Modelling habitat associations of 14 species of holothurians from an unfished coral atoll: implications for fisheries management

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ABSTRACT: Currently there is no commercial or subsistence fishing for holothurians on the Cocos (Keeling) Islands and, despite a prominent government presence, no reported cases of poaching or illegal fishing. However, because of recent interest in developing a commercial fishery for holothurians there, a survey was initiated to provide baseline data on the previously unfished local holothurian populations. Fourteen species of holothurians were recorded during the survey, with the most abundant species being Holothuria atra; only 4 other species had relatively high abundances. A total of 20 556 holothurians were counted; however, 97% of these were considered to be of low commercial value. The high- and medium-value species found in this survey were all in extremely low abundances, with restricted distributions. The distribution and abundance of holothurians was closely linked with benthic habitats, with 48% of the variation in holothurian populations explained by 13 habitat variables. Several species displayed distinct habitat preferences: H. atra was associated with sand-dominated habitats, Actinopyga mauritiana was associated with relic reefs and soft corals, while Holothuria fuscopunctata and Stichopus herrmanni were both associated with reef flats. The densities recorded in the present study represent the natural abundance and distribution of holothurian populations at this atoll. Given the low numbers of commercially important species, it is highly unlikely that a commercial fishery would be economically viable at the Cocos (Keeling) Islands and it would be more beneficial to maintain the natural holothurian population.

KEY WORDS: Holothurians \cdot Habitat associations \cdot Coral reefs \cdot Exploitation \cdot Unfished populations

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INTRODUCTION

Holothurians play an important ecological role in nutrient cycling and bioturbation processes in marine benthic communities (Uthicke 1999, Skewes et al. 2002, Mangion et al. 2004, Uthicke et al. 2004b, Purcell 2010). Often the productivity of a habitat, particularly in coral reef systems, is a result of carbon fixation and nutrient recycling provided by benthic micro-algae (Uthicke & Klumpp 1998, Uthicke et al. 2004b). Previous studies have suggested that holothurians contribute to the oxygenation of the upper sediment levels and play a role in bioturbation that, in turn, may increase the productivity of benthic micro-algae (Uthicke & Klumpp 1998, Uthicke 1999, Uthicke & Karez 1999, Uthicke et al. 2004b, 2009), providing increased food resources for other species. The ecological consequences of removing holothurians by fishing are unknown. However, given they have important functions in their environment, it is likely that removal of these animals may reduce the overall productivity of coral reefs (Uthicke et al. 2004b, Friedman et al. 2010).

Holothurians are often amongst the most valuable resources for small tropical island communities (Kinch et al. 2008, Purcell 2010). Several species are highly prized by subsistence fishers (e.g. Actinoypa mauritiana and Holothuria atra) as a direct food source (Kinch et al. 2008) and by commercial operators (e.g. Holothuria fuscogilva, H. whitmaei [formerly *H. nobilis*] and *H. scabra*) due to the high demand from Asian markets (Conand & Byrne 1993, Choo 2008, Purcell 2010). Holothurians are susceptible to overfishing, and these fisheries are typically characterised by boom and bust cycles (Conand & Byrne 1993, Uthicke & Benzie 2000, Kinch et al. 2008, Uthicke et al. 2009, Anderson et al. 2010), with most fisheries severely overexploited (Conand 2004, Toral-Granda 2006, Friedman et al. 2010, Purcell



Fig. 1. Location of Cocos (Keeling) Islands (inset), and sampling sites for holothurians around the southern atoll

2010). Conand (2004) identified 42 species under population stress as a result of commercial exploitation. Similarly, an international review of 28 countries found that 21 countries, including Australia, have overexploited holothurian stocks, 5 countries have declining stocks and Malaysia has 1 species close to extinction. Of the 28 countries reviewed, only Cuba has apparently stable stocks (Toral-Granda 2006). Despite the commercial importance of holothurians, their biology, ecology and population dynamics remain poorly understood (Conand 2004, Lovatelli et al. 2004, Friedman et al. 2010). Information on growth rates, larval ecology, recruitment processes, habitat use, their ecological role and fisheries biology is scant and in some cases only available for a few species (Lovatelli et al. 2004, McIlgorm et al. 2007, Friedman et al. 2010, Purcell 2010).

The Cocos (Keeling) Islands are an Australian territory approximately 2800 km north-west of Perth, Western Australia (Fig. 1). Their shallow marine environment supports a diversity of holothurian species (Gibson-Hill 1949, Lincoln-Smith et al. 1993, Marsh 1994, Hender et al. 2001), although only limited data exist on the distribution and abundance of holothurians there (see Hender et al. 2001). While the local community, composed of traditional Cocos Malays and mainland Australians, relies heavily on the atoll's marine resources for food and recreation, commercial or subsistence harvesting of holothurians does not occur (Hender et al. 2001). The lack of commercial or subsistence harvesting coupled with the small size and isolation of the islands, cultural preferences and beliefs of the resident population and a strong Australian Federal Police (AFP), Australian Quarantine and Inspection Services (AQIS) and Parks Australia presence means that holothurian populations at the Cocos (Keeling) Islands are considered to be unexploited (including both legal and illegal fishing).

The present paper describes a baseline investigation of the abundance and habitat preferences of holothurian species at the Cocos (Keeling) Islands, motivated in part by recent interest in initiating a commercial fishery for holothurians. While the primary aim of fisheries management is ensuring the sustainability of exploited stocks, in recent years increasing emphasis has been placed on broader ecosystem function. A critical step in this process is understanding the relationship between the abundance of organisms and the habitats in which they are found (Freeman & Rogers 2003, Bellchambers et al. 2010). Previous authors have suggested that the availability and condition of habitats and their connectivity with nearby reef systems may play a major role in structuring holothurian populations (Kinch et al. 2008). However, the majority of previous studies linking holothurian abundance and distribution and habitat type have focused on populations that have, at some point, been either legally or illegally fished (e.g. Conand & Chardy 1985, Hammond et al. 1985). The present paper is unique as it describes the abundance and habitat preferences of a diversity of holothurian species in an unexploited state. We model the relationships between holothurian assemblage structure and habitats using distancebased linear regression. Estimates are made of the abundance of holothurians based on their observed numbers and the area of the major habitats with which they are associated. Finally, the potential implications of commercial fishing are considered in light of holothurian abundance and life history.

METHODS

Study location

The Cocos (Keeling) Islands are located in the Indian Ocean (12° 12' S, 96° 54' E), approximately 2950 km north west of Perth, 900 km west-southwest of Christmas Island and 1000 km southwest of Java Head (Fig. 1) (Bunce 1988). The group is comprised of 2 separate coral atolls, consisting of 27 islands covering a total area of approximately 14 km². The southern atoll, the focus of the present study, consists of 26 islands surrounding a shallow lagoon, 2 of which are inhabited with a total population of approximately 600 people. The Islands have 3 main aquatic habitat types: the outer reef slope (sub-tidal); reef flats, including sandy and rocky shores (predominantly intertidal); and a lagoon (predominantly sub-tidal) (Berry 1989).

Survey methodology

A 4-person team undertook field surveys of holothurian densities between 7 and 24 May 2006. The study was limited to depths of <29 m and covered all habitats; intertidal reef flats, shallow lagoon habitats and the outer reef slopes. Sampling was conducted systematically across the entire atoll by dividing the atoll into 1 minute blocks (Hender et al. 2001). A site was then randomly selected within each minute block. This equated to a sampling density of 1 site per 1.8 km². Our study sites also included sites previously surveyed by Berry (1989) and Hender et al. (2001). Direct comparisons with previous studies were often not possible as the data were either qualitative (Berry 1989) or holothurians were not the primary target of the surveys (Hender et al. 2001). Similarly, survey techniques and intensity were not directly comparable; however, where they were possible, comparisons have been made. During the current study a total of 79 sites were sampled (Fig. 1).

This survey used similar rapid assessment techniques to those used in holothurian surveys at Warrior Reef, Torres Strait (Skewes et al. 1998), Timor Sea MOU Box (Skewes et al. 1999) and Milne Bay Province, PNG (Skewes et al. 2002). Either SCUBA, snorkelling, or reef walks were used, depending on the water depth at each site. Sites were located using a hand-held GPS; once located 2 divers entered the water and swam adjacent 100 m \times 4 m belt transects, spaced 10 m apart, on a predetermined bearing. Every 10 m along the transect the abundance of holothurian species was recorded and a visual assessment was made of the percentage cover of the dominate substrate and habitat types.

Paired *t*-tests indicated that there were no significant differences between the observations on the 2 replicate transects at each site, so the abundance of holothurian species and percentage cover of each habitat were averaged across the 2 transects to give the overall density of each holothurian species and the average habitat percentage cover for each site.

Habitat categories

In the present study habitat is categorised in 2 different ways: fine and broad scale. The fine-scale habitat data were collected during the current survey, using the methods described above; these data were used for the modelling component of the study. The fine-scale habitat categories used in the current study are: sand, rubble (limestone rubble), seagrass, macroalgae, massive coral (corals that are solid and similar in shape in all directions), sub-massive coral (corals less than, or not quite, solid and similar in shape in all directions), plate coral (or laminar, forming a tier), foliose coral (forming a whorl), soft coral (coral without exoskeleton), branching coral (forms with branches), branching coral dead, reef flat (limestone platform) and relict reef (old eroded limestone reef). Fine-scale habitat categories were based on those used by previous studies so comparisons could be made (i.e. Williams 1994, Hender et al. 2001). However, for estimates of holothurian standing biomass habitat categories that could be quantified across the entire lagoon were required. Therefore, each of the sites surveyed during the current study was also allocated a broad-scale habitat category, adapted from Williams (1994), to estimate the standing biomass of holothurians (see 'Results').

Statistical analysis

Permutational distance-based approaches were used to examine spatial patterns in holothurian assemblages, as the data were highly skewed and contained many zeros (Clarke & Warwick 2001). The data were transformed using log10(x + 1) to reflect the distributions of rare species (only 4 of the 14 species were reasonably common), and the Bray-Curtis dissimilarities were calculated. The relationships between holothurian abundances and finescale habitat variables were analysed using distance-based linear models (DISTLM; Legendre & Anderson 1999, McArdle & Anderson 2001) in the computer program PRIMER-E+. Forward selection based on all habitat variables was chosen, and Akaike's information criterion was used as a measure of goodness-of-fit. The most parsimonious model was chosen, and the DISTLM analysis then repeated using only those habitat variables selected for this model. A distance-based redundancy analysis (dbRDA) was included to quantify the associations between habitats and the orthogonal axes generated by the dbRDA. Sites were then qualitatively grouped according to the relationship to the first and second dbRDA axes. The SIMPER routine was used to determine which holothurians characterised the groups derived from the dbRDA.

Standing biomass was estimated by calculating the average density of holothurians per 400 m², for each broad-scale habitat type (from Williams 1994), converting individuals per hectar and then multiplying by the hectares of each habitat type. This was done for all holothurians and then for each economic category (high, medium, low, unknown; Purcell 2010).

RESULTS

Holothurians of the Cocos (Keeling) Islands

Fourteen species of holothurians belonging to 7 genera were recorded on the transects (Table 1), with 4 additional species identified outside the surveyed transects. A total of 20 556 holothurians were identified and counted, with an average density of 3252 individuals ha⁻¹, 97% of these are considered of low commercial value. The most abundant species was *Holothuria atra*, which had a mean density of 2983 individuals ha⁻¹ (±455 SE). Of the 14 species recorded during the survey, only 4 further species had relatively high abundances, albeit significantly lower than *H. atra. Holothuria fuscopunctata* was the second most abundant species, followed by *Synapta*

Table 1. Species, abundance and commercial value of holothurians surveyed at the Cocos (Keeling) Islands. Commercial values of holothurian species are from Purcell (2010). *Species present at the survey sites but outside the area encompassed by the 100 × 4 m transect. Abbreviations of species names in parentheses

Species name	Common name	Commercial value	Mean no. individuals (ha ⁻¹)	SE
Actinopyga mauritiana (KUY)	Surf redfish	Medium	3.6	1.6
Actinopyga miliaris (KUQ)	Hairy blackfish	Medium	0.63	0.5
Bohadschia argus (KUW)	Leopardfish	Low	7.4	2.5
Chiridota rigida (CRI)		Unknown	0.16	0.2
Holothuria atra (HFA)	Lolly fish	Low	2 983	455.4
Holothuria coluber (HHW)	Snake fish	Low	0.16	0.2
Holothuria edulis (HFE)	Pink fish	Low	53.6	17.1
Holothuria fuscopunctata (HOZ)	Elephant trunkfish	Low	100.2	32.7
Holothuria fuscogilva (HFN)	White teatfish	High	0.32	0.2
Pearsonothuria graeffei (EHV)	Flowerfish	Low	1.1	0.8
Stichopus chloronotus (JCC)	Greenfish	Low	36.2	11.0
Stichopus herrmanni (JCV)	Curryfish	Medium	0.63	0.3
Thelenota ananas (TFQ)	Prickly redfish	Medium	0.63	32.6
Synapta maculata (RSF)	Spotted sea cucumber	Unknown	64.4	0.3
Actinopyga echinites*	Deep water redfish	Medium		
Bohadschia marmorata*	Chalkfish	Low		
Holothuria scabra*	Sandfish	High		
Holothuria whitmaei*	Black teatfish	High		

maculata, Holothuria edulis, and *Stichopus chloronotus.* The remaining holothurian species recorded during the survey had sporadic distributions and low abundances. No holothurians were observed at 15 of the 79 sites surveyed (Fig. 1).



Fig. 2. (a) Distance-based redundancy analysis (dbRDA) demonstrating the distributions of habitats by nominal group (A to D; see 'Results'). Habitats are: sand (SND), rubble (RUB), seagrass (SG), macroalgae (MA), massive coral (MC), submassive coral (SM), plate coral (PC), foliose coral (FC), soft coral (SC), branching coral (BC), branching coral dead (BCD), reef flat (RF) and relict reef (RR). (b) dbRDA demonstrating the distributions of species by nominal group (A to D). For species abbreviations see Table 1

Habitats of the Cocos (Keeling) Islands

The fine-scale habitat data were collected at the scale of transects and used for modelling habitat associations. Within the lagoon the primary habitat is sand, with seagrass beds mainly occurring along the eastern and southern sides of the lagoon. In fact, sand was found at 76% of the sites surveyed and accounted for approximately 31% of the habitat. Massive and branching corals were also common, surveyed at 62 and 56% of the sites, respectively, but accounting for only 8 and 6.5% of the cover. Soft corals were less common (42% of sites) and accounted for 11.5% of the cover. Relic reef (13.5%) and reef flats (11.1%) were the other major

habitats with respect to cover, although their distribution was less common (48.1 and 11.4%, respectively).

Habitat preferences of holothurian species

The distance-based linear regression model indicated strong relationships between holothurian assemblages and habitat variables. The most parsimonious model contained 8 of the 13 habitat variables and explained a total of 48% of the variation in holothurians, with no significant colinearity among the habitat variables. The first dbRDA axis accounted for 29.3% of the total variation in the holothurian assemblage and distinguished sites dominated by soft corals and relic reefs from soft bottom communities. The second dbRDA axis accounted for 7.3% of the variation in the holothurian assemblage and largely discriminated living corals from reef flats (Fig. 2a).

Only 4 holothurian species were strongly correlated with the dbRDA axes. *Holothuria atra* was positively correlated with Axis 1, indicating it was positively associated with relic reef and and negatively associated with relic reef and soft corals. Axis 2 indicated *H. atra* was also positively associated with reef flats, but to a lesser extent. *Actinopyga mauritiana* (surf redfish) was negatively correlated with Axis 1, indicating a positive association with relic reefs and soft corals, while the positive correlations of *H. fuscopunctata* and *Stichopus chloronotus* with Axis 2 indicated that they are associated with reef flats.

Sites were then qualitatively assigned to 4 groups based on the distribution of the sites

Site	n	Soft coral	Foliose coral	Plate coral	Relic reef	Reef flat	Branching coral	Massive	Branching dead	Sand	Rubble	Sea- grass	Macro- algae
А	14	36.5	0	0.2	43.3	0	4.2	11.1	0.3	3.2	1.4	0	0
В	7	17.6	15.8	4.7	18.1	0	21.5	9.2	0.9	7	4.5	0	0.5
С	9	0.3	0	0	0	97.7	0	0	0	1.9	0	0	0
D	34	1.1	0	0	3.4	0	2.5	5.6	0	61.8	4.5	6.8	14.1
None	15	15.7	0.4	2.4	13.8	0	14.9	15.2	1.5	16.9	0.6	11.8	6.7

Table 2. Average percentage cover of habitat types across the groups. Grouping according to nominal group (see 'Results')

along the first 2 axes of the dbRDA (Fig. 2). Group A (n = 14) included sites strongly associated with soft coral and relic reefs (Table 2). These sites were moderately similar in terms of the holothurians present (similarity = 22.0) and were characterised by low mean abundance of Holothuria fuscopunctata (Table 3). The habitats of Group B sites (n = 7) were characterised by a wide range of corals (Table 2). In terms of holothurians, they were depauperate, with the lowest levels of abundance and diversity (Table 3): each site appeared to have low numbers of different species, resulting in a low level of similarity (similarity = 17.3). Group C sites (n = 9) were dominated by reef flat habitat (Table 2). These sites were relatively similar (similarity = 52.5) and supported, on average, high abundances of holothurians, the second highest abundances of *H. atra*, and the highest mean abundances of *H. fuscopunctata* and *Stichopus* chloronutus. These sites also had the highest levels of holothurian diversity (Table 3). Individuals in Group D (n = 34) were not associated with hard bottom reef flats or soft corals and relict reef (Fig. 2). Rather, they were characterised by sand and macroalgae (Table 2). They had the highest level of similarity (similarity = 59.7) and the highest abundance of *H*. atra (Table 3). They were also the only sites with Synapta maculata and had the highest abundances of H. edulis. H. fuscopunctata, the second most abundant holothurian in the lagoon was almost absent from the Group D sites (Table 3).

Standing abundance weighted for mean density of holothurians per broad-scale habitat type and the

areal extent of each habitat was estimated at 44.8 million holothurians (with 95% lower and upper confidence limits of 9.9 and 63.3 million) or approximately 3340 individuals ha^{-1} (Table 4). Of these 96.6% are considered to be of low economic value, mostly *Holothuria atra*, an additional 3.3% are of unknown value, while only 0.12% are of medium or high value. The most important habitat for holothurians in the lagoon was coral and algal flats; this habitat was relatively common (13.2%) and supported the highest abundances of holothurians, i.e. 39% of the standing abundance of holothurians (Table 4). Prograding sand sheets comprise only 6.5% of the area, but had the second highest density of holothurians and supported 16% of all holothurians (Table 4). Species of high economic value are found in only 2 habitats outside the lagoon; outer reef coral terrace and coral and algal flats associated with the reef flat. The outer reef coral terrace is relatively extensive (16.3%), but has low densities of holothurians, including economically important species. The coral and algal flats associated with the reef flat are moderately extensive (7.2% of the atoll), with higher densities of holothurians, but economically important species are an order of magnitude lower in abundance than on the outer reef terrace.

DISCUSSION

The current study identified a total of 14 species of holothurians at the sites surveyed, with a further 4 species identified outside the survey sites. A previous survey of holothurians at Cocos (Keeling) Islands identified 34 species of holothurians (Marsh 1994). However, it is difficult to compare the results of the 2 studies as Marsh (1994) focused on identifying species diversity by searching discrete areas, while the current study focused on quantifying the abundance

Table 3. Mean abundances (individuals ha^{-1}) of the 5 most abundant holo-thurians by group

Group	Holothuria atra	Holothuria fuscopunctata	Synapta maculata	Holothuria edulis	Stichopus chloronutus
А	0.29	5.29	0.00	0.14	0.04
В	0.57	0.00	0.00	0.07	0.50
С	112.89	26.83	0.00	0.06	4.78
D	247.16	0.03	5.99	4.90	1.99

Table 4. Standing biomass of holothurians (individuals ha⁻¹) at Cocos (Keeling) Islands by habitat and commercial value. Habitat categories are based on Williams (1994) and commercial values are based on Purcell (2010)

Habitat	Area (ha)	Percent of total	No. ha ⁻¹	No. ha ⁻¹ (lower)	—All holo No. ha ⁻¹ (upper)	thurians — Total no. by habitat	Total no. by habitat (lower)	Total no. by habitat (higher)	— Hold High	othurians b Medium	y commerci Low l	al value— Jnknown
Outer reef flat Coral terrace Reef flat	2186	16.3	146	37	200	318034	81258	436422	1093	24044	289619	3279
Coral and algal flat	961	7.2	3633	153	5374	3491852	146868	5164345	1335	8009	3482509	0
Lagoon Prograding sand sheet Searrass sand and silt flat	872 1295	6.5 0.7	8454 847	1596 0	11883 1310	7375966 1007045	1392750 0	10367574	00	3635 0	7312349 1007045	59982 0
Coral and algal flat Bhie bole mosair 1	1769 215	13.2 7 3	9825 7156	3522 0	12977 12578	17377046 2757777	6228859 0	22951140 3042841		2456 0	17320548	54042 0
Blue Hold Mosaic 2	914 914	0.8 0.8 0	5808 5808	000	9211 9211	5308893 16101	0	8418528 16101		3808	3960724 16101	1344361
Algal covered staghorn rubble	1315	9.8	30 22	0 0	30 43	28767	0	56957	0 0	00	10101 28767	0 0
Massive coral outcrops Sandy lagoon floor with coral Searcase hod (Thalascodondro	1263 685	9.4 5.1	3877 3825	$1496 \\ 214$	5067 5630	4896167 2618872	1889852 146707	6399324 3854955	0 0	2255 4279	4884891 2612454	$9021 \\ 2140$
cilliatum) with coral		0.6	388	388	388	31419	31419	31419	0	0	31419	0
Totals:	13410					44812514	9933893	63336791	2428	48487	43288775	1472825

and distribution of holothurians across the entire atoll using a spatially stratified survey. While Marsh (1994) conducted a qualitative survey, some observations on the abundance of 9 species were made. Marsh (1994) states that Holothuria atra was the most common species; H. nobilis and Thelenota ananas were the most valuable species, but they were not abundant; Actinopyga echinites and A. mauritiana were common to abundant on reef flats; and Bohadschia marmorata, H. scabra and B. argus were also common. With the exception of A. mauritiana, which was not found in the current survey, these statements are reflected in the results of our survey. In contrast, Hender et al. (2001) identified only 8 species of holothurians at Cocos (Keeling) Islands. The higher number of species identified in the current survey, compared to Hender et al. (2001), may reflect the increased spatial coverage of the present survey, which included reef slopes and reef flat habitats.

In the current study, an average total density of 3252 individuals ha⁻¹ was recorded. This is approximately half the density recorded by Hender et al. (2001) of 7512 individuals ha⁻¹. The difference in the density of holothurians between the 2 surveys may be due to the habitats surveyed or survey techniques used. Hender et al. (2001) did not sample the reef flats or crests, which may have resulted in overestimating the abundance of holothurians across the atoll. Similarly, scaling up observations of densities from relatively small areas (i.e. quadrats) to densities on larger scales (e.g. individuals ha⁻¹) may result in overestimations (Andrew & Mapstone 1987). As the 2 studies used different sampling techniques—Hender et al. (2001) surveyed holothurians species within 2×2 m quadrats, while the current study used $100 \times$ 4 m transects — this may also explain some of the variation. Previous studies have also suggested that cryptic or sheltering behaviour is common in holothurians and may lead to biases in abundance estimates (Hammond et al. 1985, Shiell & Knott 2008). However, as the current study used similar methods (surfaceor diver-based observations) and surveys were conducted throughout the day, the contrasts in density estimates may also reflect the natural variability in the abundance of holothurians at the Cocos (Keeling) Islands.

Observed densities in the present study of several holothurian species are higher than those in other locations, i.e. Holothuria atra (Skewes et al. 2002, PNG; Aumeeruddy et al. 2005, Seychelles; Dissanayake & Stefansson 2010, Sri Lanka), Actinopyga mauritiana (Skewes et al. 2002, PNG; NFA 2007, PNG) and H. fuscopunctata (Skewes et al. 2002, PNG; Aumeeruddy et al. 2005, Seychelles; NFA 2007, PNG). However, several species recorded in the current survey had lower densities than those observed in other studies, i.e. H. whitmaei (Skewes et al. 2002, PNG; NFA 2007, PNG), A. echinites (Aumeeruddy et al. 2005; Dissanayake & Stefansson 2010, Sri Lanka). Despite these differences in densities, given the current lack of subsistence or commercial fisheries targeting holothurians, the holothurian population at Cocos (Keeling) Islands represents an unexploited stock in its natural state.

The distribution and abundance of holothurians at the Cocos (Keeling) Islands is closely linked with the distribution and nature of benthic habitats. Previous authors have reported that holothurians exhibit distinct habitat preferences (Uthicke & Benzie 2000, Shiell 2004, Conand 2008, Kinch et al. 2008). For example, populations of Holothuria nobilis in northern Western Australia showed distinct preferences for outer reef zones, specifically, the reef flat and reef crest (Shiell 2004). Other studies have suggested that H. atra has no recognizable pattern of distribution (Massin & Doumen 1986, Shiell 2004); however, in the present study H. atra was primarily found in sand-dominated habitats. These habitats are common, particularly in the lagoon, and, on average, account for 31% of the habitat at Cocos (Keeling) Islands. The distribution of this species may also be due to its relatively unselective feeding habits (Uthicke & Karez 1999). In contrast, H. fuscopunctata and Stichopus chloronotus both displayed a positive relationship with reef flats, with H. fuscopunctata occurring primarily on the outer reef slopes and only a few individuals recorded within the lagoon. On the other hand, S. chloronotus occurs throughout the central region of the atoll. Previous studies have suggested that *Stichopus* spp. appear to select particular sediment types (Uthicke & Karez 1999); therefore, the patchy distribution of S. chloronotus within the lagoon may be a result of its feeding preferences. In the current study there is a distinct link between habitat variables and the abundance and distribution of holothurians; however, other factors may well be contributing to the remaining variation not explained by habitat classification. Environmental drivers such as sediment grain size and organic content, water depth and flow may also be important

drivers of holothurian distributions (Conand & Chardy 1985, Hammond et al. 1985, Uthicke & Karez 1999). Similarly, larval dispersion (Massin & Doumen 1986) recruitment (Purcell 2010) and behaviour (Shiell & Knott 2008) may also affect distribution patterns.

Despite observed patterns between holothurians and habitat, their ecology and population dynamics remain poorly understood and knowledge of the effects of reduced holothurian densities on the ecology of reefs and reef flats is limited. In a rare ecological study, abundance of the sea star Proteaster nodosus increased following a decrease in holothurian numbers due to overfishing (Tomascki et al. 1997). Ecologically, holothurians are an important component of soft bottom communities (Conand 2008) and play an important role in benthic recycling (Uthicke & Klumpp 1998, Uthicke 2001, Mangion et al. 2004). Therefore, decreases in holothurian numbers through overfishing may have a major impact on reef ecology and resilience (Uthicke 2004, Uthicke et al. 2009, Friedman et al. 2010).

Many holothurian fisheries, both tropical and temperate, are in varying stages of overexploitation (Conand 2008, Friedman et al. 2010, Purcell 2010), with limited or no scientific data available on stock size before or after fishing. Holothurians display particular characteristics that make them vulnerable to recruitment overfishing, including sessile, shallow water and patchy distributions. In addition, many holothurian fisheries are based in developing countries, where local communities are dependent on the income but lack the resources to manage these relatively dynamic fisheries (Kinch et al. 2008, Friedman et al. 2010). However, a significant number of holothurian species in countries such as Australia are also overexploited (Kinch et al. 2008). The sandfish Holothuria scabra fishery on Warrior Reef, Torres Strait, was closed in 1998 following several years of high fishing mortality (Skewes et al. 1998). The black teatfish H. whitmaei, formerly H. nobilis) fishery off the east coast of Queensland was closed in 1999 due to overfishing, with stocks on fished reefs reduced to <25% of that observed in areas closed to fishing (Uthicke & Benzie 2000). The sandfish fishery on the east coast of Australia (Hervey Bay) was also closed in 2000 due to a severe stock decline. Fishery-independent surveys have occurred since the closures of these fisheries, and to date there is little evidence of recovery (Skewes et al. 1999, Uthicke et al. 2004b). The conclusion from these Australian fisheries suggests that holothurian abundance can be severely impacted by overfishing and that recovery following such exploitation may be slow.

The Australian holothurian populations at the Cocos (Keeling) Islands are also at risk of overexploitation should a fishery be established. Currently, species of low commercial value (96% of total abundance) such as Holothuria atra are dominant, while species with high commercial value (e.g. H. fuscogilva) are relatively rare (<0.1% total abundance). As the population is unfished, the low abundance, particularly of high-value species, represents natural levels; however, there are few (if any) studies of unfished populations for comparison. High-value species, like H. fuscogilva and H. whitmaei with their low abundances, patchy distributions and prevalence in easily accessible locations (e.g. reef flats), would be highly vulnerable to overexploitation. This is further compounded by the isolation of the atoll, which may result in limited larval input from nonatoll holothurian populations (Hender et al. 2001, Uthicke et al. 2004a). As many of the high-value species are not known to reproduce asexually, a decrease in population numbers of these species from fishing activities may inhibit the population's ability to be self-sustaining (Uthicke et al. 2009). Ultimately this could lead to localised extinction of these species at the Cocos (Keeling) Islands, which could have flow-on effects on the functioning and resilience of the atoll's reef communities.

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