Zoological Studies **49**(1): 108-123 (2010)

Zoological Studies

Persistent and Expanding Population Outbreaks of the Corallivorous Starfish *Acanthaster planci* in the Northwestern Indian Ocean: Are They Really a Consequence of Unsustainable Starfish Predator Removal through Overfishing in Coral Reefs, or a Response to a Changing Environment?

Vanda Mariyam Mendonça[1,2,*], Musallam Mubarak Al Jabri[3], Ibrahim Al Ajmi[3], Mohamed Al Muharrami[3], Mohamed Al Areimi[3], and Hussain Ali Al Aghbari[4]

[1]*Expeditions International (EI-EMC), P.O. Box 802, Sur 411, Oman*
[2]*Algarve Marine Sciences Centre (CCMAR), University of Algarve, Campus of Gambelas, Faro 8005-139, Portugal*
[3]*Ministry of Environment and Climate Affairs, P.O. Box 323, Muscat 113, Oman*
[4]*Ministry of Fisheries, P.O. Box 467, Muscat 113, Oman*

(Accepted August 14, 2009)

Vanda Mariyam Mendonça, Musallam Al Jabri, Ibrahim Al Ajmi, Mohamed Al Muharrami, Mohamed Al Areimi, and Hussain Ali Al Aghbari (2010) Persistent and expanding population outbreaks of the corallivorous starfish *Acanthaster planci* in the northwestern Indian Ocean: are they really a consequence of unsustainable starfish predator removal through overfishing in coral reefs, or a response to a changing environment? *Zoological Studies* **49**(1): 108-123. Population outbreaks of the starfish *Acanthaster planci* have been persisting for at least the past 25 yr on coral reefs in the Gulf of Oman, in the northwestern Indian Ocean. A survey conducted in 2001 showed that the *A. planci* population on the Dimaniyat Is. was as abundant (around 5 individuals (ind.)/transect; equivalent to 100 ind./ha) as that recorded during an outbreak in the early 1980s. Local authorities are controlling starfish populations by culling relatively large adult individuals. These outbreaks cause considerable damage to coral communities, as observed specimens were adult individuals of about 60 cm in total diameter (no juveniles were observed). The situation has persisted for over 2 decades, and has now spread to coral reefs in the Arabian Gulf. Although *A. planci* population outbreaks were associated in the past with overfishing of starfish predators in coral reef areas, in the present study, we found no connection between this theory and starfish outbreaks, as stomach contents of carnivorous fish specimens likely to prey on this starfish species, caught on coral reefs on the Gulf of Oman, and sold at local fish markets (in Barka, Muscat, and Sur), showed no presence of *A. planci* in their diets. Therefore, the reason for *A. planci* population outbreaks could not have been due to overfishing of predator species, but is most likely to have been caused by the frequent input of nutrients, due to frequent upwelling events in the northwestern Indian Ocean, leading to planktonic blooms which thus enhance *A. planci* recruitment. http://zoolstud.sinica.edu.tw/Journals/49.1/108.pdf

Key words: *Acanthaster planci*, Coral reefs, Northwestern Indian Ocean, Starfish, Upwelling.

There are few principal areas of coral cover in the northwestern Indian Ocean, especially along the Oman coasts: the Musandam Peninsula near the Strait of Hormuz, the Capital Area coast (including the Dimaniyat Is.), along the central Oman coast (including Masirah I.), and along the Dhofar coast (including the Al Hallaniyat Is.). Although most of the coastline of Oman is also unsuitable for true reef development (either due to frequent upwelling events and/or the occurrence

*To whom correspondence and reprint requests should be addressed. V. Mendonça, Rua João Countinho Pais, 23 2EF, 8700-240 Olhão, Portugal. E-mail:vmmendonca@hotmail.com

of sandy substrate in areas of relatively strong currents), both well-developed multispecific reefs (such as those off the Dimaniyat Is.) and monospecific reefs mostly of the cabbage coral *Montipora foliosa* (such as those in the Gulf of Masirah) occur in the area (Fig. 1).

Previous studies (Sheppard and Salm 1988, Salm et al. 1993, Planes and Galzin 1999, Al Jabri 2003, MRMEWR 2003) examined the diversity of corals in Oman (where fewer than 150 species belonging to about 50 genera have been identified) and proved that the coral community is less diverse than that of the great Indo-Pacific region (with over 500 species belonging to more than 80 genera; e.g., Veron 2000).

In the northwestern Indian Ocean (ROPME 2004) and elsewhere (McClanahan et al. 2002, Bak et al. 2005, Briggs 2005, Smith et al. 2005, Edmunds 2007), coral reef decline has been a cause for concern, and it is sometimes difficult to attribute a single cause to coral degradation. In fact, the decline in coral reef health may be the result of more than 1 affecting factor. For instance, coral bleaching due to climatic change has been a major factor affecting coral communities (Ostrander et al. 2000, Barton and Casey 2005), as small changes in temperature values may cause massive mortality of corals (e.g., Bruno et al. 2001, Baird and Marshall 2002, Edmunds 2005, Graham et al. 2006 2007). However, in both the Gulf of Oman and Arabian Sea, coral reefs are continuously stressed by high summer temperatures (with seawater temperatures sometimes exceeding 32°C), and have also survived frequent temperature and salinity fluctuations due to frequent upwelling events (Tudhope et al. 1996), while displaying small signs of bleaching (Obura 2005). Coles and Brown (2003) discussed the ability of coral communities to adapt to frequent stress in the area. Similarly, palaeontological studies conducted in the Caribbean also proved the ability of coral communities to adapt and sometimes evolve into a community with a distinct species composition (Aronson et al. 2005). However, the rate at which adaptations occur in previously less-stressed communities is still a serious concern globally (e.g., Knowlton 2001, Baker et al. 2004, Donner et al. 2005, Berkelmans and van Oppen 2006, Feary et al. 2007, McClanahan et al. 2007).

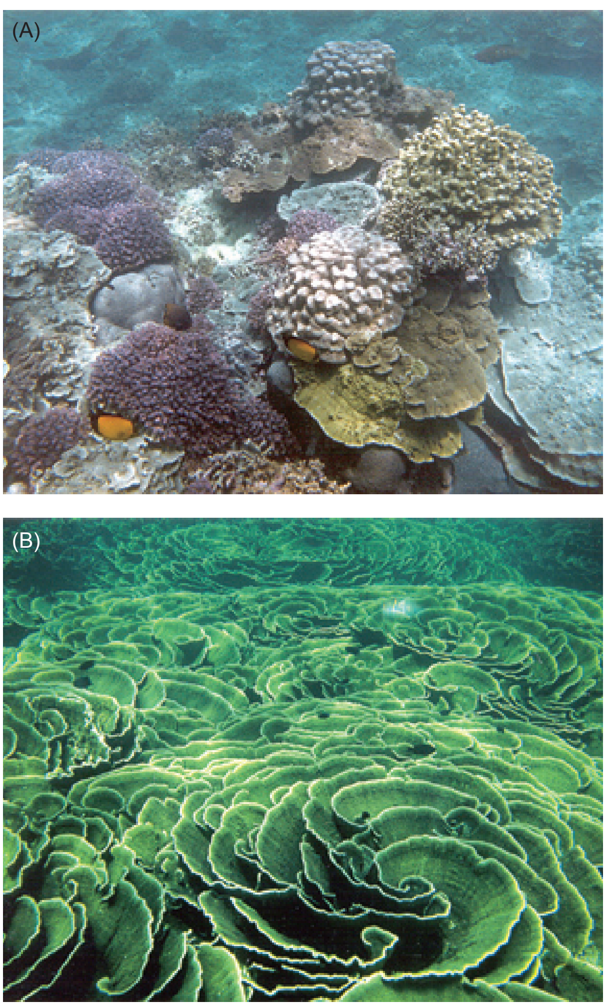

Fig. 1. Contrasting coral communities between the Gulf of Oman (multispecific reefs; plate A) and the Masirah Channel (monospecific reefs of *Montipora foliosa*; plate B)

In addition, other problems in the northwest Indian Ocean, such as coastal erosion and storm damage during the monsoons, are also important factors which must be considered (e.g., Dobbin 1992, Al Jufaili et al. 1999, Sheppard et al. 2002, Madin and Connelly 2006). Anthropogenic impacts including eutrophication (e.g., Diaz-Pullido and McCook 2005, Renegar and Riegl 2005) and siltation (Crabbe and Smith 2005) due to coastal development, pollution from land- and sea-based sources (wastes and spills; e.g., Devlin and Brodie 2005, Fabricius 2005), and fishery-related damage (including net and anchor damage, overfishing, and harmful fishing activities; e.g., Chiappone et al. 2005) are also important factors controlling coral communities.

Finally, coral communities are also stressed by biological interactions, especially from predation pressure by the corallivorous starfish *Acanthaster planci* (e.g., Glynn 1993, Benzie and Wakeford 1997) and corallivorous fish such as the butterflyfish (Chaetodontidae; Berumen and

Pratchett 2006a b 2008, Pratchett 2005 2007) and parrotfish (Scaridae; Rotjan and Lewis 2006). Coral diseases (Coles 1994, McClanahan 2002, Rosenberg and ben Haim 2002, Aeby 2005) also play important roles. Seaturtles *Chelonia mydas* and *Eretmochelys imbricata*, present in relatively large numbers year round in the northwest Indian Ocean (e.g, Mendonça et al. in press), are also coral predators, but their selective feeding habits (mostly algae for *C. mydas*, Amorocho and Reina 2007; and sponges for *E. imbricata*, e.g., Leon and Bjorndal 2002, Stampar et al. 2007) make their impacts an unlikely factor controlling coral reef communities.

However, population outbreaks of the corallivorous crown-of-thorns starfish *Acanthaster planci* are a serious cause for concern, as this is the most voracious starfish species (Pratchett 2001, Uthicke and Benzie 2001, Harriot et al. 2003), with adult specimens reaching 70 cm in diameter. In addition, starfish can well survive predation pressure by their own predators due to their regenerating abilities, so that they can discard a part of themselves which will replicate into a new individual at a fast rate (Yasuda et al. 2006). Therefore, starfish population outbreaks are a serious threat, in terms of the health of coral reefs, and may have significant negative impacts on coral communities.

Studies on predator-prey interactions and trophodynamics in other coastal ecosystems (e.g., lagoons) have shown that predation pressure is able to cause significant impacts on prey density and community structure at several levels of food webs (e.g., Mendonça et al. 2007a b 2008 2009). Similarly, significant impacts of predation pressure by *A. planci* on coral reef ecosystems were observed by Glynn (1990). Population outbreaks have been relatively frequent in the Indo-Pacific region, and may cause widespread damage to coral reefs as a single individual on a feeding occasion may leave relatively large scars on a coral colony (Bikeland 1990, Bikeland et al. 2003, Koonjul et al. 2003).

There have been several theories on the causes of outbreaks of crown-of-thorns starfish, but those with the greatest support are as follows: Fluctuations in crown-of-thorns populations may be a natural phenomenon. This theory is yet to be either proven or rejected; Removal of natural predators of crown-of-thorns starfish, through overfishing of large carnivorous fish species on coral reefs has allowed these starfish populations to expand. This theory is supported by some authors, of which Dulvy et al. (2004) can be cited; and Increased amounts of nutrients in coastal waters due to anthropogenic activities in coastal areas may induce increases in planktonic activity, and thus more food becomes available for starfish larval stages, which can grow to mature adult individuals resulting in starfish population outbreaks. This theory has been postulated for some time and is still supported by relatively recent studies (e.g., Brodie et al. 2005).

The crown-of-thorns starfish *A. planci* was particularly abundant in the Gulf of Oman in the 1980s (Fig. 2), with the abundances off the Dimaniyat Is., Muscat, and Sur, among the

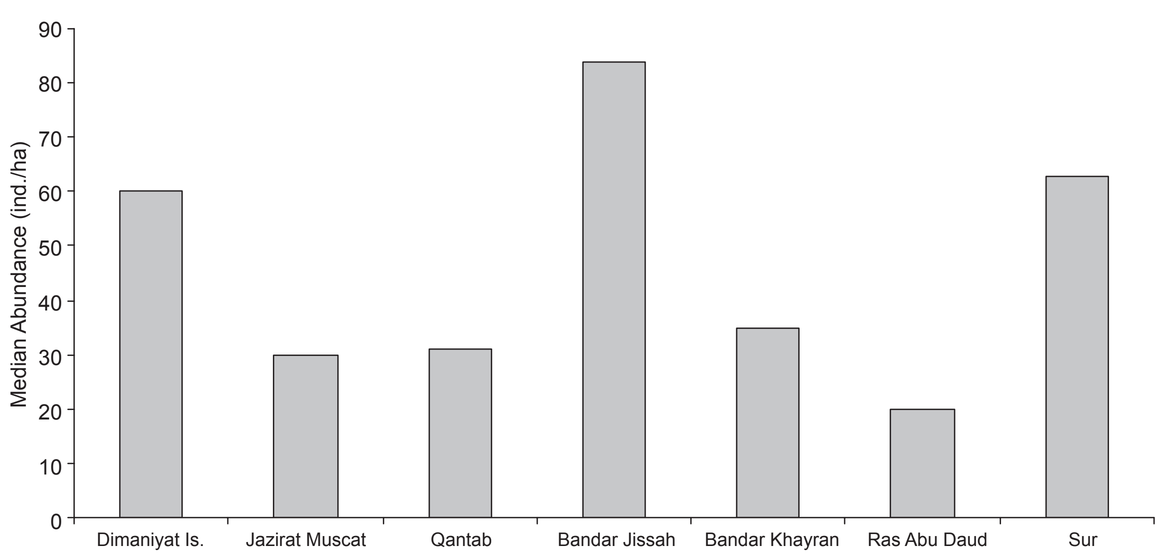

Fig. 2. Starfish abundance at several sites in the Gulf of Oman during the 1980s (adapted from Glynn 1993).

highest in the area. Therefore, local authorities, preoccupied with the preservation of the coral reefs off the Dimaniyat Is., have been culling large individuals since 1996.

The present study reviews and updates information on the coral communities of the Gulf of Oman (of which corals off the Dimaniyat Is. are the most important), and on populations of the corallivorous starfish *A. planci.* It also looks into the ecology of this starfish species, and discusses the likely causes behind starfish population outbreaks in the area.

MATERIALS AND METHODS

Study area

The Gulf of Oman includes areas from the Strait of Hormuz (separating the Arabian/Persian Gulf from the northern section of the Gulf of Oman) to Ras Al Hadd Cape in Oman (separating the southern section of the Gulf of Oman from the Arabian Sea). The area is subjected to great fluctuations in temperature, salinity, and nutrient concentrations due to frequent upwelling events brought about by the effects of both the southwesterly summer monsoon and the northeasterly winter monsoon.

Some seawater parameters measured for non-upwelled waters in late spring 2003, at a site in the southern part of the Gulf of Oman, are presented in table 1. Several parameters (temperature, salinity, dissolved oxygen, and chlorophyll a) were measured at the site using a multiparameter analysis instrument model Idronaut 316 (Idronaut 2002). Seawater samples (*n* = 3) were collected using an automated water sampler and were analyzed for nitrates, nitrites, ammonia, and phosphates using standard methods (USEPA 1983): for nitrates, the cadmium reduction method, measured at 540 nm by colorimetry, was used; for nitrites, the diazonium reduction method, measured at 540 nm by colorimetry, was used; for ammonia, the Bethelot reaction, measured at 630 nm by colorimetry, was used; and for phosphates, the antimony phospho-molybdate reaction, measured at 630 nm by colorimetry, was used. However, these parameters may present much higher values following frequent upwelling in the northern Indian Ocean, especially off the coast of Oman, as captured by remote sensing images from space (Fig. 3). The Oceanographic Data Center of the United States National Oceanographic and Atmospheric Administration (NOAA) records remotely, on a regular basis, data on the physical, chemical, and biological characteristics of seawater in the area (e.g., NOAA 2005), and these parameters were also previously recorded on site extensively by the Arabesque Project of the Joint Global Ocean Flux Study (JGFOS 1998).

Within the Gulf of Oman, coral reefs are more developed especially off the Dimaniyat Is., an archipelago of 9 islands, named D1 to D9, from east to west, with numerous satellite rocks, reefs, and shoals, formed on emergent limestone rock and fossil reefs (Fig. 4). The total land area of the islands is 85 ha, and these islands are situated 20 km offshore, about 100 km north of Muscat.

Table 1. Seawater quality (*n* = 3) of non-upwelled waters at a site northwest of Sur (22°38'N; 59°25'E), Gulf of Oman, in late spring 2003

Parameter	Median	Range
Temperature (°C)	30.00	28.60 - 32.10
Salinity (PSU)	36.50	36.40 - 36.80
Dissolved O_2 (mg/L)	6.50	5.50 - 7.07
Chlorophyll *a* (μg/L)	0.35	0.15 - 0.40
Nitrates (as N; μg/L)	10.00	0.34 - 85.00
Nitrites (as N; μg/L)	5.00	0.50 - 20.00
Ammonia (as N; μg/L)	15.00	3.00 - 22.00
Phosphates (ortho-; μg/L)	18.00	1.00 - 25.00

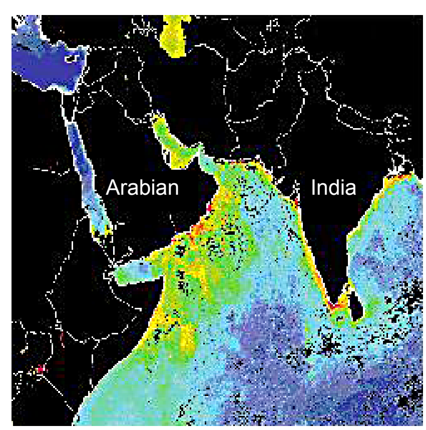

Fig. 3. Relative distribution of chlorophyll *a* recorded from space in Sept. 2003 (red color corresponds to higher concentrations and blue color to lower concentrations), indicating a phytoplankton bloom in the northwestern Indian Ocean (NWIO): with maximum intensity in areas off Oman, in the northern Arabian Sea, bordering the Gulf of Oman (Source: National Oceanographic and Atmospheric Administration, Florida, USA).

The coral reefs surrounding or near these islands are areas off islands D1-D9 and 2 main isolated shoals: one west of island D1 and another northwest off island D9. Coral reefs off the Dimaniyat Is. were first mapped by Salm (IUCN 1986), when the first genera checklist was produced for the area. These reefs support complex food webs involving high biodiversity of benthic organisms, the planktivorous whale shark *Rhincodon typus*, coral reef fish, marine reptiles (2 seaturtle species *Chelonia mydas* and *Eretmochelys imbricata*, Mendonça et al. 2001; and at least 2 seasnake species, the reef snake *Hydrophis ornatus* and the yellow-bellied snake *Pelamis platurus*, as we observed), and cetaceans (baleen whales or *Mysticeti*, Bryde's whale *Balaenoptera edeni*, toothed whales or *Odontoceti*, the Indo-Pacific humpback dolphin *Sousa chinensis*, Risso dolphin *Grampus griseus*, bottlenose dolphin *Tursiops truncatus*/*Tursiops aduncus*, pantropical spotted dolphin *Stenella attenuata*, spinner dolphin *Stenella longirostris*, common dolphin *Delphinus capensis*, pygmy killer whale *Feresa attenuata*, false killer whale *Pseudorca crassidens*, killer whale *Orcinus orca*, and sperm whale *Physeter macrocephalus*; OCRG 2004). The area also provides nursery grounds for several fish species, some of which are of commercial value.

The islands are uninhabited by humans and terrestrial mammals, due to a lack of fresh water. The absence of human settlements and the presence of large areas covered by halophytic *Suaeda* spp. shrubs have contributed to the global importance of the islands as nesting grounds for birds, especially migrating seabirds (e.g., terns *Sterna* spp., gulls *Larus* spp. and the Common Noddy *Anous stolidus*) but also resident birds of prey (Osprey *Pandion haliaetus* and the Sooty Falcon *Falco concolor*) and herons (e.g., *Egretta gularis* and *Ardea cinerea*) (Mendonça et al. 2001).

Due to the biological importance, the archipelago and surrounding waters were proclaimed a nature reserve in 1996, when efforts to protect the coral reefs, on which the complex food webs depend on, were taken more seriously, and large

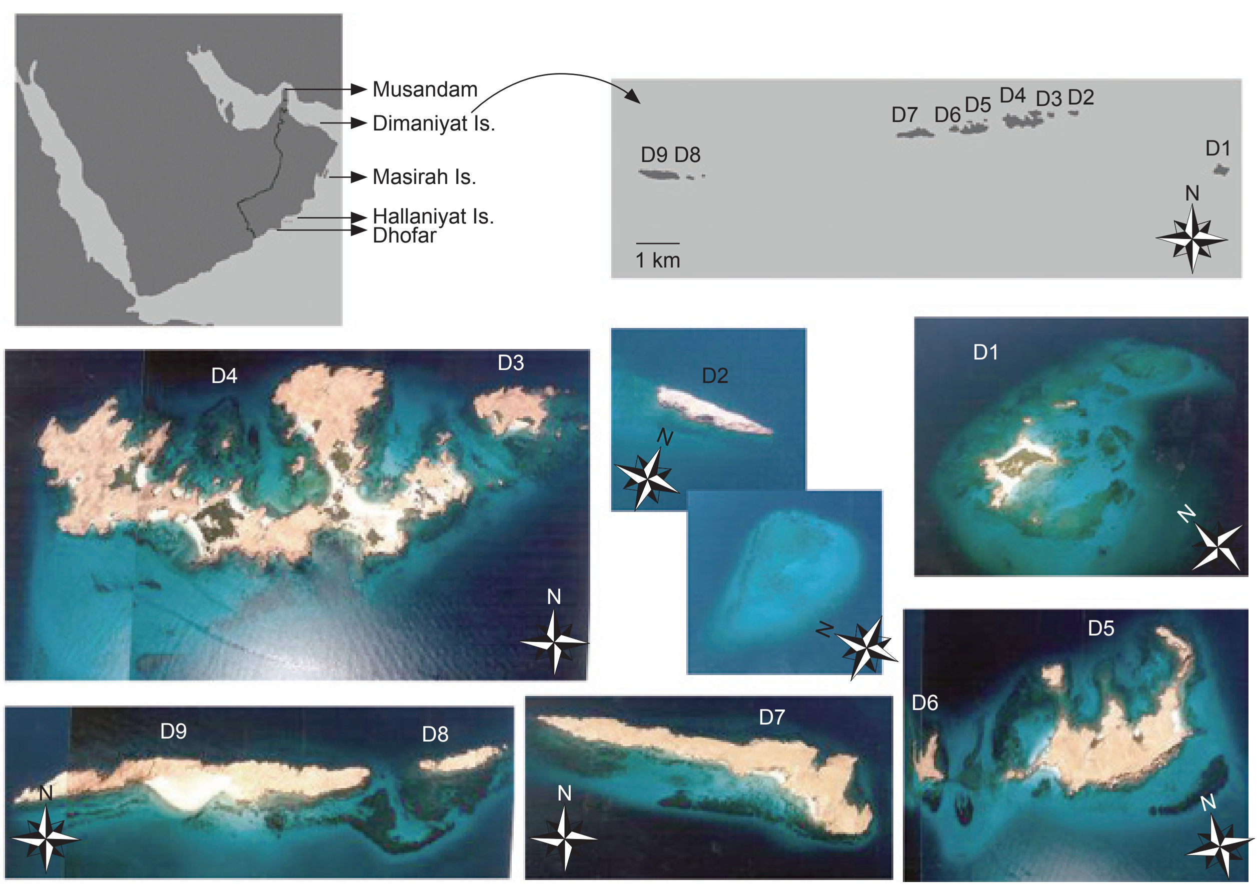

Fig. 4. Areas of true reef building corals off Oman, and aerial photographs of the Dimaniyat Is., Gulf of Oman, taken in 1998 (W, west; NW, northwest; source of aerial photos: Ministry of Environment and Climate Affairs, Muscat, Oman).

starfish culling began on a regular basis.

Assessment of coral communities

The present study compiled all available information on coral checklists for the Dimaniyat Is., conducted during 1985-1996 (IUCN 1986, Salm and Sheppard 1986, Sheppard 1986, Sheppard and Wells 1988, Salm 1993) and our own records to the species level (from shallow-water dives and snorkeling) during 1999-2001. Results for the Dimaniyat Is. were compared with other areas: Fahal I. (Muscat area, Gulf of Oman) surveyed during 2002-2004; Masirah I. (Sharqiyah region, Arabian Sea) surveyed in 2005; and Dibba and Khawr Habalayn, both on the Musandam Peninsula, surveyed in 2006. Comparisons with Dhofar used data from Salm et al. (1993).

Coral communities (using the presence/absence of corals) were compared by the following multivariate analyses (KCS 2001): cluster analyses were used to compare coral communities (both by families and species) among different sites in the Gulf of Oman and Arabian Sea, and to compare coral communities (by species) among sites within the Dimaniyat Is. Nature Reserve; DECORANA (detrended correspondence analysis) was used to compare coral communities (by species) among sites within the Dimaniyat Is. Nature Reserve; and Shannon diversity indices were used to compare coral communities by species among sites within the Dimaniyat Is. Nature Reserve. The Shannon diversity index is given by the equation: $H = - \sum p_i \ln p_i$; where i ranges from 1 to s, with s being the total number of species in the community (or richness), and for each species, the proportion of individuals or biomass that contributes to the total in the samples is p_i for the i^{th} species.

Assessment of corallivorous starfish *A. planci* populations

The present study also compiled all information recorded on the corallivorous crown-of-thorns starfish *A. planci* in the northwestern Indian Ocean since the 1980s (e.g., Glynn 1993) to more-recent studies (e.g., Planes and Galzin 1999), and data were complemented by our own observations during 1999-2008.

In the present study, updated information was obtained from sublittoral surveys (up to 25 m in depth), along 5 randomly selected radial transects perpendicular to the shoreline. This method was used either in offshore areas of the mainland or offshore the islands, and each transect was 50 m long (from the shoreline) and 10 m wide. Surveys were conducted at the following sites: Dimaniyat Is. (the D2 and D3 group, island D4, the D6 and D7 group, and the D8 and D9 group) during 1999-2001, after the starfish culling operations began in 1996; Fahal I. during 2002-2004; shores northwest of Sur in 2002-2003 and 2008; Masirah I. in 2005; and at 2 sites off the Musandam Peninsula, at Dibba in the Gulf of Oman and Khawr Habalayn in the Strait of Hormuz, in 2006. At each site, if surveyed previously by Glynn (1993), the same locations were revisited in order to compare current data with previous results. As also done by Glynn (1993), the abundance of the starfish *A. planci* (ind./transect) was transformed into ind./ha.

The median individual body size (total diameter) of the starfish *A. planci* was estimated, although these are likely to have been under-estimated since individuals were not properly measured because of problems in handling these spiny organisms. In order to compare previously available results from Glynn (1993), the total diameter (TD) was converted into a disc diameter (DD) using the relation TD = DD/0.56 (Glynn 1982).

Investigation of starfish *A. planci* presence in fish stomach contents

It is widely believed that larger carnivorous reef fish may be significant predators of *A. planci* (e.g., Dulvy et al. 2004). However, studies conducted elsewhere on the stomach contents of the most likely potential predators of *A. planci* showed that snappers (Lutjanidae), emperors (Lethrinidae), wrasses (Labridae), triggerfish (Balistidae), and pufferfish (Tetraodontidae) have varied carnivorous or even omnivorous diets, but *A. planci* has not been identified in any of their stomach contents (e.g., Allen 1985, Bean et al. 2002, Randall 2004, Disalvo et al. 2007). Similarly, although *A. planci* can be eaten by these relatively large carnivores or omnivores, no evidence was found proving that these predators had any significant impacts on the starfish population density or community structure.

In the present study, data provided by the Ministry of Agriculture and Fisheries (Table 2) and frequent visits to fish markets in Barka (in 1999-2007), Muscat (in 1999-2008), and Sur (in 1999-2008) permitted us to identify fish from coral reef areas for commercial purposes, although some bycatch reef fish with no economic interest, such as morays, were observed being discarded at sea during our field surveys, and these species were not surveyed. In order to observe whether the potential *A. planci* predators were actually feeding on this starfish, fishermen were requested to collaborate when cleaning specimens for their customers, and to put aside the stomach contents for further identification. This approach was applied in 2001 at Barka Beach (20 km from the Dimaniyat Is., and 100 km north of Muscat) and in 2008 in other fish markets in the Gulf of Oman, namely at Seeb (about 30 km north of Muscat), Mattrah (2 km north of Muscat), and Sur (200 km south of Muscat).

As no preservation method was used at the time when the fish specimens were caught, stomach contents were already very digested, but qualitative analyses (recording the presence or absence of any starfish or any other echinoderm remains, especially hard exoskeleton parts) were still possible.

At each surveyed site, stomach contents (n = 20 ind./species) of potential starfish predators, such as snappers *Lujanus bohar* and *L. johni*, emperors *Lethrinus* spp., and wrasses *Cheilinus lunatus* were observed on site using a stereo microscope. The surveyed specimens were all about 50 cm long, from snout to tail end.

RESULTS

Assessment of coral communities

The Dimaniyat Is., with clear waters, showed significant coral reefs down to 20 m, with well-developed patch reefs and fringing reefs along the southern side of the islands. On the other hand, on the exposed northern side, the maximum coral reef development was observed only at about 2 m of depth. Nevertheless, the area offers a variety of habitats for coral settlement including underwater cliffs and cavities on limestone and fossil coral substrate, and rocky outcrops in both exposed and sheltered locations, contributing to the relatively high coral diversity in the area, with at least 48 confirmed species. These coral community compositions are closer to that observed off Masirah I. on the Arabian Sea coast (Fig. 5), with higher diversity indices observed on a shoal west of D1, and off D4, the D2-D3 group, and island D7 (Figs. 6, 7).

The dominant species were *Pocillopra damicornis* and *Acropora* spp., although *Montipora* sp., *Porites lutea*, *Goniopora* sp., *Psammocora contigua*, *Pavona cactus*, *Platygyra daedalea*, *Plesiastrea versipora*, and *Leptastrea purpurea* were also common species. On the other hand, *Platygyra sinensis* and *Siderastrea savignyana* occurred only off D4, and *Anomastrea irregularis*, *Galaxea astreata*, and *Hydnophora excesa* only occurred on the shoal west of D1 (Fig. 8).

In general, the vertical growth of branching coral reefs (e.g., *Acropora* spp.) was 1-3 m, suggesting that this is still a very youthful stage of reef development. *Porites lutea* fringing reefs showed vertical growth of 4-5 m; and larger *Pocillopora damicornis* patches reached 6-7 m in thickness.

Assessment of corallivorous starfish *A. planci* populations

Table 2. Fishery landings (tons) in Oman in 2003-2005 (source: MONE 2006; N/A=not available)

Common name	Family	2003	2004	2005
Emperors	Lethrinidae	664	1582	525
Seabreams	Sparidae	600	1733	1063
Groupers	Serranidae	586	684	367
Croakers	Carangidae	1146	455	519
Sweetlips	Haemulidae	326	741	258
Snappers	Lutjanidae	3657	2819	2439
Rabbitfishes	Siganidae	101	91	18
Others	N/A	4099	4908	3454
Total national demersal landings		11,179	13,011	8643
Total national fish landings		N/A	139,235	128,879

During our surveys (1999-2008), 19 starfish species, belonging to 9 families, were identified. Most of the recorded starfish species were deposit-feeders, and the only relatively large corallivorous starfish was *A. planci* (Table 3, Fig. 9).

On island D4, the abundance of the starfish

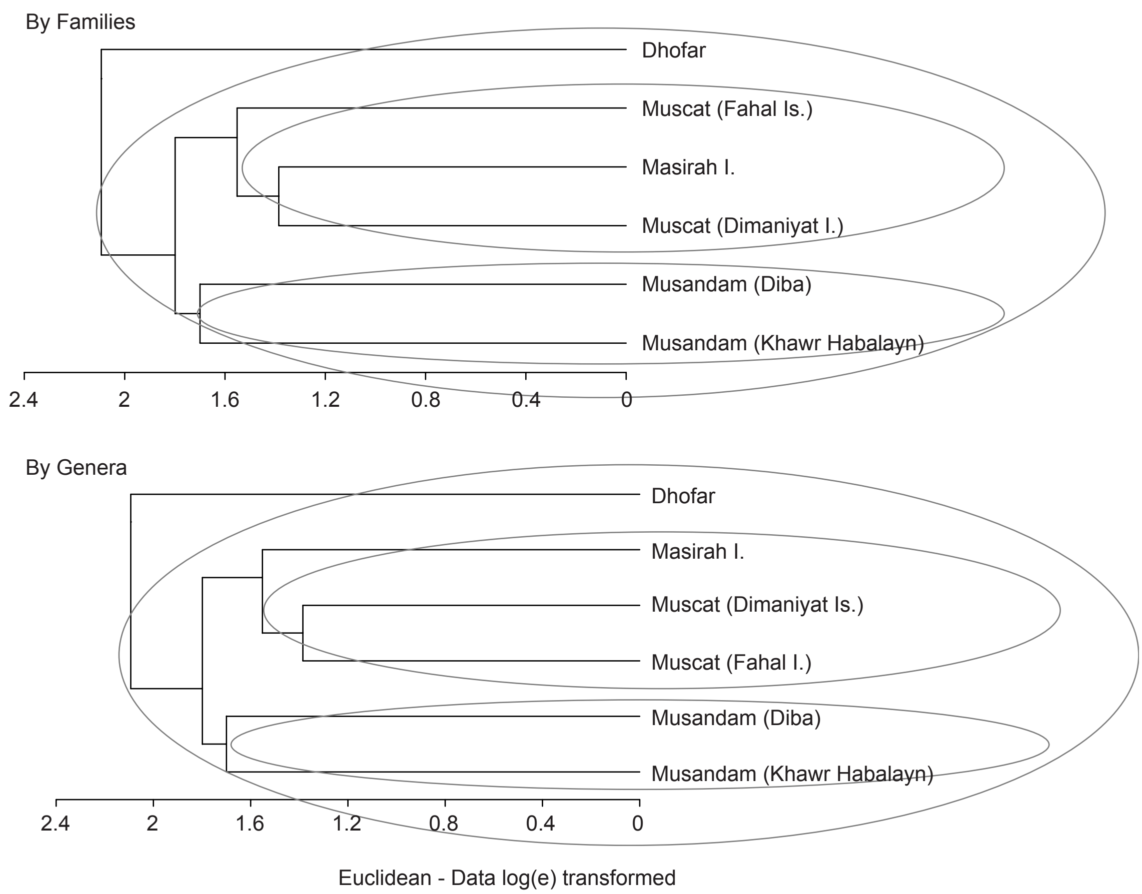

Fig. 5. Comparison of coral communities from several sites off Oman.

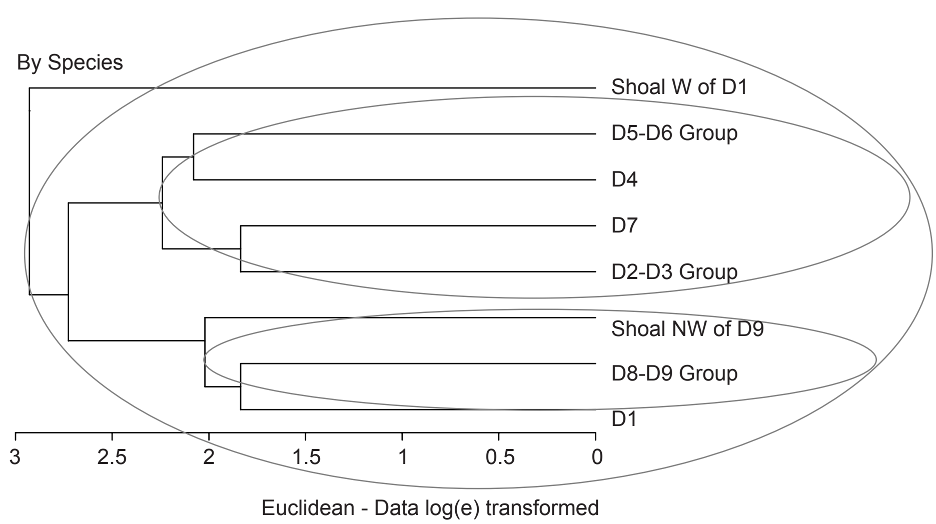

Fig. 6. Comparison of coral communities off the Dimaniyat Is., Gulf of Oman.

A. planci (around 5 ind./transect; thus 100 ind./ha) was similar to that found in 1982. However, the starfish *A. planci* density had decreased off the other islands (Fig. 10), most likely as a result of culling efforts by local authorities.

Starfish *A. planci* individuals observed in 2001 were about 50-60 cm in total diameter, corresponding to 28-33.6 cm in disc diameter. These dimensions for crown-of-thorns off the Dimaniyat Is. are larger than that registered previously in the area, although starfish of this size were previously found off Bandar Khayran and Bandar Jissah, south of Muscat (Fig. 11).

The starfish *A. planci* proved to be an opportunistic predator, feeding both on branching and non-branching corals in the Gulf of Oman (Fig. 12). In the Dimaniyat Is., in 2001, scars likely to have been caused by starfish were observed on *Platygyra* sp., and in Nov. 2002, a starfish was observed feeding on a branching *Montipora* sp. colony at 9 m in depth, northwest of Sur, in the southern part of the Gulf of Oman. In summer 2008, an adult starfish was again observed at the same site, northwest of Sur, on an area with coral cover of < 20% and dominated by *Acropora* spp.

In summer 2008 at this same site, a relatively high abundance of the ophiurid *Ophionereis* sp. on the order of 100-1000 ind./m^2 was present on rocky intertidal areas among an algal mat dominated by the brown algae *Padina* sp.

Investigation of the starfish *A. planci* presence in fish stomach contents

Off the Dimaniyat Is., of the total of 98 identified fish species (belonging to 47 families), 57 were carnivorous and 10 were omnivorous. Most of these fish individuals were however of a relatively small size, and therefore unable to feed

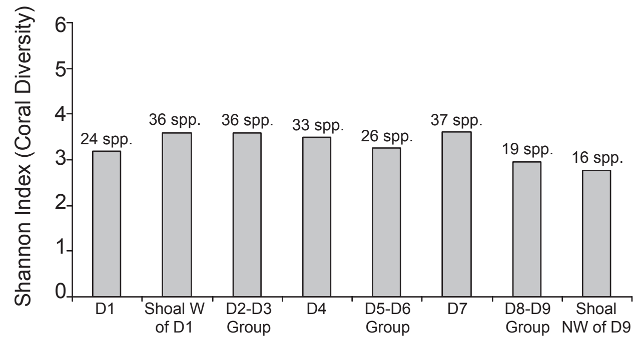

Fig. 7. Coral diversity indices off the Dimaniyat Is., Gulf of Oman.

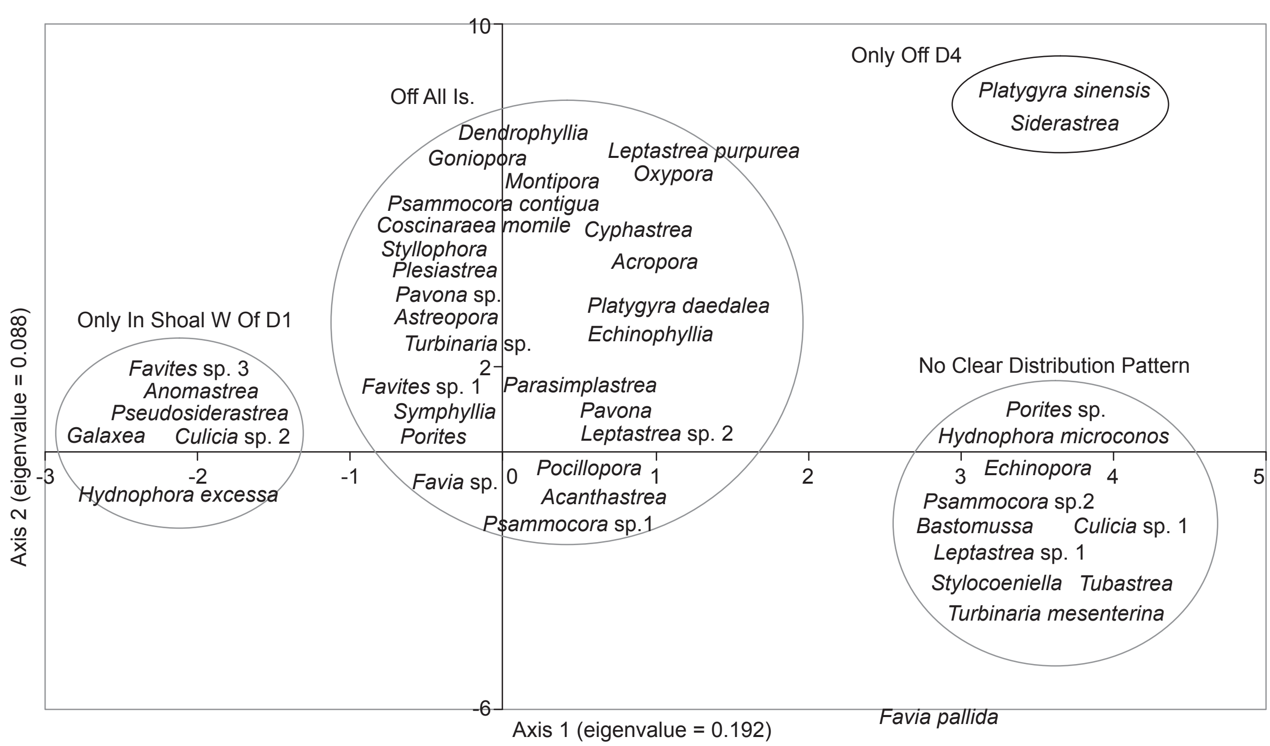

Fig. 8. Coral species distribution off the Dimaniyat Is., Gulf of Oman (full species names are indicated only when more than 1 species per genus were recorded; otherwise only the genus is given).

on large starfish. In addition, during the surveys conducted within the framework of the present study, no attempt by any individual fish to feed on crown-of-thorns was recorded.

In fact, qualitative analyses of stomach contents of fish species, either accounting for small pelagic, large pelagic, or demersal fishery landings (such as snappers *Lutjanus bohar* and *L. johni*, emperors *Lethrinus* sp., and wrasses *Cheilinus lunatus*), and which were likely to be among predators of *A. planci* starfish, failed to show any presence of this starfish in their diets at any surveyed sites (Barka, Seeb, Mattrah, and Sur fish markets).

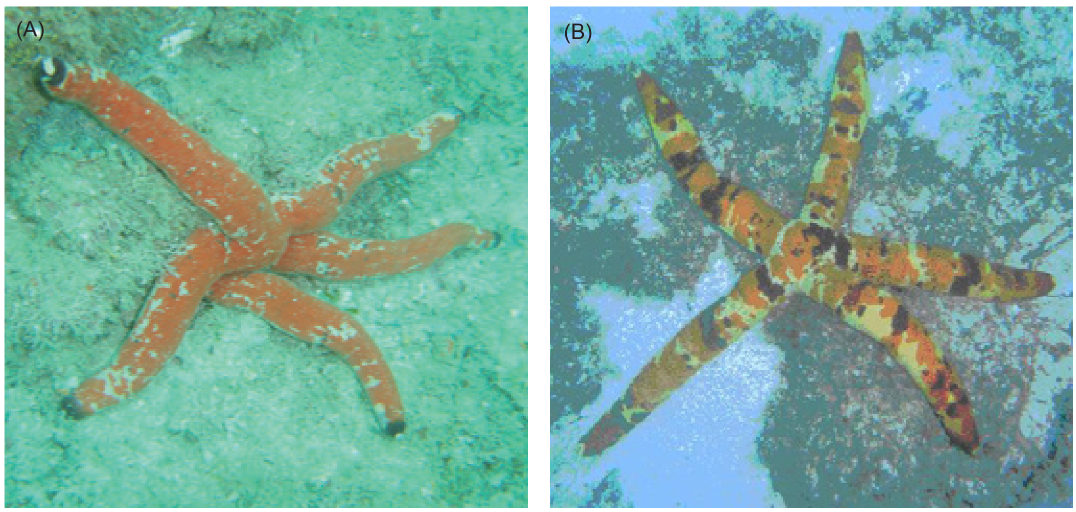

Fig. 9. Deposit-feeding starfish *Leiaster* sp. (A), and *Leiaster coriaceus* resembling the pattern of the Omani Army uniform, (B), both observed in shallow waters of the Arabian Sea.

Table 3. Identified starfish species in the Gulf of Oman and Arabian Sea, during surveys conducted for the present study in 1999-2008, complemented by information on predominant feeding strategies and maximum total diameters

Family	Species	Feeding strategy	Maximum size (cm)
		(Richmond 2002)	
Astropectinidae	*Astropecten* sp. 1	Deposit-feeder	15 (for the genus)
	Astropecten sp. 2	Deposit-feeder	15 (for the genus)
Goniasteridae	*Monachaster sander*	Deposit-feeder	8
	Stellaster childreni	Deposit-feeder	20
Oreasteridae	*Culcita schmideliana*	Corallivorous	15
	Culcita sp.	Corallivorous	15 (for the genus)
	Pentaceraster tuberculatus	Corallivorous	20
Ophidiasteridae	*Linckia multifora*	Deposit-feeder	17
	Fromia indica	Deposit-feeder	5
	Fromia milleporella	Deposit-feeder	5
	Fromia sp.	Deposit-feeder	5 (for the genus)
	Ophidiaster hemprichii	Deposit-feeder	15
	Leiaster coriaceus	Deposit-feeder	20
Asterinidae	*Asterina burtoni*	Deposit-feeder	1.5
	Asterina sp.	Deposit-feeder	7
Acanthasteridae	*Acanthaster planci*	Corallivorous	70
Asteropseidae	*Asteropsis cairnifera*	Deposit-feeder	9
Pterasteridae	*Euretaster cribrosus*	Corallivorous	10
Echinasteridae	*Echinaster purpureus*	Deposit-feeder	28

DISCUSSION

The present study, compiling previous studies and updating knowledge on coral reefs in the Gulf of Oman showed that coral diversity off the Dimaniyat Is. was larger than previously known, and further studies may increase the presently available species checklist.

Although Glynn (1993) observed scars only on the coral genera *Montipora* and *Acropora* and avoidance of *Pocillopora damicornis*, in the present study, scars were observed on those genera and also on several coral genera including *Platygyra* and *Hydonophora*. According to Cumming (2000 2002), scars caused by other coral predators, such as the gastropod *Drupella* sp., are distinct from those caused by *Acanthaster planci* since *Drupella* scars are on the edges and never in the middle of live tissue because these gastropods avoid crawling over live coral. On the other hand, *Acanthaster* scars can be in the center of a colony, surrounded by live tissue. In addition, *Drupella* also grazes the branch bases (in branching corals) first, while *Acanthaster* often feeds on the tips leaving basal parts alive.

When comparing results of starfish *A. planci* populations in 2001 with those available from 1982 (Glynn 1993), it was observed that although the population densities slightly decreased, the overall median was very similar (50 ind./ha). On the other hand, individual body sizes were slightly smaller in the Dimaniyat Is. in 1982, However, on both sampling occasions, starfish populations of *A. planci* (1982 and 2001) were likely to have been underestimated, because starfish hide themselves under corals and rocks.

As also observed by Glynn (1993) in 1982, in 2001, no juveniles were recorded, and no corallivorous gastropods were observed. Also no small scars, which could have been caused by juvenile corallivorous starfish, were observed. The list of corallivorous starfish also indicates that no other starfish predator could cause the observed large scars on corals, except for 2 distinct scars, at one of the locations near island D4, with irregular removal of the brain coral cover, which could have been caused by hawksbill turtles *Eretmochelys imbricata* (which also feed on corals and sponges, but probably prefer to ingest sponges).

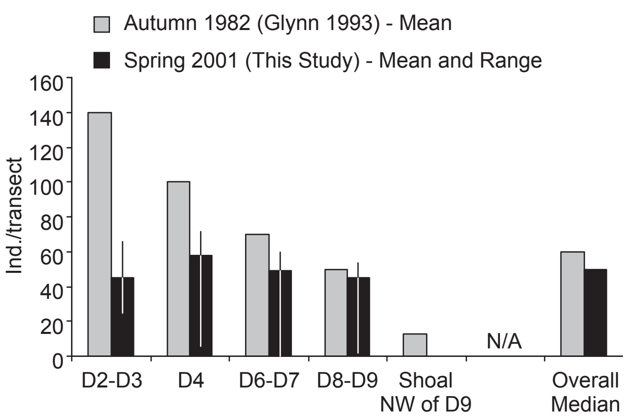

Fig. 10. Available records of abundance of the corallivorous starfish *Acanthaster planci* off the Dimaniyat Is., Gulf of Oman.

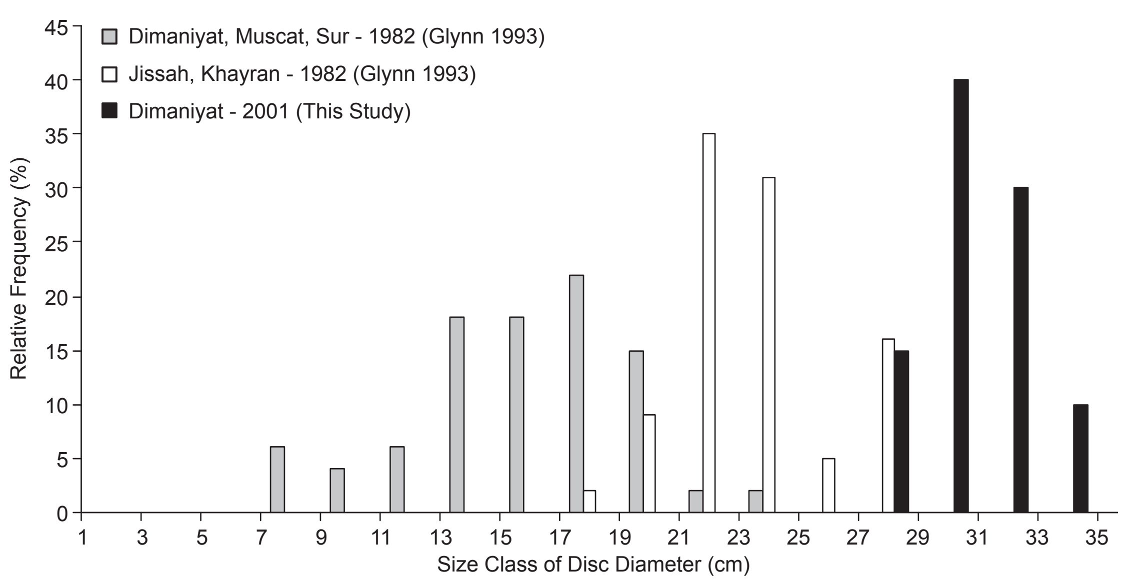

Fig. 11. Available records of size class frequency distributions of *Acanthaster planci* in the Gulf of Oman.

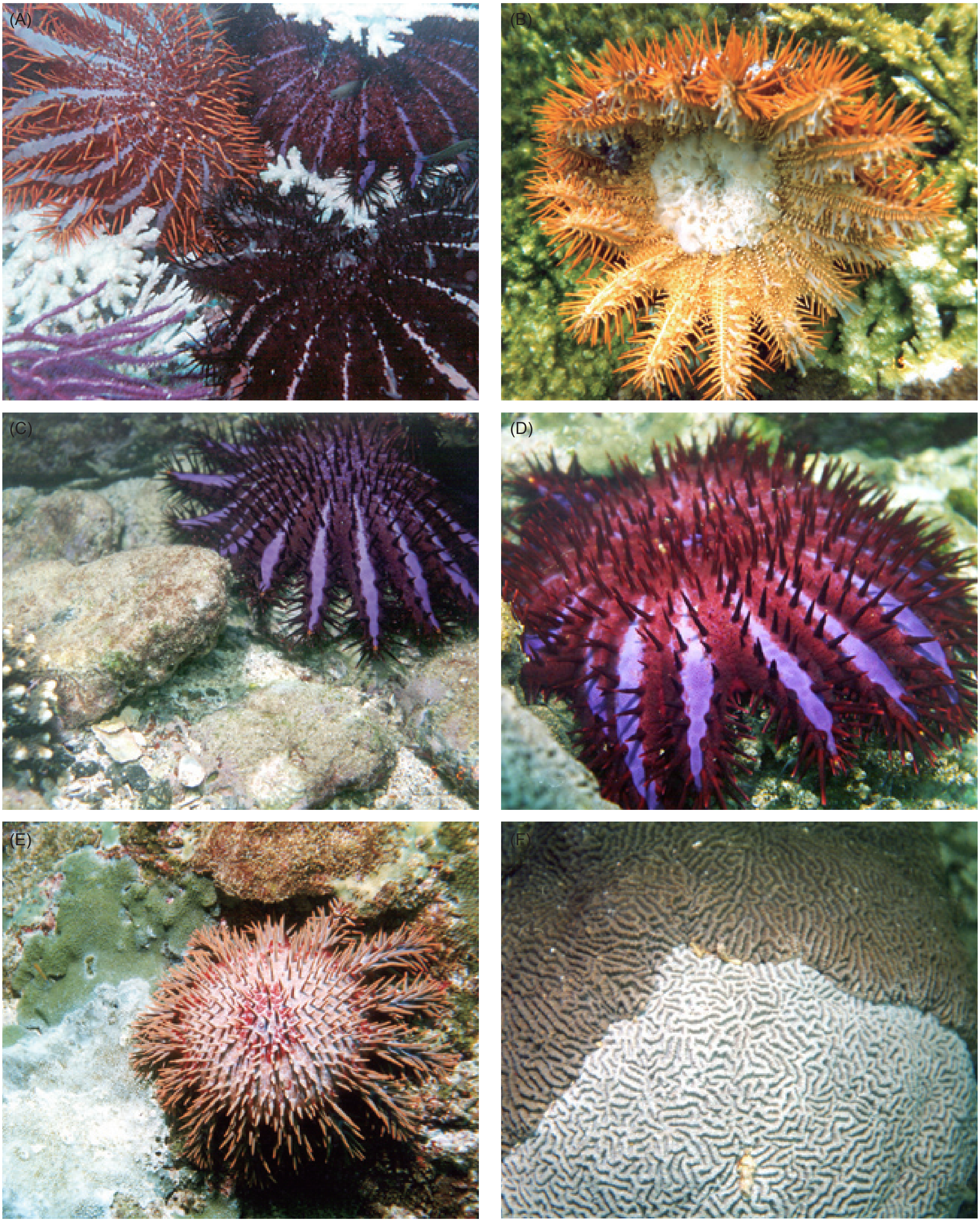

Fig. 12. (A) is an indicator of *Acanthaster planci* starfish abundance off the Dimaniyat Is. (Gulf of Oman) in the 1990s. (B) shows a starfish individual, recorded off the Dimaniyat Is., which was forcefully detached and turned upside down, showing that it had been feeding on live coral tissue. (C) and (D) show scars made by *A. planci* on live branching corals *Acropora* spp., recorded off Khalboo, 1 km north of Muscat. (E) shows *A. planci* scars on a non-branching coral *Hydnophora* sp., recorded in the Dhofar region, southern Oman. (F) shows *A. planci* scars on a non-branching coral *Platygyra* sp., also off Khalboo, Muscat.

Since the population studied in 2001 on the Dimaniyat Is. area is descendent of that studied in 1982, at the same locations, and there were some differences in individual body sizes between the observed group of individuals, with smaller-sized individuals in 1982 and larger-sized individuals in 2001, differences in diet when the same coral species are available may indicate that starfish have distinct food preferences depending on their own individual body sizes.

The lack of observations of starfish remains in stomach contents of relatively larger reef fish might not be surprising since the starfish *A. planci* is also known to be highly poisonous (e.g., Rual 1999), although their predators may have developed immunity to their venom (Dill 1983, Terry-Graham et al. 2002), as some species such as hawksbill turtles are immune to chemical substances in sponges, which are often poisonous to other species. However, bioaccumulation of these toxins in fish predators could indirectly affect humans consuming these fish species, as observed in hawksbill turtles which may be poisonous to humans (e.g., Aguirre et al. 2006). In addition, the spiny protection of the starfish generally makes them less suitable as prey for predators, as animals display resource selection, as a survival strategy, according not only to the protein content but also by avoiding injury when catching prey (e.g., Manly et al. 1993, Brown and Kotler 2004).

Although the starfish *A. planci* is reported to be a common species in the western Indian Ocean, previous reports (Salm 1993) indicated its absence off the southern coasts of the Sultanate of Oman (Arabian Sea) and also its absence in the Arabian Gulf, being only recorded in the Gulf of Oman. Glynn (1993) discussed this and suggested that the frequent upwelling conditions of the Arabian Sea may prevent spawning of starfish populations, but no explanation was put forth by that author to explain the absence of this starfish species from the Arabian Gulf. Nevertheless, a more recent study (ROPME 2004) reported *A. planci* outbreaks in the Arabian Gulf area off the United Arab Emirates which caused widespread mortality of coral reefs. Efforts by local governmental authorities in charge of managing, conserving, and rehabilitating coral reef ecosystems, in Oman and elsewhere in the region, include population control of the coral predator *A. planci* (a method also used in Australia, e.g., Harriot et al. 2003); deployment of artificial reef structures on very damaged areas; limited and controlled access by visitors; regulated fishing practices; and underwater clean-up operations.

We failed to find any evidence that larger carnivore fish can significantly affect *A. planci* populations in coral reef areas, as no crown-of-thorn remains were identified in stomach contents of fish caught in corals reefs in the Gulf of Oman. Therefore, overfishing in coral reefs, as the likely cause of crown-of-thorns outbreaks in the Gulf of Oman, also could not be supported by the results obtained in the present study. Nevertheless, off the Dimaniyat Is. and elsewhere in the region, corals and coral reefs continue to be damaged by other direct and indirect effects of fishing practices including anchoring, and damage caused by lost and/or discarded fishing nets which become entangled on reefs causing death to corals and pelagic fauna (crustaceans, cephalopods, fish, seaturtles, seasnakes, and cetaceans), including both endangered and commercially valuable species.

In fact, the causes of primary outbreaks of the coral-eating crown-of-thorns starfish *A. planci* are still subject to scientific controversy. According to Brodie et al. (2005), the possibility of primary outbreaks being linked to terrestrial runoff was postulated a number of times, suggesting that enhanced nutrient supply is critical for enhanced *A. planci* larval development. Those authors found a positive correlation between concentrations of large phytoplankton (> 2 μm) in coastal areas and higher *A. planci* larval development, and the Australian Institute of Marine Sciences recently even listed the crown-of-thorns starfish *A. planci* as a candidate bioindicator to monitor changing water quality on the Great Barrier Reef (Fabricius et al. 2006).

As upwelling events are a frequent phenomena in the northwestern Indian Ocean, leading to increased nutrient supplies and inducing phytoplankton blooms, nutrient enrichment of these coastal areas, not from anthropogenic activities but due to the monsoons, may most likely be the real reason for persistent and expanding population outbreaks of *A. planci* in the region.

Acknowledgments: From 1998 to 2001, the 1st author was supported by the Ministry of Science, Technology and High Education of Portugal (Post-Doctoral Research Fellowship Ref. PRAXIS XXI/BPD/16317/98, 25% co-financed by the European Union Social Fund). For the 2nd, 3rd, 4th and 5th authors (all of the time) and during 2002-2006 for the 1st author, the present work was conducted as an additional task after fulfilling the objectives of the Coral Reef Management Programme, while we were staff of the Ministry of Regional Municipalities, Environment and Water Resources, Oman. This ministry was split in 2007 into the Ministry of Regional Municipalities and Water Resources and the Ministry of Environment and Climate Affairs, and we must thank both ministries for the logistics and photographic evidence provided. Information available for the period of 2005-2008, was obtained while on duty for several projects, namely the Masirah Turtle Conservation Project (Foundation TOTAL, France), Al Marsa Berthing Facilities Project (Al Marsa Resorts, Oman), Mina Al Fahal Refinery Rehabilitation Project (Oman Refineries and Petrochemicals Company, Oman), and Oman India Fertilizer Company (OMIFCO) Marine Exclusive Zone Monitoring Programme (OMIFCO, Oman), in which the 1st and 6th authors were involved. Finally, we thank the NOAA for making available the remote sensing image presented in this study.

REFERENCES

Aeby GS. 2005. Outbreak of coral disease in the northwestern Hawaiian Islands. Coral Reefs **24:** 48.

Aguirre AA, SC Gardner, JC Marsh, SG Delgado, CJ Limpus, WJ Nichols. 2006. Hazards associated with the consumption of seaturtle meat and eggs: a review for health care workers and the general public. EcoHeath **3:** 141-153.

Al Jabri MM. 2003. Studies on coral communities of artificial reefs in Fahal Island, Sultanate of Oman. Master's thesis. Sultan Qaboos Univ., Muscat, Oman.

Al Jufaili SM, MM Al Jabri, A Al-Baluchi, RM Baldwin, SC Wilson, F West, AD Matthews. 1999. Human impacts on coral reefs in the Sultanate of Oman. Estuar. Coast. Shelf S. **49:** 65-74.

Allen GR. 1985. Snappers of the world: an annotated and illustrated catalogue of Lutjanid species known to date. Rome, Italy: Food and Agriculture Organisation, FAO Fisheries Synopsis, no. 125(6).

Amorocho DF, RD Reina. 2007. Feeding ecology of the East Pacific green seaturtle *Chelonia mydas* agassizi at Gorgona National Park, Colombia. Endang. Species Res. **3:** 43-51.

Aronson RB, IG MacIntyre, A Staci, NL Hilbun. 2005. Emergent zonation and geographic convergence of coral reefs. Ecology **86:** 2586-2600.

Baird AH, PA Marshall. 2002. Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. Mar. Ecol.-Prog. Ser. **237:** 133-141.

Bak RP, G Nieuwland, EH Meesters. 2005. Coral reef crisis in deep and shallow reefs: 30 years of constancy and change in reefs of Curacao and Bonaire. Coral Reefs **24:** 475-479.

Baker AC, CJ Starger, TR McClanahan, PW Glynn. 2004. Coral reefs: corals' adaptive response to climate change. Nature **430:** 741.

Barton AD, KS Casey. 2005. Climatological context for large-scale coral bleaching. Coral Reefs **24:** 536-554.

Bean K, GP Jones, MJ Caley. 2002. Relationships among distribution, abundance and microhabitat specialization in a guild of a coral reef triggerfish (Balistidae). Mar. Ecol.-Prog. Ser. **233:** 263-272.

Benzie JAH, M Wakeford. 1997. Genetic structure of crown-of-thorns starfish (*Acanthaster planci*) on the Great Barrier Reef: comparison of two sets of outbreak populations occurring ten years apart. Mar. Biol. **129:** 149-157.

Berkelmans R, MY van Oppen. 2006. The role of zooxanthellae in the thermal tolerance of corals: a nugget of hope for coral reefs in an era of climate change. Proc. Biol. Sci. **273:** 2305-2312.

Berumen ML, MS Pratchett. 2006a. Effects of resource availability on the competitive behaviour ofbutterflyfishes (Chetodontidae). Proc. Int. Coral Reef Symp. **10:** 644-650.

Berumen ML, MS Pratchett. 2006b. Recovery without resilience: persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura Reef, Moorea. Coral Reefs **25:** 647-653.

Berumen ML, MS Pratchett. 2008. Trade-offs associated with dietary specialization in corallivourous butterflyfishes (Chaetodontidae: *Chaetodon*). Behav. Ecol. Sociobiol. **62:** 989-994.

Birkeland C. 1990. Caribbean and Pacific coastal marine system: similarities and differences. Nat. Resources **26:** 1-12.

Birkeland C, R Randall, A Green, B Smith, S Wilkins. 2003. Changes in the coral reef communities of Fagatele Bay National Marine Sanctuary and Tutuila Island (American Samoa), 1982-1995. Fagatele Bay Nat. Mar. Sanctuary Sci. Ser. **2003:** 1-237.

Briggs JC. 2005. Coral reefs: conserving the evolutionary sources. Biol. Conserv. **126:** 297-305.

Brodie J, K Fabricius, G De'ath, K Okaji. 2005. Are increased nutrient inputs responsible for more outbreaks of crown-of-thorns starfish? An appraisal of the evidence. Mar. Pollut. Bull. **51:** 266-278.

Brown JS, BP Kotler. 2004. Hazardous duty pay and foraging cost of predation. Ecol. Lett. **7:** 999-1014.

Bruno JF, CE Siddon, JD Witman, PL Colin, MA Toscano. 2001. El Niño related coral bleaching in Palau, Western Caroline Islands. Coral Reefs **20:** 127-136.

Chiappone M, H Dienes, DW Swanson, SL Miller. 2005. Impacts of lost fishing gear on coral reef sessile invertebrates in the Florida Keys National Marine Sanctuary. Biol. Conserv. **121:** 221-230.

Coles SL. 1994. Extensive coral disease outbreak at Fahal Island, Gulf of Oman, Indian Ocean. Coral Reefs **13:** 424.

Coles SL, BE Brown. 2003. Coral bleaching – capacity for acclimatization and adaptation. Adv Mar. Biol. **46:** 183-223.

Crabbe MJC, DJ Smith. 2005. Sediment impacts on growth rates of *Acropora* and *Porites* corals from fringing reefs of Sulawesi, Indonesia. Coral Reefs **24:** 437-441.

Cumming RL. 2000. Distinguishing predation injuries inflicted by *Drupella* and *Acanthaster*. Reef Encounter **27:** 13-14.

Cumming RL. 2002. Tissue injury predicts colony decline in reef-building corals. Mar. Ecol.-Prog. Ser. **242:** 131-141.

Devlin MJ, J Brodie. 2005. Terrestrial discharge into the Great

Barrier Reef Lagoon: nutrient behavior in coastal waters. Mar. Pollut. Bull. **51:** 9-22.

Diaz-Pulido G, LJ McCook. 2005. Effects of nutrient enhancement on the fecundity of a coral reef macroalgae. J. Exp. Mar. Biol. Ecol. **317:** 13-24.

Dill L. 1983. Adaptative flexibility in the foraging behaviour of fishes. Can. J. Fish. Aquat. Sci. **40:** 398-408.

Disalvo LH, JE Randall, A Cea. 2007. Stomach contents and feeding observations of some Easter Island fishes. Atoll Res. Bull. **548:** 1-23.

Dobbin JA. 1992. Coastal erosion in Oman: draft regulations for the prevention of coastal erosion in the Sultanate of Oman. Muscat, Oman: Ministry of Regional Municipalities and Environment.

Donner SD, WJ Skirving, CM Little, M Oppenheimer, O Hoegh-Guldberg. 2005. Global assessment of coral bleaching and required rates of adaptation under climate change. Global Change Biol. **11:** 2251-2265.

Dulvy NK, RP Freckleton, NVC Polunin. 2004. Coral reef cascades and the indirect effects of predator removal by exploitation. Ecol. Lett. **7:** 410-416.

Edmunds PJ. 2005. The effect of sub-lethal increases in temperature on the growth and population trajectories of three scleractinian corals on the southern Great Barrier Reef. Oecologia **146:** 350-364.

Edmunds PJ. 2007. Evidence for a decadal-scale decline in the growth rates of juvenile scleractinian corals. Mar. Ecol.-Prog. Ser. **341:** 1-13.

Fabricius K, S Ulthricke, T Cooper, C Humphrey, G De'ath, J Mellors. 2006. Candidate bioindicator measures to monitor exposure to changing water quality on the Great Barrier Reef. Townsville, Australia: Australian Institute of Marine Science.

Fabricius KE. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Mar. Pollut. Bull. **50:** 125-146.

Feary DA, GR Almany, MI McCormick, GP Jones. 2007. Habitat choice, recruitment and the response of coral reef fishes to coral degradation. Oecologia **153:** 727-737.

Glynn PW. 1982. Individual recognition and phenotypic variability in *Acanthaster planci* (Echinodermata: Asteroidea). Coral Reefs **1:** 89-94.

Glynn PW. 1990. Feeding ecology of selected coral-reef macroconsumers; patterns and effects on coral community structure. *In*: Dubinsky Z (ed). Ecosystems of the world 25. Coral reefs. Elsevier, Amsterdam, pp. 365-400.

Glynn PW. 1993. Monsoonal upwelling and episodic *Acanthaster* predation as probable controls of coral reef distribution and community structure in Oman, Indian Ocean. Atoll Res. Bull. **379:** 1-66.

Graham NAJ, SK Wilson, S Jennings, NVC Polunin, JP Bijoux, J Robinson. 2006. Dynamic fragility of oceanic coral reef ecosystems. Proc. Nat. Acad. Sci. USA **103:** 8425-8429.

Graham NAJ, SK Wilson, S Jennings, NV Polunin, J Robinson, JP Bijoux, TM Daw. 2007. Lag effects in the impacts of mass coral bleaching on coral fish, fisheries and ecosystems. Conserv. Biol. **21:** 1291-1300.

Harriot V, L Goggin, H Sweatman. 2003. Crown-of-thorns starfish on the Great Barrier Reef – current state of knowledge. Townsville, Australia: Cooperative Research Centre, Reef Research Centre.

Idronaut. 2002. Idronaut Ocean Seven 316 CTD Probe. Brugherio, Italy: Idronaut.

IUCN. 1986. The proposed Dimaniyat Islands National Nature Reserve. Muscat, Oman: International Union for Conservation of Nature and Natural Resources (IUCN).

JGFOS. 1998. Arabesque Project - CDROM. Plymouth Marine Laboratory, Plymouth, UK: Joint Global Ocean Flux Study (JGFOS).

KCS. 2001. Multivariate statistical package, MVSP. Version 3.1. User's Manual. Anglesey, Wales: Kovach Computing Services (KCS).

Knowlton N. 2001. The future of coral reefs. Proc. Natl. Acad. Sci. USA **98:** 5419-5425.

Koonjul MS, V Mangar, JP Luchmun. 2003. Eradication of crown-of-thorns starfish (*Acanthaster planci*) infestation in a patch reef in the lagoon off Ille Aux Cerfs, Mauritius. Annu. Meeting Agric. Scientists **2003:** 333-338.

Leon YM, KA Bjorndal. 2002. Selective feeding in the hawksbill turtle, an important predator in coral reef ecosystems. Mar. Ecol.-Prog. Ser. **245:** 249-258.

Madin JS, SR Connolly. 2006. Ecological consequences of major hydrodynamic disturbances on coral reefs. Nature **444:** 477-480.

Manly BFJ, LL McDonald, DL Thomas. 1993. Resource selection by animals. London: Chapman and Hall.

McClanahan TR. 2002. The near future of coral reefs. Env. Conserv. **29:** 460-483.

McClanahan TR, M Ateweberhan, NAJ Graham, SK Wilson, CR Sebastian, MMM Guillaume, JH Bruggemann. 2007. Western Indian Ocean coral communities: bleaching responses and susceptibility to extinction. Mar. Ecol.-Prog. Ser. **337:** 1-13.

McClanahan TR, J Maina, L Pet-Soede. 2002. Effects of the 1998 coral mortality event on Kenyan coral reefs and fisheries. Ambio **31:** 543-550.

Mendonça VM, AA Al Kiyumi, SM Al Saady, HJ Grobler, KA Erzini. 2001. Dimaniyat Islands, Gulf of Oman: the environment on the densest known nesting grounds of the critically endangered hawksbill turtle *Eretmochelys imbricata*. Proc. 1st Int. Conf. Aquacult. Fish Environ. NW Indian Ocean **2:** 160-168.

Mendonça VM, DG Raffaelli, PR Boyle. 2007a. Interactions between shorebirds and benthic invertebrates at Culbin Sands lagoon, NE Scotland: effects of avian predation on their prey community density and structure. Sci. Mar. **71:** 579-591.

Mendonça VM, DG Raffaelli, PR Boyle. 2008. Spatial and temporal characteristics of benthic invertebrate communities, and impacts of disturbance of cockle harvesting at Culbin Sands Lagoon, NE Scotland. Sci. Mar. **72:** 265-278.

Mendonça VM, DG Raffaelli, PR Boyle, C Emes. 2007b. The ecological role of overwintering fish in the food web of the Culbin Sands lagoon ecosystem, NE Scotland: identifying major trophic links and testing effects of fish *Pomatoschistus microps* (Pallas) on benthic invertebrates. Sci. Mar. **71:** 649-660

Mendonça VM, DG Raffaelli, PR Boyle, C Emes. 2009. Trophodynamics in a shallow lagoon off NW Europe (Culbin Sands, Moray Firth): spatial and temporal variability of epibenthic communities, their diets, and consumption efficiency. Zool. Stud. **48:** 196-214.

Mendonça VM, SM Al Saady, AA Al Kiyumi, KA Erzini. 2010. Interactions between green turtles (*Chelonia mydas*) and foxes (*Vulpes vulpes arabica*, *Vulpes rueppellii sabaea*, and *Vulpes cana*) on turtle nesting grounds in the northwestern Indian Ocean: Impacts of the fox community on the behaviour of nesting seaturtles at Ras Al Hadd Turtle Reserve, Oman. Zool. Stud. (in press)

MONE. 2006. Statistical year book 2006. Muscat, Oman: Ministry of National Economy (MONE).

MRMEWR. 2003. Status of the marine environment report, SOMER 2003 – Oman. Muscat, Oman: Ministry of Regional Municipalities, Environment and Water Resources (MRMEWR).

NOAA. 2005. World Ocean Atlas. Florida, USA: National Oceanographic and Atmospheric Agency (NOAA).

Obura DO. 2005. Resilience and climate change: lessons from coral reefs and bleaching in the Western Indian Ocean. Estuar. Coastal Shelf Sci. **63:** 353-372.

OCRG. 2004. A compilation of sightings along the Oman coast. Muscat, Oman: Oman Cetacean Research Group (OCRG) for the Marine Science and Fisheries Centre, Ministry of Agriculture and Fisheries.

Ostrander GK, KM Armstrong, ET Knobbe, D Gerace, EP Scully. 2000. Rapid transition in the structure of a coral reef community: the effects of coral bleaching and physical disturbance. Proc. Natl. Acad. Sci. USA **97:** 5297-5302.

Planes S, R Galzin. 1999. Scientific mission Oman '99: the Ardoukoba Expedition. Perpingnan, France: Univ. of Perpignan.

Pratchett MS. 2001. Influence of coral symbionts on feeding preferences of crown-of-thorns starfish *Acanthaster planci* in the Western Pacific. Mar. Ecol.-Prog. Ser. **214:** 111-119.

Pratchett MS. 2005. Dietary overlap among coral-feeding butterflyfishes (Chaetodontidae) at Lizard Island, northern Great Barrier Reef. Mar. Biol. **148:** 373-382.

Pratchett MS. 2007. Dietary selection by coral feeding butterflyfishes (Chaetodontidae) on the Great Barrier Reef, Australia. Raffles Mus. Bull. Zool. **14:** 171-176.

Randall JE. 2004. Food habits of reef fishes of the West Indies. *In* Barry TF, ed. Food habits of reef fishes of the West Indies. Miami, FL: National Oceanographic and Atmospheric Administration, pp. 665-759.

Renegar DA, BM Riegl. 2005. Effect of nutrient enrichment and elevated CO_2 partial pressure on growth rate of Atlantic scleractinian coral *Acropora cervicornis*. Mar. Ecol.-Prog. Ser. **293:** 69-76.

Richmond M. 2002. A field guide to the seashores of eastern Africa and the western Indian Ocean islands. 2nd ed. Vasteras, Sweden: The Sea Trust.

ROPME. 2004. State of the marine environment report – SOMER 2003. Kuwait city, Kuwait: Regional Organization for Protection of the Marine Environment (ROPME).

Rosenberg E, Y ben Haim. 2002. Microbial diseases of corals and global warming. Environ. Microbiol. **4:** 318-326.

Rotjan RD, SM Lewis. 2006. Parrotfish abundance and selective corallivory on a Belizean coral reef. J. Exp. Mar. Biol. Ecol. **335:** 296-301.

Rual F. 1999. Marine life envenomations: example in New Caledonia. Med Trop. **59:** 287-297.

Salm RV. 1993. Coral reefs of the Sultanate of Oman. Atoll Res. Bull. **380:** 1-85.

Salm RV, RAC Jensen, VA Papastavrou. 1993. Marine fauna of Oman: cetaceans, turtles, seabirds and shallow water corals. Gland, Switzerland: International Union for Conservation of Nature and Natural Resources.

Salm RV, CRC Sheppard. 1986. Corals and coral reefs of the capital area, Oman. Gland, Switzerland: International Union for Conservation of Nature and Natural Resources.

Sheppard CRC. 1986. Marine habitats and species in Oman. Gland, Switzerland: International Union for Conservation of Nature and Natural Resources.

Sheppard CRC, RV Salm. 1988. Reef and coral communities of Oman, with a description of a new coral species (Order Scleractinia, genus *Acanthastrea*). J. Nat. Hist. **22:** 263-279.

Sheppard CRC, M Spalding, C Bradshaw, S Wilson. 2002. Erosion vs recovery of coral reefs after 1998 El Niño: Chagos Reefs, Indian Ocean. Ambio **31:** 40-48.

Sheppard CRC, SM Wells. 1988. Coral reefs of the world. Vol II. Cambridge, UK: International Union for Conservation of Nature and Natural Resources.

Smith LD, M Devlin, D Haynes, JP Gilmour. 2005. A demographic approach to monitoring the health of coral reefs. Mar. Pollut. Bull. **51:** 399-407.

Stampar SN, PF da Silva, OJ Luiz Jr. 2007. Predation on the zoantid *Palythoa caribaeorum* (Anthozoa, Cnidaria) by a hawksbill turtle (*Eretmochelys imbricata*) in Southeastern Brazil. Mar. Turtle Newslett. **117:** 3-5.

Terry-Graham LA, DI Bolrrick, PC Wainwright. 2002. Using functional morphology to examine the ecology and evolution of specialization. Integr. Comp. Biol. **42:** 265-277.

Tudhope AW, DW Lea, GB Shimmield, CP Chilcott, SM Head. 1996. Monsoon climate and Arabian Sea coastal upwelling recorded in massive corals from Southern Oman. Palaios **11:** 347-361.

USEPA. 1983. Methods for chemical analyses of water and wastewater. Ohahio, USA: Environmental Protection Agency (EPA) EPA-600/4-79-020.

Uthicke S, JAH Benzie. 2001. Restricted gene flow between *Holothuria scabra* (Echinodermata: Holothuroidea) populations along the north-east coast of Australia and the Solomon Islands. Mar. Ecol.-Prog. Ser. **216:** 109-117.

Veron JEN. 2000. Corals of the world. 3 Volumes. Queensland, Australia: Australian Institute of Marine Science.

Yasuda N, M Hagaguchi, M Sasaki, S Nagai, M Saba, K Nadaoka. 2006. Complete mitochondrial genome sequences for crown-of-thorns starfish *Acanthaster planci* and *Acanthaster brevospinus*. BioMedCentral Genom. **7:** 17.