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Enigmatic declines of Australia's sea snakes from a biodiversity hotspot

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ABSTRACT

Declines in the abundance of marine vertebrates are of considerable concern, especially when they occur in isolated locations relatively protected from most major anthropogenic disturbances. This paper reports on sustained declines in the abundance and diversity of sea snakes at Ashmore Reef, a renowned biodiversity hotspot in Australia's Timor Sea. Surveys conducted in eight years between 1973 and 2010 recorded the highest abundances (average 42–46 snakes day^{-1}) and species richness (nine species) in 1973 and 1994. In 2002 abundance had declined by more than 50% (21 snakes day^{-1}) and only five species were recorded. Since 2005 abundances have been consistently low (1–7 snakes day^{-1}), with just two species, *Aipysurus laevis* and *Emydocephalus annulatus*, recorded in significant numbers. Despite extensive searches since 2005 (especially in 2010) five species of sea snake historically abundant at Ashmore Reef have not been sighted and are presumed to have become locally extinct. These species include three Timor Sea endemics *Aipysurus apraefrontalis*, *Aipysurus foliosquama*, *Aipysurus fuscus*, and one Australasian endemic *Aipysurus duboisii*. Declines in the abundance and diversity of sea snakes at Ashmore Reef cannot be attributed to differences in survey methods among years. Ashmore Reef was declared a National Nature Reserve (IUCN Category 1a) in 1983 and, although the causes for the declines are not known, this protection has not prevented their occurrence. We discuss possible causes for these enigmatic declines however, in order to implement effective management strategies, studies are needed to determine why sea snakes have disappeared from Ashmore Reef.

1. Introduction

Biodiversity is globally threatened, in part due to the widespread declines in the distribution and abundance of many vertebrate populations (Hoffmann et al., 2010). In many cases population declines can be directly attributed to know causes, most commonly habitat loss/change and over-exploitation (Böhm et al., 2013; Gibbons et al., 2000; Stuart et al., 2004), which tend to be the focus of conservation actions. However, broad-scale and difficult to manage threats, such as climate change (Thomas et al., 2004) and disease (Pounds et al., 2006), are becoming increasingly important drivers of declining population abundances and biodiversity losses. Nonetheless, enigmatic population declines also occur (Stuart et al., 2004) despite the presence of suitable habitats and/or protection, and for which the causes are uncertain or unknown (Gibbons et al., 2000; Winne et al., 2007). These declines are of particular concern as they suggest the presence of underlying threatening processes that are cryptic and undetected, and therefore not being dealt with effectively by current conservation and management strategies.

A recent evaluation of extinction risk for the world's reptiles found that nearly one in five species is threatened with extinction (i.e. listed in the IUCN Red List Categories Vulnerable, Endangered or Critically Endangered, IUCN, 2001) and another one in five is classified as Data Deficient (Böhm et al., 2013). Moreover extinction risk is generally higher in the tropics and in aquatic habitats (Böhm et al., 2013). Although snakes were among the least threatened groups of reptiles (Böhm et al., 2013), there is evidence that terrestrial snake populations around the world have undergone declines over the past 10–15 years, with many declines occurring in well-protected locations (Reading et al., 2010; Winne et al., 2007). The cause(s) for these declines are currently unknown but the synchronous and precipitous nature of many declines suggests a possible mechanism of declining habitat quality and/or prey availability in terrestrial environments leading to reduced carrying capacity (Reading et al., 2010; Winne et al., 2007).

True sea snakes (Elapidae; Hydrophiinae) are viviparous predatory marine reptiles that occur in tropical and subtropical shallow-water habitats (<200 m) in many locations throughout the

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Indo-West Pacific. There are >60 species in 13 nominal genera (Lukoschek and Keogh, 2006) (but see Sanders et al., 2013), with the highest species diversity occurring in the tropical coastal waters of Australia (>30 species representing most nominal genera) (Cogger, 2000; Elfes et al., 2013), Malaysia and Indonesia (Elfes et al., 2013; Heatwole, 1999), with new species continuing to be described in Australia (Sanders et al., 2012; Ukuwela et al., 2013; Ukuwela et al., 2012). True sea snakes comprise two major evolutionary lineages: the *Aipysurus* lineage (11 species in 2 genera – *Aipysurus* and *Emydocephaus*), and the *Hydrophis* lineage (>45 species in 11 nominal genera) (Lukoschek and Keogh, 2006). Each lineage is represented by both widespread and endemic species, but patterns of distribution and endemism differ markedly between the two lineages. Eight of the 11 species in the *Aipysurus* lineage are restricted to Australasian waters (Cogger, 2000; Elfes et al., 2013), whereas species diversity in the *Hydrophis* lineage is highest in SE Asia, with just 15 species reliably reported from Australian waters, five of which appear to be Australasian endemics (Cogger, 2000).

The Timor Sea, which extends from Australia's north-west coast to the southern coast of Timor, has long been renowned as a sea snake biodiversity hotspot (Guinea and Whiting, 2005; Minton and Heatwole, 1975; Smith, 1926), with historical records indicating that about one quarter (14/60) of the world's species of hydrophiine sea snakes occur in its waters (Cogger, 2000; Guinea and Whiting, 2005; Minton and Heatwole, 1975). Ashmore Reef is the largest of five isolated reefs in the Timor Sea and all 14 sea snake species known from the Timor Sea have been recorded at Ashmore Reef (Table 1) (Cogger, 2000). While some species are vagrants, at least nine species have maintained resident breeding populations on this isolated reef system (Cogger, 2000; Guinea and Whiting, 2005; Minton and Heatwole, 1975) (Table 1). As early as 1926, Malcolm Smith (1926) in his '*Monograph of Sea Snakes*' commented on the high diversity and abundance of sea snakes at '*the Ashmore Reefs*'. In 1973 researchers from the RV Alpha Helix collected more than 350 sea snakes from nine species in less than two weeks at Ashmore Reef and 'many more were observed' (Minton and Heatwole, 1975), while in 1994 (Guinea and Whiting, 2005) estimated a standing stock of almost 40,000 sea snakes on the 174 km^2 reef flat of Ashmore Reef.

In addition to the high species diversity and abundance, there are high levels of endemism at Ashmore Reef. Half of the species (3/6) from the *Aipysurus* lineage recorded from Ashmore Reef (Minton and Heatwole, 1975; Smith, 1926) are restricted to the Timor Sea. These endemics almost certainly evolved in the Timor Sea (Lukoschek and Keogh, 2006; Lukoschek et al., 2007b), highlighting the pivotal role this region has played in the evolutionary history of the *Aipysurus* lineage. Moreover, four of the nine resident species and three of the five vagrant species (Table 1) are Australasian endemics (Cogger, 1975, 2000). Population genetic studies for the Australasian endemic, *Aipysurus laevis*, documented much higher genetic diversity in the Timor Sea than in all other parts of its Australian range for both nuclear microsatellites and mitochondrial sequence data (Lukoschek et al., 2007b, 2008) making the Timor Sea reefs critical for generating and maintaining sea snake biodiversity at both inter- and intra-specific levels.

The *Aipysurus* and *Hydrophis* lineages differ in their preferred habitat types. Most *Hydrophis* lineage species occur in inter-reefal soft sediment habitats, whereas seven of the 11 species from the *Aipysurus* lineage occur almost exclusively in coral reef habitats (Cogger, 2000; Heatwole, 1999). Resident species at Ashmore Reef include representatives from both lineages (Table 1), which

Table 1
Sea snake species recorded on Ashmore Reef in the Timor Sea. Resident species refers to species that typically occur on coral reefs and were seen at Ashmore in the 1920s and between the early 1970s and the late 1990s. Vagrant species are those that have only been recorded occasionally at Ashmore Reef over the past 100 years and that typically occur in non-reef soft sediment habitats. Habitat and depth ranges are those where species are typically known to occur and based on McCosker (1975). Diet information was obtained from Fry et al. (2001), McCosker (1975), and Voris and Voris (1983).

Species	Common name	Geographical range	Habitat	Depth	Diet
Resident species with breeding populations					
Aipysurus lineage					
Aipysurus apraefrontalis	Short-nosed sea snake	Ashmore & Hibernia Reefs	Reef flat and crest	0–10 m	Eels
Aipysurus duboisii	Dubois sea snake	Australia, southern PNG, Coral Sea & New Caledonia	Most reef habitats	0–20 m	Eels, Blennidae, Acanthuridae, Scaridae
Aipysurus foliosquuama	Leaf-scaled sea snake	Ashmore & Hibernia Reefs	Reef flat and crest	0–10 m	Eels, Gobidae, Labridae
Aipysurus fuscus	Dusky sea snake	Ashmore, Hibernia & Scott Reefs	Various reef habitats	0–20 m	Gobidae, Labridae, Fish Eggs
Aipysurus laevis	Olive sea snake	Australia, southern PNG, Coral Sea & New Caledonia	Reefs and inter-reefal habitats	0–50 m	Generalist – Fish and Invertebrates
Emydocephalus annulatus	Turtleheaded sea snake	Australia, Coral Sea, New Caledonia, Philippines	Most reef habitats	0–30 m	Fish Egg Specialist
Hydrophis lineage					
Acalyptophis peroni	Horned sea snake	Australia, Coral Sea, New Caledonia, south China Sea	Sandy, soft sediment reef habitats	0–30 m	Eels, Gobidae
Astrotia stokesii	Stokes sea snake	Indo-West Pacific	Reefs and sandy habitats	0–30 m	Batrachoididae, Gobidae, Apogonidae
Hydrophis coggeri	Cogger's sea snake	Australia, New Caledonia, Philippines, Indonesia, Fiji	Sandy, soft sediment reef habitats	0–30 m	Eels
Vagrant species					
Hydrophis lineage					
Hydrophis elegans	Elegant sea snake	Australian endemic	Non-reef soft-bottom habitats	0–50 m	Eels
Hydrophis occelatus	Spotted sea snake	Australian endemic	Non-reef soft-bottom habitats	0–50 m	Generalist
Hydrophis kingii	Spectacled sea snake	Australian endemic	Non-reef soft-bottom habitats	0–50 m	Eels, Plotosidae
Lapemis curtus	Spine-bellied sea snake	Indo-West Pacific	Non-reef soft-bottom habitats	0–50 m	Generalist
Pelamis platura	Yellow-bellied sea snake	Indo-West Pacific	Pelagic	Surface	Generalist

typically occur in different habitat types throughout the massive reef complex and have different levels of dietary specialisation (McCosker, 1975). Coral reefs are among the world's most vulnerable ecosystems with the abundance of corals declining on reefs globally due to pollution, habitat destruction, overexploitation, and increasing effects of climate change (Burke et al., 2011; Hughes et al., 2010; Pandolfi et al., 2011). Moreover, extensive loss of corals has led to declines in reef-dependant organisms (Pratchett et al., 2008; Wilson et al., 2006). A common view is that degradation of coral reefs and associated loss of species can be mitigated by establishing marine protected areas that reduce extractive pressure on populations (but see Graham et al., 2007). In 1983 the Australian Government declared the Ashmore Reef National Nature Reserve in recognition of the high biodiversity value of Ashmore Reef and in order to protect its ecological processes (Anon, 2002). Since then, most of Ashmore Reef (550 km^2) has been protected as a strict nature reserve (IUCN category Ia), which prohibits all public access, while a small area (33 km^2) in the western lagoon has been protected as a national park (IUCN category II), which allows public access and recreational fishing of finfish for immediate consumption (Anon, 2002). Nonetheless, despite these high levels of protection, there have been reports of declining abundances of sea snakes at Ashmore Reef, but the causes are unclear (Guinea, 2006, 2007, 2012). In order to implement effective management strategies it is important to examine trends and explore possible reasons for these declines. Here we present findings from extensive quantitative surveys conducted for sea snakes at Ashmore Reef since 2002 and synthesise information from published surveys conducted since 1973 with the aim of providing an up-to-date synopsis of the current status of sea snakes at Ashmore Reef. We use these data in conjunction with information about benthic habitats to explore trends in the diversity and abundance of sea snakes in relation to habitat quality and discuss possible causes of population declines and local extinctions.

2. Materials and methods

2.1. Study sites

Ashmore Reef (12°20′S, 123°E) is a large (ca. 583 km^2) emergent reef located 350 km off the Australian coast on the edge of Sahul Shelf (Anon, 2002). The crescent shaped reef has an unbroken southern margin with an extensive lagoon on the northern part of the reef that opens to the ocean at two large passes on the northern and north-western margins (Fig. 1).

2.2. Previously published survey data for sea snakes at Ashmore Reef

Published studies of the diversity and abundance of sea snakes at Ashmore Reef commenced in 1973 (Minton and Heatwole, 1975), with subsequent surveys conducted in 1994, 1996 and 1998 (Guinea and Whiting, 2005), 2005 (Guinea, 2006) and 2007 (Guinea, 2007). These studies targeted different areas of the massive reef complex using various survey methods, including SCUBA, snorkel, manta tow, boat transects and reef walks, and often the amount of area surveyed was not reported. A summary of the survey methods, areas and reef habitats surveyed, and survey efforts of (Guinea, 2006, 2007; Guinea and Whiting, 2005; Minton and Heatwole, 1975) is presented in Table 2 with additional details in Supplementary Tables A1 and A2.

2.3. Diversity and abundance of sea snakes at Ashmore Reef from 2002 to 2010

Surveys were conducted at Ashmore Reef by the authors as follows: 2002 (VL), 2006 (DC, MB), 2009 (ZR, MB) and 2010 (VL). Snakes were visually identified to species using external characteristics following Cogger (2000).

In September 2002, snorkel, SCUBA, manta-tow and reef flat walks were conducted at Ashmore Reef in as many locations and habitats as possible during ten days (Table 2). For each survey the location, duration (in minutes), and number of sea snakes of each species encountered was recorded (Supplementary Table A3).

In November 2006, May 2009, and August 2010 belt-transect surveys were conducted on SCUBA to estimate the abundance of sea snakes. Six sites were sampled in all three years and aimed to representatively sample all habitats and exposures (Fig. 1). Four sites were located around the perimeter of Ashmore Reef (north, east, south east and south west), and two sites were located in the west and east lagoons respectively (Fig. 1). Surveys were conducted on the reef crest (2–3 m depth) and the reef slope (8–10 m depth) with a total area of 5000 m^2 surveyed for each site by habitat (depth) combination (one hectare per site). In 2006 this was achieved using 500 × 5 m belt transects (2 replicates per habitat per site) while in

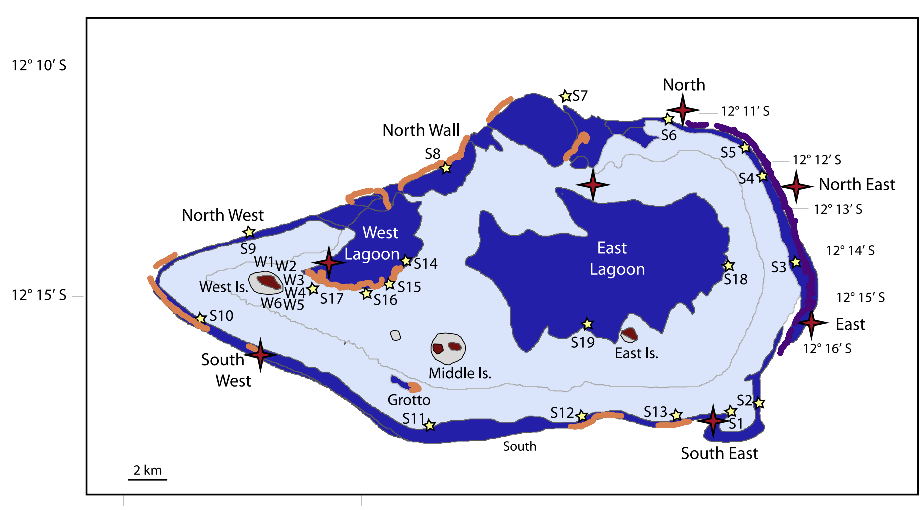

Fig. 1. Ashmore Reef in the Timor Sea showing study sites. Red stars indicate SCUBA sampling sites where transect surveys were conducted in 2006, 2009 and 2010. Orange and purple lines indicate tracks surveyed on manta-tow in 2010. Yellow stars indicate 19 snorkel sites (S1 to S19) surveyed in 2006. W1 to W6 indicate reef flat surveys conducted on foot at low tide near West Island in 2006.

Table 2
Summary of survey methods used to obtain estimates of species diversity and abundance of sea snakes at Ashmore Reef from 1973 to 2010. For each survey the following information is provided if available: Year, Ashmore locations surveyed based on the names of different parts of the reef complex given in Fig. 1, reef habitats encompassed by the surveys, estimate of survey effort as area when given or time when area was not available and the number of days of the entire field trip, survey methods employed, source of the data, and location of detailed information about the methods and results for each survey.

Year	Location	Habitats	Survey Effort	Survey Methods	Source	Details
1973	West Lagoon	Lagoon from 25 m depth to reef flat	8 days - repeat surveys of 800 m transect from boat to reef	Snorkel, SCUBA	Minton and Heatwole (1975)	Table A1
1994	West Lagoon, East Lagoon, North Wall, North	Reef Flat – High Tide	38 Ha over two days	Boat Transects	Guinea and Whiting, 2005	Table A1
1994 1996 1998	Reef Flat near West Island	Reef Flat – Low Tide	1000 m × 20 m each year	Reef Walk	Guinea and Whiting (2005)	Table A1
2002	South West, South East, West & East Lagoons, North Wall, North, Grotto, North West, Reef Flat near West Island	All reef habitats	22 h over 10 days	SCUBA, Snorkel, Manta Tow, Reef Walk	This study	Table 4 Table A3 text
2005	West & East Lagoons, North Wall, Grotto, Reef Flat near West Island	Lagoon, reef flat and crest	30 h over 10 days	Snorkel, Manta Tow, Boat Transects, Reef Walk	Guinea (2006)	Table A2
2006	South West, South East, West & East Lagoons, North Wall, North West, North, East, Reef Flat near West Island	All reef habitats	30 Ha over 12 days	SCUBA, Snorkel, Reef Walk	This study	Table 5 Table A4 text
2007	South West, South East, West & East Lagoons, North Wall, North, Grotto, North West, Reef Flat near West Island	All reef habitats	14 h over 10 days	Snorkel, Manta Tow, Boat Transects, Reef Walk	Guinea (2007)	Table A2
2009	South West, South East, North, East, West & East Lagoons	Outer reef crest and slope, lagoon crest and slope	6 Ha over 4 days	SCUBA	This study	Table A4 text
2010	South West, South East, West & East Lagoons, North Wall, North, East, Grotto, North West	All reef habitats	>100 Ha over 18 days	SCUBA, Snorkel, Manta Tow	This study	Table 6 Table A4 text

2009 and 2010 belt transects were 100 × 10 m (5 replicates per habitat per site). In 2010, an additional site (north east) was also surveyed using belt transects (Supplementary Table A4).

In November 2006, snorkel surveys and reef flat walks were also conducted at Ashmore Reef. Snorkel transects were conducted in the reef crest or upper slope at 19 sites with the aim of comprehensively sampling all exposures and habitats of Ashmore Reef (S1–S19, Fig. 1). Each snorkel transect was 500 × 5 m (2500 m^2) and four replicate transects were conducted at 17 of the 19 sites (one hectare per site). The two exceptions were sites S6 (2 transects – 0.5 Ha) and S3 (6 transects – 1.5 Ha). Thus, a total of 19 Ha was surveyed on snorkel. Reef walks (six transects 500 × 20 m: W1–W6) were conducted in the intertidal lagoon near West Island and covered the same reef flat habitats surveyed in 1994, 1996 and 1998 by Guinea and Whiting (2005).

In August 2010, we conducted extensive manta-tow surveys in order to cover as much reef area as possible (Fig. 1). An in-water observer was towed along the reef crest or upper slope at an average speed of two knots for 2-min intervals during which time horizontal visibility was recorded. A Garmin GPS recorded the track of the manta-tow at five-second intervals and a boat observer recorded the GPS location at the end of each 2-min survey. Manta-tow surveys covered 47 km of track distance during 13.5 h and encompassed most aspects of the outer perimeter of Ashmore Reef, plus large sections of each lagoon and the Grotto (Fig. 1). The average horizontal visibility was 10 m ±0.9 (SE) indicating that approximately 94 hectares of the Ashmore Reef crest and upper slope were surveyed.

Manta-tow surveys continued until a sea snake was sighted, at which time surveying stopped to catch the sea snake and obtain tissue samples for genetic analysis. Additional sea snakes encountered off manta-tow were also recorded and captured for sampling. A visible scar in the tail where the tissue sample was taken ensured that sea snakes were not inadvertently recorded more than once.

2.4. Comparing abundance estimates between surveys

Given the variation in survey methods and effort, and the fact that the only information available for 1973 is the total number of days spent at Ashmore Reef (Minton and Heatwole, 1975), we use the measure of snakes sighted (or captured) day^{-1} to compare species diversity and abundance between previously published surveys (Guinea, 2006, 2007; Guinea and Whiting, 2005; Minton and Heatwole, 1975) and the four more quantitative surveys we conducted in 2002, 2006, 2009 and 2010. Reports of surveys conducted in 2005 and 2007 (Guinea, 2006, 2007) provided information about the number of hours spent surveying different locations throughout the reef complex so we use the measure of snakes sighted h^{-1} from these two published surveys and our four surveys to document changes in the distribution and abundance at Ashmore Reef between 2002 and 2010.

2.5. Benthic composition and habitat complexity in 2010

Benthic cover and habitat complexity were quantified to explore whether these correlated with the local abundances of sea snakes, and as a baseline for future studies. Benthic composition and habitat complexity were quantified at the seven sites where SCUBA surveys for sea snakes were conducted in 2010 (Fig. 1). Benthic cover (%) was estimated using 50 m point intercept transects (three replicates per depth per site) with habitat recorded below each of 100 uniformly distributed points (50 cm apart). Benthic categories recorded were live hard coral, dead coral, soft coral, turf algae, crustose coralline algae, filamentous algae, sponge, *Halimeda*, sea grass, sand, pavement and rubble. Along each transect, habitat complexity was scored at 3 points (0 m, 20 m and 40 m) encompassing a 7 m radius (18 complexity scores per site). We used an established six-point scale whereby: 0 = no vertical relief; 1 = low and sparse relief, 2 = low but widespread relief, 3 = moderately complex relief, 4 = very complex with numerous caves and fissures, 5 = exceptionally complex with high coral cover and numerous caves and overhangs (Polunin and Roberts, 1993; Wilson et al., 2007).

3. Results

3.1. Magnitude and pattern of decline in abundance and species richness

Despite differences in survey methods, the numbers of sea snakes recorded at Ashmore Reef in 1973 and 1994 were remarkably similar, 46 and 42 snakes day^{-1} respectively. In 2002, the number of sea snakes recorded as Ashmore Reef had declined to 21 snakes day^{-1} and then declined further to an average of between one and seven sea snakes day^{-1} in 2005, 2006, 2007, 2009 and 2010 (Fig. 2). These declines occurred despite the fact that survey effort tended to increase, particularly in 2002, 2006 and 2010 (Supplementary Tables A1–A4). Reef walks in shallow intertidal habitats revealed similar declines in abundance. In 1994, 1996 and 1998 inter-tidal reef flat walks conducted by Guinea and Whiting (2005) recorded between 13 and 34 sea snakes in 2 Ha of the reef flat near West Island (Table 3). By contrast, reef flat walks conducted in 2002 (2 Ha), 2005 (10.5 h, Guinea, 2006), 2006 (6 Ha) and 2007 (entire reef flat around West Island, Guinea, 2007) did not find any sea snakes (Table 3).

Declines in the overall abundance of sea snakes from 1973 to 2005, corresponded with a marked decline in the number of species recorded at Ashmore Reef. In 1973, Minton and Heatwole (1975) collected nine species of sea snakes (*Aipysurus laevis*, *Emydocephalus annulatus*, *Aipysurus apraefrontalis*, *Aipysurus duboisii*, *Aipysurus foliosquama*, *Aipysurus fuscus*, *Acalyptophis peroni*, *Astrotia stokesii* and *Hydrophis coggeri*) in eight days (Fig. 2). The same nine species were recorded in 1994 [eight species during two days of boat surveys of the reef flat (Fig. 2) and the ninth, *A. duboisii*, reported from the West Lagoon] (Guinea and Whiting, 2005). There were differences in species-specific encounter rates between 1973 and 1994 that were probably due to the different survey

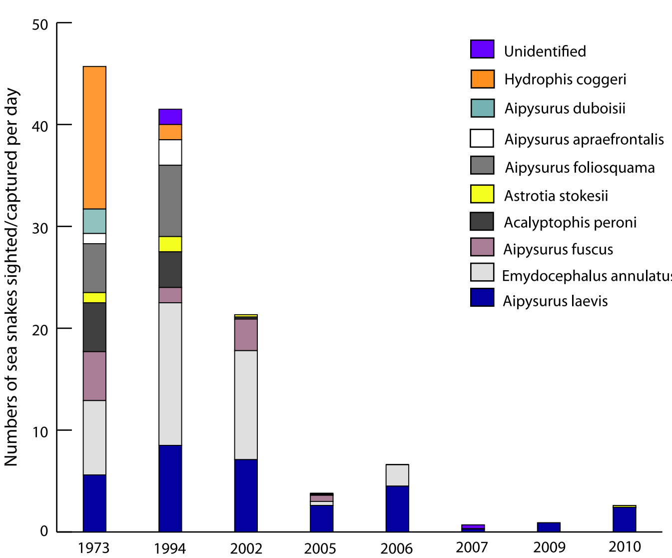

Fig. 2. Declines in abundance and species diversity of sea snakes at Ashmore Reef (shown as number of snakes per species seen per day) in surveys conducted between 1973 and 2010. Three sea snake species that were abundant at Ashmore Reef in the 1970s and 1990s, *Aipysurus apraefrontalis*, *A. foliosquama H. coggeri*, have not been sighted in any surveys conducted since 2002. *Aipysurus fuscus* and *Acalyptophis peroni* have not been seen since 2005 and *Emydocephalus annulatus*, previously one of the most abundant species at Ashmore Reef, was not sighted in 2010 during intensive surveys of the entire reef complex.

Table 3
Numbers of sea snakes encountered during surveys of the reef flat (reef flat walks) near West Island at low tide from 1994 to 2007.

Species	1994[a] 2 Ha	1996[a] 2 Ha	1998[a] 2 Ha	2002 2 Ha	2005[b]	2006 6 Ha	2007[c]
Aipysurus apraefrontalis	5	1	5	0	0	0	0
Aipysurus foliosquama	21	2	15	0	0	0	0
Aipysurus fuscus	3	3	6	0	0	0	0
Aipysurus laevis	0	2	2	0	0	0	0
Emydocephalus annulatus	1	5	3	0	0	0	0
Hydrophis coggeri	1	0	3	0	0	0	0
Total	31	13	34	0	0	0	0

[a] *Source*: Guinea and Whiting (2005). One 2 Ha transect surveyed each year.
[b] *Source*: Guinea (2006). A total of 28 reef walk surveys were conducted in 10.5 h over 10 days in 2005.
[c] *Source*: Guinea (2007). Total area surveyed not specified in the text but Fig. 4 in the report shows that the entire reef flat around West Island was surveyed.

methods used and reef habitats surveyed, Table 2). Similarly, in 1994, 1996 and 1998 reef walks recorded five to six species in just 2 Ha of reef flat near West Island (Table 3).

In 2002, only five species (*A. laevis*, *E. annulatus*, *A. fuscus*, *A. peronii*, and *A. stokesii*), were recorded at Ashmore Reef during ten days of extensive surveys across almost all reef habitats (Table 4). The same five species were recorded in 2005 (Guinea, 2006), however most snakes were *A. laevis* and sighting rates dropped markedly between 1994 and 2002 (Fig. 2). *A. laevis* and *E. annulatus* were the only species recorded in 2006 and, apart from one *A. stokesii* recorded in 2010, *A. laevis* was the only species recorded in 2007 (Guinea, 2007), 2009 and 2010 (Fig. 2). Despite our extensive surveys in 2002, 2006, 2009 and especially 2010, and those of Guinea in 2005 and 2007, four species of sea snake, *A. apraefrontalis* and *A. foliosquama*, (two Timor Sea endemics) and *A. duboisii* and *H. coggeri* have not been sighted at Ashmore Reef since 1994, and three additional species, *A. fuscus* (a Timor Sea endemic) and *A. peroni* and *E. annulatus* have not been sighted since 2005.

3.2. Distribution and habitat use

Aside from declines in both diversity and abundance of sea snakes at Ashmore Reef, there has also been a localised contraction of the range of locations and habitats in which sea snakes have been recorded. In 2002, sea snakes were found in almost all areas of Ashmore Reef (Fig. 3) with highest encounter rates (average 12 snakes h^{-1}) occurring at the north wall (Table 4). The next highest encounter rates (9 snakes h^{-1}) were in the west lagoon, the Grotto, and south east Ashmore (Fig. 3). The lowest encounter rates were at the east lagoon and south west Ashmore (Fig. 3). The only location where no snakes were seen was at north west Ashmore (Table 4). In 2005 (Guinea, 2006), encounter rates at the north wall and east lagoon had dropped to 3 snakes h^{-1}, while in the Grotto and west lagoon encounter rates were <1 snake h^{-1} (Fig. 3). The highest encounter rate in 2005 was at north Ashmore (6 snakes h^{-1}) (Fig. 3), which was not surveyed in 2002. In 2006, sea snakes were not encountered at southwest Ashmore or the west lagoon, while at the east lagoon, south east and north Ashmore encounter rates were lower than in 2002/2005 (Fig. 3, Table 5). The highest encounter rates (6 snakes h^{-1}) occurred at the north wall, which was an increase from 2005 but lower than in 2002, and at north east Ashmore (not previously surveyed) (Fig. 3, Table 5). In 2007 only seven sea snakes were seen in the west lagoon, Grotto and south east Ashmore during a minimum of 14 survey hours (Fig. 3) [(Guinea, 2007) does not provide sufficient detail to calculate the total number of hours surveyed]. In 2009, a total of three *A. laevis* were encountered in 12.5 survey hours over five days and all

Table 4
Numbers of sea snakes encountered at Ashmore Reef in September 2002 from SCUBA, snorkel and manta-tow surveys showing survey time, numbers of sea snakes per species and encounter rates (number of sea snakes per hour) at different locations.

Location	Time (h)	*Acalyptophis peronii*	*Aipysurus fuscus*	*Aipysurus laevis*	*Astrotia stokesii*	*Emydocephalus annulatus*	Total	Encounter rate
South West	1.0	0	2	2	2	0	6	6.0
South East	3.0	0	1	10	0	14	25	8.3
North Wall	10.3	0	7	45	1	73	126	12.3
West Lagoon	3.1	3	15	4	1	4	27	8.8
East Lagoon	2.0	0	3	5	0	3	11	5.5
North West	0.3	0	0	0	0	0	0	0.0
Grotto	1.7	0	3	4	0	10	17	10.2
Total	22 h	3	31	70	4	104	212	9.8

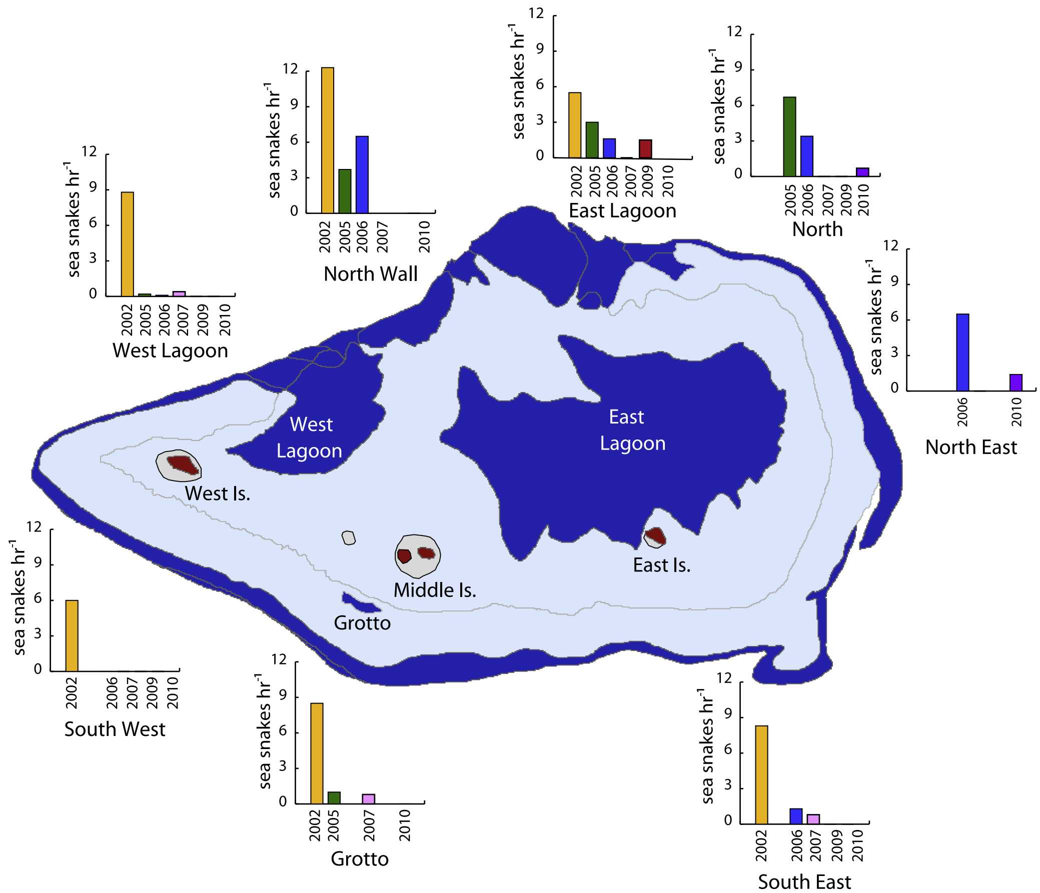

Fig. 3. Numbers of sea snakes seen per hour at eight Ashmore Reef locations, six on the outer perimeter of the reef and also the East and West Lagoons, during six surveys conducted between 2002 and 2010. Note that not all locations were surveyed each year. If a location was not surveyed in a particular year, the year is not shown on the *X*-axis of the respective graph, whereas if a location was surveyed but no snakes were sighted, then the year is shown but there is no corresponding bar on the graph. For example, north east Ashmore was surveyed only in 2006 and 2010, and snakes were seen on both occasions, whereas the West Lagoon was surveyed in each of the six surveys year but no sea snakes were seen in 2009 and 2010.

occurred in the east lagoon (Fig. 3). Sea snakes were not seen at any of the other five locations surveyed in 2009 (Fig. 3).

In 2010 a total of 46 sea snakes (45 *A. laevis* and one female *Astrotia stokesii*) were encountered during 88 survey hours over 18 days (Table 6). Despite intensive surveys of all areas of the reef complex, sea snakes were only found at north and north east Ashmore Reef (between 12°11.078′S: 123° 06.598′E to 12°14.853′S: 123° 09.423′E, see Fig. 1). Encounter rates at north east Ashmore (<2 snake h^{-1}) were much lower than in 2006 (>6 snakes h^{-1}), and at north Ashmore encounter rates were even lower (<1 snake h^{-1}) and lower than previous surveys in 2005 (>6 snakes h^{-1}) and 2006 (>3 snakes h^{-1}) (Fig. 3; Table 6). Within the north east region of Ashmore Reef, sea snakes were most abundant between latitudes 12°12′ to 12°13′ (Fig. 1), with numbers tapering off to the north and south (Table 6).

3.3. Live coral cover and habitat complexity at Ashmore Reef in 2010

Although there is limited information on the specific habitat requirements of different sea snake species (Table 1), changes in the distribution and abundance of sea snakes might be attributable to the biological or physical structure of reef habitats. In 2010, mean live coral cover differed significantly among locations at Ashmore Reef ($F_{1,6} = 23.8$, $p < 0.001$) with coral cover at north east, north, south west and south east Ashmore significantly higher than at the east and west lagoons and at east Ashmore (Fig. 4; Tukeys HSD post hoc tests having $p < 0.01$). Habitat complexity also differed significantly among locations ($F_{1,6} = 46.5$, $p < 0.001$) with mean habitat complexity scores at north (3.2 ± 0.21 SE) and north-east (2.9 ± 0.19 SE) Ashmore significantly higher than at the other five locations surveyed (Tukeys HSD post hoc tests

Table 5
Numbers of sea snakes seen at Ashmore Reef in 2006 during SCUBA and snorkel surveys showing the total number of *Aipysurus laevis* and *Emydocephalus annulatus*, seen at each location.

Location	Area (Ha)	*Aipysurus laevis*	*Emydocephalus annulatus*	Total
South West	5	0	0	0
South East	3	7	1	8
East	2.5	1	0	1
North East	2	15	11	26
North	2.5	12	5	17
North Wall	1	8	5	13
West Lagoon	5	1	0	1
East Lagoon	4	10	3	13
North West	1	0	0	0
Total	26	54	25	79

Table 6
Manta tow surveys conducted in 2010 at Ashmore Reef sites showing the total distance and time surveyed, the number of *Aipysurus laevis* encountered on manta-tow and the total numbers of snakes recorded at each location identified as male (M), female (F) or undetermined (n/a).

Reef Region	Manta-tow distance (m)	Manta-tow time (min)[b]	Sighted on manta-tow	*M*	*F*	*n/a*
North to East						
12°11′ – 12°12′	5338	100	4	1	2	1
12°12′ – 12°13′	4659	87	10	10	13	0
12°13′ – 12°14′	4895	87	7	3	6	1
12°14′ – 12°15′	4480	72	6	2	5	1
12°15′ – 12°16′	2276	58	0	0	0	0
Total[a]	21,648	404	27	16	26	3
North Wall	8188	140	0	0	0	0
North West	874	9	0	0	0	0
South West	3814	60	0	0	0	0
South East	3585	49	0	0	0	0
West Lagoon	6096	104	0	0	0	0
East Lagoon	2061	32	0	0	0	0
Grotto	736	14	0	0	0	0
Total	25,354	408	0	0	0	0

[a] The total number of snakes includes snakes sighted on manta-tow plus those sighted off manta-tow. Note that one female *Astrotia stokesii* was also encountered at north east Ashmore Reef.
[b] Note that manta-tow time does not include time spent conducting SCUBA surveys or the time between 2 min manta-tow surveys while data were being recorded, thus is only a small subset of the total time spent searching for sea snakes at Ashmore Reef in 2010.

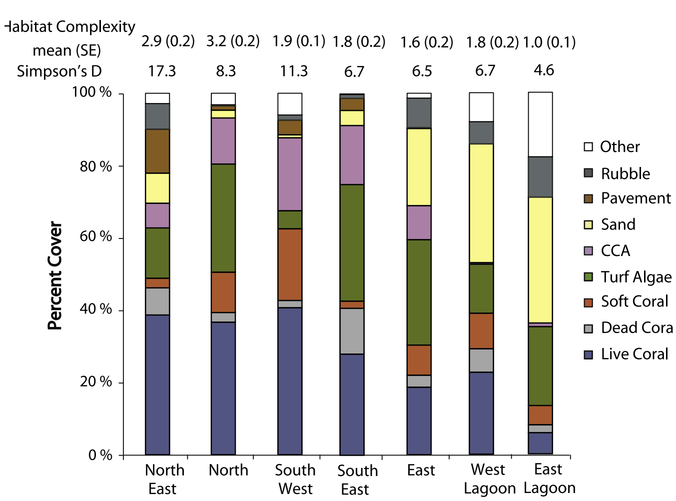

Fig. 4. Mean percent cover of nine benthic habitat types at seven Ashmore reef sites in 2010. Habitat complexity scores and Simpson D evenness index for benthic habitats (not including live coral) are shown above each bar.

having $p < 0.01$), which had mean complexity scores less than two (Fig. 4). North east Ashmore also had the highest diversity (evenness) of non-coral habitats (Simpson's $D = 17.5$ for the eight benthic habitats excluding live coral) followed by south east Ashmore (Simpson's $D = 11.3$) and north Ashmore (Simpson's $D = 8.3$) while the remaining locations had Simpson's D values ranging from 4.6 to 6.7 (Fig. 4). Non-coral benthic habitats varied among sites, typically according to the reef location, with outer exposed sites dominated by CCA while the lagoons were dominated by sand (Fig. 4).

4. Discussion

Comparisons of recent survey data with historical meta-data reveal a dramatic decline in the abundance and diversity of sea snakes at Ashmore Reef between 1994 and 2005. Even more alarming is the fact that six species of sea snakes that were formerly resident at Ashmore Reef (*A. peroni*, *A. apraefrontalis*, *A. foliosquama*, *A. fuscus*, *A. duboisii*, *E. annulatus*, *H. coggeri*,) have not been sighted for many years, despite extensive recent surveys. These declines in abundance and diversity of sea snakes have occurred during a period that Ashmore Reef has been protected as an IUCN category Ia nature reserve. Actual causes of these declines are unknown but could be the result of the combined effects of habitat degradation, emerging effects of climate change, as well as intrinsic threats to the viability of snake populations (e.g. disease and recruitment failure). Whatever the mechanism, the existing management of Ashmore Reef has not prevented the loss of its sea snake biodiversity, which was one of the criteria that lead to its protection (Anon, 2002).

4.1. Declines in diversity and abundance of sea snakes on other coral reefs

In just over a decade, populations of sea snakes at Ashmore Reef have undergone precipitous declines, resulting in very low diversity and abundance that is a stark contrast with the numbers reported at this global hotspot during the twentieth century (Cogger, 1975; Guinea and Whiting, 2005; Minton and Heatwole, 1975; Smith, 1926). However, this phenomenon is not isolated to Ashmore Reef. A 35-year study of population dynamics of *A. laevis* and *E. annulatus* in the southern Great Barrier Reef documented local extinctions on a subset of reefs (Lukoschek et al., 2007a). These reefs are also afforded considerable protection from exploitive activities, and the reasons for these local extinctions remain unknown (Lukoschek et al., 2007a). Similarly, between 2003 and 2012 counts of *E. annulatus* on a protected New Caledonian reef declined from more than six day^{-1} to less than two day^{-1} with no obvious cause (Goiran and Shine, 2013).

Compared with Ashmore Reef, sea snakes have been less well studied at nearby Timor Sea reefs (Cartier, Hibernia and Scott), however there is evidence that similar declines in species diversity have occurred at Hibernia Reef since the early 1990s. In 1973 (Minton and Heatwole, 1975) and 1992 (Guinea, 1993), Hibernia Reef (which is not a marine protected area) supported the same nine species of sea snakes as Ashmore Reef at that time, and in approximately the same proportions. In 2005 only three species (*A. laevis*, *A. fuscus*, *E. annulatus*) were recorded from Hibernia Reef (Guinea and Whiting, 2005) and in 2007 only *A. laevis* and *E. annulatus* remained (Guinea, 2007), indicating a similar loss of species diversity. Only two species of sea snakes, *A. laevis* and *E. annulatus*, have ever been recorded at Cartier Islet (protected as an IUCN category Ia nature reserve since 2000, Anon, 2002) in the six surveys conducted since 1973 (Minton and Heatwole, 1975), 1992 (Guinea, 1993), 2002 (Lukoschek Unpublished Data), 2005 (Guinea, 2006, 2007, 2007, 2009; Richards et al., 2009) and 2010 (Lukoschek Unpublished Data). Six sea snake species were recorded at Scott Reef (not a marine protected area) in 1973 (Minton and Heatwole, 1975) and four of these species (*A. laevis*, *A. fuscus*, *A. duboisii*, *E. annulatus*) were encountered in 2002 (Lukoschek Unpublished Data), however survey effort for sea snakes has been much lower at Scott Reef than at the other Timor Sea reefs.

Of great concern is the disappearance of *A. apraefrontalis* and *A. foliosquama*, two restricted-range endemic species that had previously only been reported from Ashmore and Hibernia reefs (Table 1). These two species have not been sighted on either reef since the late 1990s (Guinea, 2006, 2007) and are now listed as Critically Endangered (CR) by the IUCN Red List Assessments (IUCN, 2011) and Australia's *Environment Protection and Biodiversity Conservation (EPBC) Act 1999.* Similarly, *A. fuscus*, also endemic to reefs in the Timor Sea, has not been recorded at Ashmore Reef since 2005 and is now listed as Endangered (EN) by IUCN (IUCN, 2011).

4.2. Potential mechanisms for sea snake declines

4.2.1. Habitat loss

Reef-associated sea snakes typically shelter and forage under ledges and within the reef matrix. Reduced habitat complexity has been shown to reduce the abundance and diversity of reef fishes (Graham et al., 2007; Pratchett et al., 2008; Wilson et al., 2009); thus, it might be predicted that reductions in coral cover, diversity and habitat complexity following bleaching events have contributed to the declines of reef-associated sea snake species at Ashmore Reef. The mass bleaching event of 2003 caused significant widespread coral mortality at Ashmore Reef (Rees et al., 2003) with average coral cover reduced to 10% (Kospartov et al., 2006). The impacts of the bleaching event in 2003 were patchy, and north east Ashmore had higher live coral cover (20–25%) and species diversity than the other five reef regions surveyed (Kospartov et al., 2006). Similarly, coral cover was also highest at north and east Ashmore in 2009 (Ceccarelli et al., 2011b), and at north and north-east Ashmore in 2010 (Fig. 4). Higher coral cover (and diversity) is expected to have maintained higher habitat complexity at north east Ashmore than other parts of the reef complex, as was recorded in 2010, potentially accounting for the fact that sea snakes only occurred in this part of the reef complex.

Nonetheless, recent degradation of coral-dominated habitats at Ashmore Reef, due to temperature induced bleaching in 2003 (Ceccarelli et al., 2011b), cannot account for the declines in local populations of sea snakes. The most pronounced declines in the abundance and diversity of sea snakes occurred between the mid 1990s and 2002 (Fig. 2), preceding the 2003 coral loss. Widespread bleaching associated with the 1998 El Nino event affected many Australian reefs (Hoegh-Guldberg, 1999), including Scott Reef in the Timor Sea (Skewes et al., 1999; Smith et al., 2008), but surveys in late 1998 indicated that Ashmore Reef experienced limited coral loss during this event (Skewes et al., 1999). Moreover, surveys conducted at Ashmore Reef in May 2002 reported that reef habitats and associated reef fishes were in good health (Russel et al., 2004). As such, the disappearance of the four sea snake species, including two restricted range endemics, from Ashmore Reef between the mid 1990s and 2002 do not coincide with localised loss of coral cover or habitat complexity. In addition, two species that either disappeared (*H. coggeri*) or severely declined in abundance (*A. peroni*) during this period (Fig. 2) were predominantly associated with soft-sediment rather than coral-dominated habitats (Table 1) indicating that loss of coral cover probably was not responsible for these declines.

4.2.2. Declines in potential prey availability

The limited dietary information available suggests that most sea snake species feed on relatively sedentary fish species that are either bottom dwelling or live in burrows or reef crevices, with the most common prey being eels, gobies and apogonids (Fry et al., 2001; McCosker, 1975; Voris and Voris, 1983). Limited information about preferred prey items suggests that many species are specialists that forage on relatively few prey species (Fry et al., 2001; McCosker, 1975; Voris and Voris, 1983), indicating vulnerability to declines in the abundance of preferred prey items. The only sea snake species that has not disappeared from Ashmore Reef, *A. laevis*, is a dietary generalist that feeds on range of small fishes and eels from many families, as well as crustaceans and squid (Voris and Voris, 1983). By contrast, the dietary information that is available indicates that some species that have disappeared from Ashmore Reef had some level of dietary specialisation (McCosker, 1975). For example, the turtleheaded sea snake, *E. annulatus*, from the *Aipysurus* lineage is a dietary specialist that forages exclusively on fish-eggs, predominantly from the families Pomacentridae, Gobidae and Blennidae (Goiran et al., 2013). In 2005 and 2009 pomacentrids accounted for >50% of fishes counted at Ashmore Reef and had the highest species diversity (Kospartov et al., 2006; Richards et al., 2009). The cryptic families Gobidae, Apogonidae and Blennidae were not counted in 2005 and 2009, however, the high abundance and diversity of pomacentrids suggests that the disappearance of *E. annulatus* from Ashmore Reef was not directly linked to prey availability. Moreover, two of the three resident *Hydrophis* species forage exclusively on eels (McCosker, 1975) whereas other species from both lineages tend to have more generalised diets (Table 1). This variation in dependence on different prey items indicates that prey availability is unlikely to be the cause of the disappearance and/or declines of all nine resident sea snake species at Ashmore Reef.

4.2.3. Illegal and incidental harvests

Indonesian visitation to Ashmore Reef extends back centuries and in the 20th century was linked to over harvest of its marine resources (Whiting, 2000). In 1974, a Memorandum of Understanding (MOU) between the Australian and Indonesian Governments recognized traditional Indonesian fishing practices and delineated access and fishing restrictions to five areas on the northwest Australian continental shelf, including Ashmore Reef (Fox et al., 2009). The establishment of the Ashmore Reef National Nature Reserve in 1983 subsequently banned all fishing and collecting at Ashmore Reef, with the exception of subsistence fishing by traditional Indonesian fishers in a small area of the west lagoon zoned IUCN Category II (Anon, 2002). Prior to 2000, this protection was enforced by Environment Australia for 9 to 10 months of the year (April to December); however, illegal fishing activities were observed in the Nature Reserve during the months lacking enforcement (Whiting, 2000). Since May 2000 an Australian Customs Service vessel has been based at Ashmore Reef as a permanent surveillance platform (Whiting, 2000) but there have been intermittent periods without an enforcement presence that appeared to result in a decline in trochus and holothurian populations (Ceccarelli et al., 2011a). However, there is no evidence that traditional Indonesian fishers ever have targeted sea snakes on Timor Sea Reefs. Information about Indonesian vessels visiting Ashmore Reef, collected by National Parks officers stationed at Ashmore Reef from 1986 to end 1999 (1678 records) and by the Australian Fisheries Management Authority (AFMA) Apprehensions from 1988 to 2001 (899 records), found that the main catches were trepang (holothurians), trochus and sharkfin, followed by reef fish (Fox et al., 2009). There were no records of sea snakes in either of these databases (Fox et al., 2009). In addition, published reports list sea turtles, seabirds, seabird eggs, dolphins and giant clams as targeted by Indonesian fishers at Ashmore Reef, but sea snakes never have been listed (Anon, 2002; Russel et al., 2004; Russel and Vail, 1988). Thus, it seems unlikely that the massive declines in sea snakes at Ashmore is due to illegal fishing by Indonesian fishers.

Australian trawl fisheries are known to impact certain species and populations of sea snakes (Courtney et al., 2009; Fry et al., 2001; Stobutzki et al., 2000). The only trawl fishery operating in the vicinity of Ashmore Reef is the North West Slope Trawl Fishery; a deep-water fishery that predominant targets lobster (Emery et al., 2009). The overall bycatch for this fishery is low and detailed bycatch data from 2000 to 2008 does not record any sea snakes (Emery et al., 2009). Significant numbers of sea snakes are incidentally captured in the Northern Trawl Fishery (NTF), however, the NTF is predominantly a coastal fishery and its closest boundaries are >200 km from Ashmore Reef (Ward, 2000). Moreover, at least four sea snake species that have disappeared from Ashmore Reef (*A. apraefrontalis*, *A. foliosquama*, *A. fuscus*, *E. annulatus*) have never been reported in the NTF bycatch (Ward, 1996a,b, 2000) so there is currently no evidence to suggest that fisheries bycatch has contributed to disappearance of sea snakes from Ashmore Reef.

4.2.4. Disease, invasive species and pollution

In the past decades there has been a worldwide increase in reports of diseases affecting a wide range of marine wildlife species in both tropical and temperate regions (Harvell et al., 1999). Conditions favouring the outbreak of disease are human activity and climate variability (Harvell et al., 1999), and the trend towards a warming climate is potentially promoting the spread and prevalence of pathogens and an increased susceptibility of animals to disease (Epstein et al., 1998; Harvell et al., 2002). At the same time, increased human activity in shipping, trade in aquatic animals, and aquaculture continues to enhance the global transport of marine species, including pathogens (Harvell et al., 1999). Increasing incidences of disease outbreaks have been documented in most groups of marine vertebrates, including cetaceans, seals, sea lions, otters, turtles and fish (Epstein et al., 1998) and are increasingly being reported for terrestrial snakes, including recent cases of severe fungal infections in endangered rattlesnakes (Allender et al., 2011). A handful of disease outbreaks have been documented for amphibious sea kraits (genus *Laticauda*) in captivity, one of which resulted in numerous fatalities (Chinnadurai et al., 2008).

Although geographically remote, Ashmore Reef experiences a relatively high level of boat traffic by traditional Indonesian fishers and, to a lesser extent, illegal entry vessels, yachts, and merchant ships traversing waters in the vicinity of Ashmore Reef (Russel et al., 2004; Russel and Vail, 1988). Indonesian fishing vessels routinely shelter in the western lagoon of Ashmore Reef, with 1662 visits recorded between 1985 and 1999 (Russel et al., 2004). Most Indonesian fishing vessels originate from 'low risk' ports with clean waters, however at least 2% of vessels originating from large commercial ports in Indonesia may have introduced exotic diseases, invasive species and/or pollution into its waters (Russel et al., 2004). Although fewer in number, illegal entry vessels typically are in poor condition, heavily fouled, likely to contain pathogen-contaminated bilge water, and many originate from high-risk ports in Indonesia (Russel et al., 2004), thus are likely to act as vectors of disease, invasive species and/or pollution from Indonesia to Ashmore Reef. Arrivals at Ashmore Reef by suspected illegal entry vessels reached a peak in 2000–2001, with 41 arrivals between July 2000 and August 2001 (Russel et al., 2004), coinciding with the onset of declines in the diversity and abundance of sea snakes at Ashmore Reef.

To date there are no documented cases of disease outbreaks for sea snakes in the wild; however, the comparatively low research effort into sea snakes and the difficulty of documenting diseases in marine habitats means that it is not possible to exclude disease as an underlying or contributing cause to the loss of sea snakes at Ashmore Reef. Nonetheless, over the past 10 to 15 years there have been no reports of dead or sick snakes at Ashmore Reef (Guinea, 2006, 2007; Guinea and Whiting, 2005) and in 2002 none of the >250 sea snakes from five species captured at Ashmore Reef (by V.L.) showed any signs of disease. Snakes swam vigorously before and after being caught and there were no external signs of illness (visible tumours, bulges, injuries, fungal infections, parasites etc.). Similarly, all 45 snakes caught in 2010 appeared to be healthy; however, it is possible that snakes could have had high internal parasite loads; fungal, viral or bacterial infections; tumours or other illnesses without external signs.

4.2.5. Recruitment failure

All species of 'true' sea snakes have internal fertilization and give birth to live young after a gestation period of four to six months (Heatwole, 1999). Recruitment failure could result from reduced fecundity due to biological or environmental factors affecting the quality of eggs and/or sperm, as well as successful gestation in females. Nothing is known about the reproductive condition of sea snakes at Ashmore Reef over the past 10 to 15 years or whether disease and/or pollutants could have impacted sea snake reproduction. Sex ratios did not differ from 1:1 in 2002 and 2010 for the species examined and sea snakes were observed mating during all field trips suggesting that, if reproductive failure was the cause of population declines, it was not due to skewed sex ratios resulting in the inability of sea snakes to find mates.

4.3. Potential recovery

The causal factors underlying the loss of sea snakes at Ashmore Reef are likely to be multi-facetted and possibly related to overall ecosystem decline. If habitat degradation has driven sea snake declines at Ashmore Reef, then the increases in live coral cover between 2005 and 2009 (10.2–29.4%) (Ceccarelli et al., 2011b) and the 2010 coral cover estimates (20 to 40%) may point to the potential recovery of sea snakes. Re-establishment of sea snake populations relies on dispersal from neighbouring Cartier, Hibernia and (the more distant) Scott reefs. However, strong genetic structure and mark-recapture evidence for reef-associated sea snakes indicates limited gene flow associated with strong site fidelity to small home ranges (Guinea and Whiting, 2005; Lukoschek et al., 2007b, 2008; Lukoschek and Shine, 2012). Specifically, significant genetic divergence for *A. laevis* among Ashmore, Hibernia, Cartier and Scott reefs for mitochondrial DNA and nuclear microsatellites indicates limited dispersal among these reefs (Lukoschek et al., 2008; Lukoschek et al., 2007b) while an eight-year mark recapture study for *E. annulatus* in New Caledonia indicated long-term site fidelity for two populations separated by just 2 km of continuous reef habitat, resulting in significant genetic divergence (Lukoschek and Shine, 2012). Further, if sea snake declines were driven by disease, reproductive failure, or broad-scale changes in the marine environment (e.g. rising temperatures,), re-establishment of sea snakes is likely to be hampered by the continuation of adverse conditions coupled with Ashmore Reef's isolation. These results may point to long-term local extinctions of sea snakes at Ashmore Reef, making unaided re-establishment of populations unlikely in the near term.

4.4. Management implications and the future of Ashmore's sea snakes

Whilst marine reserves managed as no-take areas are effective in protecting reef biodiversity by mitigating direct threats, some external threats cannot be addressed (Beger et al., 2010; Jones et al., 2004). Many aspects of the ecology and biology of sea snakes are poorly understood, as are the key threatening processes impacting sea snake populations and/or species, making it difficult to identify effective management strategies, but clearly the management regime of Ashmore Reef of the past 20 years has not been able to prevent massive declines in abundance and diversity of sea snakes. Given our lack of understanding of what has caused these declines, addressing knowledge gaps about the dietary and reproductive biology, ecology, disease susceptibility and broader conservation status of Australia's reef-associated sea snakes is crucial. Ideally research effort should be focused towards biological and ecological factors that have the potential to be managed, or have previously been highlighted as important, such as disease, reproduction and predator–prey relationships. A full assessment of the status of sea snakes on other Timor Sea reefs has the potential to inform likely causes of decline, as these reefs have different management regimes and responses to impacts such as bleaching (Ceccarelli et al., 2011b; Smith et al., 2008), and is needed to assess the regional extent of snake declines. For example, *A. foliosquama*, (Critically Endangered under IUCN, 2011), had not been seen at Ashmore (or Hibernia) Reef since the late 1990s but in 2010 one dead individual, collected at Barrow Island, was deposited in the Western Australian Museum. This species is regarded as being endemic to Ashmore and Hibernia reefs so it is not clear if the Barrow Island individual was a waif or whether *A. foliosquama* occurs in locations on the WA coast. Clearly, dedicated research is needed to determine the true geographic range and population sizes of this and other Critically Endangered and Endangered sea snake species. Most importantly, we need to identify effective management actions specific to maintaining populations of reef-associated sea snake species in order to avoid similar catastrophic declines in the future.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.07.004.

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