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REPORT

Biology and ecology of the vulnerable holothuroid, *Stichopus herrmanni*, on a high-latitude coral reef on the Great Barrier Reef

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Abstract Tropical aspidochirotid holothuroids are among the largest coral reef invertebrates, but gaps remain in our understanding of their ecological roles in lagoon sediment habitats, a vast component of coral-reef ecosystems. *Stichopus herrmanni*, listed as vulnerable (IUCN), is currently a major fishery species on the Great Barrier Reef (GBR) and throughout the Indo-Pacific. It is critical to characterise how this species interacts with its environment to understand how its removal may impact ecosystem functionality. We investigated seasonal variation in movement, bioturbation, feeding and gonad development of *S. herrmanni* over 3 yr at One Tree Reef, which has been a no-take area for decades. We determined the direct influence of the deposit-feeding activity of *S. herrmanni* on sediment turnover and granulometry, and on the abundance of infauna and benthic productivity in a comprehensive in situ analysis of tropical holothuroid feeding ecology. This species is highly mobile with identifiable individuals exhibiting site fidelity over 3 yr. With the potential to turn over an estimated 64–250 kg individual^{-1} yr^{-1}, *S. herrmanni* is a major bioturbator. *Stichopus herrmanni* is a generalist feeder and influences trophic interactions by altering the abundance of infauna and microalgae. *Stichopus herrmanni* exhibited decreased feeding activity and gonad development in winter, the first documentation of a seasonal disparity in the bioturbation activity of a tropical holothuroid. Sediment digestion and dissolution by *S. herrmanni* has the potential to influence seawater chemistry, a particularly important feature in a changing ocean. Our results provide essential baseline data on the functional roles of this ecologically important species to inform development of ecosystem-based bêche-de-mer fisheries management on the GBR.

Keywords Sea cucumber · Curryfish · Sediment · Bioturbation · Bêche-de-mer

Introduction

Despite their prominence in benthic sediment systems, gaps remain in our understanding of the feeding biology and trophic ecology of aspidochirotid sea cucumbers (Holothuroidea). Aspidochirotids are epibenthic deposit feeders that ingest sediment and associated organic matter using specialised feeding tentacles (Roberts 1979; Roberts et al. 2000; Purcell et al. 2016a). They can process large amounts of sediment in association with their feeding activity, and so have been called the earthworms of the sea (Bonham and Held 1963; Purcell et al. 2016a). Active selective foraging by size and/or organic content of sediment particles has been reported for shallow-water (Yingst 1976; Uthicke 1999; Slater and Carton 2010; Slater and Jeffs 2010; MacTavish et al. 2012; Navarro et al. 2013) and deep-sea (Roberts et al. 2000; Hudson et al. 2005) species. Questions remain on the details of the diet of aspidochirotids, how they influence their environment through their

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feeding and bioturbation, and whether they are selective or non-selective feeders with respect to sediment grain size and/or nutrient profiles (Hammond 1982; Klinger and Johnson 1998; Roberts et al. 2000).

Many aspidochirotids are commercially valuable (Conand 1998, 2001; Purcell et al. 2012, 2014), harvested to generate the dried body wall product called bêche-de-mer (or trepang). This high-value product is traded in the Asian market and provides a source of income and food to millions worldwide (Purcell et al. 2013, 2014; Eriksson and Clarke 2015). Due to their ease of collection, holothuroids are particularly vulnerable to overfishing with many in a perilous state of conservation (Conand 2001; Uthicke et al. 2004; Friedman et al. 2011; Eriksson and Byrne 2015). Increased demand for bêche-de-mer is driving worldwide exploitation (Conand 1998, 2001; Purcell et al. 2013), and 16 species are now listed as threatened to extinction by the IUCN (Conand et al. 2014; Purcell et al. 2014). Many species are now locally extinct (Hasan 2005; Anderson et al. 2011; Branch et al. 2013; Price et al. 2013; Purcell et al. 2014), with at least 70% of the world's tropical holothuroid fisheries considered exploited, over-exploited or depleted (Purcell et al. 2013).

Understanding the ecological roles of exploited species is critical for ecosystem-based fisheries management (Anderson et al. 2011; Purcell et al. 2016a). Tropical aspidochirotids are among the largest and often most abundant non-coral invertebrates in coral reef carbonate sediment habitats. Reef sediment habitats are vast, sometimes accounting for up to 95% of areal benthic coverage, and constitute the majority of calcium carbonate stored in coral-reef ecosystems (Gattuso et al. 1998). In these habitats, aspidochirotids turn over vast quantities of sediment through their deposit-feeding activity (Yamanouti 1939; Bonham and Held 1963; Hammond 1982; Klinger et al. 1994; Uthicke 1999; Mangion et al. 2004; Shiell and Knott 2010). This bioturbation activity directly increases oxygen levels in the sediment (Hammond 1982), with increased sediment anoxia noted following their removal from reef flat habitats (Lee et al. 2017). The digestion and dissolution of carbonate sands in the holothuroid gut may further alter biogeochemical processes by reducing sediment grain size and increasing local alkalinity in reef environments (Hammond 1981; Schneider et al. 2011, 2013; Purcell et al. 2016a). This compensatory process could contribute to the biogenic buffering of ocean acidification, and thus reef resilience, in a changing ocean (Schneider et al. 2011, 2013).

Tropical aspidochirotids also play critical roles in trophic functionality. They are reported to consume bacteria, diatoms and microalgae, with infauna considered to be a minor food source (Moriarty 1982; Moriarty et al. 1985; Uthicke 1999; Roberts et al. 2000). Nitrogen excretion by aspidochirotids encourages benthic productivity in oligotrophic coral reef systems (Uthicke and Klumpp 1998; Uthicke 2001; Wolkenhauer et al. 2010; Purcell et al. 2016a). In manipulative experiments, seagrass growth and biomass decreased following the removal of the sandfish, *Holothuria scabra* (Wolkenhauer et al. 2010). Similarly, field-based incubations showed that the nitrogen waste products of *H. atra* promoted benthic microalgal growth and productivity, suggesting that holothuroids fertilise their own gardens (Uthicke and Klumpp 1998). Overall, the ecological consequences of removing holothuroids from coral reefs are likely to be detrimental to ecosystem functionality (Purcell et al. 2016a).

The distances covered by tropical holothuroids as they feed are not well known, largely because they are difficult to tag or track (Conand 1983, 1989, 1991; Purcell et al. 2016a, b). While they have been considered to be largely sedentary (Conand 1983, 1991; Purcell 2010), a recent study on two large tropical holothuroids, *Bohadschia argus* and *Thelenota ananas*, showed that these species moved between 2–8 and 5–9 m d^{-1}, respectively (Purcell et al. 2016b). While this suggests they are highly mobile, these species also display long-term site fidelity (Purcell et al. 2016b). The curryfish, *Stichopus herrmanni*, has been recorded to move 0.4–0.7 m h^{-1} (Purcell and Eriksson 2015), with no difference in activity between day and night (Eriksson et al. 2013). Information on the effects of season on holothuroid activity and bioturbation is limited to one study on *H. scabra*, which exhibited increased activity coinciding with annual peaks in water temperature and gonad development (Shiell and Knott 2010). These features of movement, activity and site fidelity have important implications for conservation of holothuroids and the identification of effective marine protected areas (Purcell and Kirby 2006; Purcell et al. 2016b; Wolfe and Byrne 2017), and are especially important to understand for fished species.

Globally, tropical bêche-de-mer fisheries follow a predictable pattern of serial exploitation of high-value species, with a transfer of effort to lower value species (Conand 1998, 2001; Branch et al. 2013; Purcell et al. 2013, 2014). These patterns of overfishing are typical of developing countries, but similar trends are also documented for higher-income regions including on Australia's World Heritage-listed Great Barrier Reef (GBR) (Eriksson and Byrne 2015). On the GBR, catches of the mid-value curryfish, *S. herrmanni*, increased at a rate of ~200% per year between 2007 and 2011 (Eriksson and Byrne 2015). This species is increasing in value as it becomes rarer in tropical waters worldwide (e.g. Torres Strait: Skewes et al. 2004; Papua New Guinea: Kinch et al. 2008; East Africa: Eriksson et al. 2010; GBR: Eriksson and Byrne 2015). *Stichopus herrmanni* is now listed as vulnerable to extinction (Conand et al. 2014; Purcell et al. 2014).

We investigated seasonal variation in movement, bioturbation, feeding and gonad development in *S. herrmanni* at One Tree Reef (OTR), GBR, over 3 yr. Previous studies indicated that spawning in this species occurs during summer with suppressed gonad growth in winter (Conand 1993a, b). We hypothesised that this holothuroid would be highly mobile, as shown recently for *S. herrmanni* (Purcell and Eriksson 2015), and other large tropical holothuroids (Purcell et al. 2016b). We predicted seasonal activity and bioturbation would increase in summer, coinciding with increased water temperature and gonad development, as shown for *H. scabra* (Shiell and Knott 2010). It has been suggested that *S. herrmanni* does not exhibit selective feeding behaviour (Roberts and Bryce 1982; Klinger et al. 1994), and so we hypothesised that this species is a generalist grazer with non-selective feeding traits. We compared the biota in ambient sediment to that in the oesophagus, intestine and faecal casts of *S. herrmanni* to characterise the available food source and their diet. Since the digestive biology of aspidochirotids is likely to have an important biogeochemical impact due to the dissolution of carbonate sediment in the low-pH sea cucumber gut (Hammond 1981; Schneider et al. 2011, 2013), gut pH was determined at different stages of sediment digestion. Coelomic fluid pH was also measured to assess acid–base regulation in *S. herrmanni* (Collard et al. 2013, 2014), and the reproductive cycle was assessed through gonad index analysis. The data assimilated here provide new empirical information on the ecological roles of *S. herrmanni* in a lagoon sediment habitat on the GBR, information critical for the development of ecosystem-based fisheries management (Anderson et al. 2011; Purcell et al. 2016a), and the conservation of this exploited bêche-de-mer species.

Methods

Habitat conditions

Fieldwork was conducted in the shallow (1–3 m) sandy habitat 'Shark Alley' in OTR lagoon (23°30′S, 152°05′E), southern GBR, Australia (Fig. 1a). The feeding biology and movement of *S. herrmanni* (Fig. 1b) were investigated each season (summer, autumn, winter, spring) between 2013 and 2015, with each season replicated twice. Temperature was intensively monitored in Shark Alley across 2016, using in situ HOBO loggers to determine the conditions directly experienced by *S. herrmanni* in Shark Alley. Average temperatures in 2013–2015 were also calculated for each season using average daily temperatures, available from the in situ weather station positioned inside OTR lagoon (http://data.aims.gov.au/aimsrtds/station.xhtml?station=131).

Movement and bioturbation

For each observation period, ten *S. herrmanni* (length 30.8 ± 4.0 cm; width 8.9 ± 1.0 cm; mean ± SD; $n = 80$) were tracked in situ for 5 h across afternoon low tides (neap low ~1500 hrs) to quantify their movement and bioturbation activity. Each season was repeated twice across 2013–2015, so that a total of 20 individuals were tracked per season. No surveys were conducted at night as *S. herrmanni* does not behave differently between day and night (Eriksson et al. 2013). Tagging *S. herrmanni* is notoriously difficult (Conand 1983, 1989, 1991), and so was not attempted. Identifiable individuals (i.e. by colouration, scarring, spot patterns) were noted during each survey.

To determine the distance moved and faecal cast production of *S. herrmanni*, the initial position of each individual was marked with a stake, and individuals were revisited hourly. Each hour the distance between the initial stake and new position of the holothuroid was measured. The exact route of each individual was measured following the trail of faecal casts produced (Fig. 1b), not a straight line. After measuring the distance travelled, all faecal casts were collected and the holothuroids' new position was marked. Faecal casts are encased in a thin mucous layer and were collected carefully by hand. This process was repeated hourly for each individual at low tide when OTR lagoon is ponded, removing confounding hydrodynamic interference with the integrity of faecal casts. The total distance moved and amount of sediment released in a 5-h period were then determined.

Daily movement rates were calculated from the average hourly distance moved for each individual. Analyses of the amount of sediment released each hour showed that time had no significant effect on defecation rates across the 5-h sampling periods (RMANOVA: $F_{4,80} = 1.4$, $p = 0.23$). Thus, average hourly defecation rates per individual were calculated from the total amount of sediment released over 5 h. Maximum average daily and annual defecation rates were extrapolated from this estimate, assuming that *S. herrmanni* is a continuous feeder (i.e. 24 h) (Klinger and Johnson 1998; Eriksson et al. 2013). Minimum sediment turnover rates were calculated using the 15-h feeding period determined for *S. herrmanni* by Yamanouti (1939).

Surface sediment cores were also collected adjacent to each *S. herrmanni* to compare ambient sediment to that digested by the holothuroids. Cores were taken with plastic coring tubes stoppered at 5 mm depth, as this is the estimated feeding depth of deposit-feeding holothuroids (Uthicke 1999).

The sediment grain size profiles of *S. herrmanni* faecal casts and ambient sediment cores were compared ($n = 20$ season^{-1}). Sediment samples were partitioned by wet sieving with fresh water into the size fractions 1400, 1000,

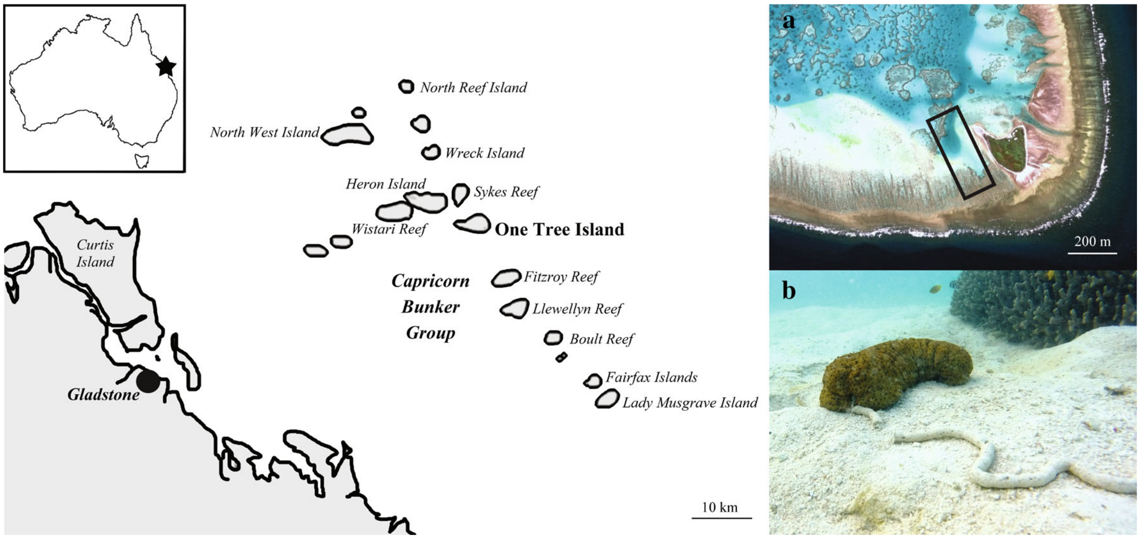

Fig. 1 Location of One Tree Island in the Capricorn Bunker Group (Great Barrier Reef, Australia), with indication of **a** Shark Alley (*black box*). **b** *Stichopus herrmanni* bioturbation and faecal cast trail

500 and <500 µm, and dried in a 60 °C oven for >24 h. The dry weight of each size class was calculated as a percentage of the total sample weight. The total dry weight (g) of each faecal cast was used to extrapolate hourly, daily and yearly bioturbation rates of *S. herrmanni* over each observation period.

Infauna in ambient, gut and faecal cast sediment

A separate set of faecal cast ($n = 10$) and ambient sediment ($n = 10$) samples were collected from Shark Alley each season and fixed in 10% formaldehyde in filtered seawater with a Rose Bengal dye. The presence of infauna (~100–1000 µm length) was determined under a dissecting microscope, identified by their pink stain. The total number of organisms present in 2-mL subsamples of sediment were counted and categorised into predominant groups: Amphipoda, Nematoda, Polychaeta, Platyhelminthes and other Crustacea (e.g. Copepoda, Ostracoda, Isopoda). Biota in the ambient sediment cores and *S. herrmanni* faecal casts were compared. To identify the infauna ingested by *S. herrmanni*, sediment samples were also taken from the oesophagus (right behind the mouth) of dissected individuals ($n = 8$), before digestive processes impaired the ability to identify gut contents.

Surface sediment photopigments

Faecal cast ($n = 6$) and ambient sediment ($n = 12$) samples were also collected each season for analysis of chlorophyll-*a*. Samples were dried in an oven at 60 °C for ~24 h, and the dry weight was measured. Chlorophyll-*a* was extracted from the dry sediment samples with 90% acetone. Samples were kept dark and cool (~4 °C) for 18–24 h before analysing the supernatant by spectrophotometry at wavelengths of 630 and 664 nm. Chlorophyll-*a* levels were calculated using formulae produced by Jeffery and Humphrey (1975), relative to the dry sediment weight. Mean values for chlorophyll-*a* were taken for each season.

Internal pH

A total of 32 *S. herrmanni* were collected from Shark Alley and quickly transported to One Tree Island Research Station (OTIRS) for analysis of internal pH. Half of the specimens were used immediately, to ensure their stomachs were filled with sediment (full; $n = 16$). The remaining *S. herrmanni* were left for >24 h in flow-through aquaria to empty their digestive tracts (empty; $n = 16$). The body wall of each individual was cut open, and the coelomic fluid drained. pH of the coelomic fluid was measured immediately. The pH probe was then carefully inserted into a small incision in the foregut of each *S. herrmanni*, and the pH was recorded. pH was also measured in incisions at the hindgut for several full and empty individuals ($n = 6$), and of ambient seawater samples ($n = 9$). All pH measurements were made using a ROSS Sure-flow sensor (Orion, Thermo Scientific) or WTW Multiline probe, calibrated to NIST buffers 7.00 and 10.02 (Hach, Radiometer Analytical).

Gonad index

The gonad index was determined for *S. herrmanni* collected in summer ($n = 29$), autumn ($n = 8$), winter

($n = 9$) and spring ($n = 24$). Collections were made over a number of years (2008–2016), due to permit restrictions on harvest numbers. *Stichopus herrmanni* were collected from Shark Alley and returned to OTIRS for dissection. Gonad index was calculated as the weight-percent of the gonads relative to the combined drained body wall and viscera weights. The weight range (drained) of individuals used for gonad index analyses was 667–2370 g ($n = 70$). Two of nine specimens completely lacked identifiable gonads in winter and were recorded as zero weight. Data were combined by season of collection.

Statistics

Average hourly movement and sediment turnover rates of *S. herrmanni* were analysed using analysis of covariance (ANCOVA), with season as the fixed factor and holothuroid size as the covariate. Year was not considered a fixed factor due to the unbalanced sampling of each season twice over 3 yr (2013–2015). Sediment granulometry (grain particle size) was analysed by converting the dry weight-percent of each sieve class into a measure of kurtosis (i.e. skewedness, tailedness, homogeneity) for each sample using the logarithmic method of the GRADISTAT package (Version 8.0, Crowthorne, UK) (Blott and Pye 2001). The value of kurtosis for each sediment sample was then analysed using a two-way ANOVA, with season and sediment type (faecal cast/ambient sediment) as the fixed factors.

Seasonal differences in infauna composition between *S. herrmanni* faecal casts and ambient sediments were visualised using non-metric multidimensional scaling (MDS) plots. Abundance data of infauna groups were arcsine transformed before visualisation in the two-dimensional MDS space. Within this space, communities that have similar compositions cluster together, while those that are different are spaced further apart. Further determination of differences in the abundance of infauna groups due to our two factors (season, faecal cast/ambient sediment) was done using PERMANOVA, calculating the *F*-statistic using 9999 permutations for all factors (Anderson et al. 2008). Similarity of percentages (SIMPER) tests were performed to examine combined effects. MDS, PERMANOVA and SIMPER tests were done using Primer V6.

Benthic photopigment data were analysed using a two-way ANOVA, with season and sediment type (faecal cast/ambient sediment) as the fixed factors. Internal pH of *S. herrmanni* was analysed using a two-way ANOVA, with gut condition (empty, full) and position in the gut (coelomic fluid, foregut, hindgut) as fixed factors. Data on the gonad index of *S. herrmanni* were analysed using one-way ANOVA, with season as the fixed factor. Homogeneity of variance and normality were checked and confirmed for all data series (Quinn and Keough 2003). Percentage data were arcsine transformed before analysis. Post hoc Tukey's HSD tests were used to determine where significant differences lay. All ANOVAs were analysed using JMP 501 (Cary, NC, USA).

Results

Habitat conditions

The average water temperature in Shark Alley was 24.5 ± 0.01 °C (mean ± SE) in 2016, with a minimum and maximum temperature of 17.5 and 32.3 °C, respectively (Electronic supplementary material. ESM, Fig. S1). The average daily water temperature in OTR lagoon 2013–2015 was 27.2 °C (±0.07) during summer, 25.1 °C (±0.14) in autumn, 21.5 °C (±0.07) in winter and 23.9 °C (±0.95) in spring (ESM Fig. S1). Based on average daily water temperatures in OTR lagoon, the maximum temperature was 29.4 °C (summer), and the minimum was 19.4 °C (winter) (ESM Fig. S1).

Movement and bioturbation

Stichopus herrmanni moved an average of 47.2 ± 9.2 cm h^{-1} across all seasons, ranging between 5.8 and 192 cm h^{-1}. The average distance moved was greatest in summer (62.4 ± 13.0 cm h^{-1}), and smallest in winter (37.5 ± 7.5 cm h^{-1}) and spring (38.8 ± 7.9 cm h^{-1}), but these data did not differ significantly (Fig. 2a; ESM Table S1). However, the spread of data indicated that the upper 25th percentile was fastest in summer (Fig. 2a). *Stichopus herrmanni* moved an average of 9 m d^{-1} in winter and 15 m d^{-1} in summer. In total, six recognisable individuals were repeatedly observed within the study area 3–4 times each over 3 yr.

There was a significant seasonal difference in the total amount of sediment released by *S. herrmanni* over the 5-h monitoring period. The length of *S. herrmanni* (range 19–44 cm) had no effect on sediment defecation (Fig. 2b; ESM Table S1). Tukey's HSD test revealed that rates of bioturbation were higher in summer (28.6 g h^{-1}) and autumn (25.2 g h^{-1}), compared to winter (13.7 g h^{-1}) and spring (11.7 g h^{-1}) (Table 1; Fig. 2b; ESM Table S1). Calculated values for minimum and maximum daily and annual defecation rates are displayed in Table 1.

Sediment grain size was dominated by small sediment particles (<500 µm) compared to larger grain sizes (>500 µm) in all seasons (Fig. 3; ESM Table S1). There was a significant difference in sediment grain size distribution (kurtosis) between the faecal casts and ambient sediment, and between seasons, but no interactive effect (Fig. 3; ESM Table S1). Tukey's HSD tests revealed that

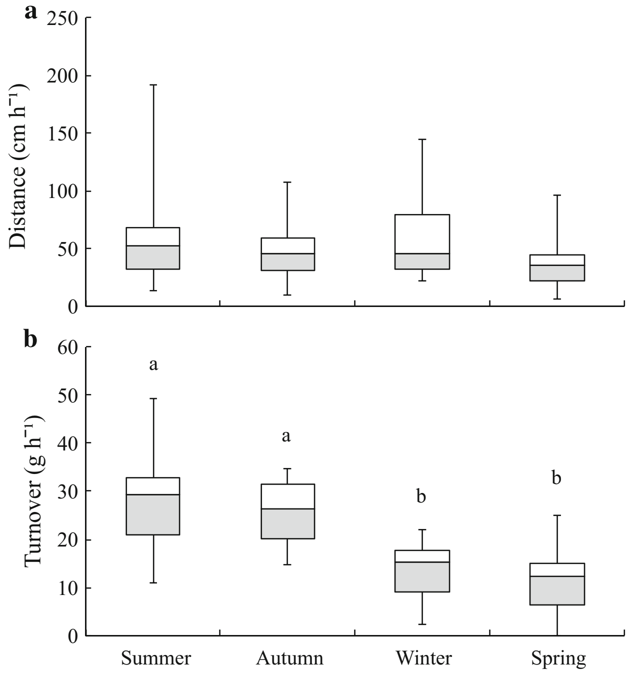

Fig. 2 **a** Distance moved (cm h^{-1}) and **b** amount of sediment turned over (g h^{-1}) by *Stichopus herrmanni* for each season ($n = 20$; ±SE). *Boxes* represent the interquartile range (25th and 75th percentile), the *horizontal line* is the median, and the *whiskers* represent the data range. *Different letters* indicate significantly different groups (Tukey's HSD test)

there were more fine sediment particles (<1000 µm) and fewer large sediment fragments (>1000 µm) in the faecal casts produced by *S. herrmanni* than in the surrounding environment (Fig. 3). Between seasons, Tukey's HSD tests showed that the kurtosis of each sample was greatest in spring and summer (i.e. least homogenous), and lowest in winter (i.e. most homogenous) (Fig. 3; ESM Table S1).

Infauna in ambient, gut and faecal cast sediment

There were clear differences in the abundance of infauna in ambient sediment (54.8 ± 2.7 individuals mL^{-1}) compared to faecal cast samples (4.05 ± 0.2 individuals mL^{-1}; Table 2; Fig. 4). There was no distinct differentiation of infauna among seasons, but infauna found in ambient sediment samples in winter were different to other seasons (Fig. 4). PERMANOVA confirmed these patterns, detecting differences in the abundance of infauna among seasons and between faecal casts and ambient sediment, with an interactive effect (Fig. 5a, b; ESM Table S2). Infauna were more abundant in ambient sediment samples (67%) than in casts produced by *S. herrmanni* (14%) (Table 2; Fig. 5a, b). There were also more organisms present in ambient sediment during summer and autumn than in winter and spring (Fig. 5a). SIMPER tests suggest that this was driven by low numbers of amphipods in spring (7%) compared to the remaining seasons

Table 1 Average (±SE) hourly sediment turnover rates of *Stichopus herrmanni* by season, including calculated minimum (15-h feeding period; Yamanouti 1939), and maximum (24 h continuous feeding; Klinger et al. 1994) daily and annual rates (see "Methods")

	Sediment turnover rate				
	Hourly (g individual^{-1} h^{-1})	Daily (g individual^{-1} d^{-1})		Annual (kg individual^{-1} yr^{-1})	
		Min	Max	Min	Max
Summer	28.6 ± 1.8	429.2	686.7	156.7	250.7
Autumn	25.2 ± 1.3	377.5	604.0	137.8	220.5
Winter	13.7 ± 1.7	205.2	328.3	74.9	119.8
Spring	11.7 ± 1.9	175.5	280.8	64.0	102.5

Fig. 3 Average weight percentage of sediment size class fractions in holothuroid faecal casts and ambient sediment cores for each season ($n = 20$; ±SE)

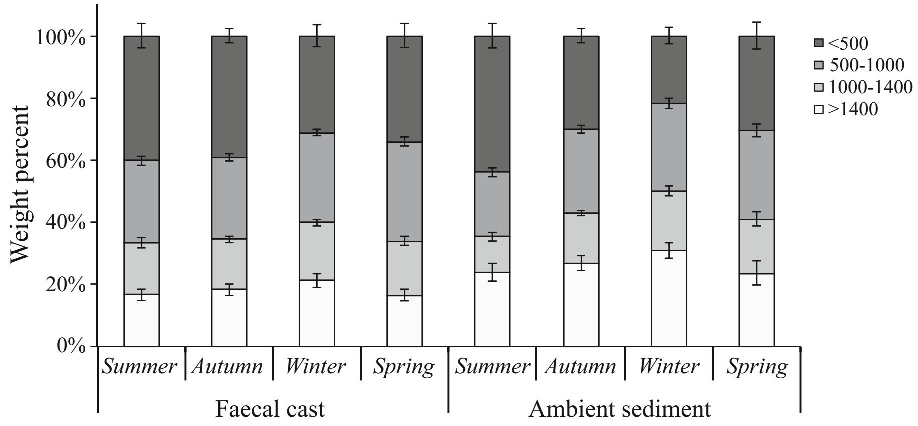

Table 2 Average (±SE) abundance of sediment infauna in (2 mL) ambient sediment samples ($n = 40$), *Stichopus herrmanni* faecal casts ($n = 40$), and oesophagus sediment samples ($n = 8$)

	Amphipoda	Nematoda	Polychaeta	Platyhelminthes	Other Crustacea
Ambient	21.2 ± 1.2	15.2 ± 0.6	5.9 ± 0.4	0.2 ± 0.05	12.2 ± 0.5
Faecal casts	1.4 ± 0.06	0.8 ± 0.03	0.3 ± 0.02	0	1.5 ± 0.08
Oesophagus	9.6 ± 0.8	8.0 ± 1.1	0.5 ± 0.2	0	1.4 ± 0.3

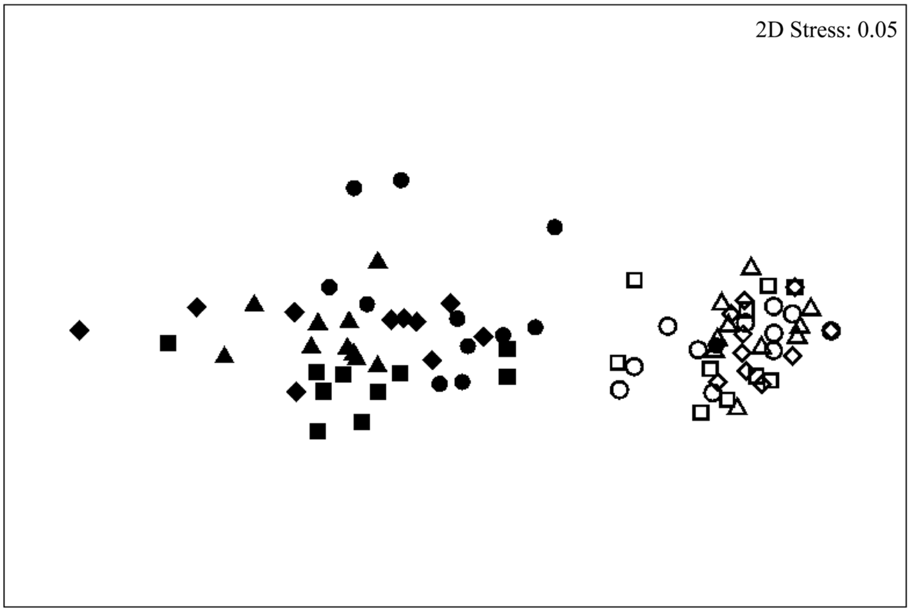

Fig. 4 Non-metric multidimensional scaling ordination plots on Bray–Curtis similarity of meiofauna community structure in Shark Alley for *Stichopus herrmanni* faecal casts (*open shapes*) and ambient sediment cores (*closed shapes*), taken during summer (*triangles*), autumn (*diamonds*), winter (*squares*), and spring (*circles*)

(14–15%) (Fig. 5a). Sediment in the oesophagus of *S. herrmanni* ($n = 8$) included the most common organisms in ambient sediment samples (Table 2).

Surface sediment photopigments

The average level of benthic chlorophyll-*a* was significantly higher in ambient sediment samples (3.00–3.28 µg g^{-1}) than in faecal casts (1.87–2.52 µg g^{-1}) (Fig. 5c; ESM Table S1). Chlorophyll-*a* did not differ among seasons in the environment or in *S. herrmanni* faecal casts (Fig. 5c).

Internal pH

The pH of the digestive tract of *S. herrmanni* was significantly different for individuals with their gut empty and full of sediment, and for measurements taken in the foregut, hindgut and coelomic fluid (Fig. 6; ESM Table S1). There was also a significant interaction between these factors (Fig. 6; Table S1). pH was highest in the coelomic fluid, regardless of whether the digestive tract was empty (pH 7.91 ± 0.03) or full (pH 7.98 ± 0.03) (Fig. 6). pH was significantly lower in the foregut than in the hindgut (Fig. 6). In digestive tracts full of sediment, the average pH of the hindgut was 7.65 (±0.07), but was 7.49 (±0.05) in the foregut (Fig. 6). In empty guts, the average pH was 7.37 (±0.06) and 7.05 (±0.09) in the hindgut and foregut, respectively (Fig. 6). The pH of ambient seawater was 8.12 ± 0.03.

Gonad index

The gonad index differed between seasons (Table 3; ESM Table S1). *Stichopus herrmanni* had a higher gonad index in the summer (4.85%) than in other seasons (Table 3; ESM Table S1). Gonads were notably reduced during autumn (0.41%) and winter (0.19%), and increased in size in spring (0.99%) (Table 3).

Discussion

Movement and bioturbation

This is the longest in situ study tracking the seasonal activity and bioturbation of individual aspidochirotids (Table 4). We showed that *S. herrmanni* moved

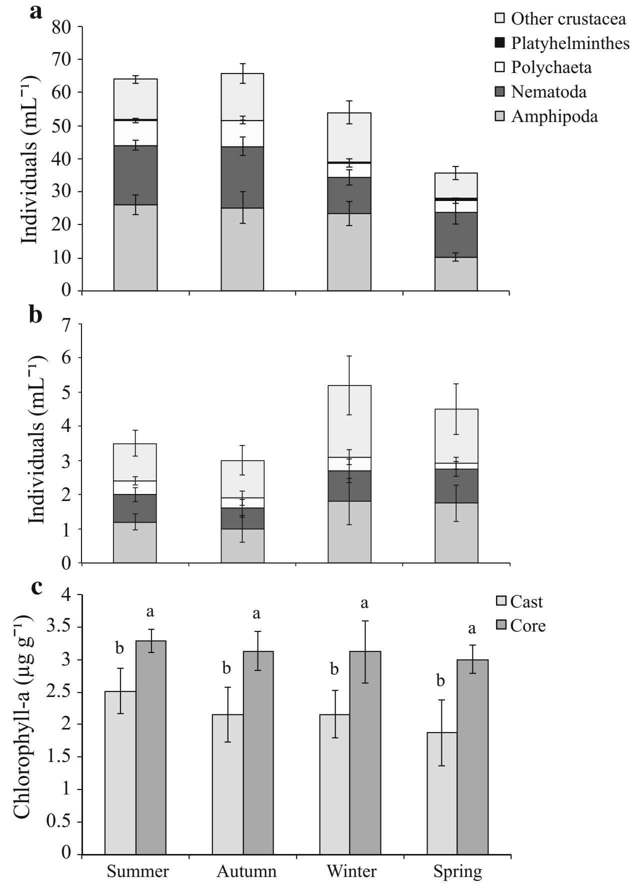

Fig. 5 Benthic community composition: average abundance of infauna (mL^{-1}) in **a** naturally occurring sediment cores and **b** casts produced by *Stichopus herrmanni* ($n = 10$ season^{-1}; ±SE). **c** Average level of chlorophyll-*a* (µg g^{-1} dry sediment) in *S. herrmanni* faecal casts ($n = 6$ season^{-1}) and ambient sediment cores ($n = 12$ season^{-1}; ±SE). *Different letters* indicate significantly different groups (Tukey's HSD test)

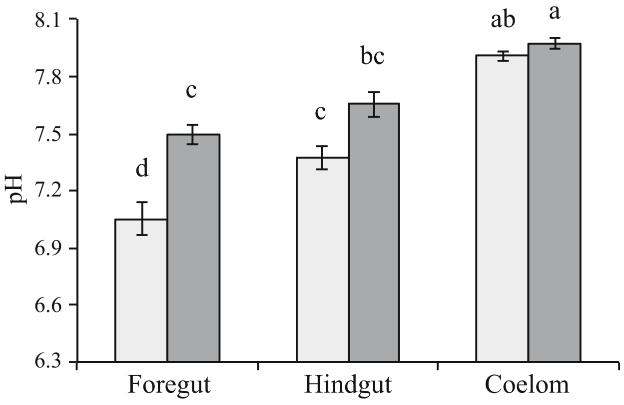

Fig. 6 Average (±SE) internal pH in the foregut ($n = 16$), hindgut ($n = 6$) and coelom ($n = 16$) of *Stichopus herrmanni* with a gut empty (*light grey bars*) or full (*dark grey bars*) of sediment. *Different letters* indicate significantly different groups (Tukey's HSD test)

Table 3 Average (±SE) gonad index for *Stichopus herrmanni* in each season, with indication of sample size (*n*)

	GI (%)	SE	*n*
Summer	4.85	0.49	29
Autumn	0.41	0.09	8
Winter	0.19	0.07	9
Spring	0.99	0.20	24

considerably, at an average rate of 47.2 cm h^{-1} throughout the year. This speed is comparable to that documented for *S. herrmanni* in New Caledonia (Purcell and Eriksson 2015), and for other tropical holothuroids (<100 cm h^{-1}: Conand 1991; Roberts et al. 2000; Uthicke 2001; Shiell and Knott 2010; Purcell et al. 2016b). However, some *S. herrmanni* reached speeds >300 cm h^{-1}. The average hourly movement of *S. herrmanni* was greater in summer and autumn (50–62 cm h^{-1}) compared to winter and spring (37–39 cm h^{-1}), but this trend was non-significant and was likely driven by several particularly active individuals. Seasonal trends of decreased holothuroid activity (movement) in winter have been documented for the sandfish, *H. scabra*, on Ningaloo Reef, Western Australia (Shiell and Knott 2010). More data are needed to identify seasonal activity patterns in *S. herrmanni*, including for lower-latitude populations that may be less influenced by seasonal change.

Stichopus herrmanni moved an average of 9 and 15 m d^{-1} during winter and summer, respectively. A recent study of other large tropical holothuroids, *B. argus* and *T. ananas*, showed that they moved 2–8 and 5–9 m d^{-1}, respectively (Purcell et al. 2016b). These two species exhibited site fidelity and long-term home ranging behaviour, as indicated by the reoccurrence of recognisable individuals over 2 yr (Purcell et al. 2016b). While we did not tag or track individuals over the years, several recognisable *S. herrmanni* were repeatedly encountered in Shark Alley. Thus, adult *S. herrmanni* may also display home range affinity. The apparent site fidelity of *S. herrmanni*, and patterns of ontogenetic migration within their recruitment reef (Eriksson et al. 2013; Palazzo et al. 2016; Wolfe and Byrne 2017), highlight their vulnerability to overharvesting on reefs open to fishing, and the potential for heavily targeted species to suffer marked population declines, local extinction and poor recovery (Gillanders et al. 2003; Uthicke et al. 2004; Hasan 2005; Purcell 2010; Friedman et al. 2011). This has important implications for fisheries management regarding connectivity between recruitment and nearby adult habitats within the same reef (Wiedemeyer 1994; Gillanders et al. 2003; Grüss et al. 2011; Bourjon and Morcel 2016).

Table 4 Sediment processing rates (g dry weight h^{-1}) of tropical aspidochirotids based on field observations and faecal casts collected in situ

Species	Sediment processed (g h^{-1})	Sample size (*n*)	Period of continuous tracking (h)	Diel difference	Seasons sampled	Habitat	References
Holothuria							
Arenicola	1.7–2.9[a]	50	24[b]	n/s	–	Sandy, reef	Hammond (1982)
Atra	3.6[a]	65	24[b]	n/s	1	Sandy, reef	Yamanouti (1939)
	6–12[a]	–	–	–	1	Reef flat, lagoon	Bonham and Held (1963)
	1.2[a]	–	–	–	1	Lagoon	Klinger et al. (1994)
	3.6	12	2	–	2	Seagrass	Uthicke (1999)
	2.9–3.8	6	24[b]	–	1	Back reef	Mangion et al. (2004)
Bivittata	5.2[a]	29	24[b]	PM > AM	1	Sandy, reef	Yamanouti (1939)
Edulis	2.5[a]	34	24[b]	n/s	1	Sandy, reef	Yamanouti (1939)
	0.9[a]	–	–	–	1	Lagoon	Klinger et al. (1994)
Flavo-maculata	1.0[a]	24	24[b]	n/s	1	Sandy, reef	Yamanouti (1939)
Leucospilota	0.7[a]	–	–	–	1	Lagoon	Klinger et al. (1994)
	3.3–4.1	6	24[b]	–	1	Back reef	Mangion et al. (2004)
Mexicana	4.6–5.0[a]	20	24[b]	PM > AM	–	Sandy, reef	Hammond (1982)
Scabra	8.2[a]	47	24[b]	PM > AM	1	Sandy, reef	Yamanouti (1939)
Vitiens	3.0[a]	39	24[b]	PM > AM	1	Sandy, reef	Yamanouti (1939)
Whitmaei	3.3–7.1	18–30	24[b]	n/s	3	Reef, lagoon	Shiell and Knott (2010)
Stichopus							
Chloronotus	0.3[a]	–	–	–	1	Lagoon	Klinger et al. (1994)
	11.5	12	2	–	2	Seagrass	Uthicke (1999)
Herrmanni	2.1[a]	64	24[b]	PM > AM	1	Sandy, reef	Yamanouti (1939)
	1.0[a]	–	–	–	1	Lagoon	Klinger et al. (1994)
	5–23	10	2.5	PM > AM	1	Sandy, lagoon	Purcell and Eriksson (2015)
	11.7–28.6	80	5	n/s	4	Sandy, lagoon	Present study
Isostichopus							
Badionotus	2.8–4.9	30	24[b]	PM > AM	–	Sandy, reef	Hammond (1982)

Values available as daily rates were converted to an hourly rate (–, no data or unclear; n/s, no significant effect)

[a] Estimated from average dry weight of single faecal casts multiplied by mean number of casts produced over 24 h, rather than faecal casts expelled over time

[b] Individuals visited several times across 24 h, not continuously followed

Rates of sediment turnover by *S. herrmanni* were significantly lower in winter and spring than in summer and autumn, providing the first documentation of a seasonal disparity in bioturbation for a tropical holothuroid (Table 4). This is likely due to low water temperatures and a reduced gonad index (i.e. reduced energetic demands) during winter, as suggested for seasonal effects on the movement of *H. scabra* (Shiell and Knott 2010). We estimate that sediment turnover by *S. herrmanni* could range from 64 to 250 kg individual^{-1} yr^{-1} (Fig. 7), depending on season and diurnal feeding patterns (Yamanouti 1939; Purcell and Eriksson 2015). Even at the calculated minimum value, the total rates of sediment turnover reported here for *S. herrmanni* are above those previously documented for this and other aspidochirotids (9–105.1 kg individual^{-1} yr^{-1}) (Table 4). This reflects our robust sampling technique, collecting all faecal casts produced over 5 h in a hydrodynamically stable environment, compared to previous studies estimating total turnover rates from single faecal casts (e.g. Yamanouti 1939; Bonham and Held 1963; Hammond 1982; Klinger et al. 1994).

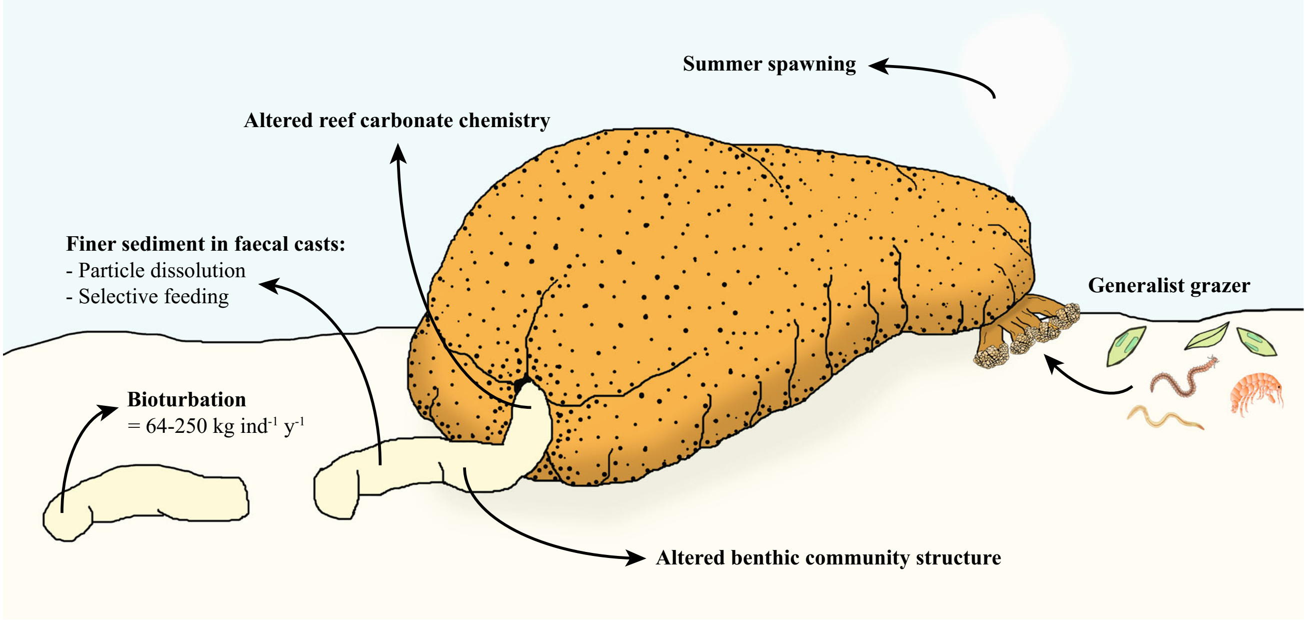

Fig. 7 Representation of the biological and ecological roles of *Stichopus herrmanni*

Considering the amount of sediment turned over by *S. herrmanni* in a year, this species is likely to be ecologically important in its lagoon habitat, influencing benthic processes and trophic interactions (Fig. 7). This is especially true for unfished reefs, such as OTR and Heron Reef, where *S. herrmanni* is abundant (31.25–1100 individuals ha^{-1}; Eriksson et al. 2013; Wolfe and Byrne 2017), and prompts the question of the ecological impact of removing this bêche-de-mer species from tropical sediment habitats.

Our understanding of the feeding mechanisms and preferences of tropical holothuroids with respect to sediment grain size, nutrient profiles and associated biota is poor. Very little new data are available since the Roberts et al. (2000) review on holothuroid feeding strategies. The ability of holothuroids to select particular sediment grain sizes appears to be species specific and associated with feeding tentacle morphology (Roberts and Bryce 1982; Roberts et al. 2000). The size range of particles ingested by shallow-water tropical species is very broad, from a median of 100 µm in *B. argus* to ~6000 µm in *H. atra* (Yamanouti 1939; Roberts et al. 2000). As shown in the profile of ambient sediment from Shark Alley, this area of OTR lagoon has a relatively uniform sediment granulometry, dominated by fine particles (~73% < 1400 µm). Early research suggests *S. herrmanni* does not reduce sediment grain size through its digestion (Yamanouti 1939). In contrast, we found the faecal casts produced by *S. herrmanni* had a comparatively finer mean grain size (~81% < 1400 µm) than the ambient environment. Whether *S. herrmanni* selects smaller sediment particles in its feeding (e.g. Roberts 1979; Roberts et al. 2000), or reduces grain size through the partial dissolution of sediment in the low-pH gut (e.g. Hammond 1981; Schneider et al. 2013) could not be determined in our study. The feeding niche and distribution of tropical aspidochirotids in lagoon systems is likely also influenced by other factors such as reef shelter (Klinger et al. 1994; Klinger and Johnson 1998), and hydrodynamic displacement (Wolfe and Byrne 2017).

Generalist consumer diet

Through an assessment of three stages of sediment processing by *S. herrmanni* (ambient sediment, oesophagus, faecal casts) we provide new insights into the trophic role of *S. herrmanni* in its tropical lagoon habitat. This is the first study to examine sediment in the oesophagus, where ingested biota can still be identified. Faecal casts had lower levels of infauna and chlorophyll-*a* than the ambient sediment, and infauna was found in the oesophagus of *S. herrmanni*, indicating that this species ingests and consumes benthic infauna and microalgae (Fig. 7). In contrast, previous studies concluded that infauna is not consumed by tropical aspidochirotids (Moriarty et al. 1985), and that infauna may not play a large role in the overall nutrition of some holothuroids (Uthicke 1999). However, these studies examined sediment in the stomach and intestines, which was likely too advanced in the digestive process to be able to identify organisms. *Stichopus herrmanni* processes large quantities of sediment, and we suggest that this species is a generalist grazer that ingests what is available in the environment. Our data suggest that *S. herrmanni* does not select for specific infauna or benthic microalgal food, as suggested previously for this species (Roberts and Bryce 1982). However, since infauna abundance was lower in the oesophagus than in ambient sediment, it is likely that some mobile species are able to escape predation by *S. herrmanni*.

Infauna were more abundant in the sediment during summer and autumn, coinciding with higher rates of bioturbation and movement by *S. herrmanni*. There was significantly less infauna during winter and spring, likely driven by low water temperatures on this southern reef, with a ~15 °C difference between summer maximum and winter minimum temperatures. Seasonal changes in the composition of benthic habitats, including infauna and algae, are common in coral reef systems (Uthicke and Klumpp 1998; Diaz-Pulido et al. 2009; de Oliveira et al. 2016; van Hoytema et al. 2016). We did not find significant seasonal changes in benthic productivity (chlorophyll-*a*) at our study site, as shown previously for OTR (Johnstone et al. 1990). However, benthic productivity can be very patchy in lagoon sediment (Koop and Larkum 1987; Johnstone et al. 1990). More research is needed to understand the seasonality of benthic algae in tropical lagoon systems, and the influence of bioturbators like *S. herrmanni* on the production or disruption of benthic algal mats and associated infauna.

Aspidochirotids can increase the productivity of benthic microalgae and seagrass systems through their bioturbation activity and increasing local nutrients (especially ammonium) through their excretory physiology (Uthicke and Klumpp 1998; Uthicke 2001; Wolkenhauer et al. 2010; Costa et al. 2014). Local enhancement of productivity by aspidochirotids has also been used to benefit integrated tropical mariculture systems (Namukose et al. 2016). This is important for the health of benthic lagoon systems in the presence or absence (i.e. fishing) of holothuroids. Information on the ecological consequences of removing bêche-de-mer species from coral-reef ecosystems is limited (e.g. Uthicke and Klumpp 1998; Wolkenhauer et al. 2010; Lee et al. 2017) and warrants greater attention (Purcell et al. 2016a). This could be examined using inclusion–exclusion experiments (e.g. Wolkenhauer et al. 2010) and/or stable isotope analyses (e.g. Slater and Carton 2010) to understand community-level responses, trophic cascades and potential phase shifts in sediment ecosystems resulting from the overharvest of large bêche-de-mer species.

Internal pH and seawater chemistry

The gut pH of *S. herrmanni* was higher when full of sediment (pH 7.04–7.81) compared to empty digestive tracts (pH 6.42–7.77), as shown previously for *H. atra*, *H. mexicana* and *Isostichopus badionotus* (Hammond 1981; Schneider et al. 2013). Tropical deposit-feeding holothuroids can play a pivotal role in the carbonate chemistry of coral-reef ecosystems, at least at the local scale (Hammond 1981; Schneider et al. 2011, 2013; Purcell et al. 2016a; Vidal-Ramirez and Dove 2016). It has been hypothesised that the digestion and dissolution of carbonate sediment in the holothuroid gut may buffer external changes in local carbonate chemistry (Fig. 7), and that this may be particularly important under scenarios of ocean acidification (Schneider et al. 2011, 2013). Our results show that the digestion of carbonate sediment in the gut of *S. herrmanni* drives an increase in gut pH, likely due to dissolution of carbonate sediment. This may influence external seawater chemistry when redeposited into the environment, potentially benefiting local reef calcifiers. This feature of their feeding biology warrants greater attention in the face of continued global change.

In contrast to changing pH in the gut, the coelomic fluid pH of *S. herrmanni* (7.91–7.98) was stable and similar to that recorded for the external environment (pH 8.12 ± 0.03; $n = 9$). Thus, coelomic fluid pH conforms to environmental pH (Fig. 7), as shown for tropical and temperate holothuroids (Collard et al. 2013, 2014). Holothuroids have a reduced ability to regulate their internal acid–base levels compared to other echinoderms (e.g. sea urchins), which may impact their physiological and metabolic processes as seawater chemistry changes due to ocean acidification (Collard et al. 2013, 2014). Conversely, as poorly calcified organisms, holothuroids may be more resilient to changing ocean chemistry compared to more heavily calcified reef species (e.g. corals, sea urchins, molluscs) (Dupont et al. 2010; Byrne 2011; Collard et al. 2013).

Reproduction

The gonad index data indicated that the reproductive activity of *S. herrmanni* on OTR peaked in summer (Dec–Feb) and that gonad growth was suppressed during winter (Jun–Aug) (Fig. 7), with two of nine individuals lacking identifiable gonads. This pattern is similar to that reported for another high-latitude population of this species in New Caledonia (Conand 1993a) and has been observed in temperate and tropical stichopodid species (Cameron and Fankboner 1989; Conand 1993b; Hu et al. 2010). Considering the time of spawning and likely planktonic duration, summer spawning of *S. herrmanni* agrees with observations of annual recruitment of juveniles in 2015 and 2016 on the GBR (Wolfe and Byrne 2017). These data on reproduction and recruitment are an important consideration for fisheries management, especially considering the likely trajectory of declining stock of this species on the GBR and elsewhere (Conand et al. 2014; Eriksson and Byrne 2015).

Implications for bêche-de-mer management on the GBR

Ecosystem resilience is strengthened by ecological functionality, which depends on species across trophic levels (Kroeker et al. 2011; Connell and Ghedini 2015). Emerging research on the contribution of holothuroids to ecosystem functionality indicates that they enhance local productivity and sediment health (Uthicke and Klumpp 1998; Uthicke 1999; Wolkenhauer et al. 2010; Purcell et al. 2016a; Lee et al. 2017) and may help buffer the effects of ocean acidification (Schneider et al. 2011, 2013). Fundamental gaps in information on holothuroid biology and ecology have not only limited our ability to gauge stock productivity, sustainable extraction rates and the ecological impacts of bêche-de-mer fisheries, it has hampered management dialogues (Wiedemeyer 1994; Anderson et al. 2011; Purcell et al. 2013; Eriksson and Byrne 2015). Improving our understanding about how these organisms interact with their environment and influence ecosystem processes is critical to understanding how bêche-de-mer fisheries impact coral reefs. This information is needed to support decision-making on conservation and ecosystem-based management (Anderson et al. 2011; Purcell et al. 2016a). Current approaches to bêche-de-mer fisheries are not viable for holothuroids (Conand 2001; Purcell et al. 2012, 2013, 2014), prompting the suggestion that a paradigm shift in fisheries management is needed.

As global patterns of exploitation continue it is likely that ecosystem function will be compromised in the absence of the ecosystem services holothuroids provide (e.g. Moriarty et al. 1985; Uthicke and Klumpp 1998; Uthicke 1999; Michio et al. 2003; Wolkenhauer et al. 2010; Costa et al. 2014; Purcell et al. 2016a; Lee et al. 2017). Biological and ecological information, as determined here, are important to inform effective ecosystem-based management strategies for target bêche-de-mer species. While we now have good information on the biology and ecology for high-latitude tropical populations of *S. herrmanni* (New Caledonia, Heron Island, One Tree Island), data are needed to determine the feeding ecology, population dynamics and spawning cycles of this species in its warmer, more tropical northern range across the Indo-Pacific (Purcell et al. 2012). It is critical that empirical data are collected for reefs both open and closed to harvest across the geographical range of bêche-de-mer targets. We urge the need for increased locally relevant information for targeted bêche-de-mer species to reduce the risk of continued global exploitation, threatened species and localised extinctions.

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