Movement dynamics, sediment turnover and sheltering behaviours of the nocturnal coral reef sea cucumber, *Stichopus* cf. *monotuberculatus*

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Abstract Animal movement and feeding studies shed light on ecological roles and can inform management strategies for fished species. However, the feeding and movement of nocturnal sea cucumbers have been rarely studied. We determined the movement dynamics, feeding ecology and sheltering behaviour of the nocturnal *Stichopus* cf. *monotuberculatus* (dragonfish) at One Tree Reef and Heron Island Reef on the southern Great Barrier Reef. The short-term movement of individual sea cucumbers were tracked, and sediment defecation rates were measured. Displacement rates averaged 3–33 cm h^{-1} across the four sites, with the sea cucumbers moving more slowly approaching sunrise and within patches of organically rich sediment. The movement paths were moderately tortuous, with larger sea cucumbers moving along straighter paths. Rates of sediment turnover averaged 7.8 g h^{-1} and were greatest for larger individuals. The faecal casts were organically richer and composed of finer grains than the ambient surface sediments, implying that *S.* cf. *monotuberculatus* avoids consuming coarse sediments and feeds on nutritionally rich particles. The sea cucumbers sheltered under hard reef substrata and moved non-directionally on the seascape, with a few individuals homing back to their original refuges. The affinity to reef substrata and short nightly net displacements of *S.* cf.

monotuberculatus have implications for the spatial management of this and other similar species. Larger individuals occupied deeper refuges, implying that projected declines in substratum rugosity on coral reefs due to climate change could impact the size structure of sea cucumber populations, with implications for fisheries.

Keywords Foraging · Deposit-feeding · Peanut fish · Holothuroid · Homing · Refuging

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Introduction

Animal movement and feeding are key ecological processes that influence the structure and dynamics of ecosystems by providing links to trophic and nutrient-flux hierarchies (Polis et al. 1997). Studies of animal movement and feeding ecology provide insight into their ecological roles (e.g., Navarro et al. 2017; Kristensen et al. 2021) and are important for harvested species to inform conservation and fisheries management (Pittman and McAlpine 2003). Despite their prominence in benthic ecosystems globally, the feeding ecology and movement patterns of many commercially exploited sea cucumbers (holothuroids) are not well understood (Eriksson et al. 2013; Navarro et al. 2014; Wolfe and Byrne 2017).

Deposit-feeding sea cucumbers are ubiquitous on coral reefs, where their sediment bioturbation and feeding behaviours have significant effects on physio-chemical processes (Purcell et al. 2016a). In these oligotrophic systems, holothuroids play a key role in recycling nutrients (Massin 1982; Uthicke 2001b; Purcell et al. 2016a). Deposit-feeding by sea cucumbers also influences local seawater carbonate chemistry, potentially mitigating the effects of anthropogenic ocean acidification at local scales (Schneider et al. 2011, 2013; Wolfe et al. 2018). Further, through their feeding activities,

holothuroids facilitate the regeneration and remineralisation of surface sediments (Purcell et al. 2016a). With some species able to turnover vast quantities of sediment, sea cucumbers play a vital role in maintaining sediment and thereby ecosystem health (Purcell et al. 2016a; Wolfe and Byrne 2017; Williamson et al. 2021).

The overexploitation of sea cucumbers for the luxury dried food commodity 'bêche-de-mer' and the production of pharmaceuticals is a major threat to benthic marine communities (Purcell et al. 2013, 2016a; Wolfe and Byrne 2022). Holothuroids are particularly vulnerable to overfishing due to their life-history traits, ease of collection (Uthicke et al. 2004; Purcell et al. 2010) and high market value (Purcell et al. 2014b). The removal of holothuroids from coral reefs has been linked to the overgrowth of algal mats (Moriarty et al. 1985; Uthicke 1999), sediment anoxia (Lee et al. 2017) and the susceptibility of hard corals to heat-activated pathogens (Grayson et al. 2022). For many species, management strategies are poorly informed due to a lack of fundamental species-specific biological data (Uthicke et al. 2004; Purcell et al. 2013).

Spatial management measures, such as no-take zones and rotational-fishing zone systems, are used to conserve relatively sedentary animals, such as holothuroids (Hastings and Botsford 2003; Uthicke 2004). Spatial protection should ideally be guided by an understanding of species mobility and the likelihood that animals will 'spillover' across reserve boundaries (Grüss et al. 2011; Hernandez-Lamb et al. 2012). Despite being regarded as sedentary, recent studies show that some sea cucumbers are highly mobile at hourly timescales (e.g., Hammond et al. 2020; Gray et al. 2022). In addition, some species exhibit site fidelity and do not displace far in the long-term (Conand 1991; Purcell et al. 2016b; Purcell et al. 2023a; Hammond and Purcell 2023). Due to the difficulties of tagging sea cucumbers (see Purcell et al. 2016b), the movement dynamics of many bêche-de-mer species are unknown (Eriksson et al. 2013; Wolfe and Byrne 2017).

Most animals do not move randomly and instead establish a home range where they undertake routine activities, such as foraging and resting (Quinn and Brodeur 1991). Within this home range, animals often move between distinct resting and feeding sites (e.g., Tuya et al. 2004). A behavioural pattern observed for several sea cucumber species is a diel cycle of diurnal sheltering and nocturnal feeding (Hammond 1982; Mercier et al. 1999). Most sea cucumber movement is associated with foraging, and many species modify their movement to feed selectively on organically rich deposits (Da Silva et al. 1986; Mercier et al. 1999; Navarro et al. 2013). Some holothuroids also feed selectively for grain size (Moriarty 1982; Uthicke 1999), while others show no preference (Uthicke and Karez 1999).

Among marine species, larger individuals tend to displace further than smaller ones (Quinn and Brodeur 1991; Allen et al. 2018), although there are exceptions (e.g., Purcell et al. 2023a). Movement behaviour can also vary among conspecifics, with some individuals exhibiting long-term site fidelity while others disperse large distances (e.g., Purcell et al. 2016b; Hammond and Purcell 2023). Refuge quality might influence movement patterns of species with diel migration between shelters and foraging grounds (Hammond 1982; Graham and Battaglene 2004).

Refuges, or shelters, are structural microhabitats individuals utilise to decrease their exposure to predators, sunlight, and unfavourable environmental conditions (Forsythe et al. 2003; Ménard et al. 2008). Marine species often occupy shelters that closely correspond to their size (Forsythe et al. 2003; Booth and Ayers 2005). Such relationships are often related to the variable protective capacity of refuges across body sizes (Eggleston et al. 1990). For some marine invertebrates, the quality and abundance of available shelters may influence population size and structure (Eggleston et al. 1990; Beck 1995). With reef substratum rugosity projected to decline due to the impacts of climate change (Rogers et al. 2014), understanding refuge selection can provide insight into the challenges facing species in a changing ocean (e.g., Fontoura et al. 2020).

The Stichopodidae is a diverse holothuroid family, with several species commercially exploited in wild fisheries and aquaculture (Byrne et al. 2010; Woo et al. 2019; Cheng et al. 2021). Across the Indo-Pacific the *Stichopus* cf. *monotuberculatus* species complex is harvested with the identity of the Pacific species uncertain, due to the inability to compare with specimens from the type locality in the Western Indian Ocean (Mauritius) (see Byrne et al. 2010). *Stichopus* cf. *monotuberculatus* is often misidentified in fishery data as the morphologically similar *S. horrens* and both are commonly known as dragonfish (Eriksson et al. 2007; Byrne et al. 2010). Hence, *S.* cf. *monotuberculatus* is probably more exploited than reported. Several recent studies have emerged on the potential for commercial mariculture and sea ranching of this species. One found high growth rates of the sea cucumbers on artificial reefs, with animals feeding on sediment detritus containing food sources such as microbes, algal debris and phytoplankton (Xu et al. 2022). In tanks, this species was more active at higher seawater temperatures and tends to move down-current in simulated flow experiments (Chen et al. 2022). Further, a recent study determined the morphometric relationships of S. cf. monotuberculatus to generate biomass estimates for fisheries stock assessments (Gray et al. 2023). Apart from it's nocturnal nature and being found sheltering in reef infrastructure during the day (Purcell et al. 2023), the ecology of this species in natural habitats is practically undocumented. This cryptic behavioural pattern has likely contributed to our limited ecological knowledge of this species and other nocturnal coral reef holothuroids.

Here, we investigated the short-term movement patterns and sediment turnover of *S.* cf. *monotuberculatus*. Our objectives were to: (1) determine trends in the displacement and directionality of individuals movement paths, (2) quantify sediment turnover and whether the species feeds selectively with respect to grain size and organic content, and (3) investigate sheltering behaviour, and whether *S.* cf. *monotuberculatus* occupies certain refuge types. The variable and distinctive colour patterns among individual *S.* cf. *monotuberculatus* provided an opportunity to use photographic records to validate individuals with temporally repeated observations. Fieldwork was undertaken at two reefs in the southern Great Barrier Reef, Australia, at localities where the species occurs in high densities. Our findings provide essential data on the movement dynamics of *S.* cf. *monotuberculatus* to inform spatial management measures, while shedding light on the species' ecological roles. These data broaden our understanding of the movement and feeding ecology of sea cucumbers and furnish a rare view of movement patterns in nocturnal reef invertebrates.

Materials and methods

Study sites

Fieldwork was undertaken at One Tree Reef (23.51° S, 152.09° E; OTR) and Heron Island Reef (23.44° S, 151.92° E; HIR) in the Capricorn Bunker Group, southern Great Barrier Reef in April–May 2022 (Fig. 1a). The study sites at OTR are located in the Great Barrier Reef Marine Park Authority Scientific Research Zone, and in the Green Zone (Marine National Park) at HIR. Both locations, One Tree Reef and Heron Island Reef, have a near-continuous rim around the reef that ponds seawater at low tide. Coral communities are diverse and there are extensive areas of soft sediments interspersed among the hard reef structures at both locations (Eriksson et al. 2013; Wolfe and Byrne 2017). Mean daily seawater temperatures in 2022 ranged 19.7–28.2 °C and diel seawater temperatures were similar between locations, ranging 23.4–26.2 °C (AIMS 2023).

Sites with sufficient populations of *S.* cf. *monotuberculatus* were identified by reconnaissance on the nights prior to monitoring. At OTR, two sites were identified in the lagoon, along the edge of a small patch reef at the channel entrance to the One Tree Island Research Station (Fig. 1b). Both sites are shallow (< 1 m deep at low tide) and are separated by approximately 30 m. At HIR, the southern (Site 1, ≤ 1.5 m corrected to zero tidal datum) and northern (Site 2, ≤ 1.7 m) sides of the HIR boat channel served as respective sites (Fig. 1c). These sites are approximately 50 m from each other and are bordered by concrete walls, which extend into the reef flat.
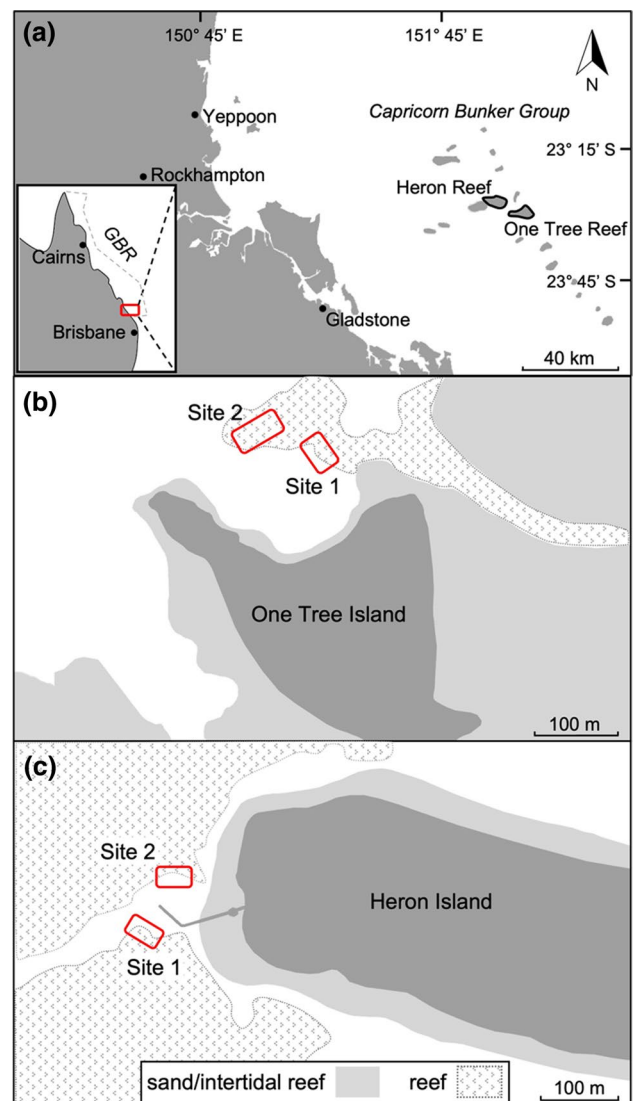

Fig. 1 **a** Location of One Tree Reef and Heron Island Reef in the Capricorn Bunker Group, southern Great Barrier Reef, Australia, and study sites located at **b** One Tree Reef, and **c** Heron Island Reef. Map source: Google Maps

Field data collection

The *S.* cf. *monotuberculatus* were located on snorkel using dive torches by searching sand, reef, and rubble habitat within the study areas. Due to their high densities at the study sites, individuals were selected for monitoring based on their distinct identifiable colour patterns (Fig. 2). Once an individual was identified, the time of each initial observation, body colour and markings were recorded. Where possible, the refuges that individuals emerged from were identified and marked with a weight and float. Simultaneously, a numbered peg with flagging tape was placed 1 cm behind the anus of each individual. Every 2–3 h from sunset to sunrise, we located the sea cucumbers and recorded

Fig. 2 The highly variable and individually distinctive colour patterns of *Stichopus* cf. *monotuberculatus*. Examples of individuals examined in the present study with various colour patterns, used to aid in verification of individuals over the observation periods. These photographs were all taken at night during the study. Photos: SW Purcell

their linear displacement (± 1 cm) from the peg to the posterior end of the sea cucumber with a measuring tape and compass bearing ($\pm 5°$ degrees from north) with a wrist-mounted dive compass. The times of all observations were recorded before the pegs were placed behind the animals. This process occurred at each observation period, making it relatively easy to locate the individuals.

To ensure that the same individuals were tracked throughout the night, we photographed each individual at the start and end of the night, and later confirmed their identity by inspection of the photographs. We referred to these initial photographs throughout the night, as needed. During the second observation period ($\sim$23:15–02:00), we measured each individual's body length and width (at midpoint; ± 0.5 cm) in situ with a ruler. Care was taken not to touch or disturb the sea cucumbers as this could influence movement rates (see Pan et al. 2015).

During the third observation period ($\sim$02:00), all faecal casts between the individuals and their respective pegs were gently scooped into labelled 70-ml vials using a tablespoon. The time that the samples were taken was recorded to later calculate defecation rates, which serve as a proxy for sediment reworking (Hammond 1982; Uthicke 1999). Faecal casts were only collected when we could be sure they were from the monitored individual (i.e., casts were not collected when multiple sea cucumbers paths crossed). Surface sediment samples ($\sim$30 ml) were also collected from the surrounding sediment 30–40 cm either side of each individual for which faecal casts were collected. The upper $\sim$3 mm of sediments were sampled as

above, approximating the depth to which sea cucumbers feed (Yingst 1982).

To determine if *S.* cf. *monotuberculatus* exhibited preferences for particular types of refuges, we recorded into broad benthic categories the type of refuge where animals had emerged at the start of the evening or, when that was not possible (HIR Site 2), at the end of the night. To examine selectivity for shelter size, we measured the refuge entrance width (± 0.5 cm; at the base of the refuge), refuge height at midpoint, and depth (i.e., how far laterally into the reef structure could a ruler be inserted). Animals were considered to be refuging if they were observed atleast partially sheltering within/under substrate at the time of encounter.

Sediment processing

In the laboratory, the seawater with each sample of faecal cast and ambient surface sediments was decanted on the day following collection and samples were rinsed with tap water three times to remove the majority of salts (3-h settling time between rinses; Purcell 1996). Samples were dried in an oven at 60 °C to constant weight before being standardised through a 2000-μm sieve (Tebbett et al. 2022) and weighed to the nearest 0.001 g using an electronic analytical balance. The dry weight of faecal cast samples was used as a proxy for the amount of sediment reworked (Hammond 1982). A standard bleaching procedure (see Tebbett et al. 2022) with minor modification was used to quantify the percentage of organic and inorganic material in the samples. Hydrogen peroxide (30%) was added slowly to the samples over ten

days until no new bubbles formed (Schumacher 2002). The fluid was decanted from the sample vials, and the samples were then dried and weighed as before to determine the inorganic particulate mass. The grain size composition of samples was quantified by dry sieving through a sieve stack (1000, 500, 250, 125, 63-μm) for 2 min (Purcell 1996, 2000). The sediment retained in each fraction was weighed to calculate the percentage grain size composition.

Mathematical procedures

Sea cucumber displacement rates (cm h^{-1}) and turning angles (°) for each observation period were derived from the raw movement data. Displacement rates were calculated by dividing linear displacement (cm) between successive movement steps by the time (hours) within the given observation period. Turning angles were calculated by subtracting the compass bearing for the previous observation period from the bearing for the subsequent observation period. Movement steps were assumed to follow a straight path, likely underestimating displacement and tortuosity (Turchin et al. 1991; Estevez and Christman 2006). The sea cucumbers movement paths were plotted using trigonometry in SigmaPlot V14, and individuals' net (Euclidian) displacements throughout the 12-h monitoring periods were calculated. The mean cosine and sine of turn angles furnished further metrics used in other movement studies.

Angular dispersion (AD) was used as a proxy for the tortuosity of sea cucumbers movement paths, i.e., the degree to which a movement path differs from a straight line (Batschelet 1981; Fisher 1995). This parameter ranges from 0 (high tortuosity) to 1 (straight line movement; Fisher 1995; Miller et al. 2011) and was calculated for individual movement paths, as per the below equation:

$$AD = n^{-1}\sqrt{C^2 + S^2}$$

where n is the number of moves (i.e., trajectories) in the movement path, and the constants C and S are the sum of all respective cosines and sines of turning angles.

The geometric mean grain size and sorting of the faecal cast and surrounding surface sediment samples were determined from the percentage grain size composition using GRADISTAT V8.0 (Blott and Pye 2001). All unspecified sediments (< 63 μm) were assumed to be > 1 μm.

Statistical analyses

The average hourly displacement rate (cm h^{-1}) and tortuosity (AD) data were analysed by a two-factor mixed-model permutational analysis of covariance (PERMANCOVA)

in PRIMER v7 based on Euclidean distances (similarity) (Anderson et al. 2008). The two reef systems, One Tree Reef and Heron Island Reef, are separated by 7 km and were considered 'Locations', with the two sites within each Location about 30–50 m apart. Location (OTR and HIR) was treated as a fixed factor; site was considered as a random factor, nested within the Location; and sea cucumber body length (cm) was the covariate. Individual sea cucumbers were considered as replicates ($n = 41$). A one-way PERMANCOVA analysed defecation rates of the sea cucumbers from the three study sites with the same design structure ($n = 18$). This second analysis did not include the data from HIR Site 2, as only a single faecal cast sample could be collected from this site. Datasets were Z-score normalised prior to analyses (Anderson et al. 2008) and PERMANCOVAs were tested under the reduced model using 9999 permutations, with Type I sequential sum-of-squares. The assumption of homogeneity of variance was met for all datasets.

To compare the granulometric characteristics of faecal casts ($n = 19$) and surface sediments ($n = 19$), data from all sites were combined. Granulometric parameters (% organic matter, mean grain size and sorting) and percentage grain size fractions (> 1000 & > 500; > 250 & > 125; > 63 & < 63 μm) were compared using separate Paired Samples t-Tests using IBM SPSS statistics v.28 software (IBM Corp 2021). Granulometric parameters were $\log_{10}$ transformed, and percentage grain size fractions were arcsine transformed prior to analyses to improve normality. Wilk–Shapiro tests confirmed that each dataset followed a normal distribution. For all tests, $\alpha = 0.05$.

To determine whether sediment organic content influenced movement and sediment turnover, separate nonlinear regression analyses were used to test the potential relationships between sediment organic content (% dry wt.) and (a) displacement rate (cm h^{-1}) and (b) defecation rates (g h^{-1}). Although the PERMANCOVA analyses applied the covariate linearly, body size may have influenced response variables in a curvilinear fashion that warranted further examination. Hence, nonlinear regressions were also run for the following variable pairs: sea cucumber body length (cm) and (a) average displacement rate, (b) tortuosity (AD), (c) defecation rates, and (d) refuge dimensions (width, height, and depth; cm). All analyses were undertaken using DataFit v9 software (Oakdale Engineering 2009). Data from the third observation period were used for all equations concerning surface sediment organic content. For all relationships, the goodness of fit was compared across the 298 equation forms available in the software, and the 2-parameter models with the highest r-squared value were identified in order to avoid overfitting with polynomial models. Only statistically significant relationships ($P \leq 0.05$) are graphed.

Results

Displacement

Displacement rates of individual *Stichopus* cf. *monotuberculatus* over the 12-h monitoring periods were variable, ranging from 7 to 46 cm h^{-1}. Across all sites, movement rates averaged 22 cm h^{-1} (± 1.3 SE, $n = 41$; Fig. 3a), and these did not vary between Locations ($F_{1,36} = 0.857$, $P = 0.631$; Table S1) but did differ at the scale of sites within Locations ($F_{2,36} = 3.963$, $P = 0.028$). Since site was a random factor, the sampling design presents no grounds for post-hoc testing here, although the differences are apparent in Fig. 3a.

The diurnal trends in displacement rates varied among individuals, sites, and observation periods (Fig. 3b). Nonetheless, at OTR Site 2 and HIR Site 2, the sea cucumbers displaced less from 04:30 to 06:45 relative to all other observation periods. These lower displacement rates coincided with our observations of individuals beginning to shelter before sunrise (Fig. 3c). Comparatively, at OTR Site 1 and HIR Site 1, displacement rates were somewhat variable across all observation periods, despite the sea cucumbers refuging at similar times.

Larger *S.* cf. *monotuberculatus* tended to displace more compared to smaller individuals, but this relationship was non-significant ($r^2 = 0.06$, $F_{1,36} = 2.12$, $P = 0.15$; Table S2). Further, the sea cucumbers moved faster where the organic content in the sediment was lowest ($r^2 = 0.53$, $F_{1,17} = 18.94$, $P < 0.001$; Fig. S1, Table S3).

Movement paths and tortuosity

The length of moves and turning angles of *S.* cf. *monotuberculatus* movement paths were variable among individuals (Fig. S2). Across the study sites, individuals displaced an average net distance of 178.5 cm (± 29.5 SE, $n = 36$) from their origin points. After emerging from their refuges, the sea cucumbers were observed feeding on sandy areas in close proximity to patches of live coral, rubble, and boulders. *Stichopus* cf. *monotuberculatus* appeared to forage with low directional persistence, regularly reversing their direction of travel before sheltering in reef structures in the early morning.

The sea cucumbers movement paths were moderately tortuous (Fig. 4a), with the direction of travel seeming unrelated to previous movement steps. The tortuosity of movement paths did not differ between OTR and HIR ($F_{1,34} = 0.03$, $P = 0.838$; Table S4) but differed among sites within Locations ($F_{2,34} = 5.35$, $P = 0.01$). Smaller sea cucumbers exhibited more tortuous movement paths than larger individuals ($r^2 = 0.10$, $F_{1,37} = 4.15$, $P = 0.049$; Fig. 4b; Table S5).
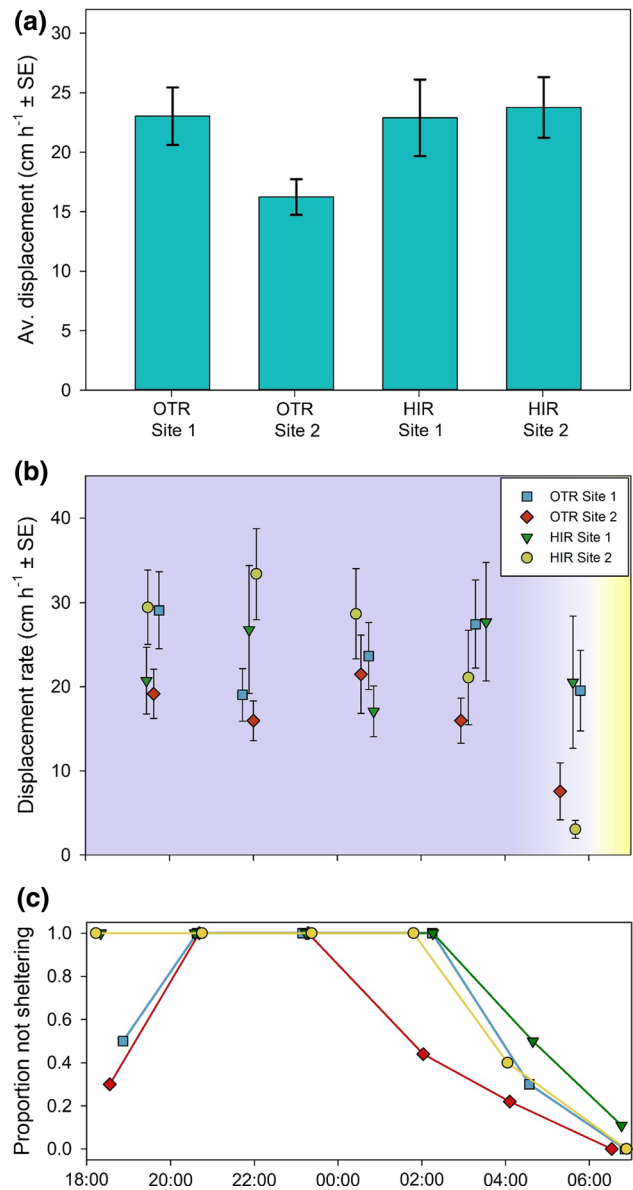
Fig. 3 a Average displacement rates (cm h^{-1} $\pm$ SE) of *Stichopus* cf. *monotuberculatus* across all observation periods at One Tree Reef (OTR) Sites 1 and 2, and Heron Island Reef (HIR) Sites 1 and 2. **b** Average displacement rates ($\pm$ SE) throughout observation periods. Data are plotted at the midpoint of observation periods; purple shading represents night-time and yellow represents daytime the following morning. **c** Proportion of sea cucumbers not sheltering. Data are plotted at the midpoint of observation periods. $n = 10$ at OTR Site 1; $n = 9$ at OTR Site 2; $n = 11$ at HIR Site 1 and 2

Feeding and sediment turnover

Sediment defecation rates of *S.* cf. *monotuberculatus* across all sites averaged 7.8 g h^{-1} (± 1 SE, $n = 19$), ranging from 1.2 to 16.1 g h^{-1} and were similar among sites ($F_{2,14} = 0.271$, $P = 0.763$; Fig. 5a; Table S6). Relative to their body size, larger sea cucumbers defecated greater volumes of sediment
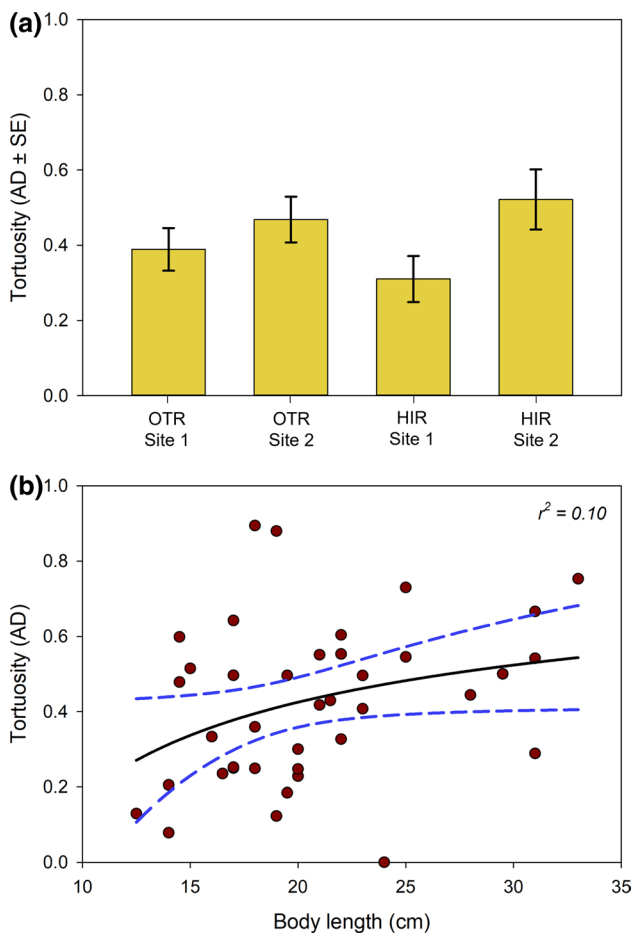
Fig. 4 a Average tortuosity (AD±SE) of *Stichopus* cf. *monotuberculatus* movement paths at One Tree Reef (OTR) Sites 1 and 2, and Heron Island Reef (HIR) Sites 1 and 2. Only paths with ≥ 3 movement steps are included. $n = 10$ at OTR Site 1, HIR Site 1 and 2; $n = 9$ at OTR Site 2. **b** Nonlinear relationship between body length x (cm) and tortuosity y (AD) for *S.* cf. *monotuberculatus* at the four study sites; $n = 39$. Black solid line is the fitted equation $y = 1.255 - 2.486/\ln(x)$; blue dashed lines are 95% CIs

Fig. 5 a Average defecation rate (g h^{-1}±SE) of *Stichopus* cf. *monotuberculatus* at One Tree Reef (OTR) Sites 1 and 2, and Heron Island Reef (HIR) Sites 1 and 2. $n = 6$ at OTR Sites 1 and 2 and HIR Site 1; $n = 1$ at HIR Site 2. **b** nonlinear relationship between body length x (cm) and defecation rate y (g h^{-1}) at the four sites ($n = 19$). Black solid line is the fitted equation $y = 2.711 + 0.002x^{2.5}$; blue dashed lines are 95% CIs

than smaller ones ($r^2 = 0.33$, $F_{1,16} = 7.74$, $P = 0.013$; Fig. 5b; Table S7). The availability of organic matter in the surrounding surface sediments had little effect on defecation rates ($r^2 = 0.09$, $F_{1,17} = 1.75$, $P = 0.204$).

The faecal cast samples contained a significantly greater proportion of very fine sand and silt ($t_{18} = 3.99$, $P < 0.001$) and coarse sand ($t_{18} = 4.16$, $P < 0.001$) than what was available in the surrounding surface sediments (Fig. 6; Table S8). There was no significant difference in the proportion of medium and fine sand between the faecal casts and the ambient ($t_{18} = 0.99$, $P = 0.337$). Defecated sediments had a finer mean grain size ($t_{18} = 5.22$, $P < 0.001$) and were more well-sorted ($t_{18} = 2.42$, $P = 0.026$) relative to the ambient surface sediments. The faecal cast samples had a significantly higher organic content than the samples of surrounding sediments ($t_{18} = 5.32$, $P < 0.001$).
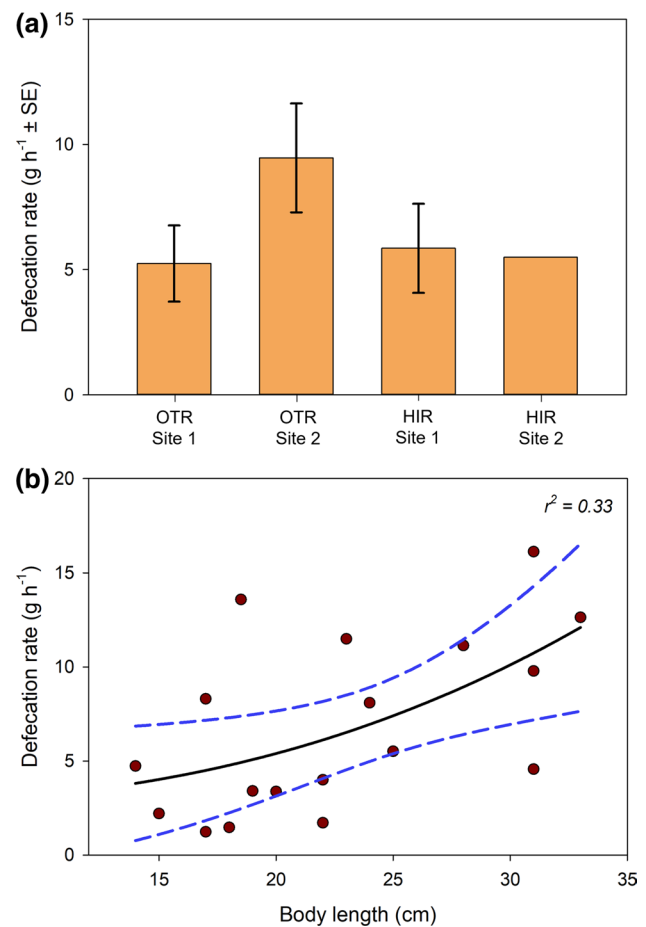
Refuging and homing behaviours

The dimensions (height, width, and depth) and microhabitat types of refuges that *S.* cf. *monotuberculatus* occupied varied among the study sites, largely due to differences in local habitat structure (Table S9; Fig. S3). At OTR, most of the sea cucumbers emerged from and returned to shelters under live *Isopora* sp. colonies, where they were present in the habitat. At HIR, *Isopora* sp. was not common, and most of the *S.* cf. *monotuberculatus* sheltered under coral rubble and in rocky crevices. Individuals that homed back to their shelters (i.e., exhibited refuge fidelity) tended to occupy relatively narrower live coral shelters compared to those that did not 'home'.

Larger *S.* cf. *monotuberculatus* tended to occupy deeper refuges (i.e., lateral intrusion into reef structures) relative to smaller individuals ($r^2 = 0.23$, $F_{1,21} = 6.23$, $P = 0.021$; Fig. 7;
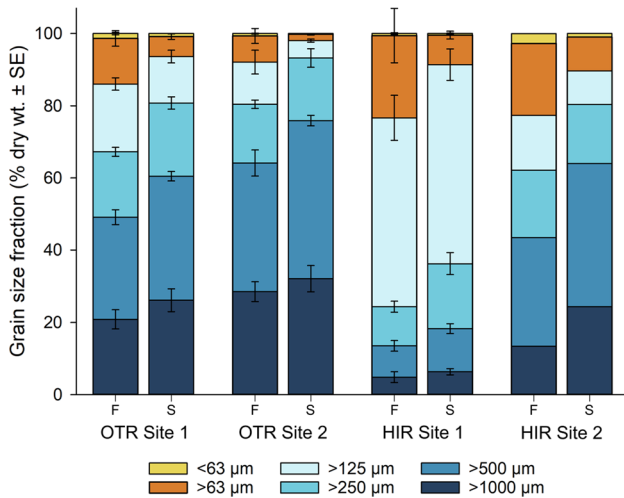
Fig. 6 Average (± SE) percentage grain size fractions (dry wt.) of *Stichopus* cf. *monotuberculatus* faecal casts (F) and surrounding sediments (S) at One Tree Reef (OTR) Sites 1 and 2, and Heron Island Reef (HIR) Sites 1 and 2. $n = 6$ at OTR Sites 1 & 2, and HIR Site 1, $n = 1$ at HIR Site 2
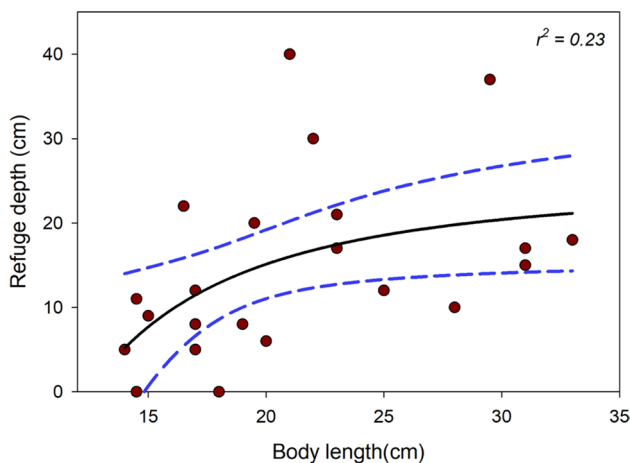

Fig. 7 Nonlinear relationship between *Stichopus* cf. *monotuberculatus* body length x (cm) and refuge depth y (cm) at the four sites ($n = 23$). Black solid line is the fitted equation $y = 24.661 - 3816.85/x^2$; blue dashed lines are 95% CIs

Table S10). However, there was no relationship between animal body length and refuge height ($r^2 = 0.03$, $F_{1,21} = 0.64$, $P = 0.43$) or body width and refuge width ($r^2 = 0.02$, $F_{1,21} = 0.4$, $P = 0.53$).

Discussion

In one of the few studies of a nocturnal sea cucumber (see Hammond 1982; Navarro et al. 2013), we successfully tracked the movement and determined sediment turnover

by individual *Stichopus* cf. *monotuberculatus* over short temporal scales. Such studies are rare for nocturnal species due to the challenges of working intermittently throughout the night. The variable and distinctive colour patterns of *S.* cf. *monotuberculatus* proved to be a useful trait for tracking individuals over short temporal scales and could also be applied to other nocturnal holothuroids (e.g., *Stichopus horrens*). Our study shows that *S.* cf. *monotuberculatus* exhibits a distinct diel pattern of diurnal sheltering and nocturnal foraging. Our observations of nocturnal activity in natural habitats concur with studies in captivity (Chen et al. 2022) and on artificial reefs (Xu et al. 2022), implying that future population assessments of *S.* cf. *monotuberculatus* would best be undertaken approximately one hour after sunset when most of the animals have emerged. The movement and feeding data presented here help to characterise the functional role of *S.* cf. *monotuberculatus*. This is also the first study to collect data on the refuge sizes and types occupied by sea cucumbers, providing valuable insight into their sheltering behaviours.

Movement and foraging patterns

Our tracking data indicate that *S.* cf. *monotuberculatus* displaces relatively small net distances, undertaking short diel foraging migrations around nearby reef shelters. Hence, movement is likely constrained by the spatial arrangement of refuges, with individuals unlikely to disperse large distances over unbounded habitats. The average hourly displacement rate determined (22 cm h^{-1}) is comparable to that for *S. chloronotus* (24 cm h^{-1}; Uthicke 2001b), which has a similar body size. Our data suggest that *S.* cf. *monotuberculatus* populations may be relatively well protected by spatial management measures that are sized similarly to those implemented for other small- to medium-bodied holothuroids. Determining whether the species exhibits long-term site fidelity would have important implications for gauging the potential spillover of this and other similar species into adjacent fishing grounds (see Grüss et al. 2011). However, assessing the movement patterns of *S.* cf. *monotuberculatus* over longer periods is difficult due to asexual reproduction through fission (Uthicke 2001a).

There was no obvious peak in movement rates of the *S.* cf. *monotuberculatus* over the night. This finding contrasts with other nocturnal holothuroids, such as *Actinopyga mauritiana,* which tend to displace further in the middle of the night (Graham and Battaglene 2004), and *Holothuria sanctori* that 'rush' before sunrise in search of refuges (Navarro et al. 2013). As for the closely related cryptic holothuroid *Stichopus horrens* (Palomar-Abesamis et al. 2018), the underlying cue for emergence in *S.* cf. *monotuberculatus* is likely to be light intensity. Thus, the activity patterns of these species are likely to vary seasonally and geographically.

While there is a general trend among marine species for larger individuals to be more mobile than smaller ones (Quinn and Brodeur 1991; Allen et al. 2018), movement rates of *S*. cf. *monotuberculatus* were comparable across body sizes. We posit that increased body size of *S*. cf. *monotuberculatus* enhances mobility by allowing larger individuals to displace directly over reef features, resulting in more linear movement paths. This coincides with our observations of large individuals climbing across the top of corals and boulders. Typically, smaller animals are more impeded by rugose substrata and require more tortuous paths to navigate their surroundings (Prevedello et al. 2010; Mancinelli and Pasquali 2016). The relationship between tortuosity and body size suggests that the more linear movement of larger individuals might translate to weaker fidelity to specific refuges and better chances of accessing foraging areas further from reef structures. More linear paths of larger individuals might also increase their chances of spilling over from within marine reserves into adjacent fishing grounds, although movement distances in this study were still rather short.

Feeding and ecological roles

The average hourly sediment reworking rate of *S*. cf. *monotuberculatus* (7.8 g h^{-1}) is comparable to that of other stichopodids, such as *S. chloronotus* (11.5 g h^{-1}; Uthicke 1999) and *Isostichopus badionotus* (2.8–4.9 g h^{-1}; Hammond 1982); but lower than for larger-bodied species, such as *S. herrmanni* at the same locality (11.7–28.6 g h^{-1}; Wolfe and Byrne 2017) and *Thelenota anax* (34 g h^{-1}; Hammond et al. 2020). It appeared that *S*. cf. *monotuberculatus* exhibited a 10-h daily feeding cycle. We estimate that each individual reworks on average 28.5 kg of surface sediment each year, although this turnover rate is likely moderated by seasonal variations in feeding activity (see Wolfe and Byrne 2017). As shown for other sea cucumbers that occur at high densities on unfished reefs (Uthicke 2001a; Williamson et al. 2021; Grayson et al. 2022), deposit-feeding by *S*. cf. *monotuberculatus* is likely to strongly influence the sediment biome in coral reef ecosystems.

Based on the model which explains defecation rates as a function of *S*. cf. *monotuberculatus* body size, we can predict that an individual 15 cm long processes 4.5 g sediment h^{-1}, while one 30 cm long processes 12.6 g h^{-1}. This exponential relationship suggests that removing large individuals through fishing may disproportionately impact ecosystem function. Further, this means that larger animals would be more efficient at remediating waste from integrated aquaculture due to the greater rates of sediment turnover.

While compensatory feeding on patches of lower organic content is reported for some holothuroids (e.g., Yingst 1982; Hammond et al. 2020), sediment organic content did not noticeably influence sediment turnover of *S*. cf. *monotuberculatus*. The variation in sediment processing rates among the reef sites highlights the need for further studies to identify factors influencing sediment turnover by holothuroids, as this will have implications for sediment health and benthic productivity, and for predictions about their influence in aquaculture settings.

Stichopus cf. *monotuberculatus* selectively ingests finer-grained particles (< 63–250 μm) and avoids ingesting coarser grains (≥ 500 μm), as found for other deposit-feeding sea cucumbers (review by Pierrat et al. 2022). This feeding selectivity may be influenced by the higher availability of organic content of smaller sediment size fractions (Jones and Jordan 1979). This finding highlights the need to supply fine sediments for pond culture and to select sites with fine granulometry for sea ranching. Moreover, by partially digesting and reconcentrating organic matter into faecal casts, *S*. cf. *monotuberculatus* is likely to provide an enriched substrate for bacterial remineralisation, as shown for other holothuroids (MacTavish et al. 2012; Purcell et al. 2016a).

Refuging and homing behaviours

Despite utilising a broad range of refuge types, our data suggest that *S*. cf. *monotuberculatus* occupied shelters non-randomly, with larger individuals inhabiting deeper refuges. Similar size relationships have been established for various crustaceans (e.g., Forsythe et al. 2003; Booth and Ayers 2005) and are related to the variable protective capacity of refuges across body sizes (Eggleston et al. 1990). With the projected decrease in reef substratum rugosity resulting from anthropogenically driven climate change (Rogers et al. 2014), our data suggest that reduced availability of suitably sized refuges might impact population size and structure of refuging sea cucumbers, such as *S*. cf. *monotuberculatus*.

Understanding the spatial distribution and demography of sea cucumber populations and the factors that influence their use of refuges is important for stock assessment and management (Félix et al. 2021; Azevedo e Silva et al. 2023). Homing *S*. cf. *monotuberculatus* (at OTR Site 2) tended to occupy relatively narrower shelters, suggesting shelter 'quality' may have influenced refuge fidelity. Hammond (1982) observed a similar behaviour for *Holothuria thomasi*, suggesting that shelters with close access to large sand patches were preferred. These observations could be incorporated into sea ranching of sea cucumbers, where provision of artificial structures with narrow openings are used to promote site fidelity, with shelter depth tailored to the size of animals being grown (Hu et al. 2021; Tian et al. 2023).

Conclusion

Here, we have shown that *S.* cf. *monotuberculatus* turns over similar volumes of sediments to that determined for diurnal sea cucumbers. Thus, often overlooked nocturnal sea cucumbers may fulfil similar ecological roles to diurnally active species. Overharvest of *S.* cf. *monotuberculatus* and other nocturnal holothuroids would lead to diminished sediment turnover on coral reef systems. Overall, the sea cucumbers displaced short net distances, with movement largely confined to foraging around reef substrata. Individuals of this species are unlikely to disperse large distances over open sandy habitats, and hence, spatial protection measures may be an effective tool for conserving *S.* cf. *monotuberculatus* populations. *Stichopus* cf. *monotuberculatus* appears to utilise available hard substrate for shelter, with the size of individuals governing refuge selection within the reef structures. This correlation between body size and reef refuge depth provides insight into factors that drive patterns of holothuroid sheltering. Finally, projected declines in reef structural complexity have implications for sea cucumber populations and their fisheries in a changing ocean.

Author contributions All authors contributed to study conception, design and fieldwork. Data analysis were performed by BCTG and SWP. The first draft of the manuscript was written by BCTG and all authors contributed to and approved the final manuscript.

Data availability The datasets generated and analysed in this study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare that they have no relevant financial or non-financial interests to disclose.

Ethical approval This is an observation study. Southern Cross University has confirmed that no ethics approval is required. Permission to undertake research was granted under GBRMPA permit no. G22/46746.1.

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