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Movement patterns of Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) linked to habitat structure and prey availability

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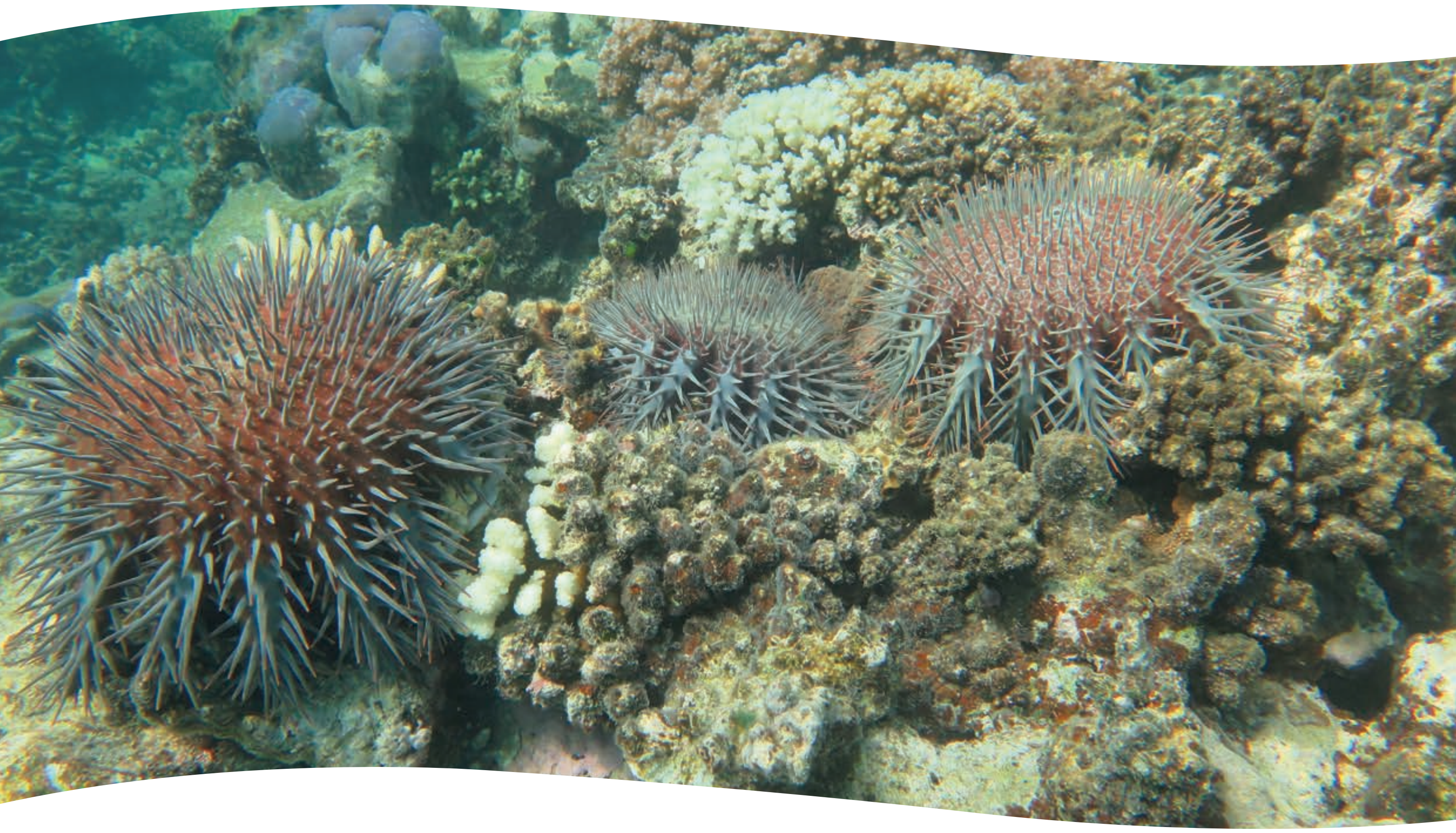

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Movement patterns of Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) linked to habitat structure and prey availability

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Cover photographs: Morgan Pratchett

CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACRONYMS

AIMS	Australian Institute of Marine Science
CoTS	Crown-of-thorns starfish
CSIRO	Commonwealth Scientific and Industrial Research Organisation
GBR	Great Barrier Reef
GBRMP	Great Barrier Reef Marine Park
JCU	James Cook University
LTMP	Long-term Monitoring Program (AIMS)
NESP	National Environmental Science Program
TWQ	Tropical Water Quality

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EXECUTIVE SUMMARY

Patterns of movement and habitat use by adult crown-of-thorns starfishes (*Acanthaster* spp.) will have a major bearing on their distribution, reproductive capacity, and impacts on coral assemblages and reef ecosystems. The spatial and temporal scales over which crown-of-thorns starfish move will also have important implications for the scales at which they will be most effectively managed. Movement patterns of crown-of-thorns starfish have been studied previously, though mostly over small distances (metres) and limited timeframes (minutes to hours). This study reports on explicit studies that measured the movement rates and movement patterns of Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) at a range of temporal and spatial scales. In the first instance, we measured the instantaneous movement rates of starfish (n = 218) across different substrates; sand, coral rubble and consolidated carbonate pavement. This study was conducted in a large (5m diameter) tank, using video recordings that were then analysed to determine the mean and maximum rates of movement over successive 15-second intervals.

To assess movement patterns of *A.* cf. *solaris* in the field, short-term tagging and movement studies were undertaken at Rib Reef, in the central GBR. All starfish (n = 357) recorded on semi-permanent transects were individually tagged using numbered pieces of flagging tape. The precise position of each starfish (where detected) was then recorded during successive surveys during day and night for up to 4 days. To further scale-up movement studies for crown-of-thorns starfish we tagged 50 crown-of-thorns starfish using V7 (69KHZ) acoustic transmitters, at Lodestone Reef or Big Broadhurst Reef. The position of these starfish relative to acoustic receivers deployed 50-200m along the edge of the reef was recorded (at 3-minute intervals) for up to 8 months. Passive acoustic monitoring was intended to provide greater insights into longer-term (weeks to months) and larger-scale (kilometres) patterns of movement for crown-of-thorns starfish, but provided much less resolution regarding fine-scale movements of individual starfish.

Instantaneous measures of movement capacity for *A.* cf. *solaris* (in aquaria) showed that these starfish are capable of moving at 20-35 cm per minute, and move fastest over sand. Despite their capacity for movement, field-based studies suggested that crown-of-thorns starfish actually move very little at scales of days to weeks, and even months. For starfish that were tagged with temporary visual markers, the minimum displacement distance recorded for the majority of starfish (88.0%) was <2m throughout the course of the study. Moreover, starfish that did move to feed (mostly at night) often returned to the same resting location between feeding bouts. Similarly, starfish tagged with acoustic transmitters for up to 6 months were only ever detected on adjacent receivers with large overlap in their ranges, suggesting that all starfish remained within 50-100m of where they were initially found and tagged for up to 6-months. The frequency and duration of passive detections varied greatly among individual starfish tagged with transmitters, with detections peaking in early hours of the morning.

While this study shows that it is possible to effectively tag crown-of-thorns starfish, both over short and longer time-frames, there were considerable logistical challenges to documenting occasional large-scale, and presumably quite rapid, displacement of individual starfish. It is clear that crown-of-thorns starfish generally move very little and remain within localised areas (even returning to the same sheltering location between successive feeding bouts) of moderate

to high coral cover. However, *Acanthaster* spp. are also capable of moving large distances when necessary, presumably when coral prey are locally depleted. It will be important to understand the nature and scale of both modes of movement to effectively manage population irruptions of crown-of-thorns starfish. Documenting the incidence and rates of movement during these infrequent events remains a priority for future research.

1.0 INTRODUCTION

Crown-of-thorns starfishes (*Acanthaster* spp.) are one of the largest and most efficient coral predators, and occur naturally on coral reefs throughout the Indo-Pacific (Chesher 1969; Birkeland and Lucas 1990; Pratchett et al 2014). More importantly, *Acanthaster* spp. exhibit periodic population irruptions, whereby local densities of starfish can increase from normally low densities of <1 to 100 starfish per hectare (Chesher 1969; Pearson and Endean 1969; Zann et al. 1990; Nakamura et al. 2014), to extreme densities of >1,000 starfish per hectare (Chesher 1969; Kayal et al. 2012). The combined feeding activities of high densities of often very large crown-of-thorns starfish almost invariably results in extensive coral depletion (e.g., Chesher 1969, Kayal et al. 2012), contributing to sustained and widespread declines in coral cover (Mellin et al. 2019). New and renewed population irruptions of *Acanthaster* spp. have been reported in many locations throughout the last decade (Lane 2012; Baird et al. 2013; Miller et al. 2015; Roche et al. 2015; Saponari et al. 2018), often in areas that have also been subject to climate-induced mass coral bleaching, as well as other more direct anthropogenic disturbances (Mellin et al. 2019; Pisapia et al. 2019). The cumulative effects of these multiple disturbances not only suppress live coral cover, but directly affects the biological and physical habitat structure (Alvarez-Filip et al. 2009, Wilson et al. 2019) with subsequent effects on biodiversity and ecosystem function (Pratchett et al. 2011; McWilliam et al. 2020). Despite increasing incidence, severity and diversity of disturbances (especially disturbance linked to ongoing human-induced environmental changes), population irruptions of *Acanthaster* spp. remain a major cause of coral loss in many locations throughout the Indo west-Pacific (Trapon et al. 2011; De’ath et al. 2012; Kayal et al. 2012; Mellin et al. 2019).

The impacts of crown-of-thorns starfish on coral assemblages and coral reef ecosystems are indelibly linked to their behaviour, and most particularly, patterns of movement and feeding (Keesing and Lucas 1992; De’ath and Moran 1998; Pratchett et al. 2009). While there has been extensive work to document and understand feeding preferences of *Acanthaster* spp. (e.g., De’ath et al. 2012), which has obvious ramifications for shifts in coral composition (e.g., Pratchett et al. 2020), there has been much less research on movement patterns of these organisms. This is however, a critical knowledge gap that has ramifications for understanding and managing population irruptions of crown-of-thorns starfish. At very high densities, crown-of-thorns starfish can form feeding fronts that gradually progress across areas of live coral cover (Barnes 1966). The movement of crown-of-thorns starfish (both in terms of direction and velocity) will, therefore, influence the rate and extent of coral depletion (Chesher 1969; Clements and Hay 2017) and the resulting broader ecological impacts. The capacity of starfish to move within and among reef habitats is also fundamental in addressing long-standing controversies surrounding the initiation and spread of population outbreaks (Pearson and Endean 1969; Talbot and Talbot 1971). Moreover, understanding the spatial and temporal scales at which adult starfish move is critical to the design of effective and efficient culling programs (Fletcher and Westcott 2013), which are the most direct and certain method for containing, if not preventing, population irruptions of *Acanthaster* spp. (Pratchett and Cumming 2019).

1.1 Capacity for movement

Crown-of-thorns starfish, like all echinoderms, move using their water-vascular system to control the extension of numerous and largely independent podia (hereafter referred to as tube feet). For asteroids, the oral side of the animal attaches to the substrate using many tube feet, which inflate, retract and extend using a hydrostatic canal system to initiate crawling (McCurley and Kier 1995). Rates of movement for echinoderms generally increase with body size, due to increases in the number and/ or size of tube feet with increases in body size (Mueller et al 2011). Most notably, small (juvenile starfish) are extremely constrained in their capacity to move quickly or over long-distances (Yamaguchi 1973; Moran 1986), especially compared to larger adult starfish. Adult crown-of-thorns starfish are reported to move at up to 30-50 cm per minute, over short distances (Moran 1986; Mueller et al. 2011). Mueller et al. (2011) suggested that unlike most starfish, there was no effect of body size on movement rates of adult crown-of-thorns starfish. This study was based on starfish ranging in size from 8-36 cm diameter (n = 38) and there was no apparent change in mean or maximum rates of movement with increasing body size (Mueller et al. 2011). There are however, marked differences in rates of movement recorded for juvenile versus adult crown-of-thorns starfish (Moran 1986; Birkeland and Lucas 1990; Table 1). Importantly, Yamaguchi (1973) showed that 2-week old juvenile starfish moved at a fairly consistent rate of 0.01 cm per minute when placed in a well-lit petri dish and invariably sought shelter in shaded locations. If this reflects their maximum movement rate, we would expect very limited capacity for newly settled crown-of-thorns starfish to move between discrete habitat types during ontogenetic development of post-settlement crown-of-thorns starfish (Wilmes et al. 2020), though Johnson et al. (1991) suggested that *Acanthaster* may settle in deep-water habitats (>50m depth), and then move to shallow water reef environments after 7-10 months around the time that they start feeding predominantly on hard (order Scleractinia) corals.

Movement rates and patterns of crown-of-thorns starfish in the wild are partly influenced by the nature (including complexity) of natural substrates (Pearson and Endean 1969; Pratchett et al. 2017). *Acanthaster* spp. move fastest over sand, where average maximum velocity (33.3 cm min^{-1}; Pearson and Endean 1969) is almost twice that recorded for other reef substrates (Moran 1986). However, crown-of-thorns starfish placed on sand rapidly move towards nearby physical habitat structures (Petie et al 2016; Sigl et al. 2016). As such, apparent differences in these movement rates may reflect differential motivations for movement, rather than the physiological capabilities of moving over different substrates. When moving within continuous reef habitats, crown-of-thorns starfish typically exhibit semi-diurnal cycles of activity, and spend <40% of time actually moving (De'ath and Moran 1998). Maximum time-averaged rates of movement for adults over extended periods are therefore only 2.50-5.75 cm min^{-1} (Moran 1986), showing that the realised rate of movement is strongly scale dependent, but also varies with size of the starfish (Pratchett et al. 2017).

Current knowledge regarding the capacity and patterns of movement for crown-of-thorns starfish comes mainly from short-term experimental studies of juveniles, especially newly settled juveniles (e.g., Yamaguchi 1973) and field-based observations of adult starfish (e.g., Ormond 1970; Aziz and Sukarno 1977). Reconciling the data arising from different studies is very difficult, largely because movement rates that are recorded are highly conditional upon the scale and methods used. Most critically, short-term observations or active tracking studies tend to report movement rates of only those individuals that are actively moving, essentially recording the capacity for movement (e.g., Pratchett et al. 2017). It is unlikely however, that these instantaneous rates of movement could or would be sustained over weeks, let alone entire days. Therefore, rates of movement inferred based on changes in the relative location of starfish in the wild, are invariably much lower than movement rates reported from active tracking of individuals (Table 1).

Field-based measurements of movement rates are also based largely on minimum displacement distances recorded over time, which may greatly under-estimate the actual movement of individuals (Keesing and Lucas 1992). Typically, field-based studies record the precise position of individually recognisable or tagged starfish at intervals of hours, days or weeks (e.g., Ormond 1970; Aziz and Sukarno 1977). When individuals are re-located in a new location, the displacement distances and rates of movement are calculated based on the straight-line distance to the original location, though it very likely starfish moved much further to achieve the apparent displacement (Keesing and Lucas 1992). The recorded displacement distances and rates of movement from such studies do not therefore, necessarily reflect the path followed by the starfish and greatly underestimate the movement capacity and patterns of movement. Keesing and Lucas (1992) directly compared minimum displacement distances recorded at daily and 5-day intervals with total distances moved by intensively tracking individual starfish. The total daily distance travelled was at least 60% further than minimum displacement distances, whereas the total distance travelled in 5-days was >160% of the recorded minimum displacement distances (Keesing and Lucas 1992).

Field-based studies of movement are also confounded by changes in behavioural modes, whereby time spent feeding or sheltering, will constrain the capacity for movement (Pratchett et al. 2017), though this provides a much more realistic representation of the movement patterns.

1.2 Movement and management

Quantifying movement rates for crown-of-thorns starfish is important, not only for understanding the initiation and spread of population irruptions, but also for optimising spatial and temporal aspects of population control (or culling) activities (Bos et al. 2013). Detailed understanding of movement patterns (at a range of different scales) will therefore, have important management implications (Vanhatalo et al. 2017; Pratchett et al. 2017).

On Australia's Great Barrier Reef (GBR), reef-wide population irruptions of the Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) originate on mid-shelf reefs in the vicinity of 14-15°S (Sweatman et al. 1998; Pratchett 2005; Wooldridge and Brodie 2015; Vanhatalo et al. 2017; but see Miller et al. 2015). In 1994, for example, population irruptions of *A*. cf. *solaris* were first recorded at Lizard Island (14°40'S, 145°27'E) and several other reefs within the immediate area, including Linnet, North Direction, and Rocky Islet (Sweatman et al. 1998). After becoming well-established on initial reefs, population irruptions spread to other nearby reefs, predominantly southwards (Kenchington 1977; Reichelt et al. 1990; Vanhatalo et al. 2017) at a rate of 100-200km every 3 years. The spread of population irruptions on the GBR has been attributed to mass migration of adult starfish, which are purported to move between reefs following localised depletion of coral prey (e.g., Talbot and Talbot 1971), though the timing and rate of spread is more readily attributable to step-wise spread through larval dispersal and establishment of high-densities of adult starfish at downstream reefs, which then reproduce and further contribute to the spread of population irruptions (Kenchington 1977; Bradbury et al. 1990; Hock et al. 2014). Nonetheless, adult crown-of-thorns starfish may well be capable of moving between nearby reefs, especially where there is contiguous reef habitat connecting reefs (Pratchett et al. 2017). If so, this will have important ramifications for control strategies and management effectiveness.

Table 1: Reported movement rates of crown-of-thorns starfish (*Acanthaster* spp.) at different life-stages

Temporal Scale	**Life stage**	**Source (Location)**	**Details of measurements taken**	**Rate Mean (Range)**
Minutes	Adults	Mueller et al. 2011 (Philippines)	Active tracking in the field, but on plastic	35.3 cm/min (0-50.9)
	Adults	Glynn 1977 (Panama)	Direct observation of a single starfish escaping predator	100 cm/min
	Juveniles (2 week old)	Yamaguchi 1973	Active tracking across petri dish	0.1 cm/min
Hours	Juveniles	Pearson and Endean 1969 (GBR)	Direct observations in the field	(1.4-4.0 m/hr)
	Adults	Barham et al. 1973 (Gulf of California)	Followed tagged individuals in the field	0.6 m/hr, but lower (0.25m/hr) in areas with high coral cover
	Adults	Pearson and Endean 1969	Direct observations in the field	(5-10 m/hr)
Days	Adults	Ormond 1970 (Red Sea)	Field-based measures of minimum-displacement distances	23 m/day (0-82)
	Adults	Aziz and Sukarno 1977 (Indonesia)	Field-based measures of minimum-displacement distances	(0.3-8.0 m/day)
	Adults	Caballes unpub. data 2006 (Guam	Field-based measures of displacement distance based on feeding scars	1.8m/day (0.9-2.3)
	Adults	Branham et al. 1971 (Hawaii)	Field-based measures of minimum-displacement distances	0-18 m/day
	Adults	Keesing and Lucas 1992 (GBR)	Repeat observations to record position of tagged individuals	2.8 m/day (0-9.6)
Weeks	Adults	Chesher 1969 (Guam)	Short-term tagging and movement in the field	250 m/wk
Months	Adults	Chesher 1969 (Guam)	Movement of feeding fronts and corresponding coral loss	1 km/month
	Adults	Ormond and Cambell 1974	Movement of aggregated population	100 m/month

Contemporary management of population irruptions of *A.* cf. *solaris* on the GBR is largely focused on culling or removing adult starfish, both to minimise coral loss caused by high densities of *A.* cf. *solaris* starfish at priority reefs, but also to reduce the reef-wide proliferation of population irruptions by reducing densities of adult starfish below reproductive thresholds (Fletcher et al. 2020). To be effective at local (within reef) scales, the crown-of-thorns starfish control program must take account of the effective scale and rates of adult movement, which will influence how fast starfish recolonise areas that have been subject to concerted culling effort. Specifically, better understanding the spatial scale of starfish movement will allow the number of within-reef management units targeted for control around a localised outbreak to be refined, and better understanding the temporal scale of starfish movement will help determine the optimal frequency with which management units should be culled. Improving estimates of crown-of-thorns starfish movement will significantly increase the efficiency and effectiveness of the overall Control Program. The capacity for crown-of-thorns starfish to undertake sustained and directional movement will also be critical in establishing the spatial extent of management effort necessary to disrupt spawning aggregation and thereby suppress reproductive output as a way of preventing further population irruptions (Rogers et al. 2017). Most critically, the capacity of starfish to move within and among reefs (including the use of deep-water habitats for settlement or refugia from adverse environmental conditions) will be important for establishing relevant management units across multiple reefs.

1.3 Study Objectives

The objectives of this study were three-fold, presented in order of increasing scale;

i) To assess the short-term (instantaneous) movement rates of crown-of-thorns starfish in captivity, essentially testing how their capacity for movement varies with body size and substrate (e.g., moving across sand versus coral rubble). While several previous studies have quantified movement rates of *Acanthaster* spp (Table 1; Moran 1986), most estimates are based on hourly or daily displacement under field conditions, with no account of the specific substrate type (e.g., Keesing and Lucas 1992). We expected that absolute rates of movement would increase with increasing size of the starfish, and that larger starfish would also be more capable of moving across complex substrates. Given that increased substrate complexity effectively increases the distance over which starfish must travel to achieve the same horizontal displacement (Flukes et al. 2012) and increases the probability and proportion of tube feet not in contact with the substrate at any point in time, we also expect that movement will be much more constrained over rubble, compared to relatively flat carbonate pavement or sand. This study was published in 2017 (Pratchett et al. 2017).

ii) To quantify diurnal and daily movement patterns of crown-of-thorns starfish, by individually tagging starfish and directly recording their position and behaviour during surveys conducted day and night for 1-4 days. This approach is very similar to that used by Keesing and Lucas (1992), who showed that starfish moved relatively little (1m/day) especially in habitats with high (>30%) live coral cover. It is possible however, that Keesing and Lucas (1992) greatly underestimated actual movement patterns of *A.* cf, *solaris*, whereby individuals may move (mostly at night) to feed and then return to essentially the same position to shelter between feeding bouts. There is conflicting evidence regarding whether *Acanthaster* spp. are predominantly nocturnal (Ormond and Campbell 1974;

De’ath and Moran 1998), which may be attributable to changing patterns of activity with ontogeny and as food becomes scarce (Moran 1986). However, there may also be geographical variation in the behaviour of crown-of-thorns starfish, linked to species-specific responses to biological or environmental conditions (Burn et al. 2020). As such, we explicitly assessed diurnal changes in the specific location and behaviour of starfish, testing for diurnal cycles of feeding versus sheltering. A portion of this research (focussing on diurnal changes in feeding behaviour and exposure) was published in Burn et al. (2020).

iii) To study larger-scale (kilometres) and longer-term (months) movement of crown-of-thorns starfish, we used passive acoustic monitoring (*sensu* Simpfendorfer et al. 2011; Welsh et al. 2012), where focal individuals are tagged with coded transmitters and their unique signal is automatically monitored using acoustic receivers. Passive acoustic monitoring is being used to track movements of a wide-range of different coral reef organisms (Heupel et al. 2004; Udyawer et al. 2016; Scott et al. 2019; Schlaff et al. 2020), providing the opportunity to track movement of individuals within complex reef environments over months to years. The specific goal of this study was to track changes in the behavioural modes of crown-of-thorns starfish following localised depletion of coral prey, expecting to show extended periods of limited movement, as starfish concentrate on feeding within distinct habitat patches, interspersed with rapid large-scale movements to new habitat patches. Given that passive acoustic monitoring has never before been conducted for *Acanthaster* spp. this study also provides an opportunity to explore the utility of this technology for assessing even larger scale movement patterns, such as inter-reef movements.

2.0 METHODOLOGY

2.1 Captive movement rates

To quantify movement rates of crown-of-thorns starfish, a total of 112 Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) were collected at or near Lizard Island (14˚40'S, 145˚27'E) on the northern Great Barrier Reef (GBR), Australia, in November 2015. Starfish were carefully transported to the experimental aquarium facility at Lizard Island Research Station and held in captivity in 1000 L plastic aquaria with continuous and rapid exchange of fresh seawater.

To quantify mean and maximum rates of movement, starfish were placed individually into a large (5m diameter) tank. Movement trials were initiated by placing a single starfish in the centre of the experimental aquarium. The movement of the starfish to the outer perimeter of the aquarium was then recorded using a GoPro camera mounted directly above the aquarium. To encourage starfish to move to the edge of the tank a 1m wide sheet of black plastic was attached to one section of the aquarium, which had otherwise white walls. The black plastic was intended to simulate the shade cast by a reef structure, representing a potential refuge detectable by photoreceptors of *Acanthaster* spp. (Beer et al 2016, Petie et al 2016). Movement trials were conducted during daylight hours and only when the sun was sufficiently elevated to directly light the bottom of the aquarium, from approximately 0830 to 1700.

Three different substrate types were tested; i) a 5 cm thick layer of sand, which was collected from intertidal areas adjacent to reef environments, ii) continuous layer of paving tiles which were coated in calcareous algae following extended deployment (up to 6 months) in reef environments before being air dried (reflective of consolidated carbonate pavement), and iii) coral rubble, comprising an assortment of coral fragments left over from previous experiments. Starfish were randomly selected from the pool of captive individuals (n = 112), ensuring that each individual was tested only once on each substrate type. Some starfish were tested on multiple substrate types, but we did not explicitly account for individual identity and so cannot compare movement rates on different substrates for each individual.

Videos were analysed using Adobe After Effects to calculate mean and maximum rates of movement. Start time was defined as the time at which starfish began directional movement and end time was determined when the individual either reached the edge of the substrate, halted movement and was removed, or disappeared into the substrate. To quantify movement rates, coordinates of the central point for each individual were recorded at 15-second intervals, and the distance between these two points was calculated and converted from pixels to cm, using measuring tapes laid across the bottom of the tank for calibration. Variation in locomotor capacity among individual starfish was analysed based on the mean rate of movement (cm/ second) averaged across all possible 15 second intervals for each starfish, and maximum rate of movement, which was the maximum distance moved (cm/ 15 sec) across all 15 sec intervals for each starfish.

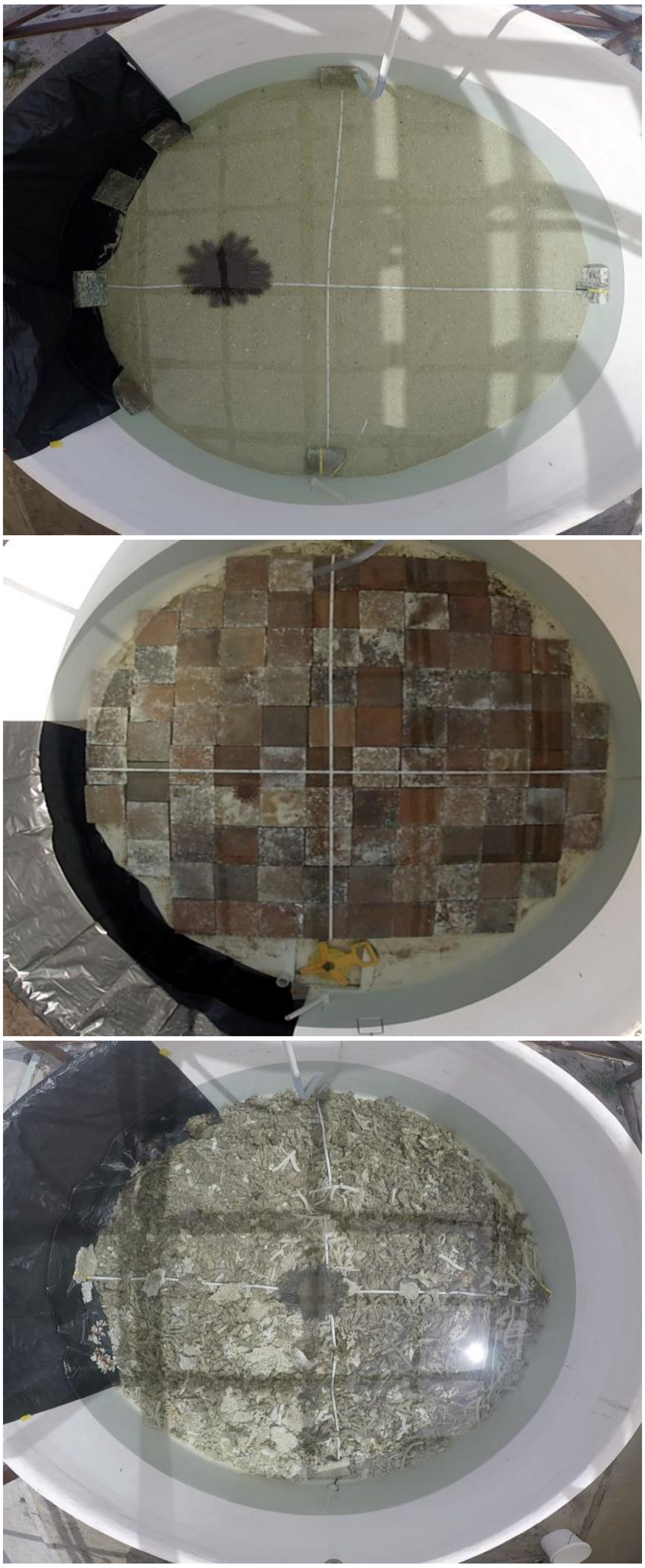

Figure 1: Experimental tests of movement capacity for Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) at Lizard Island Research Station, showing three different substrates used in captive movement trials: sand, pavers and coral rubble. Photographs: Morgan Pratchett.

2.2 Short-term tagging and movement

Short-term tagging and movement studies were undertaken at Rib Reef (18˚29'S 146˚52'E), in the central GBR. This study was conducted in 2016 to 2017, when active outbreaks of *A.* cf. *solaris* were concentrated on mid-shelf reefs in the area between Cairns and Townsville (Pratchett et al. 2019). High densities of *A.* cf. *solaris* caused extensive coral loss at Rib Reef during 2015 and 2016, though areas of high coral cover remained, mostly inside the lagoon. To document the initial position of crown-of-thorns starfish, 50m tapes were deployed parallel to the reef contour in each of two different habitats; on the reef crest (1-3m depth) which was generally characterised by high cover of tabulate *Acropora*, and on the reef slope (6-9m depth) where there was high diversity of corals, but often low coral cover, except in areas where there were mono-specific stands of sprawling staghorn *Acropora*. Between 2-5 transects were established during each of three distinct reef visits, with sampling conducted in different sites on each sampling occasion to account for prevailing conditions and changes in the distribution and abundance of starfish aggregations.

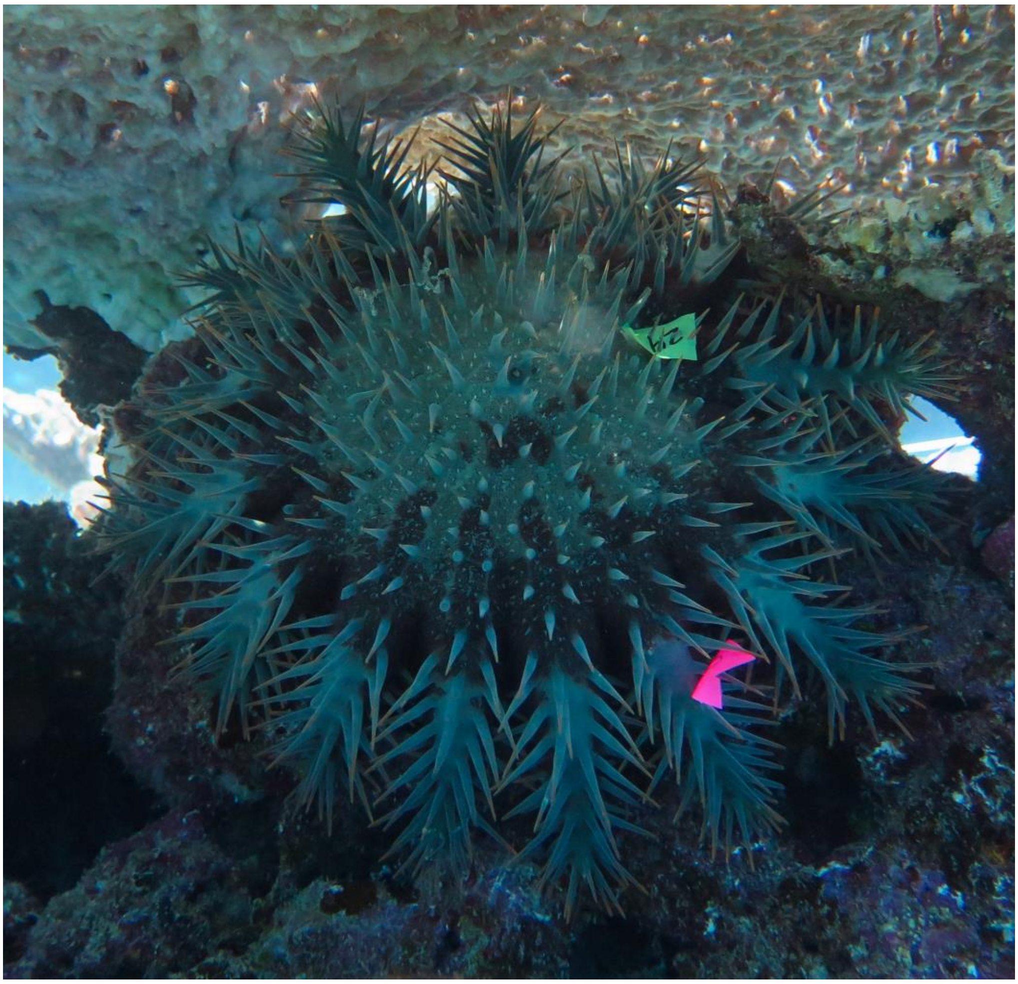

Figure 2: Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) at Rib Reef, showing temporary tags (2), whereby numbered pieces of coloured flagging tape were secured over accessible spines and were often discernible without disturbing the animal. Photograph: Morgan Pratchett.

All crown-of-thorns starfish that were located within the immediate vicinity of the transect tapes (up to 5m either side of the transect line) were tagged using uniquely numbered pieces of flagging tape, following Sigl and Laforsch (2016), and their position was recorded (to the nearest 10cm) relative to the distance along as well as the perpendicular distance away from the transect line. Temporary tags (2cm lengths of coloured flagging tape) were secured by spearing them over one or more aboral spines (wherever accessible) with aid of long-handle forceps. The size (maximum diameter) was recorded (or estimated) taking care not to disturb the starfish or cause them to move. During initial set-up (n = 75 starfish across 2 sites), we placed two independent pieces of flagging tape on every starfish (Figure 2), and then verified the subsequent identity of starfish by referring to both tags. This effectively allowed for measures of tag retention among starfish that were recorded on multiple occasions (n = 68 starfish), which was very high (94.1%; 128 out of 136 tags) over the initial study period (48-72 hours). While the dual tagging did (in some cases) make it easier to determine the identity of starfish (e.g., for starfish concealed well within the reef matrix, tags placed on opposite arms increased the likelihood that at least one tag would be visible without disturbing the starfish), subsequent starfish were mostly tagged with only a single temporary tag.

To assess fine-scale movement patterns of *A.* cf. *solaris* at Rib Reef within and among diel intervals, transect tapes were left in position for up to 4 days, and re-surveyed on multiple occasions. Each of the transects was surveyed at least once during diurnal (0700-1700 hrs) and nocturnal periods (1900-0500 hrs). Transects were established during daylight hours and at least one survey was conducted after dark. During each survey we recorded the position (as described above) of every tagged starfish. We also tagged and recorded all new starfish detected during each successive survey. While not an initial or intentional objective of this study, this accounting of all newly detected starfish (as distinct from *re-captures*) allowed for mark-recapture estimates of the local population size and detection probabilities of starfish in different size classes, following MacNeil et al. (2016). Detectability was assessed by comparing the total number of adult *A.* cf. *solaris* recorded during the first diurnal and first nocturnal survey on each transect to the estimated overall population size based on ratios of tagged starfish versus un-tagged starfish recorded across all successive surveys on each transect. Estimated overall population size was calculated using a loglinear model in Rcapture, (Baillargeon and Rivest 2007) assuming a closed population, given the short period that elapsed (<24 hours) between surveys.

Aside from recording the position of starfish, the extent to which individuals were exposed (visible from directly above) was recorded to the nearest 10%. We also recorded whether starfish were moving versus stationary, and/ or feeding. Feeding was determined based on whether stomachs were everted (even partially) versus completely retracted, by carefully lifting one or more arms until it was possible to observe the everted stomach or mouth. Local coral cover and composition was also recorded using the point intercept method (at 50cm intervals) along each of the transects. All live corals were identified to genus, while points that did not intersect live corals were categorised as either carbonate pavement, loose rubble or sand.

2.3 Passive acoustic monitoring

To study larger-scale (hundreds of metres) and longer-term (months) movement of crown-of-thorns starfish, we tagged individual starfish (n = 50) using V7 69KHZ acoustic transmitters and remotely monitored their position relative to 8 acoustic receivers (VR2W – 69 KHZ receivers by Vemco) deployed along continuous reef tracts. Two separate and successive monitoring studies were undertaken: i) Lodestone Reef (18˚41'S, 147˚06'E) where receivers were installed on March 5th 2019 to either side of a small aggregation of starfish that was located along the north-western corner of the reef (Figure 3), and ii) Big Broadhurst Reef (18˚56'S, 147˚43'E), where receivers were installed on November 21st 2019 in a continuous line on the southwestern edge of the reef (Figure 4). At Lodestone Reef, the two central receivers (number 4 and 5) were spaced 50 m apart, increasing to 100 m either side for the next receiver (3 and 6) and 200 m for the two outermost receivers (1 and 2; 7 and 8). At Big Broadhurst Reef, all receivers were set 100m apart at a depth between 3.5m and 7m. These sites were selected following extensive surveys (manta tow searches) at mid-shelf reefs in the central section of the GBR, including Hopkinsons Reef, Grub Reef, and Centipede Reef, to identify sites with reasonable densities of crown-of-thorns starfish but also moderate coral cover, and in areas with limited habitat structure that would interfere with signals between tagged starfish and receivers.

Acoustic receivers were painted in marine anti-foul paint, arranged in a relatively straight line and secured using either a stake hammered into sand or rubble, or chained to large section of carbonate reef matrix (Figure 3). At Lodestone Reef, receivers were arranged in a line as close as possible to the continuous reef structure, but there were lots of tall patch reefs that could potentially reduce detections of starfish, except when they were on the top or seaward side of the patch reefs. At Big Broadhurst Reef receivers were deployed in relatively deep water, away from the reef edge and crest (to avoid damage during low tides and rough weather, as well as ensuring they did not pose a hazard for local boat traffic) but were secured well above the surrounding substrate to maximise detection rates (Figure 3). It was expected (given the complexity of the reef habitat) that tagged starfish would only be detected if out in the open, such as moving between reef structures and patch reefs.

Figure 3: Location of the 8 acoustic receivers at Lodestone Reef, central GBR, and VR2W acoustic receiver at Lodestone Reef in March 2019. Photograph: Vanessa Messmer.

Vemco V7 (69KHZ) transmitters were the smallest transmitters available that could be attached externally to crown-of-thorns starfish. Transmitters were painted with marine anti-foul paint to avoid settling organisms that might affect the transmission, and were programmed to emit a signal every 3 minutes (180 seconds) for up to 12 months. Transmitters were attached to crown-of-thorns starfish using 17 LB (0.38 mm diameter) fishing line that was fed through the calcified ring within the central disc of the starfish, which is located just outside of the ring of madreporites. Holes were pre-drilled in the central disk using a 19G x 3.5” Terumo spinal needle, which was rotated by hand, after first using it to locate the calcified ring. The fishing line was then fed through the needle (whilst still in place) and through the body of the starfish. For the first tagging study (n = 12 starfish; March 2019) the fishing line was tied to the eyelet of the transmitter before securing around the closest armpit. However, all subsequent starfish were tagged by drilling two holes (2 to 3 cm apart) through the calcified ring to ensure the transmitter remained on the aboral surface of the starfish. The fishing line was passed down and then back up through adjacent holes and then tied to V7 transmitter on the aboral surface before connected the ends of the fishing line using A1 crimp sleeves (1.4 mm diameter). The fishing line was secured with only very slight tension to minimise the likelihood of getting snagged, while ensuring that fishing line did not tear the dermal tissues of the starfish (Figure 5). All starfish were tagged immediately after collection, on nearby areas of open sand. Following tagging, each starfish was released to the precise (temporarily marked) location where it was originally located.

Data SIO, NOAA, U.S. Navy, NGA, GEBCO
Image © 2019 Maxar Technologies
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Figure 4: Location and spacing of 8 acoustic receivers at Big Broadhurst Reef on the central GBR. Receivers were spaced at regular intervals, ~100m apart

To assess coral cover around each receiver, 3 replicate 20 m point intercept transects were run either side of the receiver and approximately parallel to the reef edge. Surveys were conducted at Lodestone Reef on 28-29 June 2019 at, and Big Broadhurst Reef on 21-22 November 2019. Live coral or the type of substrate underlying the transect tape was recorded every 0.5m, as described above.

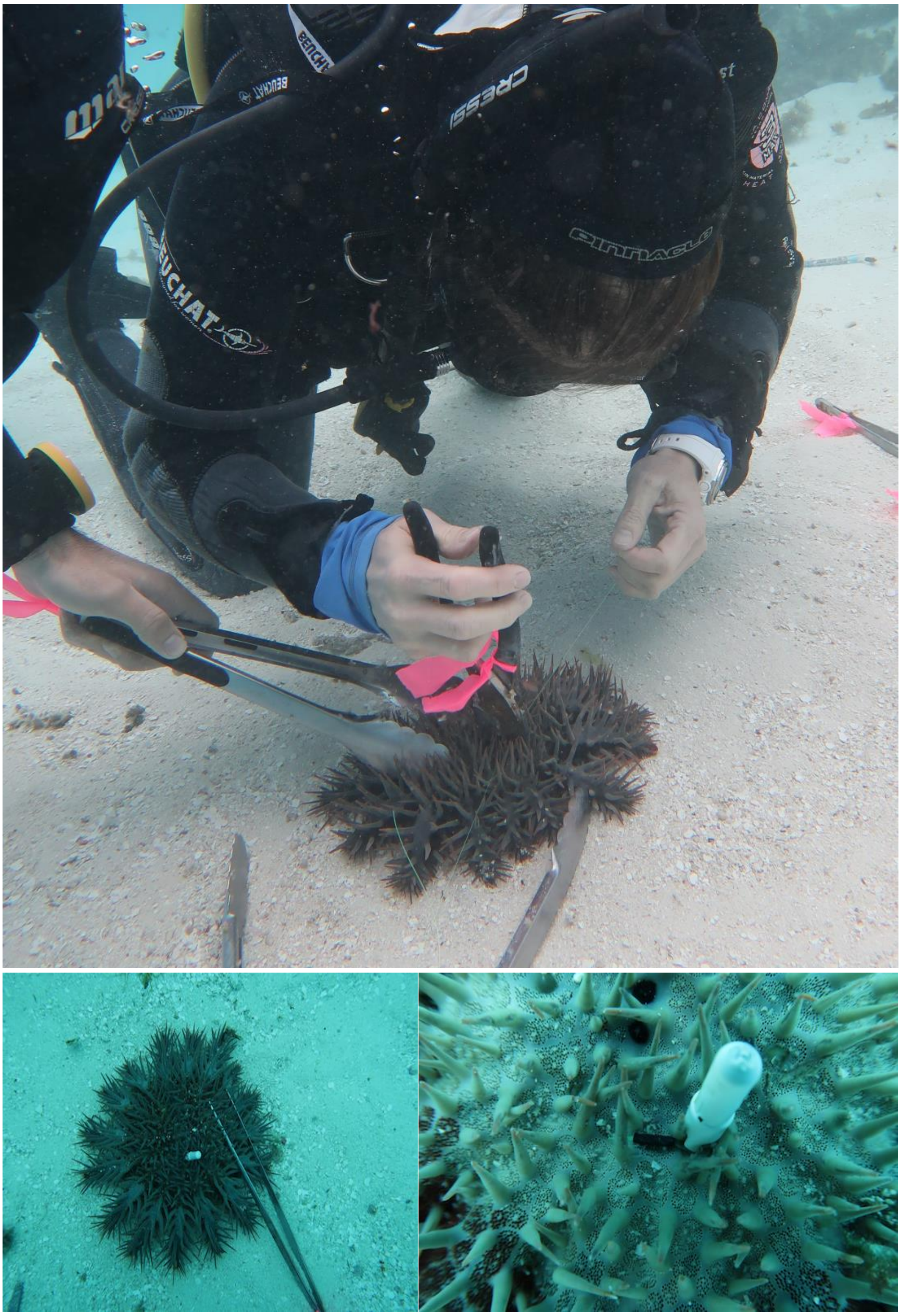

Figure 5: *In situ* tagging of crown-of-thorns starfish (*Acanthaster* cf. *solaris*) with V7 transmitters, showing specific location of tags after procedure was completed. Photographs: Deborah Burn and Vanessa Messmer.

3.0 RESULTS AND DISCUSSION

3.1 Captive movement rates

Crown-of-thorns starfish placed in the centre of an open and well-lit tank almost invariably (91.7%, n=218) and immediately moved toward the outer perimeter of the tank, which is consistent with an inherent avoidance of exposed habitats (Moran 1986; Petie et al. 2016). Exceptions to this pattern were smaller starfish that were able to seek refuge beneath large pieces of coral rubble, and thereafter remained stationary and concealed. For starfish that did progress to the outer edge, most (75.0%) headed towards the black plastic sheet, highlighting the importance of vision in orientation by crown-of-thorns starfish and their inherent preference for habitat structure (Beer et al. 2016; Petie et al. 2016). However, we did notice that most starfish tended to have a distinct anterior-posterior axis, as reported by Rosenberg (1972), whereby the initial direction of movement was determined by the orientation of the dominant arm(s), which were held upwards, presumably to maximise the visual field in the direction of movement (*sensu* Beer et al. 2016). This tendency for non-random behavioural orientation was most apparent for starfish that were initially orientated and started moving perpendicular to the direction of the black plastic sheet and then circled around to move in the direction of the sheet. Accordingly, some starfish may not have detected the black plastic sheet, simply because they were initially orientated with their dominate arm(s) in the opposite direction.

The rates of movement (averaged across all 15 second observations for each individual) recorded for starfish varied significantly with body size (GLM: $F_{1,214} = 6178$, $p < 0.05$; Figure 6). The average rate of movement for individuals <150 mm total diameter was 23.99 cm per minute (±1.02 SE) compared to 33.41 cm per minute (±1.49SE) for individuals >350mm total diameter. This is very similar to reported rates of movement for adult crown-of-thorns starfish from studies (e.g., Mueller et al. 2011) conducted at equivalent temporal scales (Table 1). As for mean velocity, maximum velocity (the maximum speed recorded in a 15 second period) generally increased with increasing body size (GLM: $F_{1,214} = 9858$, $p < 0.05$; Figure 6a). However, the maximum recorded rate of movement (107.24 cm per minute) was recorded for a starfish that was just 205mm in diameter. This seemingly anomalous rate of movement was only sustained for a very short period (15 seconds), but may suggest that sustained rates of movement were well below what these starfish are actually capable of (e.g., if being pursued by a predator). Overall, the maximum velocity recorded for each individual movement assay was 53.07% (cv = 0.74) above the mean velocity recorded as starfish moved from the centre to the edge of the tank. This suggests that starfish were moving at a moderate and sustained rate.

While mean and maximum rates of movement for crown-of-thorns starfish increased with increasing body size, it is unclear what inherent morphological features facilitate increased movement capacity at larger size. For crown-of-thorns starfish considered in this study, both the length (GLM: $F_{1,41} = 22743$, $p < 0.05$) and number of tube feet (GLM: $F_{1,41} = 10148$, $p < 0.05$) were positively related to body size (Pratchett et al. 2017). However, if we account for the size of starfish (recording movement rates based on body length per minute) the rate of movement effectively declines with increasing body size (see also Montgomery and Palmer 2012). The average rate of movement for individuals <150 mm total diameter (n = 58) was

0.205 body lengths per minute (±0.008 SE) compared to 0.084 body lengths per minute (±0.004 SE) for individuals >350mm total diameter (n = 82).

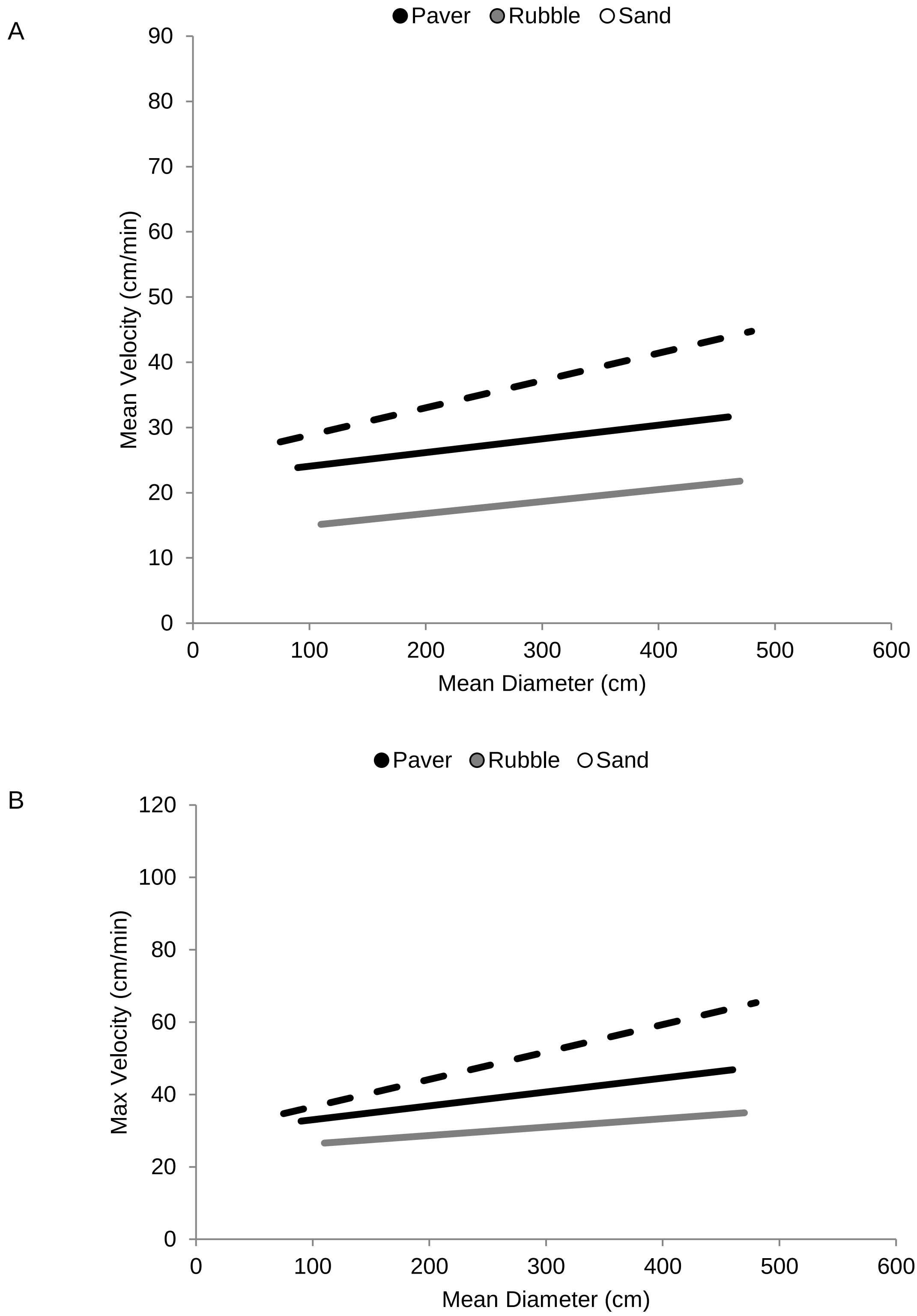

Figure 6: Relationships for a) mean velocity and b) maximum velocity with the total diameter of crown-of-thorns starfish (n = 42). Movement rates were quantified for three different substrate-types: paver (black circles), rubble (grey circles) and sand (white circles). Lines indicate the line of best fit for each different substrate type (paver: black line, rubble: grey line, sand: dashed line).

Despite marked size-based differences in rates of movement recorded, substrate type also had a significant effect on the short-term rates of movement (GLM: $F_{1,212}$ = 9848, $p < 0.05$; Figure 6). This study showed that *A cf. solaris* moved faster over sand (36.53 ± 1.31 cm min^{-1}) than on either rubble or consolidated pavement (Tukey's test: $p < 0.05$). Starfish had the slowest average rate of movement when moving across rubble (17.25 ± 0.63 cm min^{-1}), which was significantly slower for sand or pavers (Tukey's test: $p < 0.05$). Substrate type also had a significant influence on maximum velocity (GLM: F1,212 = 6089, $p < 0.05$; Figure 6b). A significant interaction was detected between starfish mean diameter and substrate type (GLM: F1,209 = 341, $p < 0.05$; Figure 6b). The highest overall maximum velocity was recorded on sand. However, maximum velocity on sand was only significantly higher than rubble (Tukey's test: $p < 0.05$). The difference in maximum velocity between sand and paver increased with increasing size of starfish, but was not significant (Tukey's test: $p > 0.05$).

It is to be expected that substrate type would influence the potential rates of movement by benthic invertebrates (e.g., Thompson and Thompson 1982), but this study presents the first explicit test of effects of substrate-type on movement rates for crown-of-thorns starfish. We found that crown-of-thorns starfish moved slowest across rubble (Figure 6), which was the most structurally complex of the three substrate types tested. Three factors likely contribute to this. Firstly, individuals must navigate a greater surface area to achieve the same degree of horizontal displacement (Flukes et al. 2012). Second, tube feet adhesion strength is significantly higher when starfish are moving over rough surfaces (Santos et al. 2005); therefore, starfish may be slowed down on rough surfaces due to the need to break the stronger adhesive bond between their tube feet and the substrate, which could also explain why the effect of substrate was stronger in larger starfish (due to the greater number of tube feet and hence strength of attachment). Finally, the capacity of starfish to bend sufficiently to keep all tube feet in contact with the substrate will decrease with the substrate's topographical complexity, and this effect should be greater for larger starfish. Interestingly and unexpectedly, crown-of-thorns starfish exhibited consistently and significantly higher velocities on sand compared with flat, unstructured, consolidated pavement (Figure 6). Functionally, we would expect movement rates to be somewhat constrained by the instability of sand and reduced adhesion of tube feet, limiting the capacity for starfish to pull themselves across the substratum. The greater velocities on sand versus pavement, might therefore, be due to motivation rather than physical capabilities (see also Thompson and Thompson 1982) or to the ease of breaking adhesion to sand surfaces.

Birkeland and Lucas (1990) suggested that the maximum rate of movement for crown-of-thorns starfish is approximately 1 body length (diameter) per minute, regardless of size, which would effectively account for size-based changes in reported movement. However, the movement rate reported by Glynn (1977), at 1m per minute for a starfish that was 250mm total diameter, would equate to 4 body lengths per minute. Average and maximum rates of movement recorded in this study were much less than 1 body length per minute, and generally <0.5 body lengths per minute, and decreased with increasing body size (Figure 76). This might suggest that starfish (even at the maximum recorded rates of movement) were not moving at anything close to the maximum possible rates of movement. If so, this would suggest that very high rates of movement are energetically costly and reserved for extreme situations, such as escaping predators (Glynn 1977). Interestingly, the size-corrected average rates of movement were much more similar across the range of sizes considered when travelling over rubble, compared to sand or pavers (Figure 7). This suggests that constraints imposed on rates of movement over highly complex substrates are largely independent of body size.

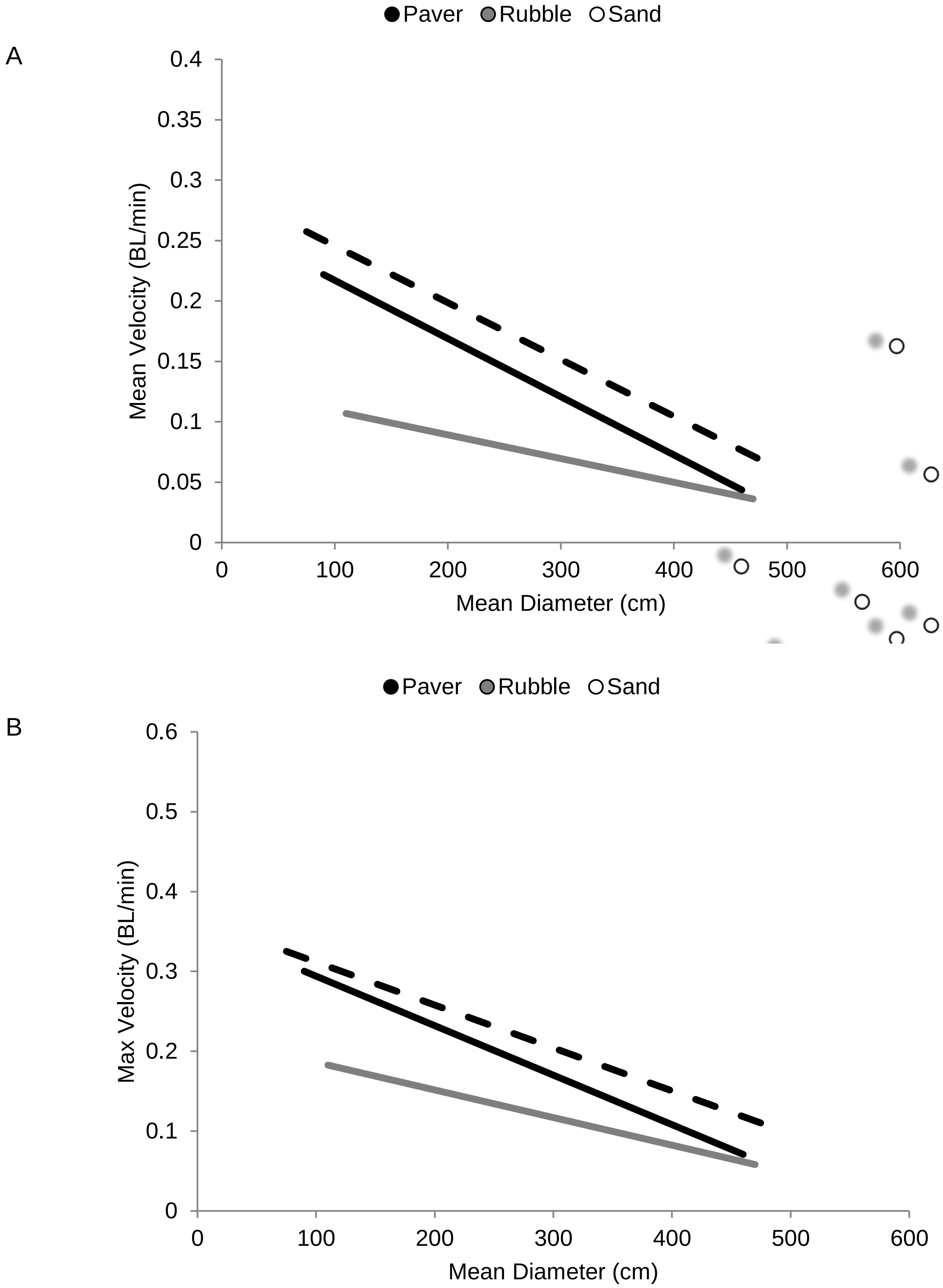

Figure 7: Relationships for a) mean velocity and b) maximum velocity with the total diameter of crown-of-thorns starfish (n = 42). Movement rates were quantified for three different substrate-types: paver (black circles), rubble (grey circles) and sand (white circles). Lines indicate the line of best fit for each different substrate type (paver: black line, rubble: grey line, sand: dashed line).

3.2 Short-term tagging and movement

3.2.1 Movement

A total of 357 individual crown-of-thorns starfish, ranging in size form 100mm diameter to 560mm dimeter were recorded and tagged (with temporary tags) on 12 transects across five sites at Rib Reef. Repeat surveys of all *A.* cf. *solaris* recorded along these transects yielded 448 discrete movement events, recorded as the minimum distance between where each starfish was detected and the location where it was last recorded. Minimum displacement distances ranged from 0 to 22.8m, while the period between successive detections ranged from 2 to 82 hours. The distribution of minimum displacement distances was highly skewed towards very limited or no movement (Figure 8); for 194 (out 448) observations the starfish did not noticeably move between successive surveys (minimum displacement distance = 0), while minimum displacement distance was <2m for 368 out of 448 (82.1%) starfish.

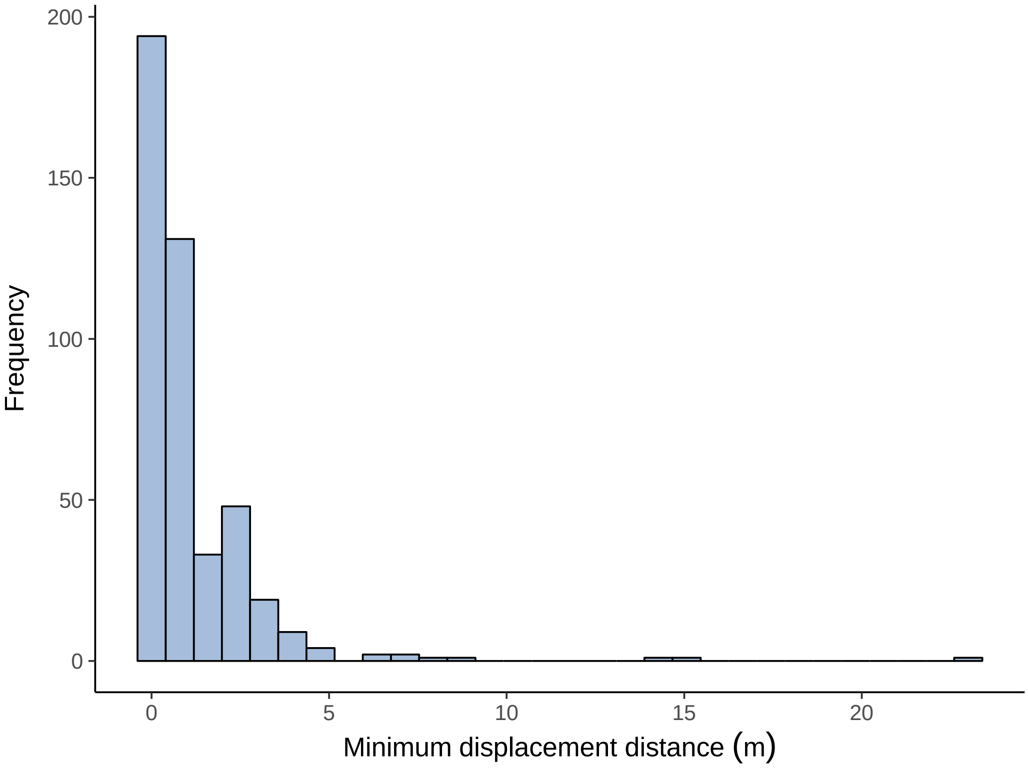

Figure 8: Frequency distribution of minimum displacement distances (n=448) recorded during successive surveys of 357 individual crown-of-thorns starfish at Rib Reef, central Great Barrier Reef.

Across all discrete movement events, the average minimum displacement distance recorded was 0.96m (95%CI: 0.79-1.14m), and the corresponding movement rate (accounting for time in hours between successive detections) averaged 0.08m per hour (95%CI: 0.07-0.10m per hour) or 1.9m per day. The average minimum displacement distance and average rate of movement was consistently low across all size-classes of crown-of-thorns starfish (Figure 9), though there were noticeable increases in both the measures of movement among large (>500mm diameter) individuals (n=3). Keesing and Lucas (1992) found that movement rates for larger crown-of-thorns starfish (≥400mm diameter) were at least twice that of smaller starfish (<400mm diameter), but we did not detect such a marked difference with size.

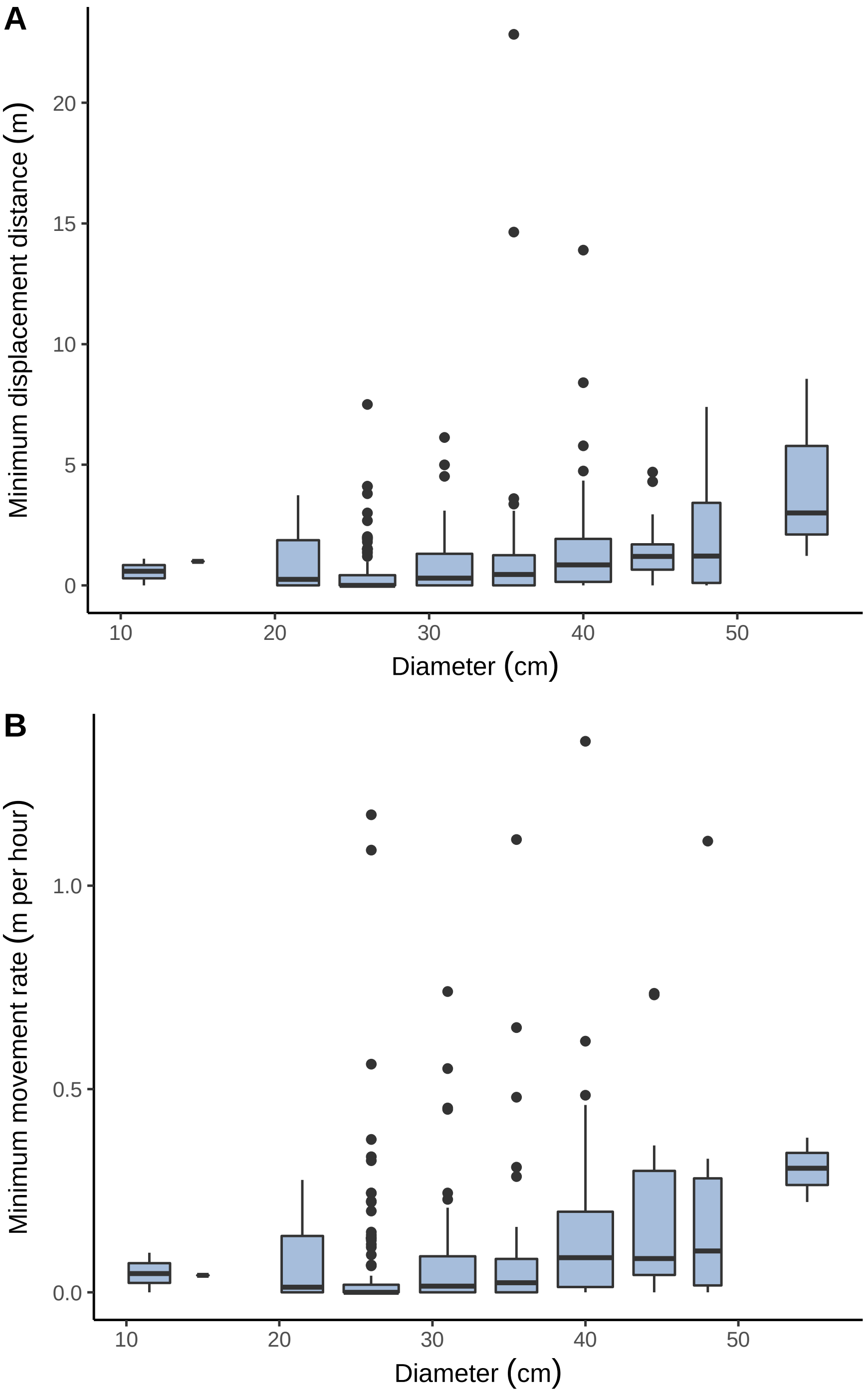

Figure 9: Box-plots showing size-based differences in recorded movement (A – minimum displacement distances, and B- minimum rate of movement) for crown-of-thorns starfish at Rib Reef, central Great Barrier Reef.

These data show that *A.* cf. *solaris* move very little on diel timescales. Even for starfish that changed their behavioural mode (e.g., between sheltering versus feeding), they moved only short distances (<2m) from sheltering positions to feeding locations. These findings are consistent with findings from other comparable short-term tagging and monitoring studies (e.g., Ormond 1970). However, it is also apparent that these methods are biased towards increased detection of starfish that move very little; there was an inherent tendency to concentrate searching in areas where starfish had previously been recorded, leading to increased likelihood of detecting starfish that had not moved, whereas starfish that had moved even just a few metres perpendicular to the transect line may have moved outside of the search area and would be unlikely to be detected. Notably, 25 out of 258 (9.7%) that were tagged during initial establishment of transects were never recorded on any subsequent surveys. This may reflect the proportion of individuals that moved sufficient distances so as to be undetectable in subsequent surveys.

Previous studies (e.g., Keesing and Lucas 1992) show that movement patterns of crown-of-thorns starfish are strongly influenced by the local availability of coral prey, which makes sense given that the prime motivation for movement (at least outside of reproductive seasons) is to access food resources. Keesing and Lucas (1992) found that *A.* cf. *solaris* in areas with low densities of starfish and high cover (>30%) of prey corals moved only 1m per day, whereas conspecifics occupying reef habitats with low (<10%) coral cover moved >4 m per day. These differences in daily rates of movement are directly attributable to the availability of coral prey, such that starfish do not have to travel as far to access food in areas with high coral cover (Keesing and Lucas 1992). However, there were also differences in recorded rates of movement between reefs (e.g., Davies Reef versus Little Broadhurst Reef) in areas with comparable coral cover (Keesing and Lucas 1992), suggesting that daily movement rates are also influenced by reef structure and availability of shelter.

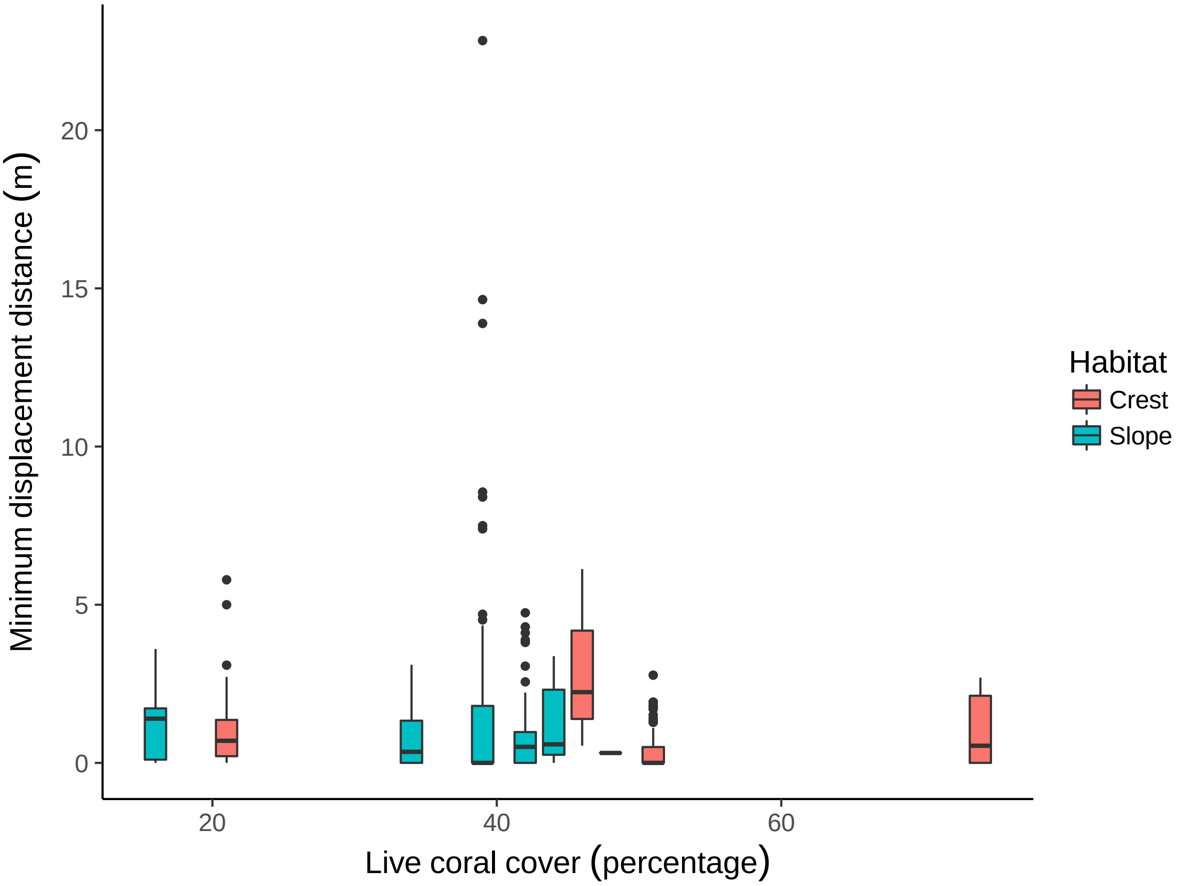

Figure 10: Box-plots showing differences in recorded movement for crown-of-thorns starfish (minimum displacement distances) relative to local cover across 10 transects at Rib Reef, central Great Barrier Reef.

Coral cover ranged from 16% to 74% among transects where we recorded diel movement patterns of *A.* cf. *solaris* at Rib Reef (Figure 10). Coral cover was generally higher on the reef crest (49.1% ±5.9 SE) than reef slope (35.0% ±5.0 SE), and particularly at Site B where there was very high coral cover (75%) recorded on the reef crest, with extensive cover of tabular *Acropora*. Tabular *Acropora* accounted for >50% of coral cover (and up to 84%) recorded on the reef crest at all sites, except Site E, where virtually all tabular *Acropora* had been recently killed (presumably by crown-of-thorns starfish). Despite marked differences in local coral cover, we found no consistent change in the minimum displacement distance recorded among transects relative to coral cover. This finding is counter to previous studies that show local coral cover has a strong influence on movement patterns of crown-of-thorns starfish (e.g., Keesing and Lucas 1992), though this might reflect the scale mismatch between our measure of coral cover (which is calculated at the scale of each 50m transects, with no specific accounting of changes in cover along each transect) versus fine-scale variability in prey availability for individual crown-of-thorns starfish.

3.2.2 Detectability

Aside from assessing small-scale movement patterns of *A*. cf. *solaris*, this short-term tagging study provided important insights into the diel patterns of behaviour, such as exposure (Burn et al. 2020) and also enabled direct estimates of detectability. In all, we recorded 357 individuals across all surveys (3-5) on 12 transects at 5 different sites (A through E). During initial deployment of transects, we recorded just 266 (74.5%) out of 357 crown-of-thorns starfish ultimately recorded (across all surveys). Based on log-linear analysis of all capture-recapture data the estimated population across all transects was 365.6 starfish (95%CI: 359.5-372.3). Based on this population estimate, our overall detectability (across successive surveys) was 95.9-99.3% (Table 2). However, nocturnal surveys increased the number of starfish detected by an average of 21.05% across all transects. Based on the single initial surveys, which were conducted during daylight hours (generally in the morning), the average level of detectability for individuals ≤250 mm diameter was 46.3%, compared to 82.4% and 85.6% for individuals 260-350mm dimeter and >350mm diameter, respectively. This likely reflects levels of detectability that would be achieved by control divers culling crown-of-thorns starfish within coral reef environments.

Differences in detectability were most apparent among different size classes of crown-of-thorns starfish (Table 2; Figure 11), as has been reported previously (MacNeil et al. 2016). MacNeil et al (2016) used very similar methods to those reported herein to assess the detectability of *A*. cf. *solaris* (n = 114 starfish) across 8 transects at two reefs (Undine Reef and Rudder Reef) in the northern GBR. MacNeil et al (2016) found that average detectability of crown-of-thorns starfish was 82%, but varied greatly depending on the size of the starfish and the time of day. In our study, overall detectability of small (≤250 mm diameter) starfish was much lower than that of starfish >250mm diameter, and there was no apparent difference in detectability between medium and large sized individuals (Figure 11). Moreover, the effect of time of day on detectability was much more pronounced for smaller (≤250 mm diameter) individuals (Table 2), presumably reflecting the increased tendency for smaller starfish to stay hidden during the day (Moran 1986).

Table 2: Estimates of detectability based on log-linear analyses of mark-recapture data, whereby crown-of-thorns starfish were surveyed at least 3 time along each of 12 transects. Estimated population size (M0) is based on capture probabilities across all surveys. The original (*ui T1*) and subsequent (*ui T2*) number of starfish detected is shown to emphasise the contribution that nocturnal surveys made to overall detections. Population estimates are shown for different size classes of starfish, different habitats and each transect (where possible).

Treatment	N	*M0*	Detectability (%)	*ui T1 (Day)*	*ui T2 (Night)*	Nocturnal addition (%)
Overall	357	365.6	97.65%	266	56	21.05%
Small (≤250 mm)	108	116.6	92.62%	54	36	66.67%
Medium (260-350 mm)	171	173.6	98.50%	143	34	23.78%
Large (>350 mm)	135	136.7	98.76%	117	16	13.68%
Crest (3m)	168	172.6	97.33%	127	20	15.75%
Slope (6m)	189	193	97.93%	139	36	25.90%
Transect A-01	67	67.9	98.67%	49	18	36.73%
Transect A-02	27	27	100.00%	26	0	0.00%
Transect B-01	83	87.7	94.64%	70	4	5.71%
Transect B-02	83	83.9	98.93%	72	11	15.28%
Transect C-01	21	24.5	85.71%	10	6	60.00%
Transect C-02	6	6.1	98.36%	5	1	20.00%
Transect C-03	1	NA	NA	1	0	0.00%
Transect C-04	3	NA	NA	2	1	50.00%
Transect D-01	33	48.5	68.04%	11	4	36.36%
Transect D-02	17	18.1	93.92%	14	3	21.43%
Transect E-01	4	4.1	97.56%	3	1	33.33%
Transect E-02	12	12.5	96.00%	5	7	140.00%

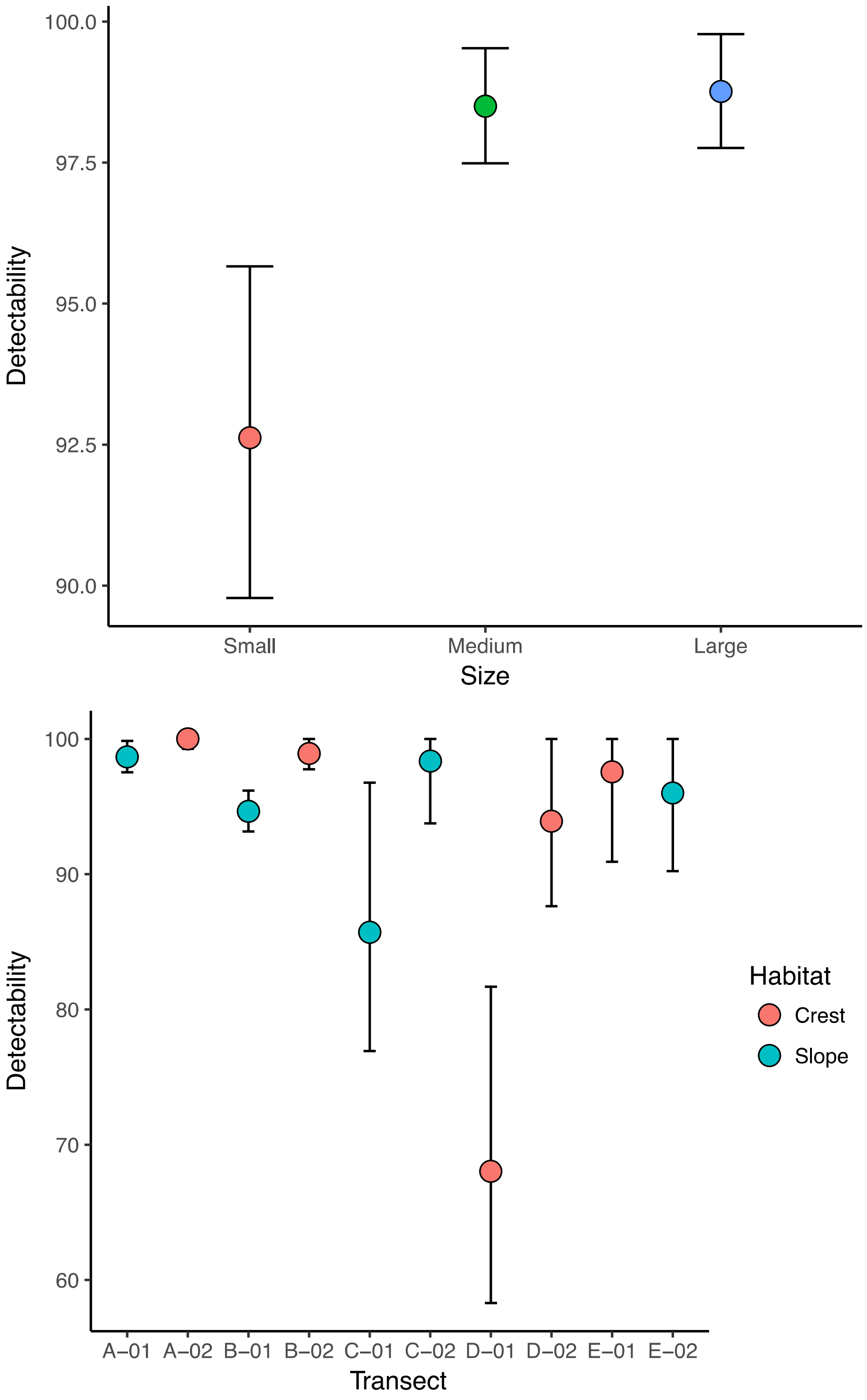

Figure 11: Detectability of Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) at Rib Reef, based on actual number of individuals recorded versus estimated population sizes for A) different size classes (as per Table 2), and B) different transects. Data is shown for only 10 (out of 12) transects, as population estimates for transects with very low numbers of starfish detected were considered erroneous. Standard error for detectability estimates was calculated based on variability in population estimates (Table 2).

3.3 Passive acoustic monitoring

Of the 12 *A.* cf. *solaris* that were initially tagged (with V7 69KHZ transmitters) at Lodestone Reef in March 2019 (transmitter numbers 39-50), only eight individuals were detected post-tagging. There were a total 938 detections across all individuals over the total sample period (from March 5th to October 27th, 2019), though only 3 individuals were detected beyond the first 2-3 days after they were tagged. One starfish (transmitter number 39) was consistently, though infrequently, detected over 6 months (Figure 12). All 12 starfish were located, tagged, and returned to the area between receivers 4 and 5 and detections were limited to these receivers, and mainly receiver number 5. Given limited long-term (>1 week) detections at Lodestone Reef, a further 12 individuals were tagged (transmitter numbers 51-62) on June 27th 2019. At this time, the entire area between receivers 4 and 5 was intensively searched for previously tagged individuals, though none were found. Given the relatively narrow strip of reef along the northern edge of Lodestone Reef, it is unlikely (but not impossible) that previously tagged individuals moved perpendicular to the line of receivers. The reef edge was lined by sand on the deeper side and a shallow reef flat with virtually no corals on the shallow side. Each receiver is theoretically capable of receiving signals from any and all V7 69KHZ transmitters located within a 100m radius. However, the signal has to be emitted within line of sight, which is a significant limitation within complex reef habitats (Welsh et al. 2012), added to which, crown-of-thorns starfish are often very cryptic and shelter or even feed on the underside of corals. It is also possible that the signal would be limited if transmitters slid to the under (oral) side of the animal (which was subsequently prevented by changing the tagging protocols, see Section 2.3). Aside from limited detectability, it is possible that transmitters were lost from crown-of-thorn starfish, where transmitters may become snagged on the substrate and then tear out of the body of the starfish as they continue to move away. However, no injured starfish were located, despite careful search concentrated in the area between receivers 4 and 5.

Of the 12 additional *A.* cf. *solaris* that were tagged on June 27th 2019 (using the modified tagging method), 9 starfish were detected post-tagging, and there was a total of 2,537 detections across all individuals from June 27th to October 27th, 2019 (Figure 13). Differences in detection rates between the two tagging events within the same location may be attributable to changes in the tagging protocols; By feeding the fishing line back through the calcified ring (rather than around the nearest arm pit), there is no possibility of the transmitter moving to the oral side of the animal. Also, the risk of getting snagged is greatly reduced, given that there was only a very small length of fishing line exposed (on both the oral and aboral sides of the starfish). However, individual differences in the frequency and duration of detections were very apparent for both groups of crown-of-thorns starfish, and it is possible that this second group of starfish were more active, or generally more exposed.

Despite frequent and extended detections of crown-of-thorns starfish, all individuals were only ever detected by the receivers immediately adjacent (receivers 4 and/ or 5) to where the starfish were initially found and released (post-tagging). These results suggest that crown-of-thorns starfish move very little (<100m) even at temporal scales of weeks to months. This is consistent with previous suggestions (e.g., Ormond 1970) that crown-of-thorns starfish tend to restrict their movements within circumscribed areas of habitat for several weeks, as long as food remains sufficiently abundant. However, the limited long-term detections (other than for individuals with transmitter numbers 39 and 61) may suggest that tagged starfish have effectively moved outside of the area encompassed by the array of receivers, potentially moving perpendicular to the reef, into deeper water or up over the reef crest. It is also possible that tagged starfish remained concealed within the reef matrix or outside of line of sight of the receivers, and may have ultimately died or lost their tags. While the current tagging method was developed and tested in captivity, where tag retention was 100% for 3 weeks (n = 6 starfish), it may be that tag retention is much lower in complex reef habitats compared to aquaria.

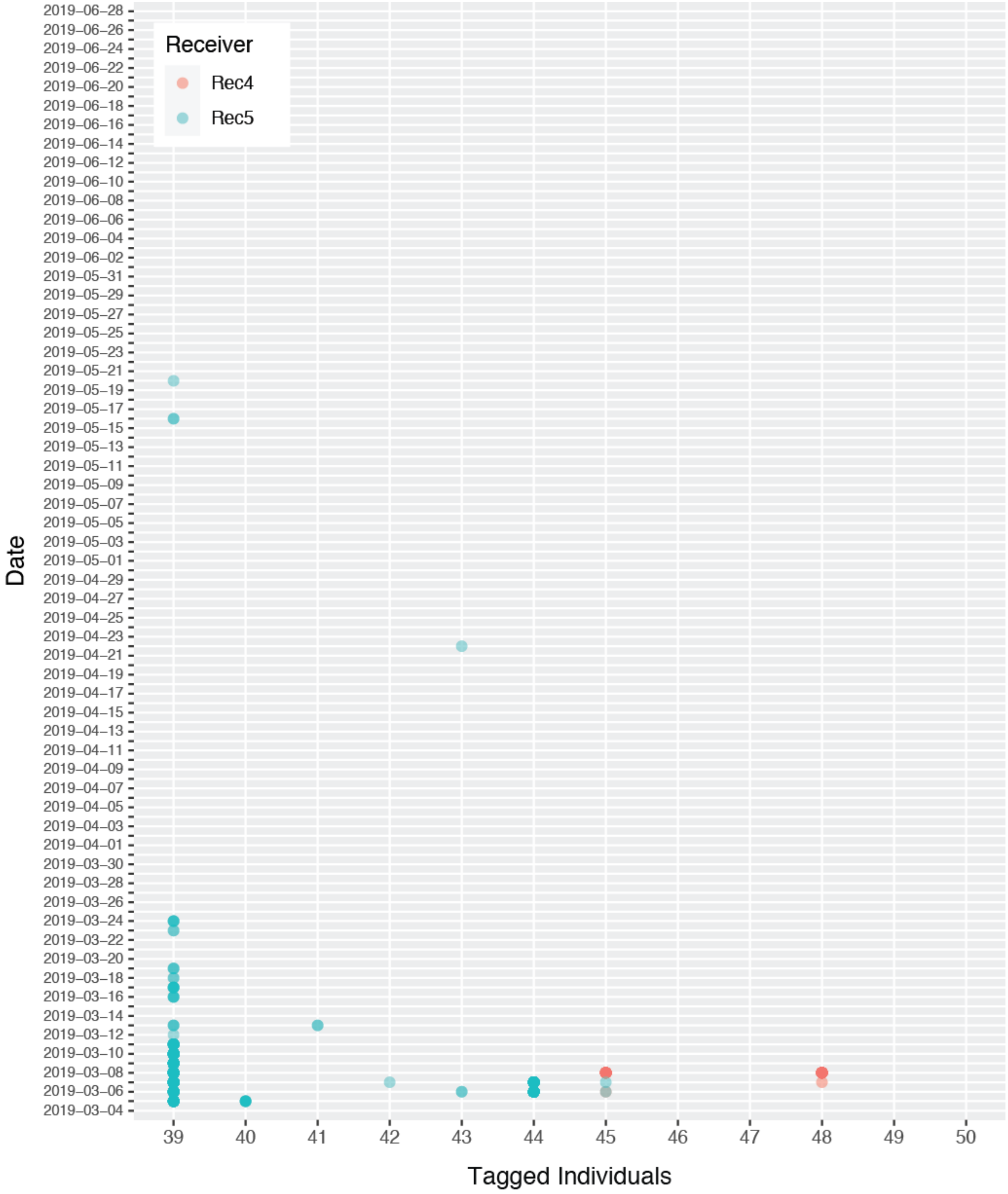

Figure 12: Detections of tagged Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) at Lodestone Reef, GBR between March 5th and June 27th 2019. Each circle represents detections for a given individual on a day and shading is proportional to the number of detections for that particular day. Data for individual 39 extends well beyond the range of days shown (see Figure 13).

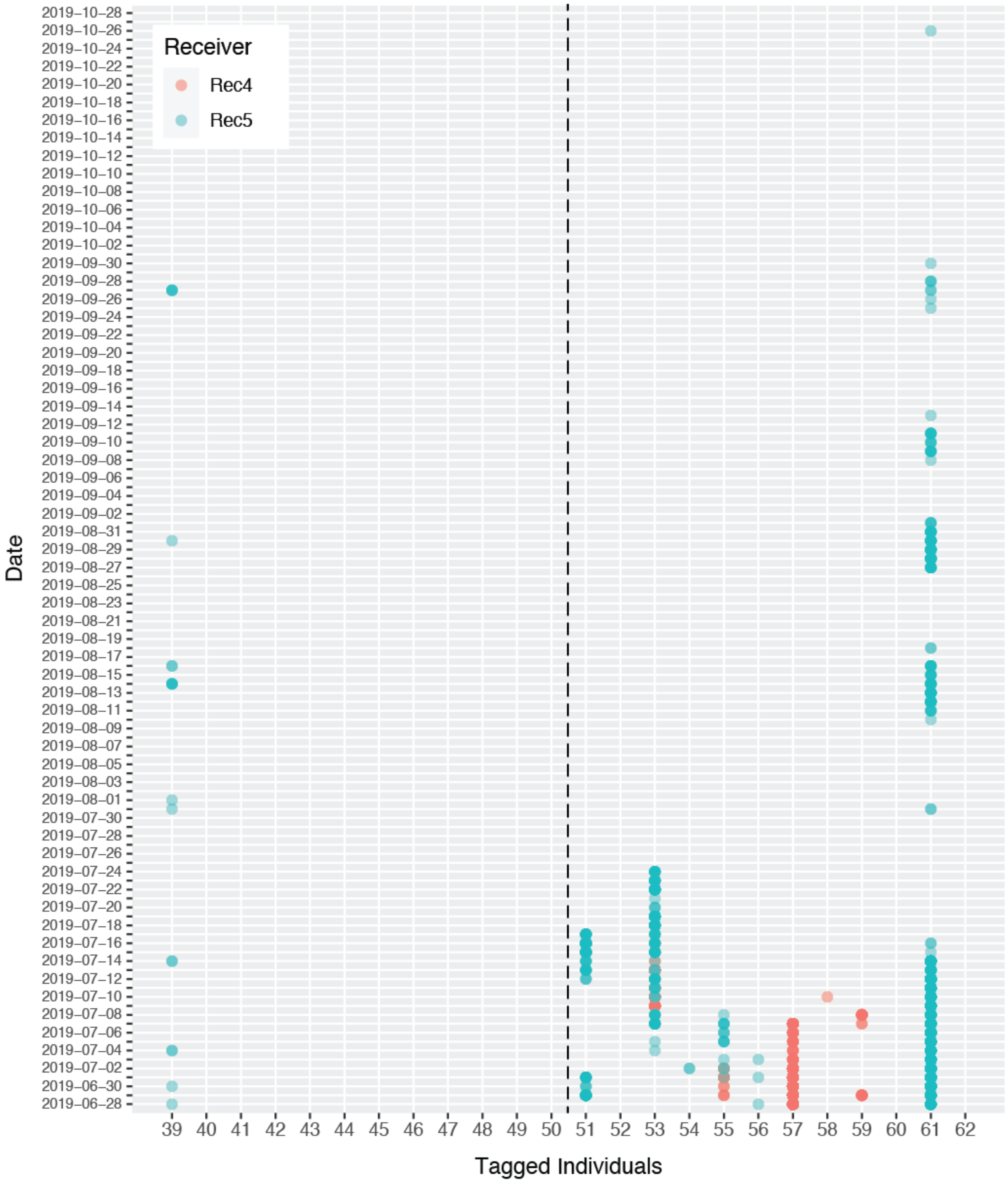

Figure 13: Detections of Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) tagged on March 5th 2019 (39-50) and 12 additional individuals tagged on June 27th 2019 (51-62) at Lodestone Reef, GBR. Data downloaded from Receivers 4 and 5 between June 27th and October 27th 2019. Each circle represents detections for a given individual on a day and shading is proportional to the number of detections for that particular day. This data continues from Figure 12, and as such, all starfish tagged on March 5th are also shown.

Figure 14: Detections of tagged Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) at Big Broadhurst Reef, GBR between November 21st 2019 and January 29th 2020. Each circle represents detections for a given individual on a day and shading is proportional to the number of detections for that particular day

The overall number and rate of detections were higher at Big Broadhurst Reef, with 4321 detections over just 2 months, compared to 3475 detections over 8 months at Lodestone Reef. Coral cover recorded at Big Broadhurst Reef (44.05% ±5.00SE) was slightly higher than recorded at Lodestone Reef (36.61% ±4.81SE), but the overall structure of the habitat was much more amenable to passive acoustic tracking, which probably contributed to increased levels of detection. At Big Broadhurst Reef, 23 out of 26 tagged individuals were detected post-release, though 8 individuals were only detected the day they were released (Figure 14). For the remaining individuals (n=15), detections were highest in the last week of November and first two weeks of December, potentially coinciding with the onset of the reproductive season (Figure 14). Only 3 individuals (64, 66, 73) were detected after this period and up until receivers were retrieved on January 29th, 2020. Notably, there were very few *A.* cf. *solaris* detected (and mostly smaller individuals) within the vicinity of the acoustic array at Big Broadhurst Reef in late January 2020, especially compared to the notable abundance and large size of starfish when this array was established in November 2019. This would suggest that larger starfish had died or moved (possibly into deeper water) through the summer period, which coincided with marked and sustained increases in water temperature over this period from 25.5°C at the start of November 2019 to 29.5°C in late January 2020 (AIMS 2020).

Declines in detections of tagged individuals, and apparent declines in the size and abundance of starfish, from November 2019 to January 2020 may suggest *A.* cf. *solaris* are vulnerable to elevated temperatures. The only study that has explored temperature sensitivity for adult crown-of-thorns starfish to date, measured changes in oxygen uptake of three relatively small (120mm diameter) individuals at experimental temperatures ranging from 25 - 33°C (Yamaguchi 1974). Yamaguchi (1974) showed that *A.* cf. *solaris* are adversely affected by temperatures ≥31°C, while prolonged exposure to ≥33°C is likely to be lethal (Yamaguchi 1974). It is possible that larger individuals will be even more sensitive to elevated temperatures, and especially in the weeks prior to spawning, when baseline metabolic rates are likely to be greatly increased. It is impossible to know whether declines in abundance and detectability of adult crown-of-thorns starfish from November through January at Big Broadhurst Reef relate to changes in behaviour, their distribution, or survivorship, but these results suggest that research into responses of adult *Acanthaster* spp. to increasing temperatures is warranted, especially given increasing incidence and severity of marine heatwaves.

Comparing across all tagged individuals (n= 50), the overall duration of detections averaged 4.78 days (±1.14 SE) and ranged from 0 to 44 days (Figure 15). This data suggests that crown-of-thorns starfish are amenable to passive acoustic tracking, but far greater sampling will be required to detect occasional long-distant displacements using this method. Passive acoustic tracking might also be used to assess fine-scale movement (e.g., Schlaff et al. 2020), though this study was intentionally designed to test for larger scale (hundreds of metres) movements. However, crown-of-thorns starfish (even if remaining within the detection range of receivers) are only detectable infrequently, which probably coincides with periods that they are out in the open. The time of day at which starfish were detected was greatest between 0400-0700 hours, and lowest in late morning and early evening (Figure 16). If these diel patterns of detections reflect periods of greatest activity, it suggests that movement is greatest at night and escalates from 0000 to 0700 hours, with another period of heightened activity in late afternoon.

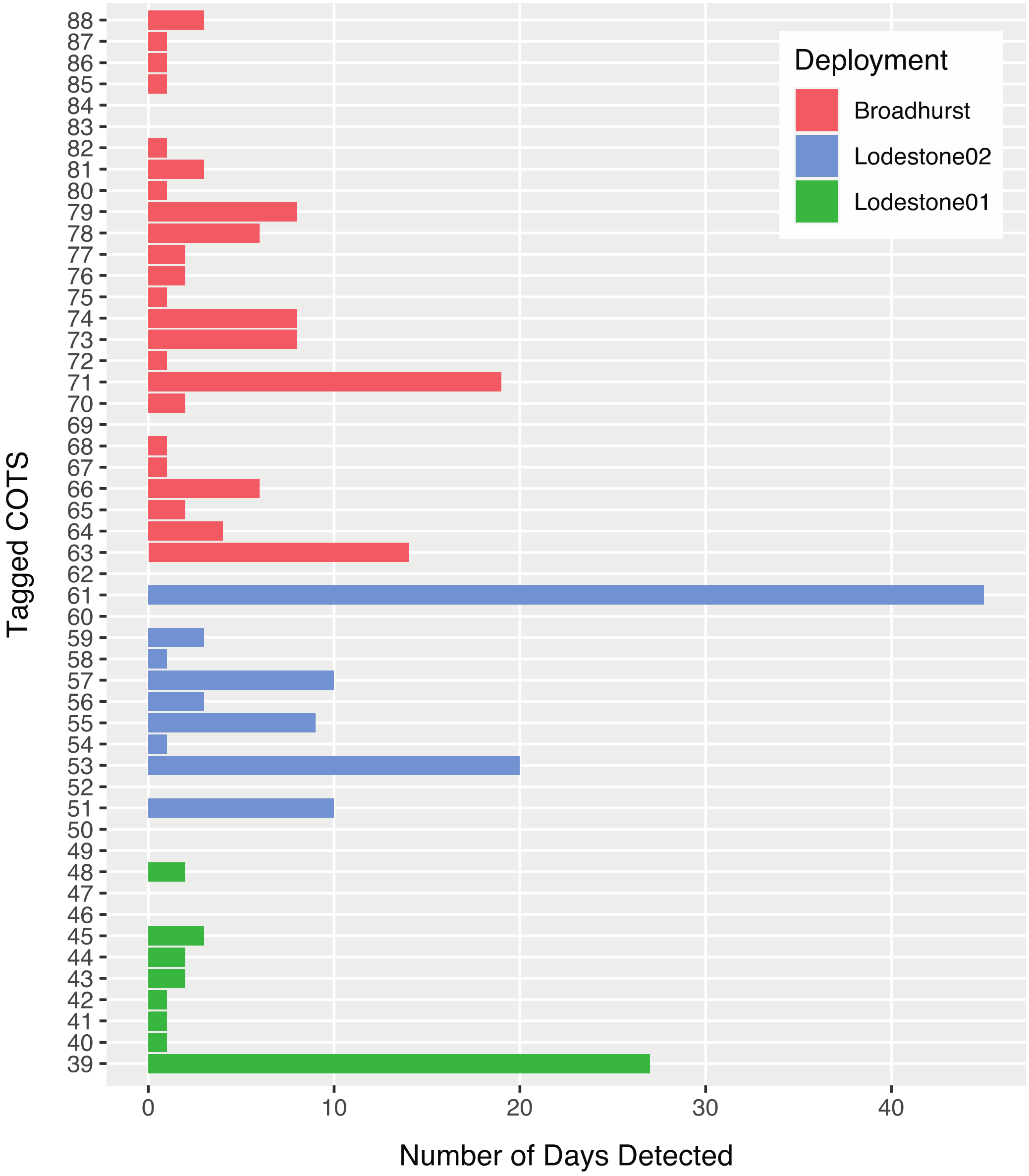

Figure 15: Total duration (in days) of detections for tagged Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) at Lodestone Reef and Big Broadhurst Reef. The lack of any bars indicates that these starfish (10 individuals) were never detected post tagging and release.

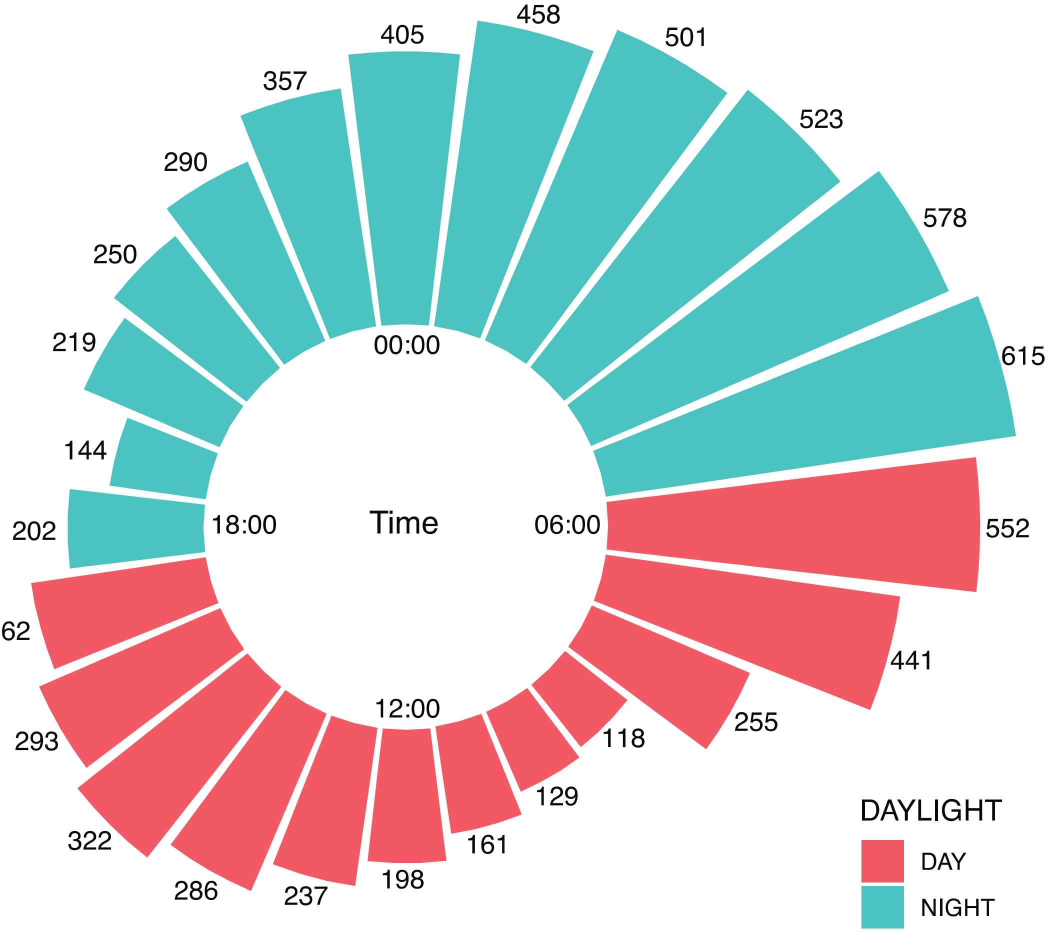

Figure 16: Total number of detections recorded at hourly intervals across all (n=50) Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) tagged (with V7 69KHZ transmitters) at Lodestone Reef and Big Broadhurst Reef in 2019

4.0 RECOMMENDATIONS AND CONCLUSIONS

Information on potential and realised movement by crown-of-thorns starfish is important for optimising spatial and temporal aspects of localised culling and removal activities (e.g., Bos et al. 2013, Fletcher et al. 2020), which is currently the most direct and viable method for managing population irruptions of *Acanthaster* spp. (Pratchett and Cumming 2019). On the GBR, extensive time and effort is invested in preventing coral loss at select locations (mostly high-value tourism locations) through direct culling (Westcott et al. 2016), by injecting individual starfish with bile salts solution (Rivera-Posada et al. 2014) or vinegar (Boström-Einarsson and Rivera-Posada 2016). To be effective and efficient, ecological control programs must be structured at spatial and temporal scales relevant to the scales at which individual organisms move through the landscape (Fletcher and Westcott 2013). Most notably, the rate at which individuals can move from uncontrolled to controlled portions of a reef and the scale of those movements will directly affect the efficacy with which the control program can protect sites of economic importance, and has important ramifications for necessary size of buffers required around areas to be protected, and the frequency revisitations to each site (Fletcher et al. 2015).

While crown-of-thorns starfish are clearly capable of moving across reef landscapes (Chesher 1969), the overwhelming result of this study (and previous studies) is that adult *Acanthaster* spp. generally move very little (Ormond 1970; Ormond and Campbell 1974), especially in habitats with reasonable (if not high) coral cover and thereby, ready access to coral prey within close proximity of sheltering locations. Moreover, we showed that crown-of-thorns starfish often exhibit high fidelity for specific sheltering locations (see also Ling et al. *In review*), returning to the same place to shelter between recurrent feeding bouts, as has been shown for urchins (Flukes et al. 2012; Ling et al. 2016). It is likely therefore, that crown-of-thorns starfish will move as required in response to changes in prey availability, though it remains unclear how far adult starfish can and will move to find viable sources of coral prey. Most critically, the question remains whether adult *Acanthaster* spp. move between reefs. If average rates of movement measured in captivity can be sustained, in combination with strong directionality, displacement distances of crown-of-thorns starfish could range from 150-520 m per day. However, it is unknown how long crown-of-thorns starfish can sustain these rates of movement and the maximum previously reported large-scale displacement of adult starfish is 1km/month (Table 1). Inter-reef movements probably occur only very rarely and contribute little to the overall spread of outbreaks, but are nonetheless very important in terms of structuring management and control actions that can reduce the impact of starfish at local scales (Westcott et al. 2016).

4.1 Future Research

This study has contributed greatly to understanding movement patterns for crown-of-thorns starfish, but has once again highlighted logistic constraints associated with effectively documenting individual plasticity in behaviour at larger temporal and spatial scales (Birkeland and Lucas 1990). While short term tagging and direct sampling provides a viable means to establish fine-scale patterns of movement and diel patterns of behaviour (Burn et al. 2020), at least for individuals that remain in the local area, there remains a considerable knowledge gap pertaining to periodic and large-scale movements of individuals and populations. Even using passive acoustic monitoring at Lodestone and Big Broadhurst reefs, we failed to detect any large-scale movements of individually tagged crown-of-thorns starfish. The mean duration of detections for these starfish (4.78 days ±1.14 SE) was broadly comparable to the temporal extent of sampling achieved using temporary tagging and monitoring (section 2.2), and so it is probably not surprising that we failed to detect instances of large-scale movements. However, it is also unclear why the extent (especially temporal duration) of detections was so limited.

This study does show that crown-of-thorns starfish are amenable to passive acoustic tracking, which provides considerable opportunities to address foremost questions relating to the movement patterns and corresponding impacts of *Acanthaster* spp. in reef environments. Most importantly, this study should be repeated with acoustic receivers placed in a much more concentrated arrangement within the immediate vicinity of where starfish are initially tagged and released (e.g. Schlaff et al. 2020), with secondary receivers placed at increasing distance to detect occasional large-scale movements. The array needs to be maintained long enough to capture changes in behaviour following localised depletion of prey resources. Importantly, receivers should be placed both along and across the reef edge with the explicit aim of detecting starfish that move into deep water or up on to the reef crest. Passive detections on acoustic receivers should also be complemented by direct searches for tagged individuals using hand-held detectors, both to recover transmitters, but also establish the location and fate of tagged crown-of-thorns starfish.

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