly marine. They are found in both tropical as well as arctic regions with habitats ranging from tidal pools, mud, sandy bottoms, and coral reefs to kelp forests, seagrass, and the deep-sea (Ferdinand and Megwalu, 2018; Lawrence J.M., 2013). Starfish are primarily benthic organisms, living on the sea floor throughout their adult lives, although many species have pelagic planktonic larval stages (Brusca Richard C. et al., 2016).

Despite their habitat diversity, starfish share several distinctive anatomical traits. Their general morphology is a flattened body with a central disk and five or more arms extending from it, defined by an oral and aboral side. The aboral side may have different textures and come in various colours (Figure 1). The oral side consists of hundreds of tube feet operating via a hydraulic system, the water vascular system, that allows locomotion, adhesion, feeding, gas exchange, and sensing their surroundings. Water enters the system through a special structure called the madreporite on the aboral side (Ferdinand and Megwalu, 2018). All starfish have a mouth at the centre of the oral side, and some can extend out their stomach to feed externally on their prey. Starfish are opportunistic feeders and predate on benthic invertebrates such as bivalve molluscs, gastropods, or crustaceans (Brusca Richard C. et al., 2016). They can reproduce sexually, with eggs and sperm cells being released in the water (Vickery and McClintock, 2000). Most starfish possess a high capacity for regeneration, allowing them to regrow lost or damaged body parts, and some species are also capable of arm shedding in response to predator interactions (Hayashi and Motokawa, 1986); Ben Khadra et al., 2015). In certain taxa, detached arms that retain a portion of the central disc may develop into a complete individual, representing a form of asexual reproduction, although arm loss itself is not actively performed for reproductive purposes (Ben Khadra et al., 2015).

Starfish play an important ecological role. They have diverse diets and help keep their local ecosystem in balance by controlling populations and growth of their preferred prey (Paine, 1971, 1966). Starfish

can also have a negative effect on ecosystems. The species complex *Acanthaster planci*, known as the Crown-of-Thorns starfish (COTs), feeds on Scleractinia coral polyps (Kayal et al., 2012). When this species complex reaches high population densities, often referred to as outbreaks, it can cause substantial degradation of the coral reef it inhabits (Chesher, 1969; Moran P. J., 1986; Pratchett et al., 2017). Outbreaks of COTs in Northeast Australia and French Polynesia have caused a noticeable decline in coral density (Brodie et al., 2005). Outbreaks also have large ecosystem impacts by changing the composition of coral communities and the dominating coral genera. This leads to alterations of the coral cover and thereby also changes in the coral-associated organisms (Pratchett et al., 2021). Outbreaks are best studied and most reported from the Great Barrier Reef in Australia and from Japan (Pratchett et al., 2017; Uthicke et al., 2023). Accordingly, it is important to target behavioural studies on these organisms to better understand how to manage their outbreaks. An increased understanding of ecology and behaviour provides an opportunity to assess the impacts of these corallivores.



Figure 1. The diversity of starfish. Different types of starfish from marine coastal systems (showing aboral side). Note their similar features: radial symmetry and flattened body with five or more arms, while they display different colours and textures on the aboral side.

The corallivore Crown-of-Thorns starfish, *Acanthaster planci*

This report focuses on the species complex *A. planci* (excluding *A. brevispinus*). A species complex refers to a group of closely related organisms that are morphologically very similar and often difficult to distinguish using traditional morphological characters, but which are genetically, reproductively, or ecologically distinct lineages (Bickford et al., 2007). The species complex can be found in many tropical regions from the Red Sea and the east coast of Africa across the Indian Ocean to Western Australia, as well as from the Indo-Pacific down to the Great Barrier Reef and across to western Americas (Moran P. J., 1986; Pratchett et al., 2017) (Figure 2). Research is suggesting that at least four different species occur in the world's oceans (Vogler et al., 2013, 2012, 2008) (Figure 2). The species that inhabit the Western Pacific, where this research was done, is identified as *Acanthaster* cf. *solaris* (Schreber, 1793; Vogler et al., 2013, 2008). The general morphology of the *A. cf. solaris* is a central disc with 11-17 arms and long, poisonous spines protruding from the aboral side. The aboral body colour of the *A. cf. solaris* is blue and grey with dark red spots spread over the central disc (Labnao et al., 2024) (Figure 3).

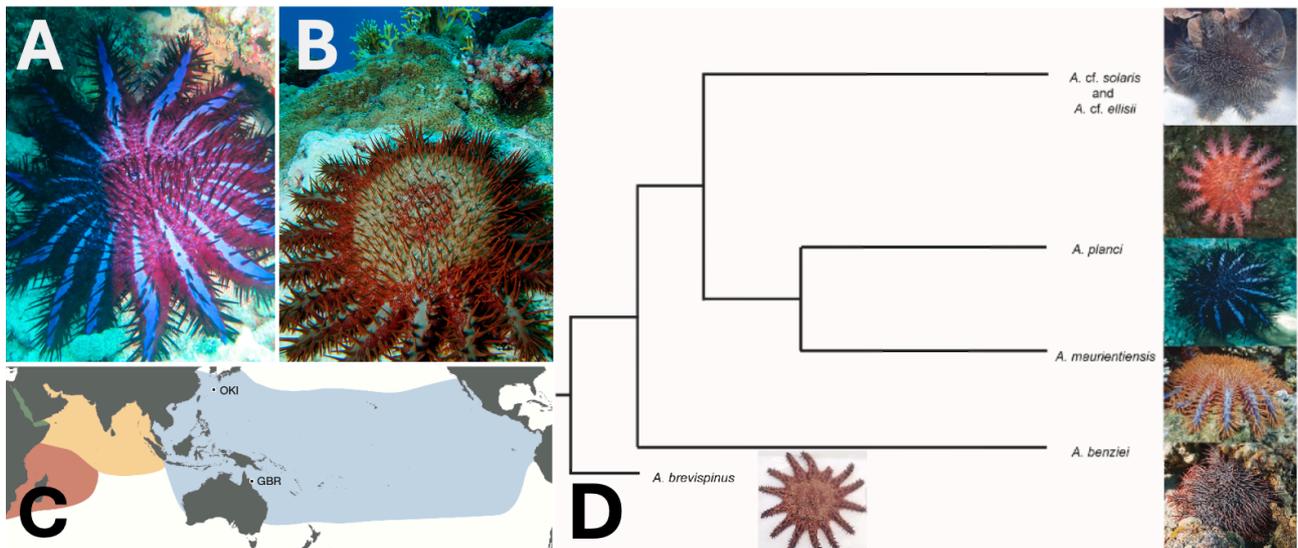


Figure 2. *Acanthaster planci* species complex. **A)** *Acanthaster planci* from the North Indian Ocean, photo taken by M. Pratchett in the Maldives. **B)** *Acanthaster* cf. *solaris* from the Pacific Ocean, photo taken by C. Caba. A) and B) borrowed from Pratchett et al., (2017). **C)** Distribution of different COTs species. Genetic clades displaying green for the Red Sea, red for the Southern Indian Ocean, yellow for the Northern Indian Ocean, and blue for the Pacific, including two sample sites in Okinawa (OKI) and the Great Barrier Reef (GBR), displaying 98.8% nucleotide identity between populations of *A. cf. solaris*. Borrowed from Hall et al., (2017). **D)** Phylogenetic tree displaying the four species, with potentially two different species distinctively living in the east and west Pacific (Dr. Shawna Foo, The University of Sydney, and Dr. Cristian Moisés Galván-Villa, University of Guadalajara). Tree drawn after Uthicke et al., (2023). Borrowed from Foo et al., (2024).

These morphological features intersect with a highly specialized dietary strategy, which influences the ecology of coral reefs worldwide. The feeding preferences for *Acanthaster cf. solaris* from the Western Pacific are *Acropora* corals, while *Porites* corals are less preferred (Birkeland, 1990; Keesing, 2023; Moran P. J., 1986; Pratchett et al., 2017). *Acropora* will therefore be more frequently consumed by *A. cf. solaris* than other genera of corals, leaving them to be depleted first from reefs with outbreaks (Goreau et al., n.d.; Pratchett et al., 2017, 2009). However, the feeding pattern alone does not fully describe the species' behaviour.

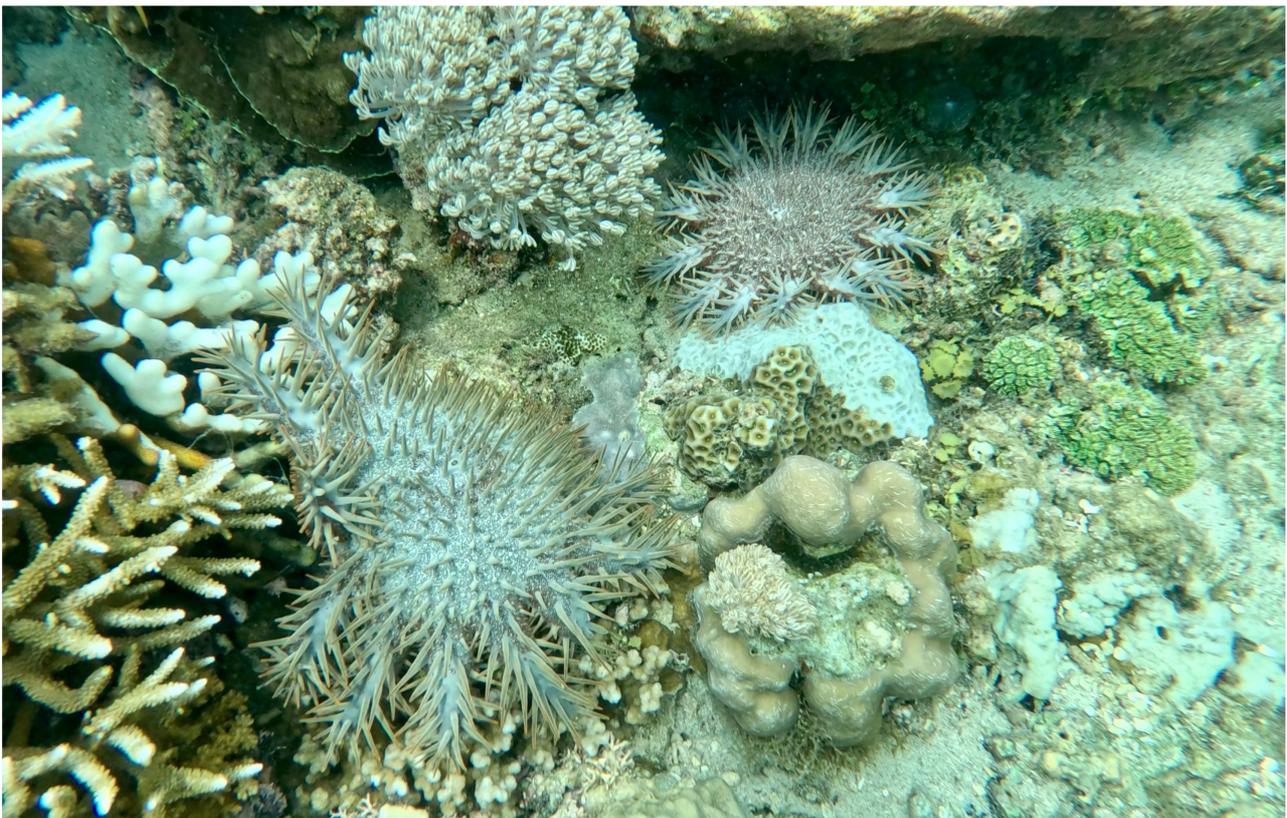


Figure 3. *Acanthaster. cf. solaris* appearance. Sample photos of *Acanthaster cf. solaris* in its natural habitat. Note the multiple arms, long, orange-toned spines, and blue and grey coloured body. Individual sizes here are between 15-20 cm.

Diel activity patterns and nocturnality in *A. planci*

The species complex, *A. planci*, is considered nocturnal, though there is some conjecture in the literature. Some say the starfish remains hidden in daytime and becomes active at night when they occur in normal numbers on reefs (Burn et al., 2020). Literature also concludes that feeding takes place continuously day and night if they occur in outbreaks (Branham et al., 1971; Chesher, 1969; Endean, 1969). On the other hand, Ormond R.F.G. and Campbell A.C., (1974) concluded that feeding activity in the Red Sea population of *Acanthaster benziei* was exclusively nocturnal, regardless of

density. In addition to this, Wilson B.R. and Marsh L.M. (1975) found diurnal feeding of *A. cf. solaris* even in very low-density populations in Western Australia, as well as in Mexico (Dana T. F. and Wolfson A. A., 1970) and Panama (Glynn, 1974). Overall, the literature indicates considerable uncertainty regarding the nocturnality of the species complex, *A. planci*. Nocturnal behaviour might have evolved as a response to the threat of predation, as the availability of prey to *A. planci* doesn't change on a daily rhythm (Keesing, 2023). Another study showed significantly more movement at nighttime compared to daytime, and that for crepuscular times, movement speed was twice that of what was observed at night for the species *A. cf. solaris* in the Great Barrier Reef (Ling et al., 2020). The reported occurrence of nocturnal and crepuscular activity on *A. cf. solaris* raises questions about the sensory mechanisms underlying activity during low-light conditions.

The sensory biology of Asteroidea, with focus on *A. planci*

Like most other animals, starfish rely on several sensory modalities to navigate their surroundings. Behavioural data regarding mechanoreception, chemoreception, and phototaxis demonstrate how starfish navigate life with these senses (Castilla J. C., 1975; Cobb and Stubbs, 1981; Garm, 2017; Garm and Nilsson, 2014; Lawrence J.M., 2013; Sloan and Northway, 2003). Starfish are known to be radially symmetric and have no centralized brain. Still, they have a complex nervous system consisting of a nerve ring around the mouth and a radial nerve going along each arm. The radial nerve is positioned along the ambulacral region of each arm. The peripheral nerve system forms 2 distinct networks. The first network is embedded within the epidermis, where it mediates environmental sensing through a distributed array of sensory neurons capable of detecting mechanical and chemical stimuli (Burke et al., 2006; Cobb and Stubbs, 1981). The second network lines the coelomic cavity and is associated primarily with the regulation of internal physiological processes, including coordination of muscle activity and modulation of coelomic fluid dynamics (Mashanov V.S. et al., 2016). These two networks are interconnected via radial nerve cords, allowing integration between sensory input and motor or autonomic outputs. The structural and functional differentiation of these networks highlights the complexity of echinoderm neuroanatomy, despite the absence of a centralized brain.

Mechanoreception

Mechanoreception in starfish covers their ability to detect physical forces such as touch, gravity, and water movement. There seems to be no accepted studies on the sense of touch in asteroids. However, there are indications of sensory cells in the epithelia of starfish, which could support touch sensitivity

in the skin (Roberts et al., 2017). Moreover, starfish seem to have a sense of gravity. Their response to gravity might be guided by the shear pressure and weight of the starfish's body on their tube feet (Castilla J. C., 1975; Reese E., 1966). For this mechanism to be in place, the species would need a kind of stretch receptor in the tube feet, and such receptors have not been identified so far. A complex nervous system is known from the tube feet, though, which possibly includes these receptors (Moore and Thorndyke, 1993).

In addition to detecting direct mechanical forces acting on the body, starfish might also be able to perceive water movement (rheotaxis) in their environment. Rheotaxis is the oriented movement of an organism in response to a current of water. Animals can exhibit positive rheotaxis, moving against the direction of the current, or negative rheotaxis, moving with the current. Asteroids have been shown to display positive rheotaxis. Data indicate that *Luidia sarsi* preferred to move against the direction of the current (Fenchel, 1965). Others (Castilla J., 1971; Castilla and Crisp, 1973) did a more in-depth study on different environmental factors influencing the movement of *Asterias rubens*. In this study, the starfish responded to currents as slow as 0.15m/s, and this made the authors contemplate a possible presence of specialized receptors to detect a current (Castilla and Crisp, 1973). More recently, the rheotaxis of *A. cf. solaris* was studied in their natural habitat (Sigl et al., 2016). The authors found *A. cf. solaris* displays negative rheotaxis in strong currents (>15cm/s) but no reaction in weaker currents. However, the specific receptors and how they mediate rheotaxis remain unknown.

Chemotaxis

Regarding chemo sensation, authors have shown that *A. rubens* very accurately locate their preferred prey, *Mytilus edulis*, using olfaction (Castilla, 1972; Castilla and Crisp, 1970). Others also found that olfaction plays a very important role in the detection of cryptic prey items such as clams and mussels, the preferred prey for many starfish (Güler and Lök, 2015; Thompson et al., 2004). Other studies also show that the juvenile stages of *A. planci* respond to different chemical cues. The juvenile COTs are herbivorous, feeding on crustose coralline algae (CCA) for approximately six months before transitioning to coral-prey diet (Lucas, 1984). Herbivorous-stage Crown-of-Thorns starfish moved towards waterborne cues from coral rubble covered in CCA and live coral, indicating attraction to these habitat cues. When presented with both CCA and live coral, juveniles showed a stronger preference for coral. Furthermore, juveniles tended to move away from chemical cues from adult conspecifics (Webb et al., 2024). Another study suggested that chemicals from corals can activate

attraction or feeding responses in adult *A. planci* (Huxley, 1976; Roberts et al., 2017). Molecular evidence also shows that *A. planci* has a dedicated chemosensory receptor repertoire (Roberts et al., 2017). All these findings highlight a chemosensory framework that guides *A. planci* through life, however, the extent to which these chemical signals are integrated with or superseded by visual cues under low-light conditions remains undiscovered.

Phototaxis

Phototaxis refers to the direct movement of an organism in response to light. Almost all Asteroidea carry a compound eye, also known as the optic cushion, at the tip of each arm (Birk et al., 2018; Garm, 2017; Penn and Alexander, 1980; Yoshida and Ohtsuki, 1966). The eye is positioned at the base of the distal-most tube foot, a modified tube foot, and consists of multiple ommatidia (Figure 4). The eye seems to be the distal-most tip of the radial nerve (Garm, 2017). Adult starfish have between 10 and 300 ommatidia, depending on the species. The eyes develop throughout life, though no research has proven at exactly what stage the eye first appears. Well-fed COTs develop an increasing amount of ommatidia throughout their growth, resulting in an ever-growing eye (Petie et al., 2016b). Two types of cells make up the ommatidia: pigment cells and photoreceptors. In adult starfish, there are around 100-150 of each type in each ommatidium (Eakin and Brandenburger, 1979; Garm and Nilsson, 2014; Petie et al., 2016b). The photoreceptors are centrally positioned within the unit, with their light-sensitive outer segments oriented toward incoming light (Garm and Nilsson, 2014). These photoreceptors are surrounded by pigment cells that absorb excess light and help each ommatidium respond mainly to light coming from a specific direction. Moreover, the screening pigment of the cell is red in all examined species. This suggests a spectral sensitivity in the short wavelength of the visual spectrum. Indeed, electroretinograms have shown a lack of colour vision with a spectral sensitivity peaking around 470 nm for *Linckia laevigata* and *A. planci* (Garm and Nilsson, 2014; Petie et al., 2016b). Each ommatidium is thought to create one pixel of the image, and combining output across multiple arms creates a visual field that supports directional movement (Petie et al., 2016b). The spatial resolution is sufficient to extract biologically relevant information from the environment. Studies on *A. planci* have shown that the number and arrangement of ommatidia allow detection of large, high-contrast features such as reef structures, which is essential for orientation and habitat localization (Garm and Nilsson, 2014; Petie et al., 2016b).

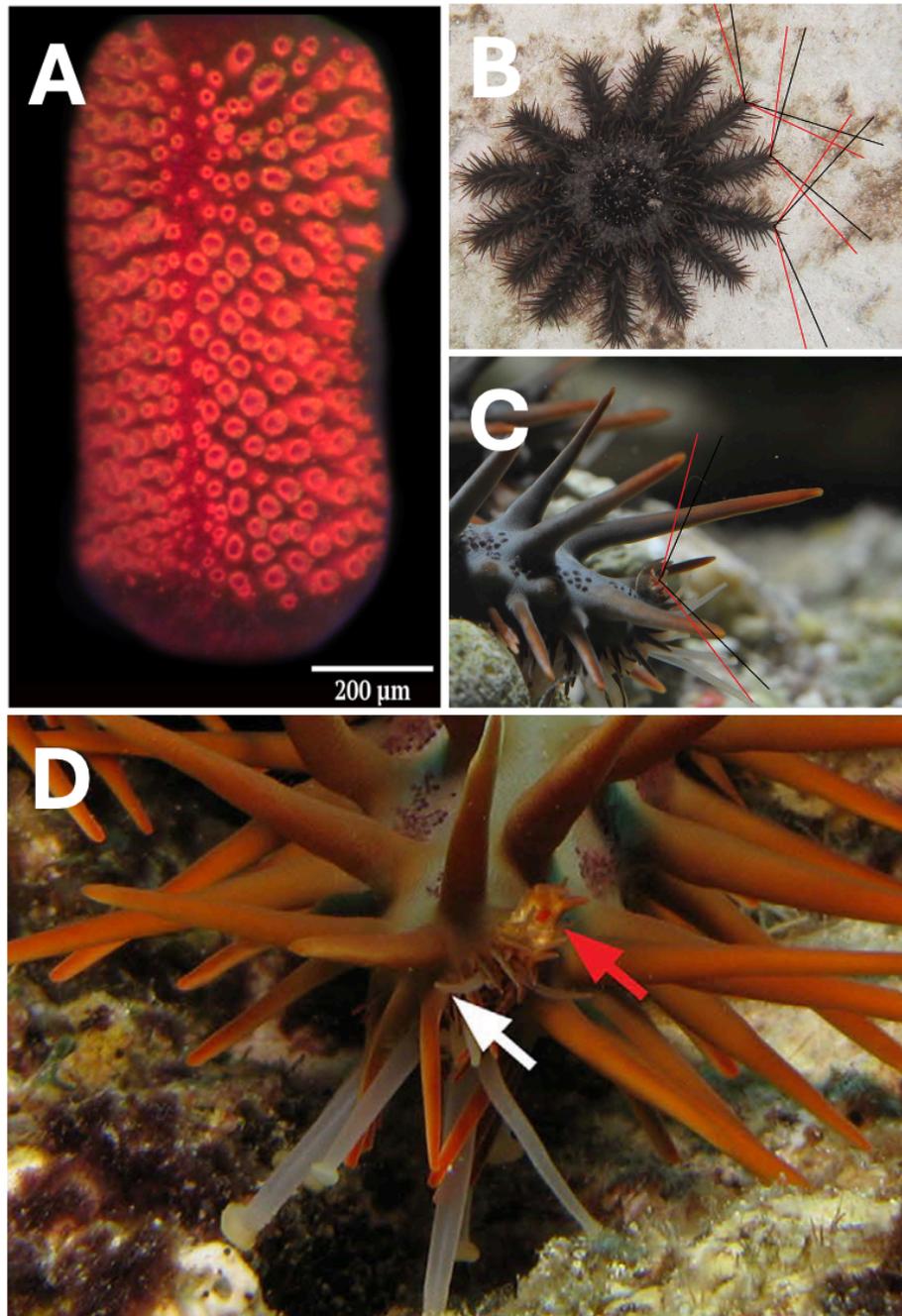


Figure 4. Visual system of *A. planci*. **A)** The compound eye of an adult *A. planci*, displaying approximately 250 ommatidia. Note the red screening pigment of pigment cells surrounding the photoreceptors in one ommatidium. Borrowed from Korsvig-Nielsen et al., (2019). **B)** Displaying the horizontal visual field of *A. planci*. **C)** Displaying the vertical visual field of *A. planci*. **D)** Tip of moving arm from *Acanthaster planci*, showing the red compound eye (red arrow) and the extended sensory tube feet (white arrow). B), C), and D) borrowed from Sigl et al., (2016).

L. laevigata and *A. planci* are the most well-documented species when it comes to vision in Asteroidea. Evidence from previous work demonstrates that both *L. laevigata* and *A. planci* use visual cues to navigate to their feeding grounds, the coral reefs. Individuals with intact visual systems moved towards a large coral boulder when placed one meter away, while individuals with eye amputations

moved in random directions. These studies showed that vision is essential for navigation and that olfaction cannot compensate for eyesight (Garm and Nilsson, 2014; Petie et al., 2016b). Moreover, they have been proven to form true images, shaping strong contrasts between the reef structure and the blue backdrop (Garm and Nilsson, 2014; Petie et al., 2016a; Sigl et al., 2016) (Figure 5). *Acanthaster planci* has an oval-like visual field with 100° horizontally and 30° vertically (Petie et al., 2016a), leading to a possible 360° horizontal visual field. In addition, the starfish eye has low spatial vision, ranging from approximately 8° in *A. planci* to around 16° in *L. laevigata* (Garm and Nilsson, 2014; Petie et al., 2016a, 2016b). Crown-of-Thorns starfish also seem to have the lowest temporal resolution and thereby the slowest vision ever recorded in any animal, with a flicker-fusion frequency of 0.5Hz (Petie et al., 2016b). This matches the movements of the animal and the importance of detecting large non-moving coral boulders. All this has led different scientists to suggest that starfish can detect larger stationary objects, like a coral boulder, within short distances (Garm and Nilsson, 2014; Petie et al., 2016a, 2016b).

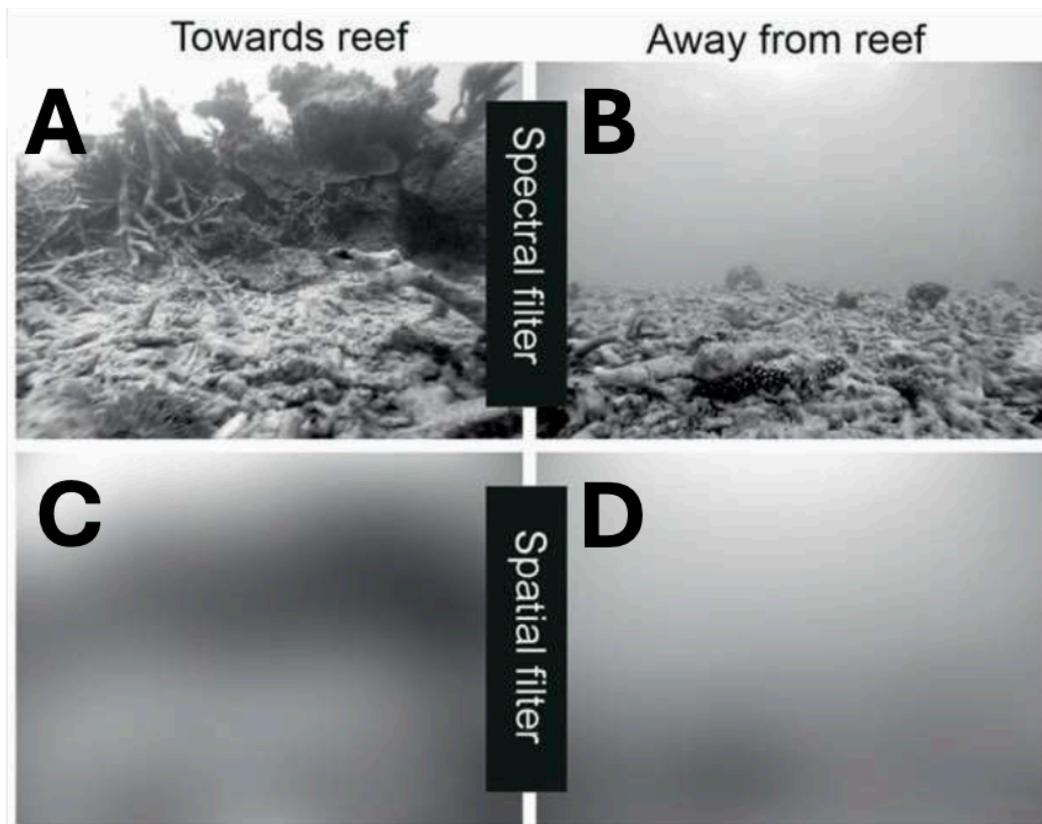


Figure 5. Visual image from *A. planci*. A) Showing the view towards the reef and B) showing the view away from the reef. C) and D) showing those views with a Gaussian blur filter with an 8° radius, simulating the visual image as seen from a Crown-of-Thorns. Borrowed and altered from Garm et al., (2023).

Beyond the structural properties of starfish eyes, recent studies have shown that vision is not passive but can be actively adjusted through coordinated movements of the arms. This allows them to modify where visual information is gathered. Beer et al., (2016) conducted a series of experiments examining how *A. planci* controls its field of view during different behavioural tasks. Their observations showed that the starfish actively adjusts the position of its arms to modify the direction in which its eyes are oriented. Rather than rotating the eyes themselves, *A. planci* alters its vertical field of vision by lifting or lowering individual arms. During movement, the arms leading in the direction of travel were often raised above the horizontal plane, likely improving visual detection of coral structures ahead. In contrast, arms trailing behind remained close to the substrate, although the tips of these arms frequently bent sharply upwards, sometimes more than 120°, directing the eyes towards the space above the animal. This may help detect predators or assess ambient light conditions (Beer et al., 2016) (Figure 6). Taken together, existing research demonstrates that vision in *A. planci* is sufficiently developed to support spatial orientation, providing a strong foundation for investigating its role under nocturnal conditions.

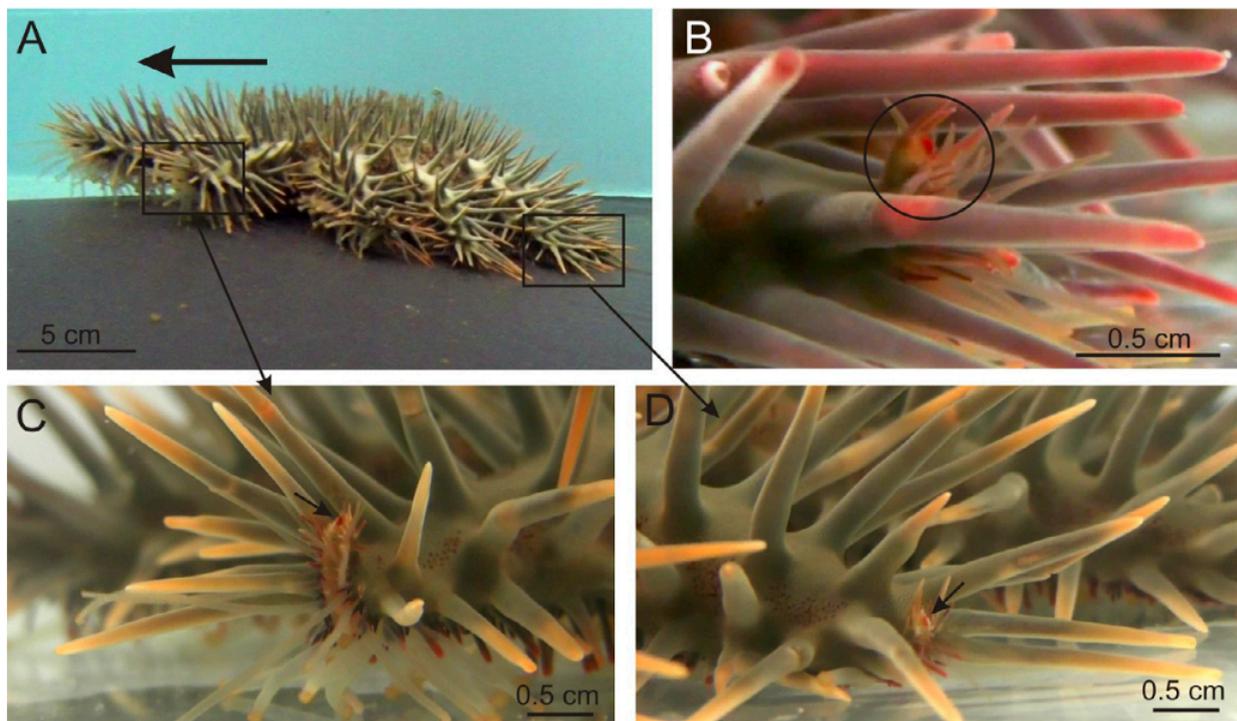


Figure 6. Active visual control in *A. planci*. **A)** A moving COTs with leading arms lifted vertically, moving on stretched out tube feet and trailing arms lowered to the bottom. The black arrow indicates the moving direction. **B)** Compound eye situated at the base of the terminal tube foot, pointing upwards, bending independently from the rest of the arm. **C)** The black arrow pointing to the compound eye on one of the leading arms, lifted upward on stretched tube feet. **D)** The black arrow pointing to the compound eye on one of the trailing arms, pressed to the substrate. Figure 4 borrowed from Beer et al., (2016).

Research gaps in the nocturnal behaviour of *A. planci*

Studies have shown that *A. planci* uses vision to navigate its habitat; however, all research to date has been conducted under daylight conditions (Beer et al., 2016; Garm and Nilsson, 2014; Petie et al., 2016b). Although field observations suggest that the species is often active at night, it is unknown whether it can use vision under these dim conditions or relies on other senses such as chemoreception or rheotaxis. Electroretinograms indicate that the eyes of *A. planci* are adapted for daylight intensities, supporting the idea that vision is most effective during daylight (Petie et al., 2016b). This highlights a substantial gap in our understanding of nocturnal navigation and foraging in this species. Clarifying which sensory pathways guide movement could inform strategies to manage their impact on coral reefs.

The possible role of lunar illumination in nocturnal navigation

Nocturnal navigation and the use of lunar illumination as a navigational cue are well documented in many marine species. This provides a biological basis for investigating similar capabilities in *A. planci*. For example, sea turtle hatchlings use the moonlight reflecting off the sea surface to locate the ocean shortly after hatching, demonstrating that nocturnal light can be sufficient for effective navigation (Witherington and Bjorndal, 1991). Similar patterns are seen in other taxa, such as glass eels. The juvenile *Anguilla anguilla* migratory movements change predictably with the lunar cycle (Cresci et al., 2019). More broadly, many marine organisms adjust their behaviour, like foraging, reproducing, and movement patterns, according to the moonlight (Ritter and Tessmar-Raible, 2024). These examples make it reasonable to wonder whether *A. planci* might also use moonlight to navigate around the habitat. However, very few studies have been undertaken at night, leaving a substantial research gap about the nightly behaviour of *A. planci*.

Compound eyes in deep-sea starfish

The possibility of low-light vision has been hinted at from a recent study about the eyes of deep-sea starfish (Birk et al., 2018), which showed that 12 of the 13 examined semi-deep-sea and deep-sea species of starfish have a compound eye at the tip of each arm (Figure 7). These findings indicate that starfish vision remains useful under very low light, likely allowing them to detect bioluminescent signals or navigate along the seafloor. Together with the previously mentioned studies portraying image formation in *L. laevigata* and *A. planci* (Garm and Nilsson, 2014; Petie et al., 2016a, 2016b), these studies suggest that visual systems in some starfish could be adapted either to deep-sea darkness or night-time coastal environments.

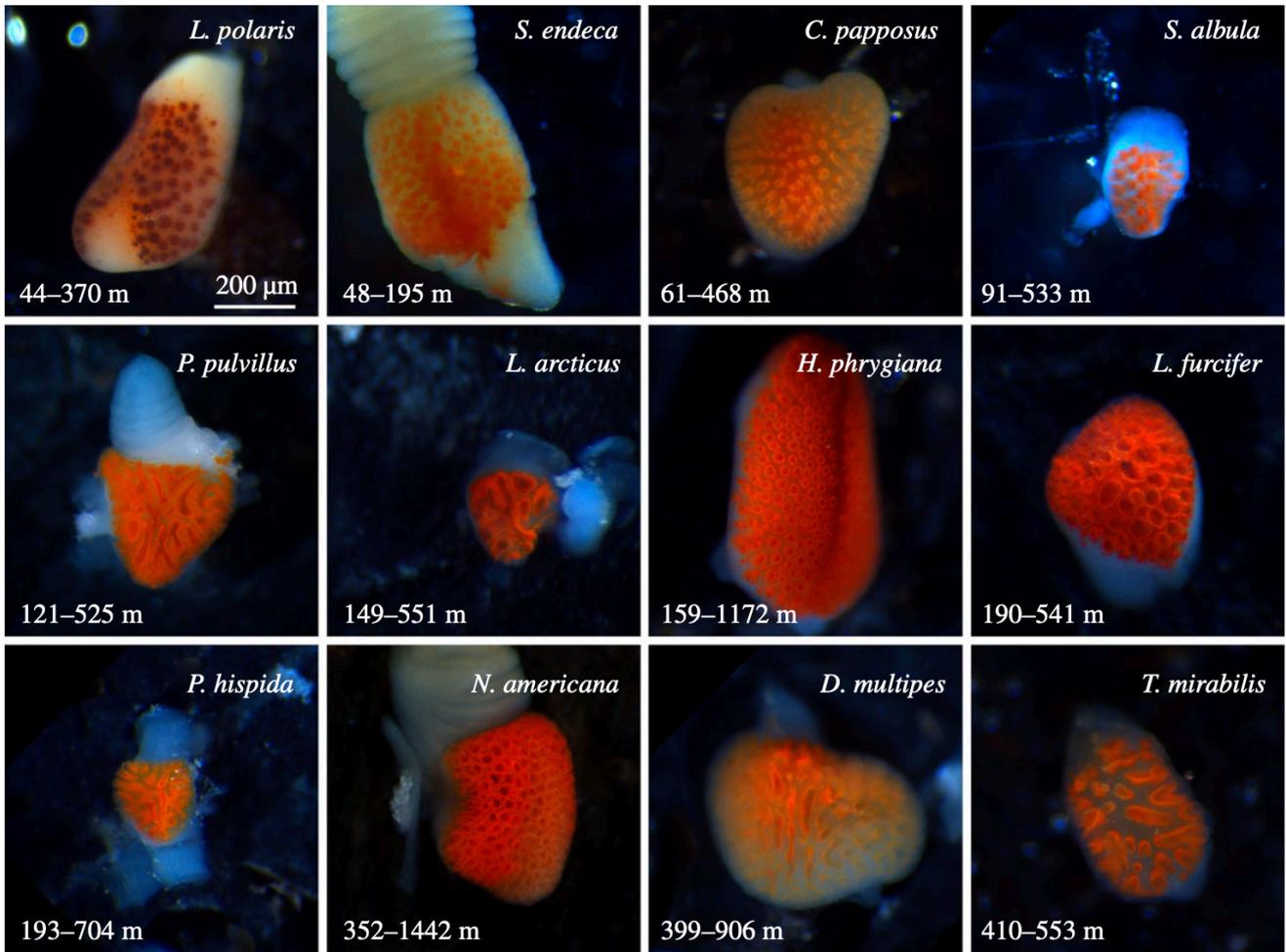


Figure 7. Compound eyes of 12 deep-sea starfish. Distinct eye shapes and sizes of ommatidia. Pictures arranged according to their depth distribution as noted on the figure, from shallow to deep, from left to right. Note an increase in ommatidia size with depth distribution and different shapes of ommatidia in different species. Borrowed from Birk et al., (2018)

Research aims

This study aims to determine whether *A. cf. solaris* can use visual cues to orient towards reef structures at night. Specifically, I examined whether movement trajectories differed between new moon, full moon, and daytime illumination. By combining behavioural experiments under different light conditions with eye ablation experiments, the study clarifies how important vision is for navigation in low-light environments. Finally, it is assessed if rheotaxis has an influence on the direction of movement by comparing the current direction with individual trajectories.

Hypothesis

Since *A. cf. solaris* often is actively feeding at night, this study hypothesises that *A. cf. solaris* uses visual cues to successfully orient towards a reef structure under nocturnal light conditions, and that

the success rate increases with increasing lunar illumination intensity. Furthermore, it is hypothesised that eye-ablated *A. cf. solaris* cannot successfully orient towards a reef structure, causing it to move in random directions. Lastly, this study hypothesizes that the trajectories of *A. cf. solaris* will not be affected by the current directions.

Methodology

Experiment location

Experiments were conducted at Andulay dive site in the municipality Siaton, southern Negros Oriental, in the Philippines (Figure 8). Andulay dive site was experiencing a Crown-of-Thorns starfish breakout and was therefore chosen as the experimental location to ensure ample sample size. A part of the area is a marine protected area (MPA), and the behavioural experiments were conducted about one hundred meters outside of the MPA. The collection of COTs happened both outside and inside the MPA.

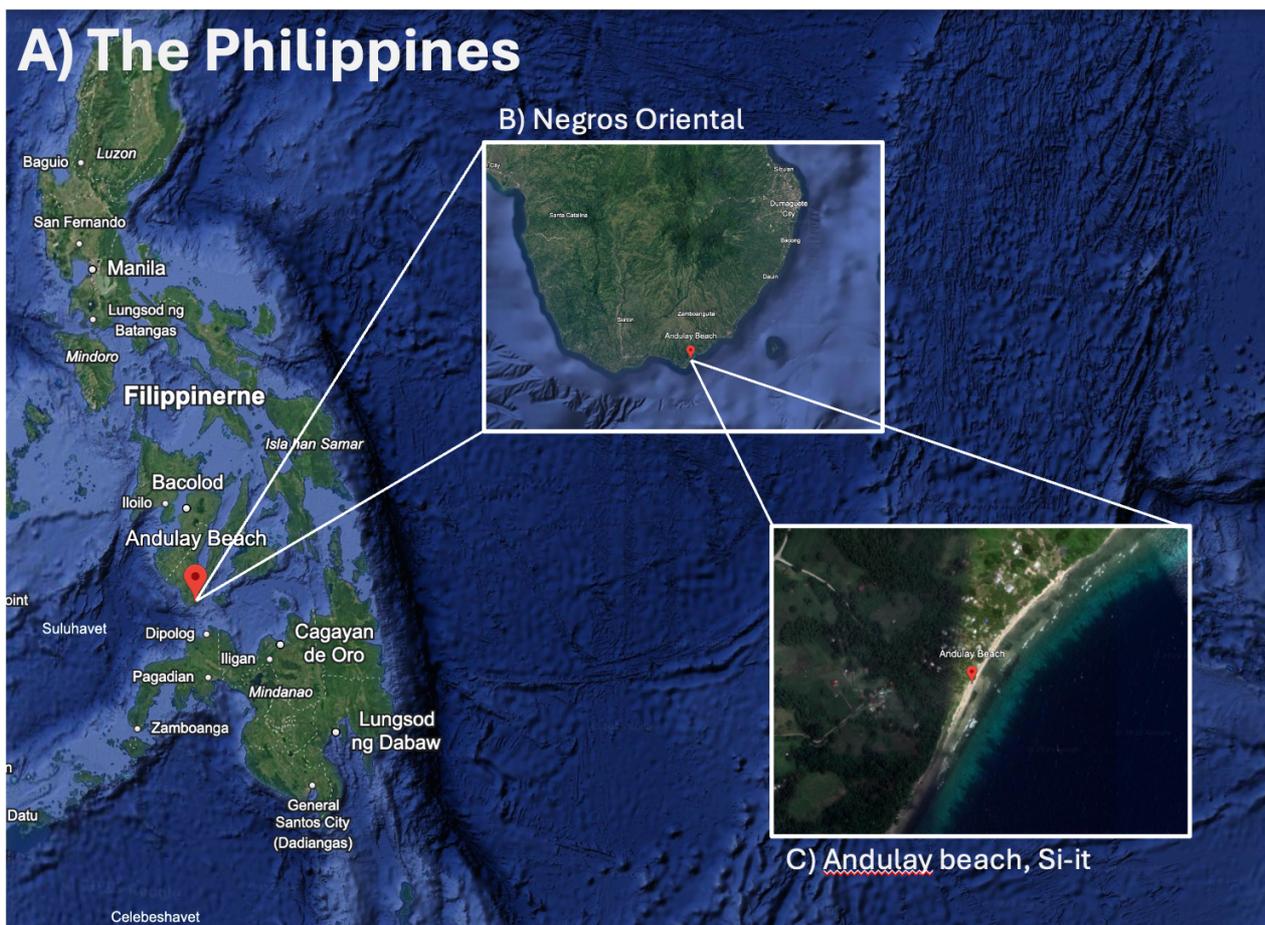


Figure 8. Experimental location. A) Map of the Philippines, red map pin is Andulay beach. B) South Negros Oriental. C) Andulay beach, Si-it. (9.058458470818572, 123.13743710504502). Maps taken from Google Earth.

Study species

Acanthaster planci is a species complex associated with coral reefs all over the world. The proposed species living in the Philippines is *Acanthaster cf. solaris*. For consistency, *A. cf. solaris* or COTs will be used to refer to the study species for the remainder of this report. Individuals with an arm to arm diameter between 15-20 cm were collected from the Andulay dive site (Figure 9) at depths of 2 - 4 m. The size of the COTs was measured to control for ontogenetic variation in sensory and behavioral performance. The COTs were found hidden in small crevices or feeding on branching coral. All animals were handled with gloves and tongs to ensure safety and to prevent damage to individuals. Every *A. cf. solaris* was tested in only one trial and thereafter culled. Cullings were performed by injecting 20 ml of vinegar into the central body using a syringe. All individuals were collected within one hour before the experiment, except for the blinded individuals, which were collected and blinded 24 hours before the experiment. A 24-hour recovery period was implemented to ensure no immediate surgical stress while still maintaining a functionally blinded state. Although *A. planci* exhibits regenerative capacity, this process in asteroids typically follows a multi-stage timeline where the first 48 hours are limited to wound closure (Ben Khadra et al., 2015). Consequently, the individuals in this study remained visually impaired throughout the experimental trial, as functional photoreceptors had not yet begun to reform.

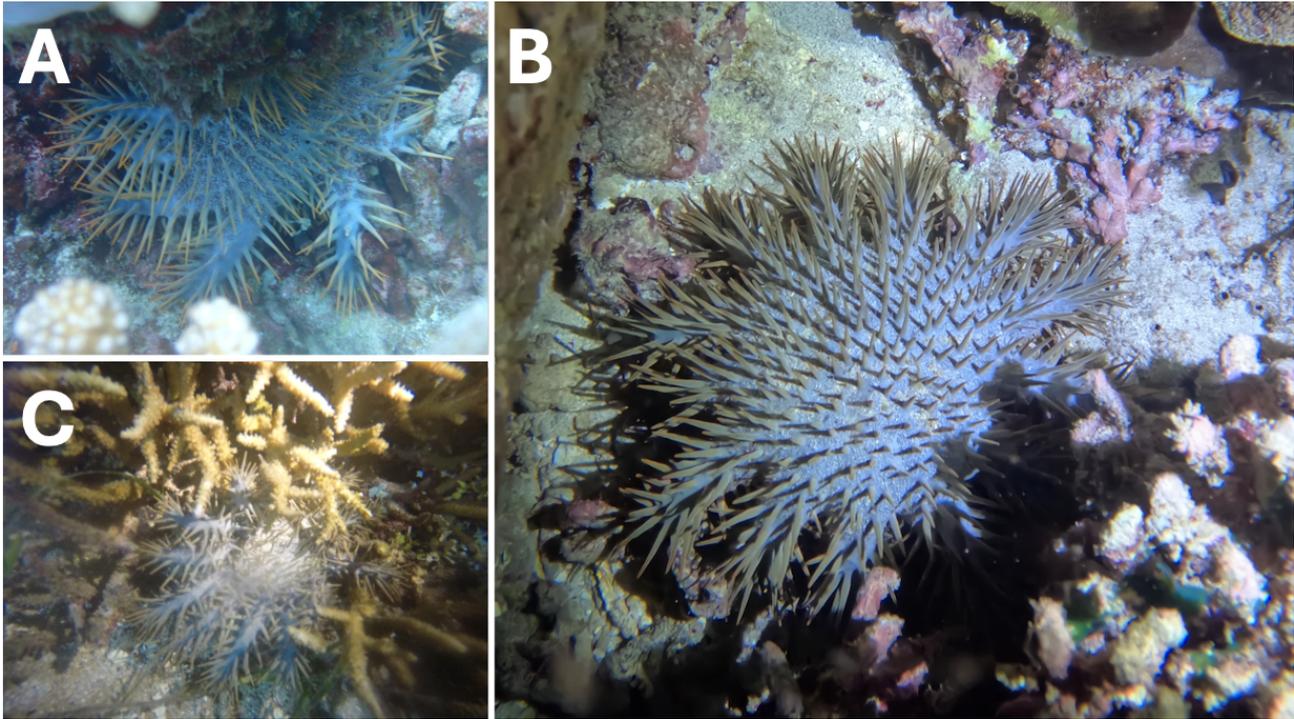


Figure 9. Individual *A. cf. solaris* from Andulay dive site. A) and B) showing different individuals hiding or resting in between coral crevices. C) Showing *A. cf. solaris* feeding on coral.

Light Conditions

Mainly, two ambient light conditions were tested, while daylight was used as a positive control test. The two light conditions were new moon (with no lunar illumination) and full moon (with maximum lunar illumination). All trials were conducted with a calm sea and under similar tidal conditions (high tide) to reduce environmental variability. Light conditions varied naturally throughout the experiment, with predominantly cloudless conditions.

Experimental design

The experiments were inspired by (Garm et al., 2014; Sigl et al., 2016; Petie et al., 2016b). The experiments were conducted in a shallow area containing a single, isolated reef structure approximately 2 m tall and 4 m wide, with no adjacent reefs visible within the animal's field of view. The sea floor topography at the location was sand with patches of seagrass (like *Enhalus acoroides*, approx. 5-8cm in height). The setup of the experiment consists of 2 x 2 m reels forming a T to ensure identical data collection (Figure 11). A delayed surface marker buoy (DSMB) was deployed to analyse the direction and strength of the current, as well as to serve as an anchor with 4-pound weights at the end. This ensured stable image capturing as a diver would float above the setup while holding on to the DSMB line. At the start of each trial, three to five *A. cf. solaris* were placed 1 m from the

reef front, and individual sizes were measured (Appendix B). Movements were recorded with an overhead camera held by a diver at 1-minute intervals for 10 minutes per trial. All divers would hover in full darkness 2-3 meters above and behind the horizontal reel (Figure 11), to be out of the visual field of *A. cf. solaris*. Multiple assistant divers would light up the experiment for 5 seconds per minute (8.33% of the time - to minimize light disturbances) as one diver took a photo.

Experimental manipulations

Three experimental factors were manipulated:

1. Daylight conditions

Trials under daylight were conducted with a total of 9 individuals to assess visual orientation during daylight intensities. These trials were conducted approximately between 10 am and 2 pm during high tide conditions.

2. Nightlight conditions

Trials were performed during full moon and new moon phases, each with 17 individuals, for a total of 34 individuals. Experiments were conducted over 3 months of moon cycles in late September, October, November and early December of 2025. All these trials were conducted between 7 pm and 10 pm, making sure the moon was high above the horizon.

3. Blinded individuals

A total of 8 starfish were collected 24 hours before the experiment, and their ocular structures were removed shortly after capture. The terminal ossicle, terminal tube foot, including the compound eye, was removed from all arms, a total of 120 eyes (figure 10). These blinded individuals were allowed at least 24 hours of recovery in a controlled plastic housing on the reef before being tested under full moon conditions.

This design allowed evaluation of how *A. cf. solaris* navigates towards reef structures under varying light conditions, as well as the role of visual structures in orientation.

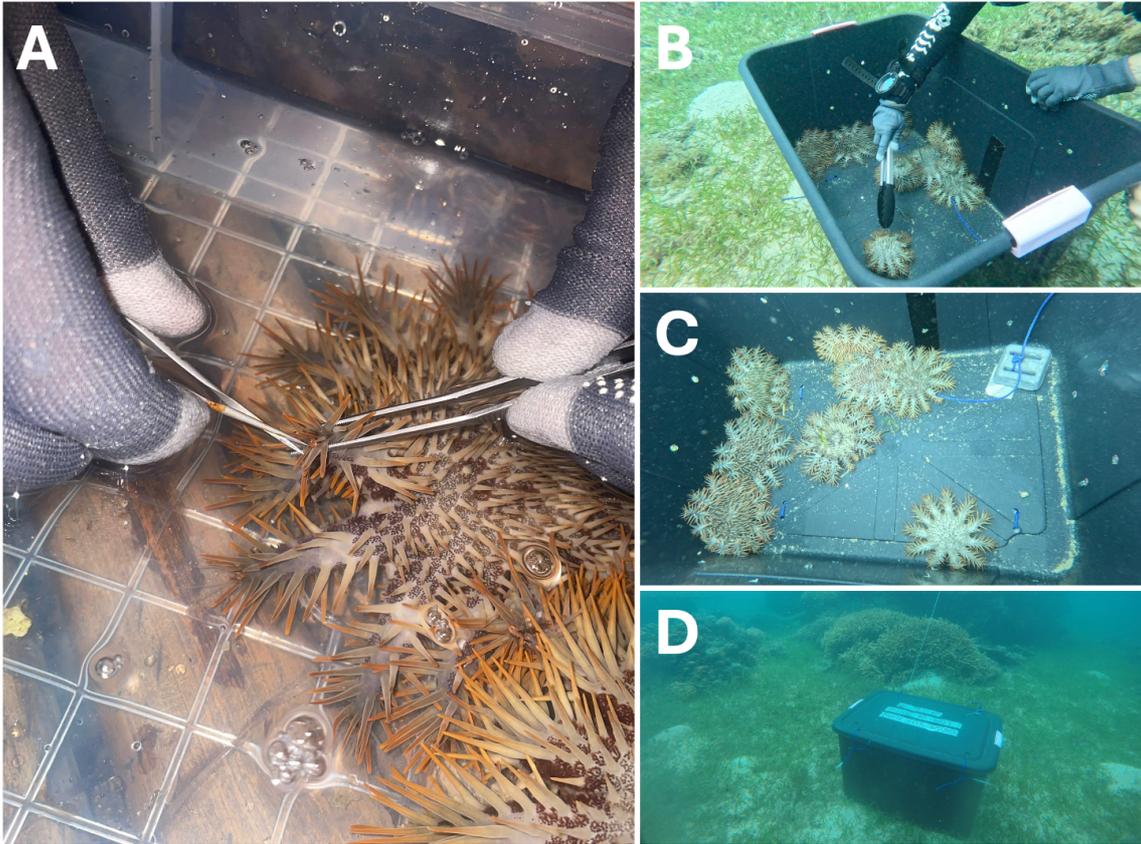


Figure 10. Eye ablation. A) Surgical removal of a compound eye with fine scissors and tweezers. B), C), and D) placement and housing of eight eye-ablated individuals for at least 24-hour recovery.

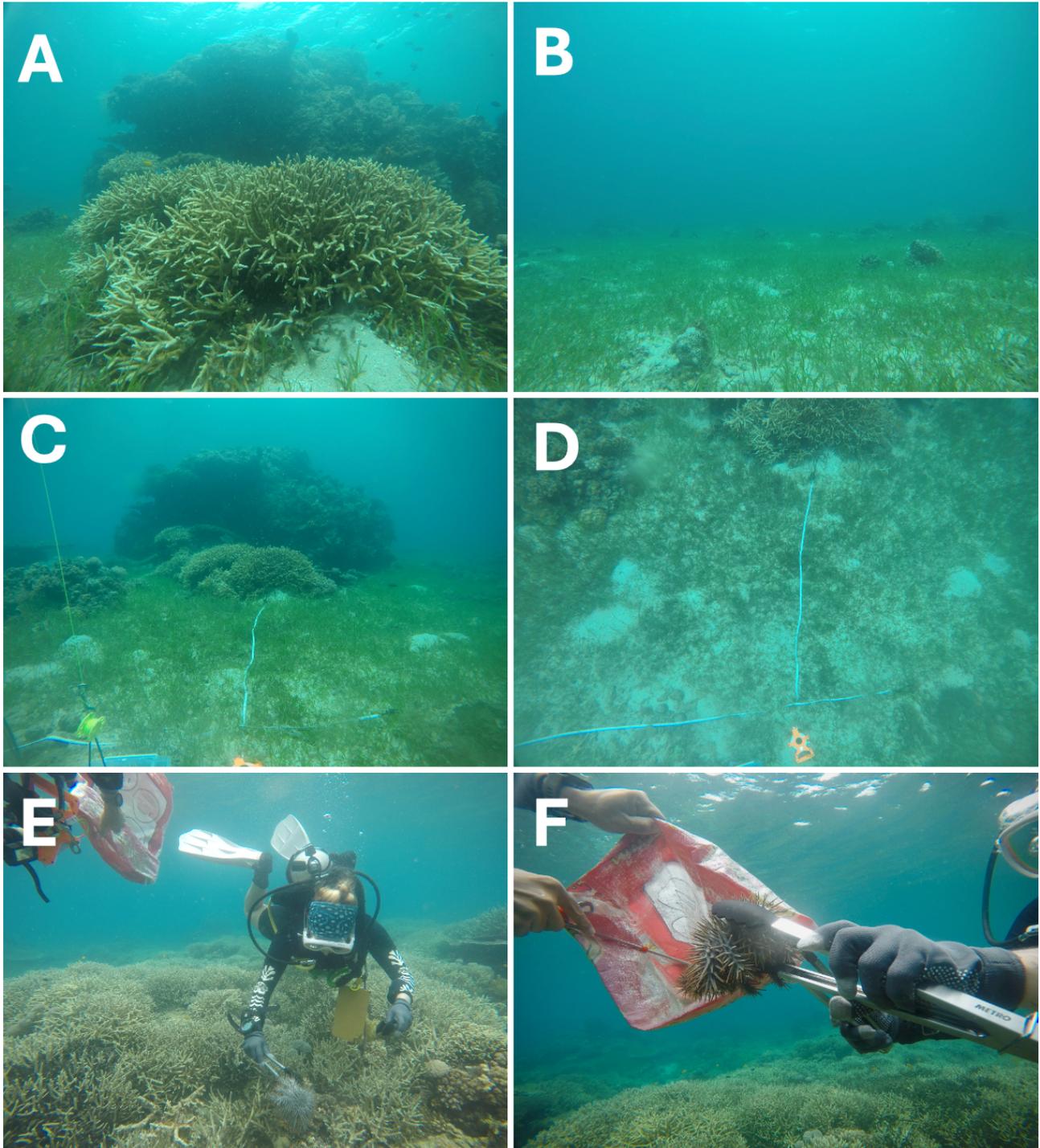


Figure 11. Experimental setup and catching *A. cf. solaris*. **A)** Showing the view towards the coral boulder, and **B)** showing the view away from the coral boulder. Not the preferred feeding grounds (Acropora corals) in A), and no adjacent coral boulders in B). **C)** and **D)** displaying the experimental setup with 2 x 2 m reels forming a T formation to ensure identical data collection. In panel C), the delayed surface marker buoy (DSMB) line is shown, used to stabilize the photographing diver. **E)** and **F)** show a diver collecting one *A. cf. solaris* from the coral reef at Andulay dive site. COTs were collected by divers using gloves and tongs.

Data collection and analysis

Animal trajectories were reconstructed through the analysis of sequential time-lapse photography at 1-minute intervals. Using GeoGebra, movement patterns were mapped by stacking sequential frames to visualize the orientation pathway of each individual (Figure 12) (Appendix A for trajectories). For each trial, the shortest linear distance to the reef was established as the primary reference vector, designated at 0° . The angular displacement was then quantified by circular measurement between the start and terminal placement relative to this reef-ward axis (Figure 13) (Appendix B for all measured angles). This approach enabled the statistical analysis of directional orientation using circular geometry, ensuring that all movement was measured against the shortest distance to the reef.

Results

In total, 14 trials of 3-5 individuals, as well as 8 blinded individuals, were completed across three light conditions: new moon, full moon, and daylight. This totalled to 52 individuals.

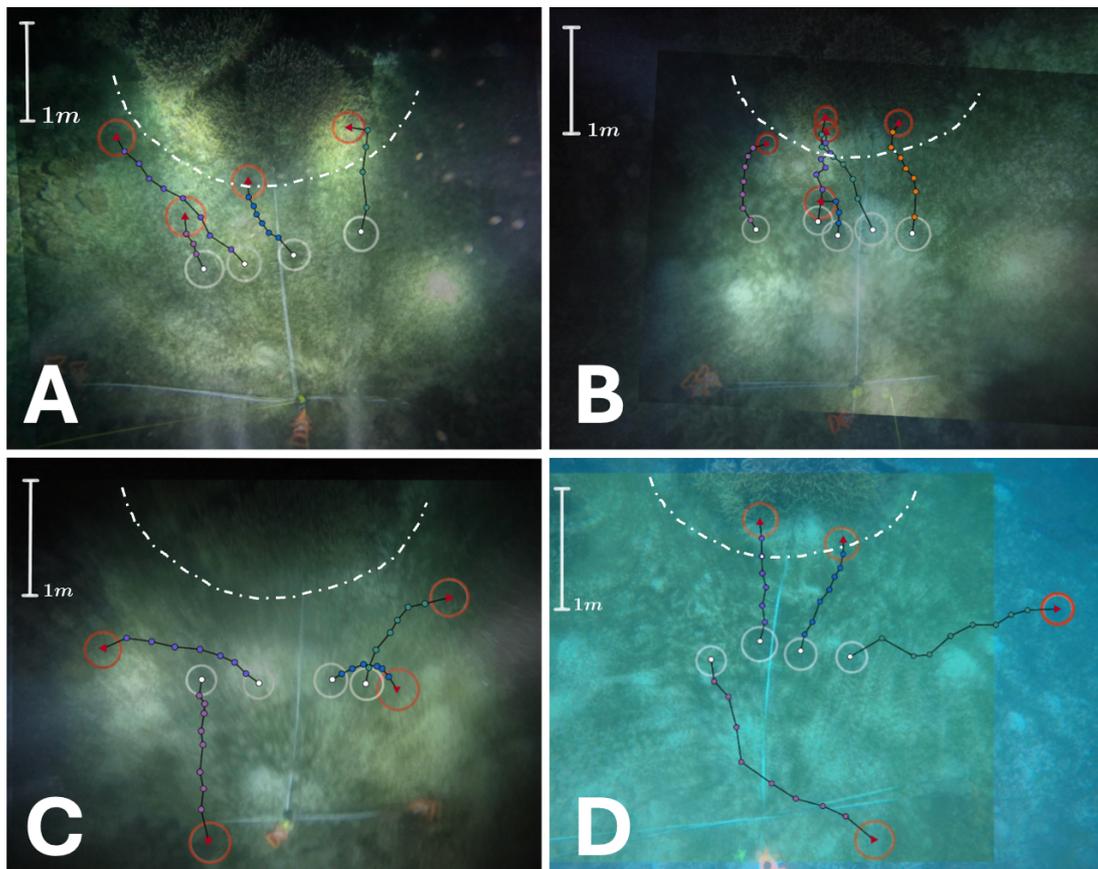


Figure 12. Movement trajectories of *A. cf. solaris* under different light conditions. In all panels, the white (translucent) circle and dot indicate the starting position of each individual, while the red circle and arrow indicate the final position and direction of movement

for each individual. Individual trajectories are shown in different colours: pink, purple, blue, green, and orange. The reef position is marked with a white dotted line. **A)** movement trajectories of five intact individuals during new moon conditions, all orienting toward the reef front. **B)** Movement trajectories of four intact individuals during full moon conditions, all orienting towards the reef front. **C)** Movement trajectories of four blinded individuals during full moon conditions, all moving in random directions. **D)** movement trajectories of four intact individuals during daylight conditions, where two move towards the reef, and two move away from the reef.

Orientation patterns

Movement patterns for new moon and full moon phases clearly show oriented movement towards the coral reef, while daylight and blinded individuals moved in what seems like random directions (Figure 12). Circular statistical analyses on the angular displacement were conducted using the software Oriana (Kovach Computing Services) to statistically test their trajectories.

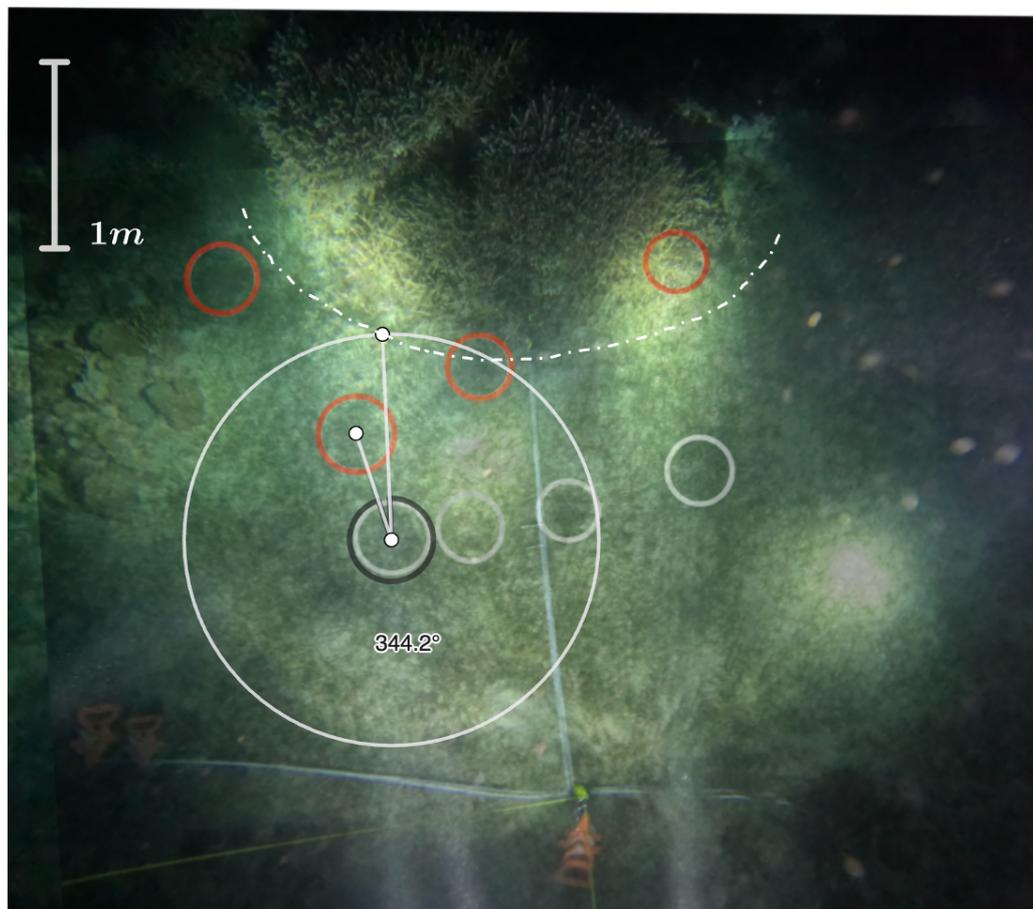


Figure 13. Angular displacement. The orientation angle was calculated by measuring the angular displacement of the terminal position relative to the reference axis of the shortest distance to the reef. All geometric calculations and vector mappings were performed using GeoGebra software. A small white circle represents the start position of one individual *A. cf. solaris*, a red circle represents the final position of that same individual, and the large white circle represents the circular measurement used to determine the angular displacement. The reef position is marked with a white dotted line. Note the angular displacement here is 344.2° , rounded down to 344° (nearest whole degree) to reflect the estimated limit of measurement precision.

Both conditions tested at night (new moon and full moon conditions) showed strong directional orientation toward the reef (0°). The mean vectors of 8° (New moon) and 350° (Full moon) indicate high accuracy, supported by high r-values of 0.7 (for both), which demonstrate strong clustering around the mean. The Rayleigh tests for both nocturnal groups yielded highly significant results (Rayleigh's full moon $Z = 8.463$, $p = 6.5 \cdot e^{-5}$ and Rayleigh's new moon $Z = 8.645$, $p = 5.02 \cdot e^{-5}$), confirming that the movement was not random. In contrast, both the daylight group and the eye-ablated group failed the Rayleigh test for uniformity (daylight $Z = 0.125$, $p = 0.888$ and blinded $Z = 0.74$, $p = 0.492$). Their low r-values (daylight $r = 0.1$ and blinded $r = 0.3$) and mean vectors (daylight $\mu = 237^\circ$ and blinded $\mu = 103^\circ$) indicate that, without functional vision or under daylight conditions, the individuals were unable to maintain a consistent heading (Table 1).

Table 1 Circular statistics for *Acanthaster cf. solaris*. Significant p-values for new moon and full moon trials, with mean vectors pointing towards the reef (0°) and 0.7 length of mean vector for both conditions, displaying a strong clustering around the mean. These conditions also have a 95% CI that includes the direction of the reef, confirming the movement was oriented towards the reef. No significant p-values for daylight or eye-ablated trials, with mean vectors not pointing towards the reef, and low values of the length of the mean vector indicating a weak clustering around the mean.

	New moon	Full moon	Daylight	Eye-ablated COTs
Sample size (n)	17	17	9	8
Mean vector (μ) (°)	8	350	237	103
Length of μ (r)	0.7	0.7	0.1	0.3
95% CI (°)	345 - 30	327 - 13	*****	318 -248
Rayleigh Z	8.645	8.463	0.125	0.74
Rayleigh p	5.02E-05	6.50E-05	0.888	0.492

Directional orientation

For trials showing non-random orientation (new moon and full moon), directional bias toward the reef was assessed by testing whether the reef direction (0°) was included within the 95% confidence interval of the mean vector. For the full moon (95% CI = 327° - 13°) and the new moon data (95% CI = 345° - 30°), the confidence interval showed they moved towards the reef (Table 1).

The lunar illuminations' effect on orientation accuracy

A qualitative comparison of the nocturnal trials indicates that navigational accuracy remained consistent regardless of lunar phase. Both new moon and full moon groups exhibited identical mean vector lengths ($r = 0.7$), demonstrating an equal degree of directional clustering toward the reef. Furthermore, the 95% confidence intervals for both conditions show substantial overlap, suggesting that the mean orientation headings are statistically indistinguishable, though it has not been tested.

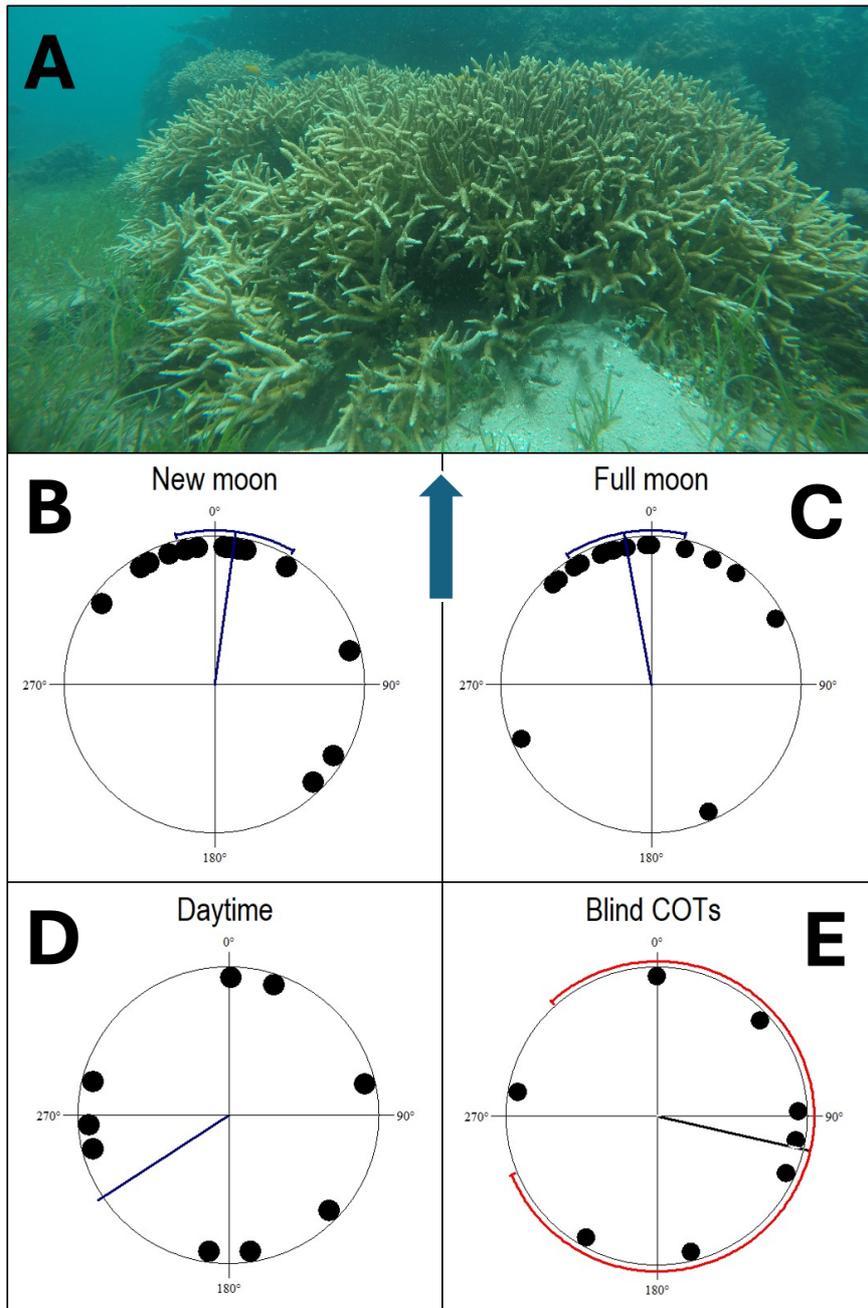


Figure 13. Circular plots illustrating COT orientation. Black dots represent the final positions of individual *A. cf. solaris*. Blue lines represent the mean vector direction and blue arcs indicate the 95% CI of the mean direction for trials with significant orientation, while red arcs indicate non-significant 95% CI. The direction toward the reef is defined as 0° and visualized with a blue arrow pointing to

the reef front. **A)** Reef front. **B)** and **C)** show significant directional movement of 17 individuals during new moon and full moon conditions, respectively, with the 95% CI including the reef front (0°) in both graphs. **D)** 9 individuals during daylight conditions, showing non-significant orientation. **E)** 8 eye-ablated individuals during full moon conditions, also showing non-significant orientation.

The influence of rheotaxis on navigation

While variations in water current direction were recorded across trials (ranging from 30° to 255° , see figure 14), these fluctuations did not appear to qualitatively influence the navigational headings of *A. cf. solaris*, though it was not statistically tested. It is likely that the benthic topography, specifically the 5-8cm tall seagrass cover (*E. acoroides*), served as a layer that weakened the current velocity at the benthic level. This could potentially have reduced the reliability of rheotaxis. A table showing the current direction at every trial is attached under the appendices.

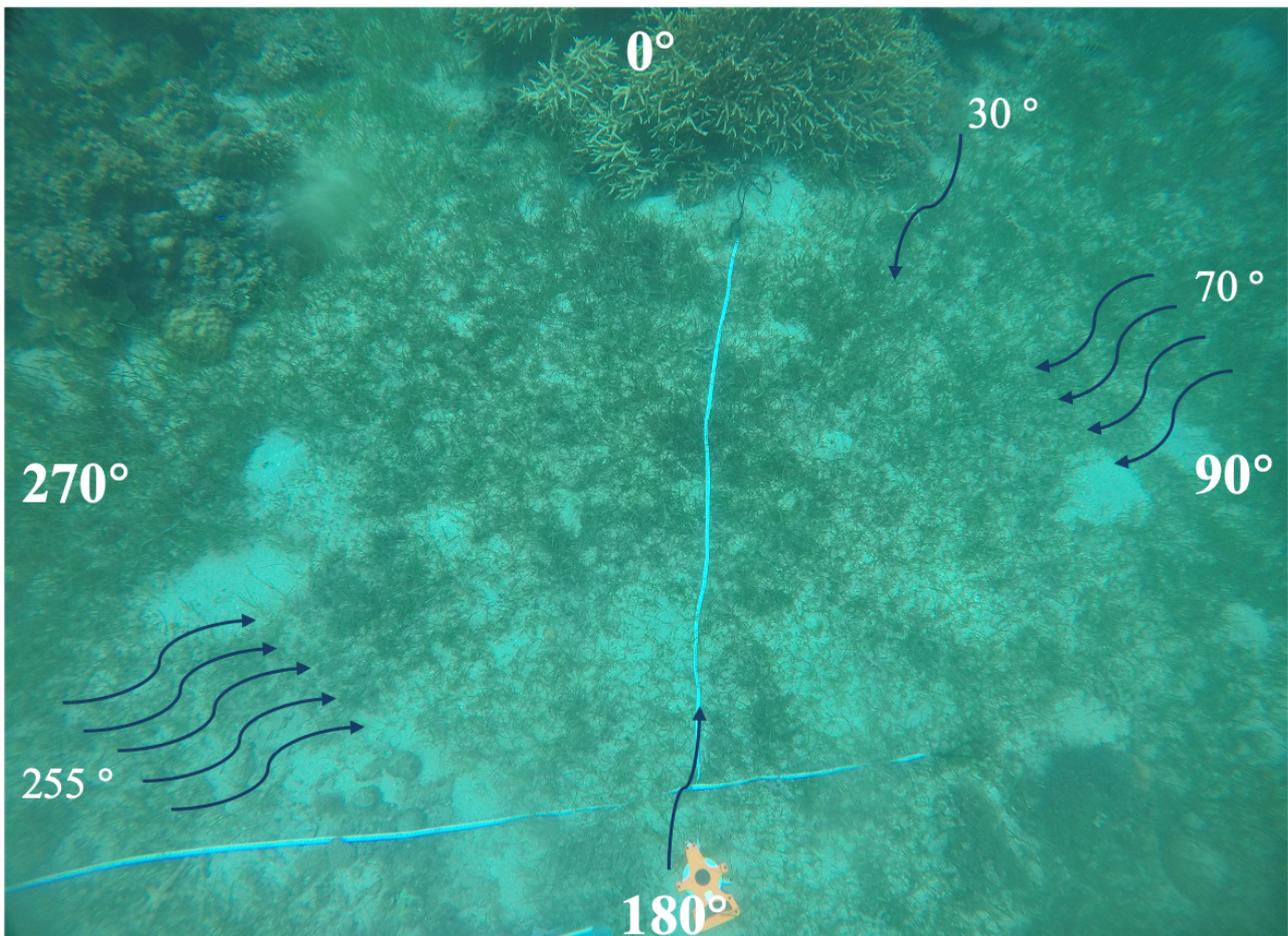


Figure 14. General current directions. Black arrows indicate the general direction of the current during the experiments. One arrow indicates one trial, with 5 trials showing current direction from 155° , 4 trials from 70° , 1 trial from 180° and one trial from 30° , with 3 trials having no detectable current direction.

Discussion

This study explored whether *A. cf. solaris* are able to visually orient toward reef structures under nocturnal conditions, and whether the lunar phase and ocular input influence this behaviour. The results demonstrate that *A. cf. solaris* shows random movement patterns during daylight conditions and significant, directional movements toward reef structures at nighttime conditions, under both new moon and full moon, while blinded individuals display random movement patterns (under full moon conditions). Together, these findings provide strong evidence that visual input plays a central role in nocturnal navigation in this species and that they can locate reef structure even under low light levels.

Daytime orientation

The daytime trials revealed random movement patterns, indicating an absence of visually orienting towards the reef. The hypothesis that *A. cf. solaris* uses vision for orientation towards reef structures under daylight conditions cannot be supported by these results. This finding differs from previous behavioural studies demonstrating visually guided reef localization in COTs under daylight conditions (Petie et al., 2016a; Petie et al., 2016b; Sigl, Steibl & Laforsch 2016). However, individuals used in these studies were collected either from the Great Barrier Reef or Moorea, French Polynesia, species considered to belong to *Acanthaster cf. solaris*, the same species assumed to be occurring in the Philippines, where the present study was conducted. Despite this taxonomic similarity, it remains possible that the observed differences in visually guided behaviour reflect population-level differences or potentially unresolved species-level variation within the *Acanthaster planci* complex. Crown-of-Thorns starfish from different geographic regions may represent distinct populations with varying sensory abilities and associated behaviour.

One possible explanation is that the population examined in this study possesses particularly light-sensitive eyes that are well adapted to low-light or nocturnal conditions but less effective in bright daylight, reducing visual performance. Such heightened sensitivity could result in diminished orientation ability during daytime trials, while enhancing navigation under nocturnal conditions. This interpretation aligns with the broader finding that *A. cf. solaris* is capable of effective nocturnal navigation. To verify this idea, future studies should employ electroretinogram recordings to directly quantify sensitivity.

The role of vision in nocturnal navigation

The results of this study provide clear evidence of nocturnal visual navigation in *A. cf. solaris*, as intact individuals demonstrated highly significant directional orientation toward the reef (0°) under both new moon and full moon (Table 1). The high mean vector lengths for both nocturnal groups further indicate a robust navigational accuracy that persists even under minimal light levels.

As mentioned above, previous studies have demonstrated that *A. planci* possesses compound eyes at the tips of each arm and that these eyes are required for reef-directed movement under daylight conditions (Garm and Nilsson, 2014; Petie et al., 2016a, 2016b). However, whether this visual capacity extends into nocturnal conditions has remained unclear. The present results show that orientation towards reef structures persists in darkness, even during new moon conditions when ambient light intensities are minimal.

A key strength of this study is the inclusion of blinded individuals. This provides direct evidence for the role of vision in nocturnal navigation. Eye-ablated starfish displayed random movement patterns, in contrast to the directed movement observed in intact individuals. This finding strongly suggests that visual input, rather than chemoreception or rheotaxis alone, supports reef-directed movement in this experimental context. While chemoreception undoubtedly plays an important role in prey detection, the present findings indicate that it is insufficient for orientation towards reef structures in *A. cf. solaris* in nocturnal conditions.

A factor that may facilitate nocturnal visual orientation in *A. cf. solaris* is the extremely low temporal resolution of their visual system. COTs integrate visual information over long time periods compared to other animals. Such slow vision likely increases photon capture under dim light conditions, allowing the visual system to accumulate enough light to detect contrasts between large reef structures against the surrounding seascape. This prolonged integration time may therefore compensate for low ambient illumination and help generate a coarse but usable visual image for navigation. The combination of long integration times and contrast-based image formation supports the interpretation that *A. cf. solaris* can extract sufficient visual information to orient towards reef structures at night. However, direct physiological evidence for increased sensitivity under low light is still limited.

Lunar illumination and orientation accuracy

Contrary to the hypothesis, no qualitative difference in orientation success was observed between new moon and full moon conditions. Both phases showed significant clustering of movement towards the reef, as well as similar accuracy of movements towards the reef. This suggests that *A. cf. solaris* collects sufficient visual information even under low-light conditions like the new moon phase. While lunar illumination is known to support the behaviour of many marine organisms, including turtle hatchlings and glass eels, the present findings indicate that *A. cf. solaris* do not rely on moonlight intensity for successful orientation (Ritter and Tessmar-Raible, 2024; Witherington and Bjorndal, 1991).

Ecological and theoretical implications

From an ecological perspective, the ability of *A. cf. solaris* to navigate towards a reef at night has important implications for understanding its behaviour and impact on coral ecosystems. *Acanthaster cf. solaris* is thought to be a predominantly nocturnal feeder, and effective nocturnal navigation likely enhances its foraging efficiency and contributes to its ability to apply strong top-down control on coral communities. Therefore, visual orientation at night might play an important role in facilitating COTs to feed more efficiently, by allowing individuals to locate the reef structures more reliably.

These findings contribute to a growing body of literature challenging the assumption that sophisticated visual behaviour requires high spatial resolution or bright light environments. These findings add to a growing body of literature showing that effective visual orientation can occur even under low-light conditions and that vision can be ecologically meaningful even when it provides only coarse information.

Methodological considerations

Although care was taken to minimize disturbance, the use of white light for photographing and recording movement trajectories may have altered the natural nocturnal light environment and potentially affected orientation behaviour. This may have influenced movement direction or contrast perception during trials. Future studies would benefit from using red light illumination or infrared video recording, which are less likely to be detected by *A. cf. solaris*.

Future research recommendations

Future research would benefit from addressing uncertainties about the species complex by explicitly identifying COTs species and populations across their geographic range using standardized genetic, morphological, and physiological approaches. Electroretinogram recordings could be useful to quantify spectral sensitivity, temporal resolutions, and absolute light sensitivity to clarify visual performance under both daylight and nocturnal conditions. Providing valuable insight into how visual performance varies between species or populations. Clarifying whether population-level or species-level differences exist in visual ecology would greatly improve our understanding of how vision shapes navigation and behaviour in Crown-of-Thorns starfish.

Furthermore, additional studies should repeat similar orientation experiments in a controlled environment to allow precise manipulation of light intensity, spectrum, and contrast. Such controlled conditions would help confirm whether orientation is driven purely by visual input or would improve with input from other senses, as well as confirm at exactly what light intensities the eyes of COTs effectively work. As discussed above, in-habitat experiments using infrared light sources rather than white light would also further confirm the use of vision by *A. cf. solaris*, as it removes white light disturbances. Moreover, understanding which visual and neural features might support night-time vision would strengthen the interpretation of behavioural results. This would provide insight into how visual performance changes between different light conditions. Altogether, this would provide a more complete understanding of nocturnal navigation in COTs.

Conclusions

This study demonstrates that *A. cf. solaris* is capable of visually guided orientation towards reef structures under nocturnal light conditions, independent of lunar phase. Intact individuals displayed highly directional movement during both full moon and new moon nights, with mean vectors consistently pointing towards the reef and 95% confidence intervals including the reef direction. Lunar illumination had no observable effect on orientation accuracy, indicating that even minimal nocturnal light is sufficient for navigation. In contrast, blinded individuals moved randomly, confirming that the observed nocturnal orientation relies on functional vision.

Daylight trials, however, showed no significant directional orientation. These findings suggest that the visual system of *A. cf. solaris* is adapted for low-light conditions, allowing individuals to locate reef structures efficiently in the dark. Overall, this study provides strong evidence that vision is the primary sensory modality driving nocturnal navigation in *A. cf. solaris*.

Acknowledgements

I would like to sincerely thank my supervisor, Anders Lydik Garm, for his invaluable guidance, feedback, and support throughout this project. I am also grateful to Naomi Westlake as well as other staff members from Marine Conservation Philippines (MCP) for coordinating and overseeing my research in the field, and to my assistant divers – Manuel Seguí, Rie Schmidt-Nielsen, and Maelle Cowey – for their essential help with fieldwork.

I would like to acknowledge the University of Copenhagen (UCPH) and the Faculty of Science for providing the environment and opportunity that made this research possible. Lastly, I extend a heartfelt thanks to my friends at MCP and the UCPH, as well as my family, for their continuous encouragement and support.

Reference list

- Beer, S., Wentzel, C., Petie, R., Garm, A.,** 2016. Active control of the visual field in the starfish *Acanthaster planci*. *Vision Res* 127, 28–34. <https://doi.org/10.1016/j.visres.2016.05.007>
- Ben Khadra, Y., Ferrario, C., Benedetto, C., Said, K., Bonasoro, F., Candia Carnevali, M.D., Sugni, M.,** 2015. Re-growth, morphogenesis, and differentiation during starfish arm regeneration. *Wound Repair and Regeneration* 23, 623–634. <https://doi.org/10.1111/WRR.12336>;PAGE:STRING:ARTICLE/CHAPTER
- Bickford, D., Lohman, D.J., Sodhi, N.S., Ng, P.K.L., Meier, R., Winker, K., Ingram, K.K., Das, I.,** 2007. Cryptic species as a window on diversity and conservation. *Trends Ecol Evol* 22, 148–155. <https://doi.org/10.1016/j.tree.2006.11.004>
- Birk, M.H., Blicher, M.E., Garm, A.,** 2018. Deep-sea starfish from the Arctic have well-developed eyes in the dark. *Proceedings of the Royal Society B: Biological Sciences* 285. <https://doi.org/10.1098/rspb.2017.2743>
- Birkeland C., Lucas J.S.,** 1991. *Acanthaster planci*: Major Management Problem of Coral Reefs. CRC Press, Boca Raton, Florida.
- Branham, J.M., Reed, S.A., Bailey, J.H., Caperon, J.,** 1971. Coral-eating sea stars *Acanthaster planci* in Hawaii. *Science* (1979) 172, 1155–1157. <https://doi.org/10.1126/SCIENCE.172.3988.1155>;WEBSITE:WEBSITE:AAAS-SITE;JOURNAL:JOURNAL:SCIENCE;WGROUPE:STRING:PUBLICATION
- Brodie, J., Fabricius, K., De'ath, G., Okaji, K.,** 2005. Are increased nutrient inputs responsible for more outbreaks of Crown-of-Thorns starfish? An appraisal of the evidence. *Mar Pollut Bull* 51, 266–278. <https://doi.org/10.1016/j.marpolbul.2004.10.035>
- Brusca R. C.,** 2016. Introduction to the Deuterostomes and the Phylum Echinodermata, in: *Invertebrates*. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts, U.S.A., pp. 967–1006.
- Burke, R.D., Angerer, L.M., Elphick, M.R., Humphrey, G.W., Yaguchi, S., Kiyama, T., Liang, S., Mu, X., Agca, C., Klein, W.H., Brandhorst, B.P., Rowe, M., Wilson, K., Churcher, A.M., Taylor, J.S., Chen, N., Murray, G., Wang, D., Mellott, D., Olinski, R., Hallböök, F., Thorndyke, M.C.,** 2006. A genomic view of the sea urchin nervous system. *Dev Biol* 300, 434–460. <https://doi.org/10.1016/j.ydbio.2006.08.007>

- Burn, D., Matthews, S., Caballes, C.F., Chandler, J.F., Pratchett, M.S.,** 2020. Biogeographical variation in diurnal behaviour of *Acanthaster planci* versus *Acanthaster* cf. *Solaris*. PLoS One 15. <https://doi.org/10.1371/journal.pone.0228796>
- Castilla J.C.,** 1971. Responses to light of *Asterias rubens*, in: Crisp D. (Ed.). Cambridge University Press, Cambridge, pp. 495–511.
- Castilla, J.C.** (1971) ‘Responses of *Asterias rubens* to Gravity’, *Marine Biology*, 11(3), pp. 273–278.
- Castilla, J.C.,** 1972. Avoidance behaviour of *Asterias rubens* to extracts of *Mytilus edulis*, solutions of bacteriological peptone, and selected amino acids. *Marine Biology* 1972 15:3 15, 236–245. <https://doi.org/10.1007/BF00383553>
- Castilla, J.C., Crisp, D.J.,** 1973. Responses of *Asterias rubens* to water currents and their modification by certain environmental factors. *Netherlands Journal of Sea Research* 7, 171–190. [https://doi.org/10.1016/0077-7579\(73\)90043-4](https://doi.org/10.1016/0077-7579(73)90043-4)
- Castilla, J.C., Crisp, D.J.,** 1970. Responses of *Asterias Rubens* to Olfactory Stimuli. *Journal of the Marine Biological Association of the United Kingdom* 50, 829–847. <https://doi.org/10.1017/S0025315400005075>
- Chesher, R.H.,** 1969. Destruction of Pacific Corals by the Sea Star *Acanthaster planci*. *Science* (1979) 165, 280–283. <https://doi.org/10.1126/SCIENCE.165.3890.280>
- Cobb, J.L.S., Stubbs, T.R.,** 1981. The giant neurone system in ophiuroids - I. The general morphology of the radial nerve cords and circumoral nerve ring. *Cell Tissue Res* 219, 197–207. <https://doi.org/10.1007/BF00210028/METRICS>
- Cresci, A., Durif, C.M., Paris, C.B., Thompson, C.R.S., Shema, S., Skiftesvik, A.B., Browman, H.I.,** 2019. The relationship between the moon cycle and the orientation of glass eels (*Anguilla anguilla*) at sea. *R Soc Open Sci* 6. <https://doi.org/10.1098/rsos.190812>
- Dana T. F., Wolfson A. A.,** 1970. Eastern Pacific crown-of-thorns starfish populations in the lower Gulf of California. *Transactions of the San Diego Society of Natural History* 16, 83–90.
- Eakin, R.M., Brandenburger, J.L.,** 1979. Effects of light on ocelli of seastars. *Zoomorphologie* 92, 191–200. <https://doi.org/10.1007/BF00994084/METRICS>
- Endean, R.,** 1969. Report on investigations made into aspects of the current *Acanthaster planci* (crown of thorns) infestations of certain reefs of the Great Barrier Reefs /. Fisheries Branch, Brisbane:

- Fenchel, T.**, 1965. Feeding biology of the sea-star *Luidia sarsi* Düben & Koren. *Ophelia* 2, 223–236.
<https://doi.org/10.1080/00785326.1965.10409601>;JOURNAL:JOURNAL:SMAR19;ISSUE:ISSUE:DOI
- Ferdinand, O., Megwalu**, 2018. *The Sea Stars (Echinodermata: Asteroidea): Their Biology, Ecology, Evolution and Utilization.*
- Foo, S.A., Millican, H.R., Byrne, M.**, 2024. Crown-of-thorns seastar (*Acanthaster* spp.) feeding ecology across species and regions. *Science of the Total Environment.*
<https://doi.org/10.1016/j.scitotenv.2024.172691>
- Garm, A.**, 2017. Sensory biology of starfish - With emphasis on recent discoveries in their visual ecology, in: *Integrative and Comparative Biology.* Oxford University Press, pp. 1082–1092.
<https://doi.org/10.1093/icb/icx086>
- Garm, A., Nilsson, D.E.**, 2014. Visual navigation in starfish: First evidence for the use of vision and eyes in starfish. *Proceedings of the Royal Society B: Biological Sciences* 281.
<https://doi.org/10.1098/rspb.2013.3011>
- Garm, A., Sundberg, D., Korsvig-Nielsen, C.E.**, 2023. Dispersed Vision in Starfish: A Collection of Semi-independent Arms 87–115. https://doi.org/10.1007/978-3-031-23216-9_4
- Glynn, P.W.**, 1974. The Impact of *Acanthaster* on Corals and Coral Reefs in the Eastern Pacific. *Environ Conserv* 1, 295–304. <https://doi.org/10.1017/S037689290000494X>
- Goreau, T.F., Lang, J.C., Graham, E.A., Gareau, P.D.**, n.d. Structure and Ecology of the Saipan Reefs in Relation to Predation by *Acanthaster planci* (Linnaeus).
- Güler, M., Lök, A.**, 2015. Foraging behaviors of sea stars, *Marthasterias glacialis* and *Astropecten aranciacus* (Asteroidea), and predator–prey interactions with warty venus clam, *Venus verrucosa* (Bivalvia). *J Exp Mar Biol Ecol* 465, 99–106.
<https://doi.org/10.1016/J.JEMBE.2014.12.018>
- Hall, M.R., Kocot, K.M., Baughman, K.W., Fernandez-Valverde, S.L., Gauthier, M.E.A., Hatleberg, W.L., Krishnan, A., McDougall, C., Motti, C.A., Shoguchi, E., Wang, T., Xiang, X., Zhao, M., Bose, U., Shinzato, C., Hisata, K., Fujie, M., Kanda, M., Cummins, S.F., Satoh, N., Degnan, S.M., Degnan, B.M.**, 2017. The crown-of-thorns starfish genome as a guide for biocontrol of this coral reef pest. *Nature* 544, 231–234.
<https://doi.org/10.1038/nature22033>

- Hayashi, Y., Motokawa, T.,** 1986. Effects of Ionic Environment on Viscosity of Catch Connective Tissue in Holothurian Body Wall. *Journal of Experimental Biology* 125, 71–84.
<https://doi.org/10.1242/jeb.125.1.71>
- Huxley, C.J.,** 1976. Response of *Acanthaster planci* (L.) to partial stimuli. *J Exp Mar Biol Ecol* 22, 199–206. [https://doi.org/10.1016/0022-0981\(76\)90096-4](https://doi.org/10.1016/0022-0981(76)90096-4)
- Kayal, M., Vercelloni, J., de Loma, T., Bosserelle, P., Chancerelle, Y., Geoffroy, S., Stievenart, C., Michonneau, F., Penin, L., Planes, S., Adjeroud, M.,** 2012. Predator Crown-of-Thorns Starfish (*Acanthaster planci*) Outbreak, Mass Mortality of Corals, and Cascading Effects on Reef Fish and Benthic Communities. *PLoS One* 7, e47363.
<https://doi.org/10.1371/journal.pone.0047363>
- Keesing, J.K.,** 2023. Feeding Biology of the crown-of-thorns starfish, *Acanthaster Planci* (Linnaeus). *Jcu.edu.au*. <https://doi.org/https://researchonline.jcu.edu.au/24112/1/01front.pdf>
- Korsvig-Nielsen, C., Hall, M., Motti, C., Garm, A.,** 2019. Eyes and negative phototaxis in juvenile crown-of-thorns starfish, *Acanthaster* species complex. *Biol Open* 8.
<https://doi.org/10.1242/bio.041814>
- Labnao, A.N., Sienes, P.M., Palomar-Abesamis, N.,** 2024. Morphological and Molecular Analysis of Western Pacific Crown-of-thorns Starfish *Acanthaster* cf. *solaris* (Schreber, 1793) in Southern Negros Island, the Philippines. *The Philippine journal of science* 153.
<https://doi.org/10.56899/153.6a.20>
- Lawrence J.M.,** 2013. *Starfish: Biology and Ecology of the Asteroidea*. Johns Hopkins University Press.
- Ling, S.D., Cowan, Z.L., Boada, J., Flukes, E.B., Pratchett, M.S.,** 2020. Homing behaviour by destructive crown-of-thorns starfish is triggered by local availability of coral prey. *Proceedings of the Royal Society B: Biological Sciences* 287. <https://doi.org/10.1098/rspb.2020.1341>
- Lucas, J.S.,** 1984. Growth, maturation and effects of diet in *Acanthaster planci* (L.) (Asteroidea) and hybrids reared in the laboratory. *J Exp Mar Biol Ecol* 79, 129–147.
[https://doi.org/10.1016/0022-0981\(84\)90214-4](https://doi.org/10.1016/0022-0981(84)90214-4)
- Mashanov V.S., Zueva O.R., García-Arrarás J.E.,** 2016. Echinoderm nervous system: organization and evolution, in: *Evolution of Nervous Systems*.
- Moore, S.J., Thorndyke, M.C.,** 1993. Immunocytochemical mapping of the novel echinoderm neuropeptide Sulfamide 1 (S1) in the starfish *Asterias rubens*. *Cell Tissue Res* 274, 605–618.
<https://doi.org/10.1007/BF00314559/METRICS>

- Moran P. J.**, 1986. *The Acanthaster phenomenon*. Aberdeen University Press, Townsville.
- Ormond R.F.G., Campbell A.C.**, 1974. Formation and breakdown of *Acanthaster planci* aggregations in the Red Sea. *Proceedings of the Second International Coral Reef Symposium* 1, 595–619.
- Paine, R.T.**, 1971. A Short-Term Experimental Investigation of Resource Partitioning in a New Zealand Rocky Intertidal Habitat. *Ecology* 52, 1096–1106. <https://doi.org/10.2307/1933819>
- Paine, R.T.**, 1966. Food Web Complexity and Species Diversity. *Am Nat* 100, 65–75. <https://doi.org/10.1086/282400>
- Penn, P.E., Alexander, C.G.**, 1980. Fine structure of the optic cushion in the asteroid *Nepanthia belcheri*. *Mar Biol* 58, 251–256. <https://doi.org/10.1007/BF00390773>/METRICS
- Petie, R., Garm, A., Hall, M.R.**, 2016a. Crown-of-thorns starfish have true image forming vision. *Front Zool* 13. <https://doi.org/10.1186/s12983-016-0174-9>
- Petie, R., Hall, M.R., Hyldahl, M., Garm, A.**, 2016b. Visual orientation by the crown-of-thorns starfish (*Acanthaster planci*). *Coral Reefs* 35, 1139–1150. <https://doi.org/10.1007/s00338-016-1478-0>
- Pratchett, M.S., Caballes, C.F., Cvitanovic, C., Raymundo, M.L., Babcock, R.C., Bonin, M.C., Bozec, Y.M., Burn, D., Byrne, M., Castro-Sanguino, C., Chen, C.C.M., Condie, S.A., Cowan, Z.L., Deaker, D.J., Desbiens, A., Devantier, L.M., Doherty, P.J., Doll, P.C., Doyle, J.R., Dworjanyn, S.A., Fabricius, K.E., Haywood, M.D.E., Hock, K., Hoggett, A.K., Høj, L., Keesing, J.K., Kenchington, R.A., Lang, B.J., Ling, S.D., Matthews, S.A., McCallum, H.I., Mellin, C., Mos, B., Motti, C.A., Mumby, P.J., Stump, R.J.W., Uthicke, S., Vail, L., Wolfe, K., Wilson, S.K.**, 2021. Knowledge Gaps in the Biology, Ecology, and Management of the Pacific Crown-of-Thorns Sea Star *Acanthaster* sp. on Australia's Great Barrier Reef. <https://doi.org/10.1086/717026> 241, 330–346. <https://doi.org/10.1086/717026>
- Pratchett, M.S., Caballes, C.F., Wilmes, J.C., Matthews, S., Mellin, C., Sweatman, H.P.A., Nadler, L.E., Brodie, J., Thompson, C.A., Hoey, J., Bos, A.R., Byrne, M., Messmer, V., Fortunato, S.A.V., Chen, C.C.M., Buck, A.C.E., Babcock, R.C., Uthicke, S.**, 2017. Thirty years of research on crown-of-thorns starfish (1986-2016): Scientific advances and emerging opportunities. *Diversity (Basel)*. <https://doi.org/10.3390/d9040041>
- Pratchett, M.S., Schenk, T.J., Baine, M., Syms, C., Baird, A.H.**, 2009. Selective coral mortality associated with outbreaks of *Acanthaster planci* L. in Bootless Bay, Papua New Guinea. *Mar Environ Res* 67, 230–236. <https://doi.org/10.1016/J.MARENRES.2009.03.001>

- Reese E.**, 1966. The complex behaviours of echinoderms. Intersciences publications, New York.
- Ritter, A., Tessmar-Raible, K.**, 2024. Time me by the moon: The evolution and function of lunar timing systems. *EMBO Rep* 25, 3169–3176. <https://doi.org/10.1038/s44319-024-00196-5>
- Roberts, R.E., Motti, C.A., Baughman, K.W., Satoh, N., Hall, M.R., Cummins, S.F.**, 2017. Identification of putative olfactory G-protein coupled receptors in Crown-of-Thorns starfish, *Acanthaster planci*. *BMC Genomics* 18. <https://doi.org/10.1186/s12864-017-3793-4>
- Schreber, J.C.D. von**, 1793. Beschreibung der Seesonne, einer Art Seesterne, mit 21 Strahlen. *Der Naturforscher* (Halle a. d. Saale).
- Sigl, R., Steibl, S., Laforsch, C.**, 2016. The role of vision for navigation in the crown-of-thorns seastar, *Acanthaster planci*. *Sci Rep* 6. <https://doi.org/10.1038/srep30834>
- Sloan, N.A., Northway, S.M.**, 2003. Chemoreception by the asteroid *Crossaster papposus* (L.). *J Exp Mar Biol Ecol* 61, 85–98. [https://doi.org/10.1016/0022-0981\(82\)90023-5](https://doi.org/10.1016/0022-0981(82)90023-5)
- Thompson, M., Drolet, D., Himmelman, J.H.**, 2004. Localization of infaunal prey by the sea star *Leptasterias polaris*. *Marine Biology* 2004 146:5 146, 887–894. <https://doi.org/10.1007/S00227-004-1497-1>
- Uthicke, S., Pratchett, M.S., Bronstein, O., Alvarado, J.J., Wörheide, G.**, 2023. The crown-of-thorns seastar species complex: knowledge on the biology and ecology of five corallivorous *Acanthaster* species. *Mar Biol* 171. <https://doi.org/10.1007/s00227-023-04355-5>
- Vickery, M.S., McClintock, J.B.**, 2000. Effects of food concentration and availability on the incidence of cloning in planktotrophic larvae of the sea star *Pisaster ochraceus*. *Biol Bull* 199, 298–304. <https://doi.org/10.2307/1543186>
- Vogler, C., Benzie, J., Barber, P.H., Erdmann, M. V, Ambariyanto, Sheppard, C., Tenggardjaja, K., Gérard, K., Wörheide, G.**, 2012. Phylogeography of the Crown-of-Thorns Starfish in the Indian Ocean. *PLoS One* 7, e43499. <https://doi.org/10.1371/journal.pone.0043499>
- Vogler, C., Benzie, J., Lessios, H., Barber, P., Wörheide, G.**, 2008. A threat to coral reefs multiplied? Four species of crown-of-thorns starfish. *Biol Lett* 4, 696–699. <https://doi.org/10.1098/rsbl.2008.0454>
- Vogler, C., Benzie, J.A.H., Tenggardjaja, K., Ambariyanto, Barber, P.H., Wörheide, G.**, 2013. Phylogeography of the crown-of-thorns starfish: genetic structure within the Pacific species. *Coral Reefs* 32, 515–525. <https://doi.org/10.1007/s00338-012-1003-z>

- Webb, M., Clements, M., Selvakumaraswamy, P., McLaren, E., Byrne, M., 2024.**
Chemosensory behaviour of juvenile crown-of-thorns sea star (*Acanthaster* sp.), attraction to algal and coral food and avoidance of adult conspecifics. *Proceedings of the Royal Society B: Biological Sciences* 291. <https://doi.org/10.1098/RSPB.2024.0623/104637>
- Wilson B.R., Marsh L.M., 1975.** Seasonal behaviour of a 'normal' population of *Acanthaster* in Western Australia. Australian Government Publishing Service, Canberra.
- Witherington, B.E., Bjorndal, K.A., 1991.** Influences of Wavelength and Intensity on Hatchling Sea Turtle Phototaxis: Implications for Sea-Finding Behavior. *Copeia* 1991, 1060.
<https://doi.org/10.2307/1446101>
- Yoshida, M., Ohtsuki, H., 1966.** Compound ocellus of a starfish: Its function. *Science* (1979) 153, 197–198.
<https://doi.org/10.1126/SCIENCE.153.3732.197;PAGE:STRING:ARTICLE/CHAPTER>

Appendixes

Appendix A: Individual trajectories.

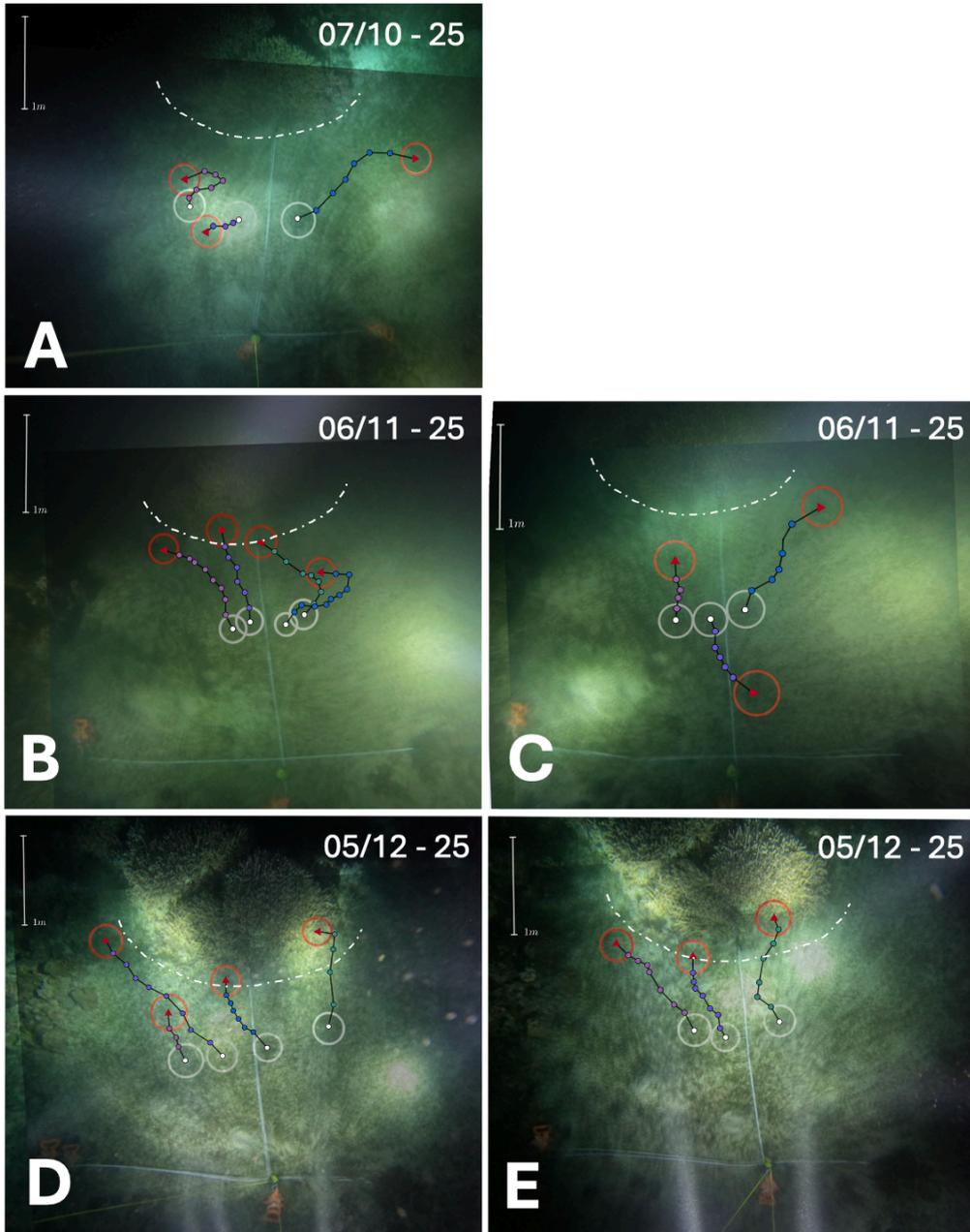


Figure A1. Individual trajectories for full moon trials. In all panels, the white (translucent) circle and dot indicate the starting position of each individual, while the red circle and arrow indicate the final position and direction of movement for each individual. Individual trajectories are shown in different colours: pink, purple, blue, green, and orange. The reef position is marked with a white dotted line. Note that most of the starfish seem to move towards the reef (dotted white line).

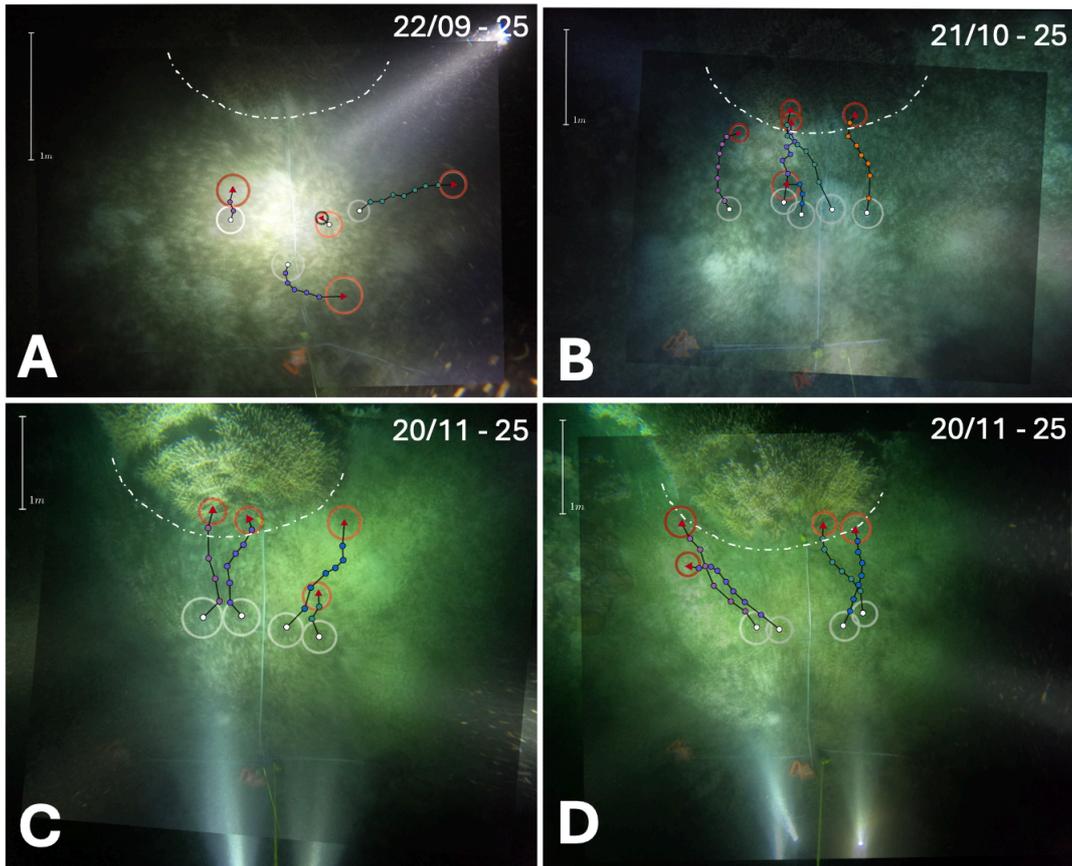


Figure A2. Individual trajectories for new moon trials. In all panels, the white (translucent) circle and dot indicate the starting position of each individual, while the red circle and arrow indicate the final position and direction of movement for each individual. Individual trajectories are shown in different colours: pink, purple, blue, green, and orange. The reef position is marked with a white dotted line. Note that most of the starfish seem to move towards the reef (dotted white line).

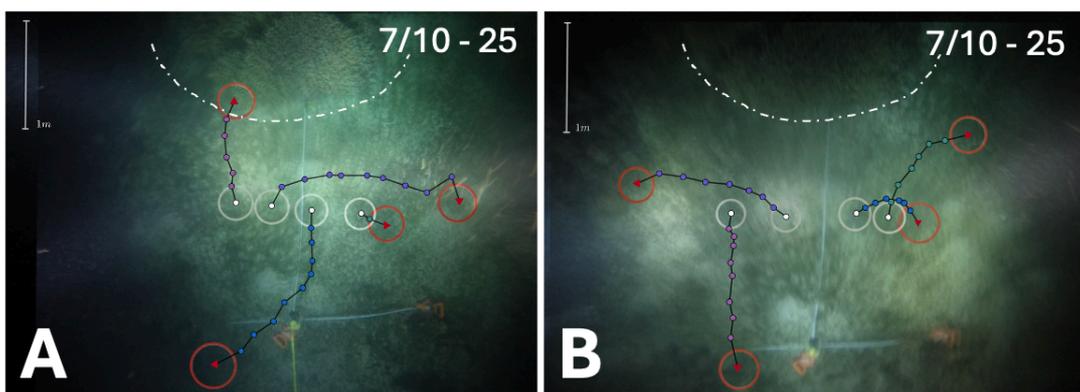


Figure A3. Individual trajectories for the eye ablated trials. In both panels, the white (translucent) circle and dot indicate the starting position of each individual, while the red circle and arrow indicate the final position and direction of movement for each individual. Individual trajectories are shown in different colours: pink, purple, blue, green, and orange. The reef position is marked with a white dotted line. Note that the starfish appear to walk in random directions.

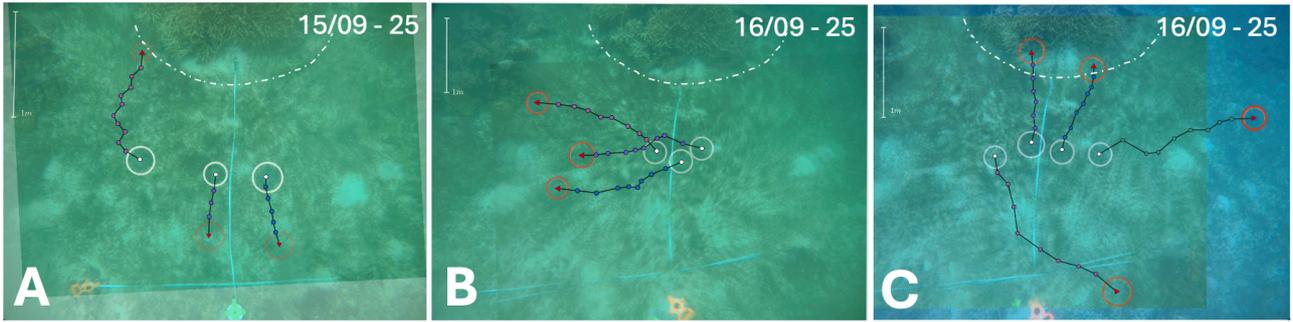


Figure A4. Individual trajectories for the daylight trials. In all panels, the white (translucent) circle and dot indicate the starting position of each individual, while the red circle and arrow indicate the final position and direction of movement for each individual. Individual trajectories are shown in different colours: pink, purple, blue, green, and orange. The reef position is marked with a white dotted line. Note that the starfish appear to walk in random directions.

Appendix B: Experimental data

Summary of individual orientation and environmental parameters for all experimental trials.

Table B1. Full moon data.

Date	Individual ID	COTs Diameter (cm)	Current Direction (°)	Angular displacement (°)
7/10 2025	COTN2-01	20	Nondetectable	339.7
7/10 2025	COTN2-02	19	Nondetectable	247.5
7/10 2025	COTN2-03	18	Nondetectable	62.8
06/11 2025	COTN4-01	16	255 W/S	327.3
06/11 2025	COTN4-02	20	255 W/S	350.4
06/11 2025	COTN4-03	12	255 W/S	345.2
06/11 2025	COTN4-04	17	255 W/S	26.8
06/11 2025	COTN4-05	14	255 W/S	0.1
06/11 2025	COTN4-06	15	255 W/S	156.1
06/11 2025	COTN4-07	17	255 W/S	37.2
05/12 2025	COTN6-01	18	70 N/E	344.2
05/12 2025	COTN6-02	16	70 N/E	319.5
05/12 2025	COTN6-03	18	70 N/E	330.1
05/12 2025	COTN6-04	20	70 N/E	14.6
05/12 2025	COTN6-05	18	70 N/E	316.6
05/12 2025	COTN6-06	16	70 N/E	341.1
05/12 2025	COTN6-07	19	70 N/E	358.2

Table B2. New moon data.

Date	Individual ID	COTs Diameter (cm)	Current Direction (°)	Angular displacement (°)
22/09 2025	COTN1-01	16	255 W/S	8.9
22/09 2025	COTN1-02	19	255 W/S	121.9
22/09 2025	COTN1-03	12	255 W/S	135.5
22/09 2025	COTN1-04	10	255 W/S	76.3
21/10 2025	COTN3-01	15	180 S	13.7
21/10 2025	COTN3-02	17	180 S	7.4
21/10 2025	COTN3-03	16	180 S	332.6
21/10 2025	COTN3-04	20	180 S	341.7
21/10 2025	COTN3-05	18	180 S	353
20/11 2025	COTN5-01	18	70 N/E	6.9
20/11 2025	COTN5-02	18	70 N/E	5.1
20/11 2025	COTN5-03	19	70 N/E	31.9
20/11 2025	COTN5-04	18	70 N/E	4.6
20/11 2025	COTN5-05	20	70 N/E	328.5
20/11 2025	COTN5-06	14	70 N/E	306.9
20/11 2025	COTN5-07	18	70 N/E	10.8
20/11 2025	COTN5-08	15	70 N/E	348.7

Table B3. Eye-ablated individuals during full moon data.

Date	Individual ID	COTs Diameter (cm)	Current Direction (°)	Angular displacement (°)
07/10 2025	COTB1-01	18	Nondetectable	0.2
07/10 2025	COTB1-02	18	Nondetectable	88.1
07/10 2025	COTB1-03	20	Nondetectable	210.8
07/10 2025	COTB1-04	20	Nondetectable	114.5
07/10 2025	COTB1-05	20	Nondetectable	166.2
07/10 2025	COTB1-06	15	Nondetectable	280.4
07/10 2025	COTB1-07	19	Nondetectable	100.8
07/10 2025	COTB1-08	17	Nondetectable	47.2

Table B2. Daylight data.

Date	Individual ID	COTs Diameter (cm)	Current Direction (°)	Angular displacement (°)
15/09 2025	COTC1-01	17	30 N/E	18.2
15/09 2025	COTC1-02	22	30 N/E	188.1
15/09 2025	COTC1-03	15	30 N/E	171.9
16/09 2025	COTC2-01	15	255 W/S	134.4
16/09 2025	COTC2-02	16	255 W/S	1.5
16/09 2025	COTC2-03	18	255 W/S	19.5
16/09 2025	COTC2-04	19	255 W/S	77.6
16/09 2025	COTC2-05	17	255 W/S	266.6
16/09 2025	COTC2-06	15	255 W/S	256
16/09 2025	COTC2-07	17	255 W/S	284