Population trends of remote invertebrate resources in a marine reserve: trochus and holothurians at Ashmore Reef

DANIELA M. CECCARELLI^{1,6*}, MARIA BEGER², MARIE C. KOSPARTOV³, ZOE T. RICHARDS^{4,7} and CHICO L. BIRRELL⁵

Marine protected areas (MPAs) have a high capacity to protect fish and invertebrate resources, given adequate surveillance and enforcement. Ashmore Reef National Nature Reserve (Ashmore Reef) was closed to commercial fishing and harvesting of invertebrates such as trochus (Trochus niloticus) and holothurians in 1983. We evaluate population trends in trochus and holothurians during eight years of monitoring, focusing largely on the differences between their populations before and after a lapse of surveillance. The trochus population increased in density from 1998 to 2005, followed by a slight decline in all surveyed habitats in 2006. This decline followed approximately five consecutive months without surveillance. Amongst populations of 18 species of holothurians, densities declined in five, and remained relatively stable in the others. Densities of commercially valuable holothurians (primarily Holothuria whitmaei and H. fuscogilva) were too low to allow the detection of trends. Continuous enforcement of the fishing closure is important to ensure successful conservation of Ashmore Reef, as are standardized monitoring techniques to enable temporal trends to be detected with confidence.

Key words: Marine Protected Area, Coral Reef, Trochus, Holothurian, Fisheries, Management, Monitoring.

INTRODUCTION

FISHERY stocks are in decline globally, with many already fished to commercial extinction (Zeller and Pauly 2005). Coral reef fisheries are no exception, with over 55% of island countries exploiting their coral reef resources in unsustainable ways (Newton et al. 2007; Rhodes and Tupper 2007). In most regions of the world, coral reef fisheries are shallow water, artisanal, subsistence operations that have been operating for centuries (Jackson 2001). Species commonly targeted in these fisheries include economically valuable macroinvertebrates such as trochus and holothurians, which also play important ecological roles within reef ecosystems (e.g., Uthicke 2001). Recovery of these populations from exploitation can require decades or longer (Bell et al. 2005), especially for rare species or in isolated locations, and exploitation may result in localized ecological extinction (Bell 2008).

MPAs protect invertebrate fisheries directly through the cessation of harvesting pressure and indirectly through wider ecosystem protection (Jones et al. 2007). However in the past, the design of MPA systems has rarely incorporated invertebrate data, and those developed to protect particular taxonomic groups are likely to be inefficient for other taxa (Beger et al. 2007). At present, mollusc and echinoderm stocks are actively managed throughout many parts of the Pacific Ocean (Fagolimul 1987; Smith 1987; Tsutsui and Sigrah 1994; Evans et al. 1997; Foale and Day 1997; Foale 2008), where management efforts are traditionally based on stock assessments through spatial monitoring (Foale and Day 1997).

Trochus (*Trochus niloticus*) and holothurians are highly valued macro-invertebrates, and large declines in population sizes of commercially valuable species have been recorded in the Pacific (Foale and Day 1997; Kinch et al. 2008). Patterns of dispersal of holothurians are poorly understood, making it difficult to predict the fate of depleted populations (Uthicke and Benzie 2003). However, genetic studies of a commercially high-value species, *Holothuria* scabra, have revealed isolated populations over large geographic distances, suggesting poor dispersal capabilities (Uthicke and Purcell 2004). This "isolation-by-distance" phenomenon has been observed for both *H. scabra* and *H. whitmaei* (Uthicke and Benzie 2003; Uthicke et al. 2005). Therefore, it is highly likely that holothurian populations on isolated coral reefs are dependent on self-replenishment, making them more vulnerable to over-exploitation than those on reefs with better connectivity to alternative sources of propagules.

In this paper we synthesize the available information on temporal trends in population densities of trochus and holothurians at Australia's Ashmore Reef National Nature

^{*}Corresponding author

¹C&R Consulting (Geochemical and Hydrobiological Solutions Pty Ltd), PO Box 1777, Thuringowa QLD 4817, dmcecca@gmail.com

The University of Queensland, School of Biological Sciences, The Ecology Centre and Commonwealth Research Facility for Applied Environmental Decision Analysis, Brisbane, QLD 4072, Australia, m.beger@uq.edu.au.

PO Box 532, The Gap, Queensland 4061, Australia. marie.kospartov@mailservice.ms.

ARC Centre of Excellence for Coral Reef Studies and School of Marine and Tropical Biology, James Cook University, Townsville, Australia, zoe.richards@jcu.edu.au.

Australian Institute of Marine Science, 35 Stirling Highway UWA (M096), Crawley WA 6009, Australia, CLBirrell@gmail.com.

Present address: PO Box 215, Magnetic Island QLD 4819, Australia, dueccca@gmail.com.

⁷Present address: Australian Museum, 6 College Street, Sydney, NSW 2010, Australia, zoe.richards@austmus.gov.au

Reserve, and examine in detail the effects of a short period of no surveillance and enforcement (5 months). We discuss the implications for the management of invertebrate resources in the Ashmore Reef National Nature Reserve.

This study focuses on the results of the most recent surveys undertaken by the authors, employing methods as close as possible to those of preceding surveys. We demonstrate the low overall abundance of invertebrate stocks and their further decline within 6 months of the cessation of intensive surveillance. This study also considers data and reports encompassing three previous surveys of Ashmore Reef over a period of eight years (Table A1). Changing monitoring protocols and unstandardized reporting present many data inconsistencies, prohibiting detailed comparisons over longer time frames. Despite this, we are able to contrast short term trends (2005-6) with general longterm trajectories, and we highlight the inadequacy of using data from different sampling strategies for the monitoring of marine reserves.

MATERIALS AND METHODS

Study site

Ashmore Reef National Nature Reserve (12° 17'S, 123° 02' E) encompasses an open ocean platform reef located on the north western extremity of the Sahul Shelf in the Arafura Sea (Eastern Indian Ocean; Fig. 1). Traditional Indonesian fishers have utilized the marine resources and coral cays of Ashmore Reef and nearby reefs since the early eighteenth century (Fox 1988; Commonwealth of Australia 2002). Historically, fishing has primarily targeted holothurians, trochus, giant clams, turtles, sharks and other fishes. Ashmore Reef was declared a MPA in August 1983 and is managed by the Commonwealth Government of Australia with a near-permanent enforcement presence. An Australian customs vessel has been stationed in the Western Lagoon of Ashmore on a permanent basis, with two vessels switching duty on a two-weekly basis. Daily surveillance flights are also made over the reserve. The surveillance provided by the vessel, but not the flights, ceased for a period of 5 months in 2005/2006, but was reinstated in 2006.

STUDY SPECIES

Trochus

Trochus (*Trochus niloticus*) is a gastropod mollusc whose mother-of-pearl shell has been collected for centuries to make buttons, jewellery and other decorative items. Trochus become sexually mature at two to three years of age

when they are between 5.5 cm and 7 cm in basal diameter (Foale and Day 1997). They are a herbivorous, mobile species that can move up to 24 m per day (Crowe *et al.* 2002; Clarke *et al.* 2003). They are found in a range of habitats, but generally require a consolidated substrate with a high degree of habitat complexity (Castell 1997; Skewes *et al.* 1999; Colquhoun 2001).

Holothurians

Holothurians occur throughout the Indo-Pacific and are subject to high fishing pressure in most locations. They are an important component of reef ecosystems, recycling detrital matter and oxygenating the sediment (Uthicke 1994; Uthicke 2001). Sixteen species of holothurians have been recorded at Ashmore Reef (Table 1). Holothurians are valued as food in many Asian cultures and a number of these occur at Ashmore Reef, including five commercially high-value species (Holothuria whitmaei, H. fuscogilva, Stichopus chloronotus, S. hermanii and Thelenota ananas). Some species of holothurians aggregate or display high localized densities (e.g., Rees et al. 2003), and most are habitatspecific (Table 1).

Data collection and analysis

A total of 41 sites were visited in 2005 and 2006. Sites were selected in accordance with previous monitoring sites, located using GPS points and habitat maps published by Skewes et al. (1999), Rees et al. (2003) and Andréfouët et al. (2006), (Fig. 1). Sites were replicated in five habitats: lower reef slope, upper reef slope, spur and groove (described below), reef crest, and reef flat. These habitats were surveyed along the north, south, and east sides of Ashmore Reef, which corresponded to sheltered, exposed and medium-exposed outer reef habitats (the reef has no distinct western side, as it tapers to a point; see Fig. 1) (Table A1).

At each site, trochus and holothurians were counted between the hours of 8:00 am and 5:00 pm using three 500 m \times 5 m belt transects within each habitat (Fig. 1). The length and width of the transects were the same as those used in previous surveys, to facilitate comparisons with the results of those previous surveys (Skewes et al. 1999; Rees et al. 2003). Reef flat and crest transects (depth: 0.5-2 m) were swum on snorkel, while deeper slope and lagoonal transects (depth: 8-10 m) were swum on SCUBA. Each transect was swum by one observer, at a pace that allowed the scanning of the entire belt and the detection of trochus in complex reef crest and upper slope habitats. All holothurians and trochus present within the transect were recorded (holothurians to species level) and basal shell widths of all trochus were measured.

Table 1. Commercial value and habitat preference of sea cucumber species recorded at Ashmore Reef (after Skewes *et al.* 1999, Gayfer and Saunders 2003, P. Purwati, pers. comm.; Gayfer and Saunders 2003)

Species	Market value	Habitat preference
Holothuria whitmaei	High	Sandy areas of reef flats, slopes and shallow seagrass beds
Holothuria scabra	High	Inner reefs flats; burrows in sandy-muddy bottoms
(last seen in 1978)	8	, , ,
Holothuria fuscogilva	High	Oceanic-influenced lagoons and passes
Holothuria lessoni	High	Outer lagoons
(last seen in 1857)	8	O
Stichopus chloronotus	Medium to high	Reef flats and upper slopes on hard substrates
Stichopus hermanii	Medium to high	Seagrass beds, rubble and sandy-muddy bottoms
Thelenota ananas	Medium to high	Reef slopes and near passes, rubble and sandy bottom
Actinopyga lecanora	Medium	Hard substrates, nocturnal
Actinopyga mauritiana	Medium	Outer reef flats on hard substrates, mostly in the surf zone
Actinopyga miliaris	Medium	Low densities in deeper oceanic waters, nocturnal
Holothuria atra	Low	High densities in shallow lagoonal waters, on sand
Holothuria coluber	Low	Shallow lagoon
Holothuria leucospilota	Low	High densities in shallow lagoonal waters, on sand
Holothuria edulis	Low	Inner reef flats, on sandy-mussy ground with coral or rubble patches
Holothuria fuscopunctata	Low	Reef slopes and shallow seagrass beds
Holothuria fuscorubra	Low	Sandy lagoon
Bohadschia argus	Low	Outer lagoons on white sand
Pearsonothuria graeffei	Low	Reef slopes
Bohadschia vitiensis	Low	Reef slopes on sand
Thelenota anax	Low	Rubble and sand patches on reef slopes, outer lagoons and near
		passes

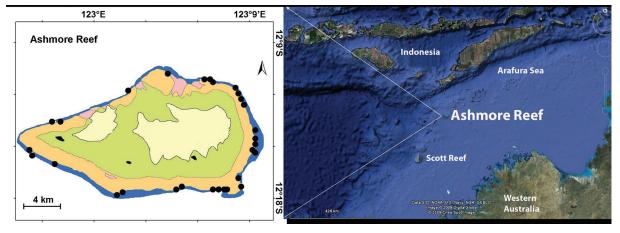


Fig. 1. Location of Ashmore Reef within the regional setting of Western Australia, and the locations of 2005 and 2006 sampling sites (black circles) around the perimeter of the reef. Blue: reef slope, orange: reef crest and flat, green: intertidal reef flat, yellow: sandy lagoons, pink: channels. Habitat classification modified from Millennium coral project (Andréfouët 2005).

Count data for each transect were converted to densities (individuals per hectare) for ease of comparison among surveys, and ANOVA tests were conducted to compare trochus and holothurian densities between habitats and years. Assumptions of normality and homogeneity of variance were examined through the Šhapiro-Wilks Test and Levene's Test, respectively (Zar 1999). Data that did not meet these assumptions of ANOVA were log₁₀-transformed. The highly complex, wave-swept spur and groove habitat on the outer edge of the reef was recognized as a discrete habitat only in the trochus analyses, as trochus appear to recognize and favour this habitat (Rees et al. 2003; Kospartov et al. 2006), but holothurians do not.

This study focuses on the results of the most recent surveys undertaken by the authors, employing methods as close as possible to those of preceding surveys. We demonstrate the low overall abundance of invertebrate stocks and their further decline within six months of the cessation of intensive surveillance ceased. This study also considers data and reports encompassing three previous surveys of Ashmore Reef over a period of eight years (Table A1). Changing monitoring protocols and unstandardized reporting present many data inconsistencies, hindering the precise interpretation of (and comparison to) earlier surveys. Despite this, this study contrasts short term trends (2005-6) with a long-term trajectory, and

highlights the inadequacy of using data from different sampling strategies for the monitoring of marine reserves.

RESULTS

Trochus

The estimated reef-wide density of trochus declined between 2005 and 2006 (37.7 to 23.75 ind ha⁻¹; $F_{1,130} = 5.75$, p < 0.05) (Table 2). Densities differed significantly among habitats $(F_{2,122} = 3.36, p < 0.05)$, but declines were consistent between years (ANOVA Year × Habitat, $F_{2,122} = 2.39$, NS). The decline was most pronounced in the spur and groove habitat, while variability in the other habitats meant that the differences were less pronounced (Fig. 2). High trochus densities were found most consistently in the vicinity of the reef crests, particularly where high topographic complexity was provided by deep grooves in the reef framework (the "spur and groove" habitat). In 2005, the highest densities were found just above the crest (on the reef flat), while in 2006

densities were higher just below the crest (on the upper reef slope). The reef slopes supported generally low numbers with the occasional aggregation (Fig. 2).

High variability distinguished the long-term temporal trends in trochus density, even when comparisons were consistently split between "high-density" southern sites and "low-density" northern and eastern sites (Fig. 3). The long-term trends of reef-wide trochus densities between 1999 and 2005 suggest a general density increase prior to 2006. A thorough meta-analysis between reports was hindered by variable reporting styles and categorizations of habitat, preventing a detailed statistical analysis between all years.

Holothurians

Holothurians were recorded in all habitats, with the highest densities found in areas of the lagoon, the reef crest and reef flat. When all species were combined there was no significant difference in reef-wide holothurian densities

Table 2. ANOVA tests for trochus density between years, habitats and sides of Ashmore Reef. The test was conducted on the differences between the years 2005 and 2006. *Degrees of freedom (df) are given in the format of "numerator,denominator". Significant results (p<0.05) are presented in bold.

Test	Factor	df(x,y)*	F	р
Year by habitat	Year	1,122	11.369	0.001
	Habitat	4,122	3.048	0.020
	Year x Habitat	4,122	2.159	0.045
Year by reef side	Year	1,124	9.375	0.003
	Reef Side	2,124	1.657	0.195
	Year x Reef Side	2,124	0.57	0.994

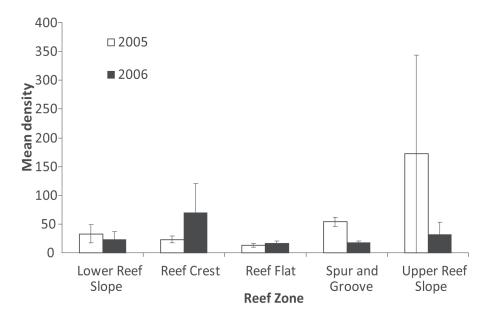


Fig. 2. Estimated trochus density (ind ha⁻¹) at Ashmore Reef in a) 2005 and b) 2006 for each site-by-habitat combination. NS = not surveyed.

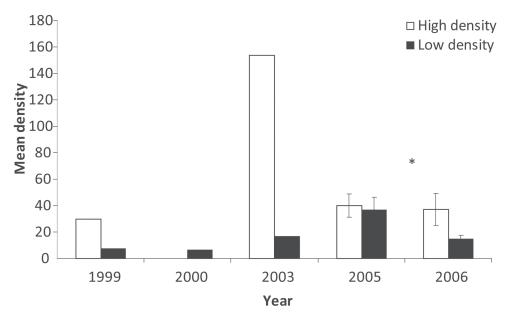


Fig. 3. Comparison of estimated mean trochus densities (ind ha¹) for surveyed habitats between years for Ashmore Reef. "High-density" sites were those on the southern exposed side of Ashmore Reef, as determined in 2003, while "low-density" sites are on the sheltered eastern and northern sides. Error bars (+/- 1 S.E.) are shown when they were reported. The asterisk indicates a significant difference between 2005 and 2006 – see Table 2.

between 2005 (1.58 \pm 0.87 SE) and 2006 (1.69 \pm 1.26 SE) (F_{1.219}=0.96, NS).

Holothurian community composition did not change significantly between the 2005 and 2006 surveys (MANOVA $F_{36,21}$ = 0.91, p = 0.74). The holothurian community at Ashmore Reef was dominated by two common species that are both capable of asexual reproduction by fission (H. atra and Stichopus chloronotus) while the majority of other species had very small population sizes (Fig. 4). Twelve species (H. whitmaei, Thelenota ananas, T. anax, S. hermanii, Actinopyga mauritiana, H. fuscopunctata, Bohadschia argus, H. fuscogilva, B. vitiensis, A. lecanora, A. aff. miliaris, H. fuscorubra) were present in very low densities and are likely to be below the minimum viable population size (Bell 2008). For example, for H. whitmaei has a mean density of above 12.5 ind ha⁻¹ is considered viable (Kinch et al. 2008).

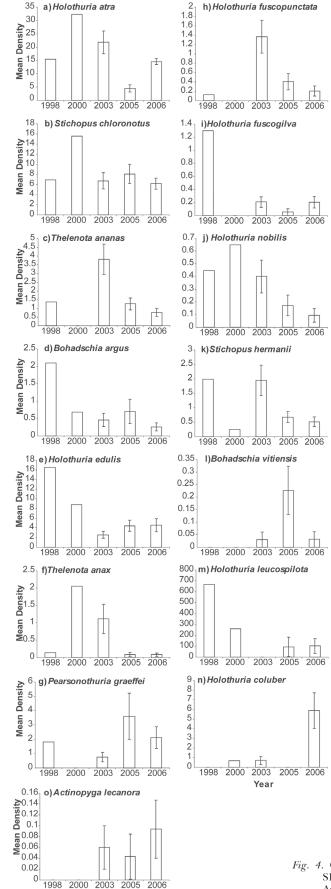
Within the statistical limitations of very low densities, surveys suggested a decline in several species in the past few years. Reef-wide Holothuria atra densities declined from ca. 32 ind ha⁻¹ in 2000 to 15 ind ha⁻¹ in 2006. Holothuria fuscopunctata occurred in extremely low densities throughout the study, but recent years have seen a decline from 1.4 ind ha-1 in 2003 to 0.2 ind ha-1 in 2006. Stichopus chloronotus densities peaked at over 15 ind ha-1 in 2000, but have remained largely constant around 7 ind ha-¹ during the last five years. H. fuscogilva peaked at the already very low 1.4 ind ha-1 in 1998, and was recorded at densities of below 0.2 ind ha-1 during the last 5 years. H. whitmaei, a commercially high value species, occurred at around 0.5 ind ha⁻¹ during the late 1990s and in 2000. Since then, densities have dropped to 0.1 ind ha⁻¹. However, these extremely low numbers were often based on a single individual that was recorded, and mostly illustrate the extremely low population size of these species rather than presenting a reliable trend.

DISCUSSION

A positive trend in the trajectory of trochus density was present up until 2005, and a decline is evident in the following year. This decline coincides with the temporary cessation of MPA enforcement for 5 months in 2006, which raises the possibility that populations were subject to fishing pressure during that time. Holothurian populations at Ashmore Reef are characterized by very low population sizes. Most have been depleted to the point where recovery is either proceeding very slowly, or may require assistance (Bell 2008). No further declines were detected during the 2005 to 2006 interval, likely due to the already low densities.

Trochus

Long-term trends suggest that MPA enforcement had a positive long-term effect on trochus population density, and several factors could have contributed to the decline in numbers recorded in 2006. Firstly, the density differences could be due to the aggregating and migrating behaviour of trochus, whereby the aggregations recorded in 2005 were not encountered in 2006, although they may have still existed somewhere on the reef. This is considered a realistic



Year

Fig. 4. Comparisons of mean density (± SE) of holothurians (ind ha⁻¹) at Ashmore Reef between surveys. Note the different y-axes for each species.

possibility, as the aggregations described in 2003 were not found in 2005, despite using the same sites marked with GPS points, and covering a large area at each site.

Secondly, illegal harvesting may have occurred during the temporary absence of surveillance and enforcement during the first half of 2006. Ashmore Reef has been subject to historic fishing pressure (Skewes *et al.* 1999), and anecdotal evidence of events of non-compliance with fishing closures has been recorded (Australian Customs Service, pers. comm.).

Thirdly, region-wide trochus harvesting continues on unprotected reefs in the Arafura Sea, potentially contributing to the overall depletion of the regional trochus resource pool (Gayfer and Saunders 2003; Department of Primary Industries Australia 2008). Coral reefs in the region surrounding Ashmore Reef, with the exception of Cartier Reef (also a marine reserve), are subject to continuing exploitation. The sources of larvae for Ashmore Reef are currently unknown, but many isolated reefs are largely reliant on self-seeding (Ayre and Hughes 2004). Small local populations together with depleted regional stocks are likely to slow the recovery of the trochus population at Ashmore Reef. Research indicates that trochus stocks are vulnerable to over-exploitation (Castell 1997), but may be more resistant to population collapse than other commercially valuable invertebrates (Foale 2008). Depleted populations can be replenished from remnants in deeper areas or on high-energy reef crests that are difficult to access for fishing in rough weather. Trochus recruits were present in reef flat habitats, but had not yet migrated to their adult habitats in the 2006 survey.

Trochus density was habitat and depth specific, with some less accessible habitats such as the exposed spur and groove and the deeper reef slopes providing a "refuge" from exploitation, as previous studies have suggested (Castell 1997; Skewes *et al.* 1999; Colquhoun 2001). The habitat-specific patterns added a degree of complexity to the trends of trochus populations. The most marked difference between years was

in reef crest densities on the southern side, driven by a very high density in 2003 and highlighting the propensity for trochus to aggregate (Castell 1997; Lincoln-Smith et al. 2006). Trochus aggregations at Ashmore Reef have been observed previously (e.g., Rees et al. 2003) for both juveniles and adults in their preferred habitats of shallow reef flats and complex reef crests, respectively (Castell et al. 1996; Castell 1997). Habitat characteristics such as algal types, sediment loads and quality of refugia can strongly influence aggregation sites, numbers and growth rates (Purcell et al. 2004). Since it is impossible to survey the entire reef, it is highly likely that some aggregations are missed in each monitoring cycle. Trochus are reported to move up to 24 m in a day (Crowe et al. 2002; Clarke et al. 2003), and there is evidence that movement occurs from the reef flat towards the reef crest upon reaching a certain size threshold or sexual maturity (Castell 1997).

Populations with patchy distributions require sampling at the appropriate scale, so that each sampling unit intercepts at least one aggregation. A further limitation for the assessment and prediction of population recovery of invertebrates is the lack of consistent comparisons with unprotected reefs in the region. In four transects at Scott Reef South, trochus exhibited very low densities of 0.05 ind ha-1 (Skewes et al. 1999), almost 20-fold lower than the densities recorded at Ashmore Reef during the same surveys. No other published estimates exist with which to evaluate the effects of protection on spatial and temporal dynamics of trochus stocks relative to other possible factors affecting these dynamics (but see Table 3).

Despite the limitations posed by dynamic trochus distributions, the data for 2005 and 2006 are likely to have the same systematic errors because a large number of sites were surveyed, the same sites were visited, and the same methods were utilized. Therefore, the statistically significant difference in trochus density between 2005 and 2006 probably documents a real decline over this period.

Table 3. Comparison of *Trochus niloticus* densities for different localities, reefs and habitats in the Indo-Pacific. N/A: Not available.

Location	Habitat	Protection Level	Publication	Mean density (ind ha ⁻¹)
Orpheus Island,	Inner reef flat,	GBRMPA Scientific	(Castell 1997)	1,150-1,780
Inner GBR	juveniles	Research Zone – No-take		
Swains Group, outer GBR	Exposed reef crest	N/A	(Nash 1993)	761
Guam	Outer reef flat	No protection	(Smith 1987)	30 - 123
Kosrae	Shallow reef slope	No protection	(Tsutsui and Sigrah 1994)	1,290
Guam	Not stated	N/A	(Nash 1993)	65-1,015
New Caledonia	Not stated	N/A	(Nash 1993)	8,050

Holothurians

Over the last 8 years of surveys at Ashmore Reef, densities of holothurians have potentially declined for eleven species, and densities were extremely low for commercially high-value species, rendering a statistical comparison hard to interpret. The population densities of a few species fluctuated without evidence of consistent trends, but with consistently low density values. This is especially true of commercially high-value species, such as *Holothuria whitmaei* and *H. fuscogilva*. Despite being highly diverse (18 species were recorded in the most recent surveys), the holothurian community is numerically dominated by two commercially low-value species.

Holothurian life history characteristics, especially high recruitment variability, make them prone to overharvesting. Population decline that shows little or no recovery despite subsequent protection has been previously documented (Uthicke et al. 2009). The failure of population replenishment through recruitment for those species that only reproduce sexually can result in a shift to a community dominated by species that can reproduce asexually by fission, as seen in this study. To replenish communities of holothurians at Ashmore Reef, connectivity with outside sources of propagules is vital (Jones et al. 2007), yet populations on the surrounding unprotected reefs in the Arafura Sea are also highly depleted. Moreover, fishing effort is likely to be displaced by the MPA to reefs nearby (Richardson et al. 2006), thus further depleting regional larval sources (Hilborn et al. 2004; Hilborn et al. 2006). Some species on Ashmore Reef may be depleted beyond recovery, as sexually reproducing populations are likely to be highly self-recruiting.

CONCLUSIONS

Monitoring provides a measure of the success of management actions (Gerber et al. 2005). The use of the same methods and survey sites between the 2005 and 2006 surveys facilitated the identification of complex spatio-temporal dynamics within the mobile invertebrate populations at Ashmore Reef. While on-site surveillance temporarily ceased in 2006, the ensuing reports of fishing vessels sighted by aerial surveillance prompted a management response and reactive monitoring. Reactive monitoring greatly increases the chances that causes and effects of disturbance events can be detected and understood, and adaptive responses such as increasing enforcement efforts help to ensure that the MPA is better protected.

Ensuring that monitoring protocols are consistent in terms of sites and methods is paramount, especially in the near future as there is a need to identify the nature of the response of populations to management actions (i.e., increased surveillance and enforcement). Additionally, some invertebrate populations (eg. trochus) can respond well to protection from exploitation (Foale 2008). However, the future of invertebrate populations at Ashmore Reef is ultimately dependent on continued active management, particularly because this area is far from the public eye.

ACKNOWLEDGEMENTS

We thank the Department of the Environment, Water, Population and Communities for facilitating the surveys, and the crew of the Patrol Vessel Walcott for providing transportation and assistance in the field. We also thank S. Kropman, M. Maly, R. Basham and N. Gemmell for helpful discussions during the preparation of this manuscript, and R. Gimin who provided expert advice on the Indonesian trochus market.

REFERENCES

- Andréfouët, S., 2005. Institute for Marine Remote Sensing (IMaRS) Millennium Coral Reef Mapping Project. http://imars.usf.edu/corals/
- Andréfouët, S., Muller-Karger, F. E., Robinson, J. A., Kranenburg, C. J., Torres-Pulliza, D., Spraggins, S. A. and Murch, B., 2006. Global assessment of modern coral reef extent and diversity for regional science and management applications: a view from space. 10th Int. Coral Reef Symp., Japan.
- Ayre, D. J. and Hughes, T. P., 2004. Climate change, genotypic diversity and gene flow in reef building corals. *Ecol. Lett.* 7: 273–278.
- Beger, M., McKenna, S. A. and Possingham, H. P., 2007. Effectiveness of surrogate taxa in the design of coral reef reserve systems in the Indo-Pacific. *Cons. Biol.* 21: 1584–1593.
- Bell, J. D., Rothlisberg, P. C., Munro, J. L., Loneragan, N. R., Nash, W. J., Ward, R. D. and Andrew, N. L., 2005. Restocking and stock enhancement of marine invertebrate fisheries. *Adv. Mar. Biol.* 49: 1–370.
- Bell, J. J., 2008. Connectivity between island Marine Protected Areas and the mainland. *Biol. Cons.* 141: 2807–2820.
- Castell, L. L., 1997. Population studies of juvenile *Trochus niloticus* on a reef flat on the northeastern Queensland coast, Australia. *Mar. Freshw. Res.* **48**: 211–217.
- Castell, L. L., Naviti, W. and Nguyen, F., 1996. Detectability of cryptic juvenile *Trochus niloticus* Linnaeus in stock enhancement experiments. *Aquaculture* 144: 91–101.
- Clarke, P. J., Komatsu, T., Bell, J. D., Lasi, F., Oengpepa, C. P. and Leqata. J., 2003. Combined culture of *Trochus niloticus* and giant clams (Tridacnidae): benefits for restocking and farming. *Aquaculture* 215: 123–144.
- Colquhoun, J. R., 2001. Habitat preferences of juvenile trochus in Western Australia: implications for stock enhancement and assessment. *SPG Trochus Information Bulletin* **7**: 14–20.
- Commonwealth of Australia, 2002. Ashmore Reef National Nature Reserve and Cartier Island Marine Reserve Management Plans. Environment Australia, Canberra.

- Crowe, T. P., Lee, C. L., McGuinness, K. A., Amos, M. J., Dangeubun, J., Dwiono, S. A. P., Makatipu, P. C., Manuputty, J., Nguyen, F., Pakoa, K. and Tetelepta, J., 2002. Experimental evaluation of the use of hatcheryreared juveniles to enhance stocks of the topshell *Trochus niloticus* in Australia, Indonesia and Vanuatu. Aquaculture 206: 175–197.
- Department of Primary Industries Australia, 2008. Annual status report 2007 East Coast Trochus Fishery. Department of Primary Industries and Fisheries, Brishane
- Evans, S. M., Gill, M. E., Retraubun, A. S. W., Abrahamz, J. and Dangeubun, J., 1997. Traditional management practices and the conservation of the gastropod (*Trochus nilitocus*) and fish stocks in the Maluku Province (eastern Indonesia). Fish. Res. 31: 83–91.
- Fagolimul, J., 1987. A survey of Yap outer islands recently seeded with Trochus. Yap State Marine Resources Division.
- Foale, S. 2008., Appraising the resilience of trochus and other nearshore artisanal fisheries in the Western Pacific. SPC Trochus Information Bulletin 14: 12–15.
- Foale, S. and Day, R., 1997. Stock assessment of trochus (*Trochus niloticus*) (Gastropoda: Trochidae) fisheries at West Nggela, Solomon Islands. *Fish. Res.* **33**: 1–16.
- Fox, J., 1988. Reefs and Shoals in Australia-Indonesian Relations: Traditional Indonesian Fisherman. in Australia in Asia: Episodes ed by A. Milner and M. Quilty. Oxford University Press, Melbourne.
- Gayfer, G. and Saunders, K., 2003. A Report on Operation Snapshot. Australian Fisheries Management Authority and Department of Fisheries, Perth.
- Gerber, L. R., Beger, M., McCarthy, M. A. and Possingham, H. P., 2005. A theory for optimal monitoring of marine reserves. *Ecol. Lett.* 8: 829–837.
- Hilborn, R., Micheli, F. and De Leo, G. A., 2006. Integrating marine protected areas with catch regulation. Can. J. Fish. Aquat. Sci. 63: 642–649.
- Hilborn, R., Stokes, K., Maguire, J. J., Smith, T., Botsford, L. W., Mangel, M., Orensanz, J., Parma, A., Rice, J. and Bell, J., 2004. When can marine reserves improve fisheries management? *Ocean Coast. Manage.* 47: 197– 205.
- Jackson, J. B. C., 2001. What was natural in the coastal oceans? *Proc. Nat. Acad. Sci. U. S. A.* **98**: 5411–5418.
- Jones, G. P., Srinivasan, M. And Almany, G. R., 2007. Population connectivity and conservation of marine biodiversity. *Oceanography* 20: 100–111.
- Kinch, J., Purcell, S., Uthicke, S. and Friedman, K., 2008. Population status, fisheries and trade of sea cucumbers in the Western Central Pacific. Pp 7-55 *in* Sea cucumbers. A global review of fisheries and trade ed by V. Toral-Granda, A. Lovatelli and M. Vasconcellos. FAO Fisheries and Aquaculture Technical Paper. No. 516, Rome.
- Kospartov, M., Beger, M., Ceccarelli, D. And Richards, Z., 2006. An assessment of the distribution and abundance of sea cucumbers, trochus, giant clams, coral, fish and invasive marine species at Ashmore Reef National Nature Reserve and Cartier Island Marine Reserve: 2005. Report for the Department of the Environment and Heritage by UniQuest Pty Ltd, Brisbane.
- Lincoln-Smith, M. P., Pitt, K. A., Bell, J. D. and Mapstone, B. D., 2006. Using impact assessment methods to determine the effects of a marine reserve on abundances and sizes of valuable tropical invertebrates. Can. J. Fish. Aquat. Sci. 63: 1251–1266.

- Nash, W. J., 1993. Trochus. Pp 452-495 in Nearshore Marine Resources of the South Pacific. Ed by A. Wright and L. Hill. International Centre for Ocean Development, Fiji.
- Newton, K., Cote, I. M., Pilling, G. M., Jennings, S. and Dulvy, N. K., 2007. Current and future sustainability of island coral reef fisheries. *Curr. Biol.* 17: 655–658.
- Purcell, S. W., Amos, M. J. And Pakoa K., 2004. Releases of cultured sub-adult *Trochus niloticus* generate broodstock for fishery replenishment in Vanuatu. *Fish. Res.* 67: 329–333.
- Rees, M., Colquhoun, J., Smith, L. and Heyward, A., 2003. Surveys of Trochus, Holothuria, giant clams and the coral communities at Ashmore Reef, Cartier Reef and Mermaid Reef, Northwestern Australia: 2003. Report Produced for the Department of Environment and Heritage by AIMS, Townsville.
- Rhodes, K. and Tupper, M., 2007. A preliminary market-based analysis of the Pohnpei, Micronesia, grouper (Serranidae: Epinephelinae) fishery reveals unsustainable fishing practices. *Coral Reefs* **26**: 335-344.
- Richardson, E. A., Kaiser, M. J., Edwards-Jones, and Possingham, H. P., 2006. Sensitivity of marine-reserve design to the spatial resolution of socioeconomic data. *Cons. Biol.* **20**: 1191–1202.
- Skewes, T. D., Dennis, D. M., Jacobs, D. R., Gordon, S. R., Taranto, T. J., Haywood, M., Pitcher, C. R., Smith, G. P., Milton, D. and Poiner, I. R., 1999. Survey and stock size estimates of the shallow reef (0-15 m deep) and shoal area (15–50 m deep) marine resources and habitat mapping within the Timor Sea MOU74 Box. CSIRO Marine Research, Hobart.
- Smith, B. D., 1987. Growth rate, distribution and abundance of the introduced topshell *Trochus niloticus* Linnaeus on Guam, Mariana Islands. *Bull. Mar. Sci.* 41: 466–474.
- Tsutsui, I. and Sigrah, R., 1994. Natural broodstock resources in Kosrae, Federated States of Micronesia. *Trochus Information Bullettin* **3**: 9-11.
- Uthicke, S., 1994. Distribution patterns and growth of 2 reef flat holothurians, *Holothuria atra* and *Stichopus chloronotus*. *Echinoderms through time: 8th Int. Echinoderm Conf.*: 569–576.
- Uthicke, S., 2001. Nutrient regeneration by abundant coral reef holothurians. J. Exp. Mar. Biol. Ecol. 265: 153–170.
- Uthicke, S. and Benzie, J. A. H., 2003. Gene flow and population history in high dispersal marine invertebrates: mitochondrial DNA analysis of *Holothuria nobilis* (Echinodermata: Holothuroidea) populations from the Indo-Pacific. *Mol. Ecol.* 12: 2635–2648.
- Uthicke, S. and Purcell, S., 2004. Preservation of genetic diversity in restocking of the sea cucumber Holothuria scabra investigated by allozyme electrophoresis. *Can. J. Fish. Aquat. Sci.* **61**: 519–528.
- Uthicke, S., Purcell, S. and Blockmans, B., 2005. Natural hybridization does not dissolve species boundaries in commercially important sea cucumbers. *Biol. J. Linn. Soc.* **85**: 261–270.
- Uthicke, S., Schaffelke, B. and Byrne, M., 2009. A boombust phylum? Ecological and evolutionary consequences of density variations in echinoderms. *Ecol. Monogr.* **79**: 3–24.
- Zar, J. H., 1999. Biostatistical Analysis. Prentice Hall, New Jersey.
- Zeller, D. and Pauly, D., 2005. Good news, bad news: global fisheries discards are declining, but so are total catches. *Fish Fish.* **6**: 156–159.