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Stranding and mortality of pelagic crustaceans in the western Indian Ocean

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Recent observations of unusual mass stranding and mortality of two Indian Ocean crustacean species, the swimming crab Charybdis smithii *and the mantis shrimp* Natosquilla investigatoris*, are documented and analysed. Strandings of* C. smithii *were observed for the first time in the equatorial Indian Ocean, the main area of its pelagic distribution. Strandings of mantis shrimps are reported from throughout the western Indian Ocean; occurrences of mass stranding in the Maldives Archipelago mark an extension of the known range of* N. investigatoris *into the central Indian Ocean. Mortality of crabs probably represents a 'catastrophic event'. In contrast, mantis shrimp strandings, which were always associated with a sudden increase of its biomass ('blooms'), are apparently post-reproduction mortalities indicating potential semelparity for this species.*

Keywords: *Charybdis smithii*, *Natosquilla investigatoris*, stranding, mortality, new records, range extension

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INTRODUCTION

The swimming crab *Charybdis smithii* MacLeay, 1838 (Portunidae) and the mantis shrimp *Natosquilla investigatoris* (Lloyd, 1907) (Squillidae) are common crustaceans of the tropical Indian Ocean. They exhibit peculiar life cycles with an extended pelagic phase for larvae, juveniles, sub-adults and even adults (Losse & Merrett, 1971a; Romanov *et al.*, 2009). They are found periodically offshore in dense aggregations, both at the surface and through the upper mixed layer.

Adult *C. smithii* are demersal; their reproduction is associated with shelf and slope habitats (Apel & Spiridonov, 1998; Türkay & Spiridonov, 2006, Romanov *et al.*, 2009). This swimming crab is a short-lived species with an annual lifespan (van Couwelaar *et al.*, 1997). Individuals may reach 75 mm in carapace width (CW) (van Couwelaar *et al.*, 1997) and become mature at 45–50 mm of CW (Balasubramanian & Suseelan, 1998). The biology of the mantis shrimp *N. investigatoris* is poorly known. Apart from infrequent extreme abundance events reported from pelagic waters (Losse & Merrett, 1971a; Potier *et al.*, 2007a), this species has been recorded in a few rare instances from the benthic environment of the western Indian Ocean (Lloyd, 1907; Chopra, 1939; Venema, 1975, 1976). Most of the time, *Natosquilla investigatoris* likely persists at very low population densities or occupies areas and depths that are rarely surveyed.

Charybdis smithii and *N. investigatoris* play an important role in the pelagic ecosystem both as predators of small fish and cephalopods (Losse, 1969; Losse & Merrett, 1971a; Balasubramanian & Suseelan, 1998; Mincks *et al.*, 2000) and as prey for top predators such as tunas, billfishes, lancetfish, dolphinfish, sharks and rays (Potier *et al.*, 2007a; Romanov *et al.*, 2009). At times, these swimming crabs and mantis shrimps may constitute the main prey item of tunas, contributing more than 50% by wet weight to the diet (Losse & Merrett, 1971a; Potier *et al.*, 2007a; Romanov *et al.*, 2009).

The western Indian Ocean is a highly dynamic monsoon-driven ecosystem exhibiting seasonally alternating oceanographic regimes that follow seasonal variability in the atmospheric circulation. In particular, the north-west part of this area is the location of one of the strongest seasonal upwellings in the world ocean (Longhurst, 2007). Monsoon seasonality and upwelling-induced productivity has a profound effect on the pelagic ecology of the region, and is likely to be an important influence on both the distribution and periodic extreme abundance of the two species discussed here (Potier *et al.*, 2007b; Romanov *et al.*, 2009).

Both species have occasionally been found stranded (Losse & Merrett, 1971a; Branch, 1984) but such events remain poorly documented. Stranding of swimming crabs, including the event which led to the original taxonomic description of this species (MacLeay, 1838), have been reported from South African coasts (Figure 1A) (Branch, 1984; van Couwelaar *et al.*, 1997; Branch *et al.*, 2002), even though

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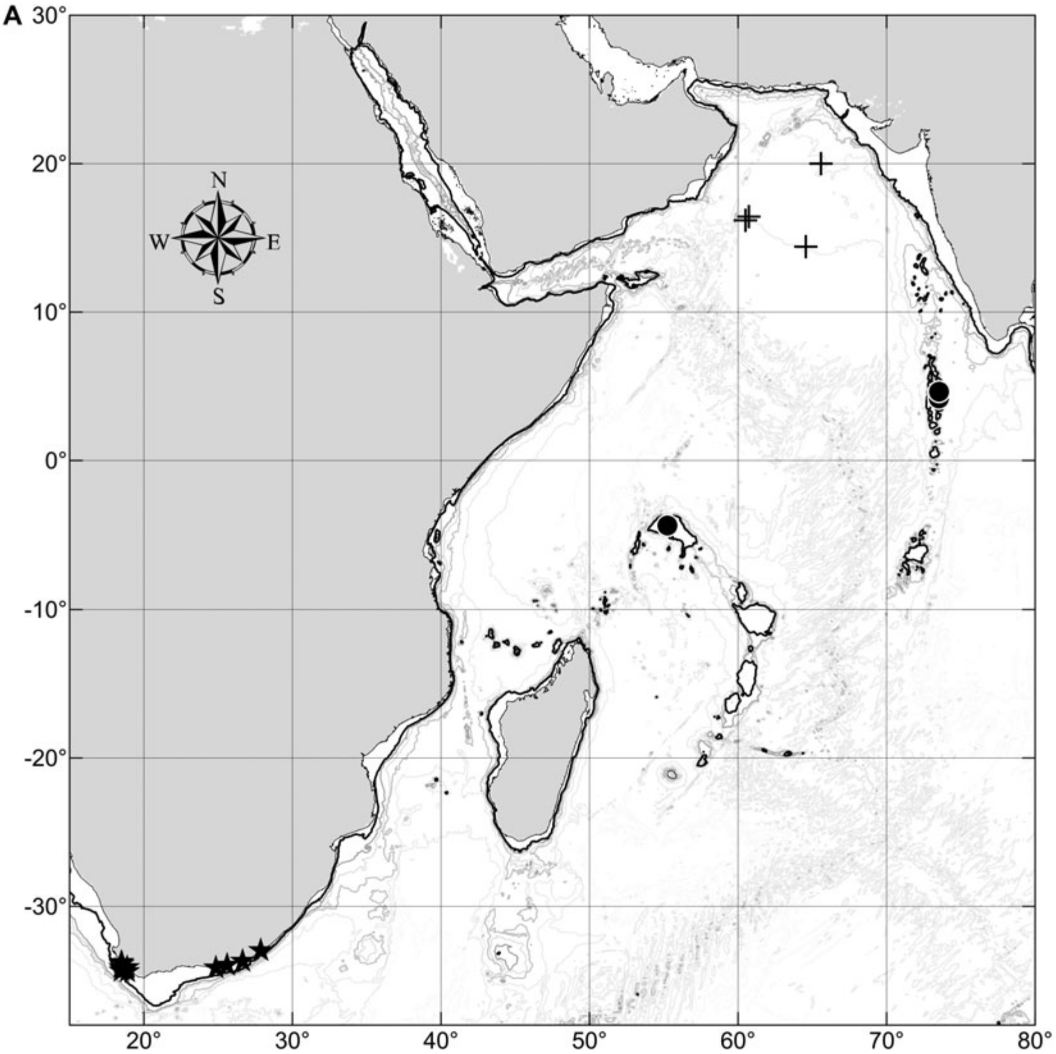

Fig. 1. Geographic distribution of stranding and sedimentation records of *Charybdis smithii* MacLeay, 1838 and stranding observations of *Natosquilla investigatoris* (Lloyd, 1907) in the Western Indian Ocean: (A) Swimming crab *Charybdis smithii*. This study: *dots* are strandings. Published records: *stars* are strandings (MacLeay, 1838*; Branch, 1984*; van Couwelaar *et al.*, 1997*), and *crosses* are sedimentation from pelagic realm (Christiansen & Boetius, 2000); (B) Mantis shrimp *Natosquilla investigatoris*. This study: *dots* are strandings, and *oblique crosses* are reports from telephone survey in the Maldives. Published records: *stars* are strandings (Losse & Merrett, 1971a; Anonymous, 2002**; Fonteneau *et al.*, 2004**; Kamukuru & Mgaya, 2004**; MBREMP, 2005*; Asseid *et al.*, 2006**). For references marked with * positions of observations were estimated from the description published in the original paper, for references marked by ** central position of island, where stranding occurs was used. On all panels the 200 m isobath (dark line) and bathymetry from 1000 to 5000 m (in 1000 m steps, light lines) are shown. Positive latitude is north from equator, negative is south from equator; longitude is east from the prime meridian. Coastline and bathymetry data are from GEBCO (GEBCO, 2010).

mass pelagic occurrences of *C. smithii* are unknown from this region (Kensley, 1977; van Couwelaar *et al.*, 1997; Türkay & Spiridonov, 2006; Romanov *et al.*, 2009). Strandings of *N. investigatoris* were noted in 1967 on two remote islands of the Seychelles Archipelago during a large-scale episode of pelagic swarming in the equatorial western Indian Ocean (Losse & Merrett, 1971a). More recently, strandings were observed along the east African coast (Tanzania) (Kamukuru & Mgaya, 2004; MBREMP, 2005; Asseid *et al.*, 2006) and on islands of the Seychelles Archipelago (Anonymous, 2002; Fonteneau *et al.*, 2004) (Figure 1B).

Mass mortalities may reflect either the consequences of a natural life cycle (semelparity, i.e. single reproductive episode before death (Green, 2008)) or a catastrophic event, as has been suggested for *C. smithii* stranding (Branch, 1984). However, no explanation has yet been proposed for stranding in *N. investigatoris*.

In this work we report for the first time observations of mass mortalities associated with stranding of *C. smithii* in the equatorial Indian Ocean within the main area of its pelagic distribution, as well as several similar events affecting the mantis shrimp *N. investigatoris* in the same region. For *N. investigatoris* we document an extension of its known range to the Maldives Archipelago. We provide also a summary of all stranding events for both species recorded in the Indian Ocean. Finally for each species we discuss hypotheses of likely causes of stranding based on field observations and available biological information.

MATERIALS AND METHODS

Stranding sites are tiny oceanic islands and/or coral atolls scattered in the western Indian Ocean from east African waters to

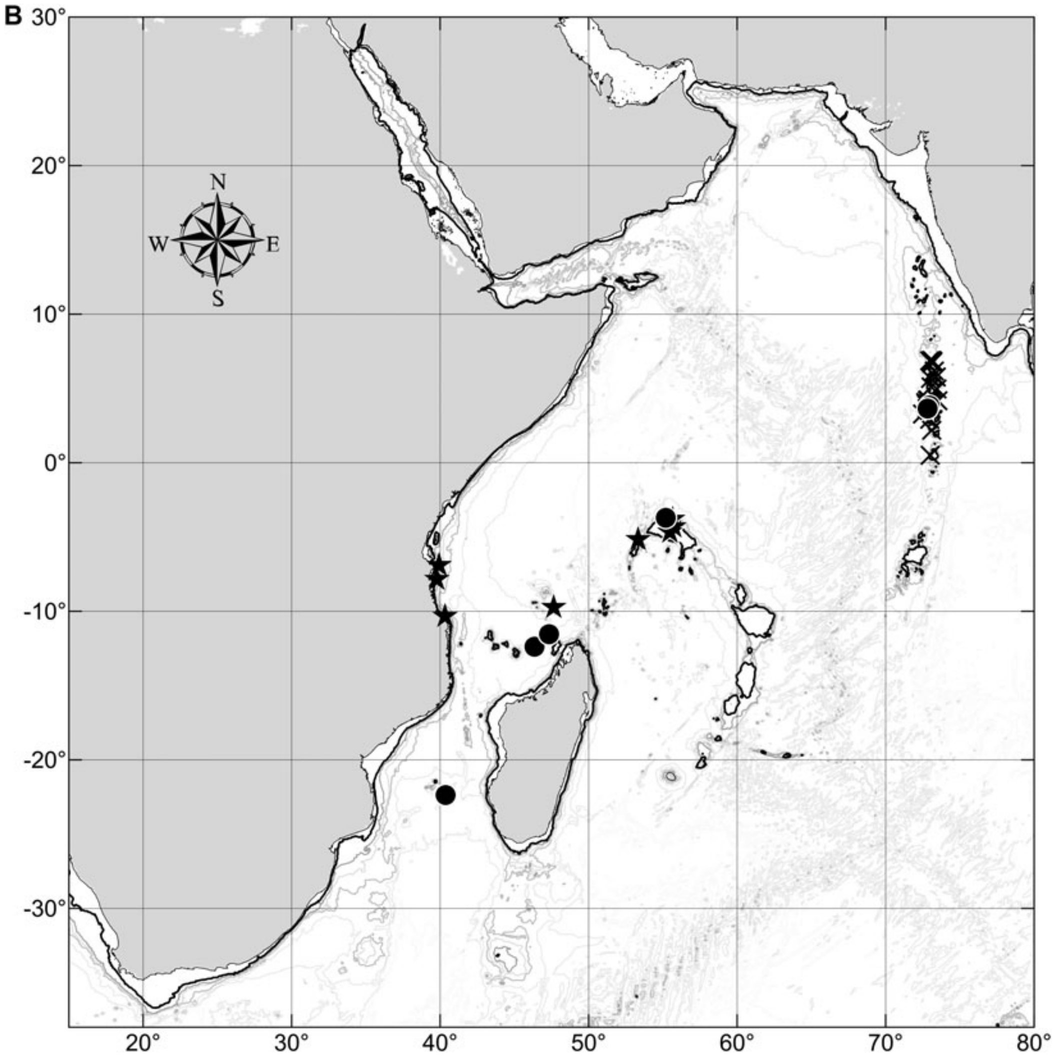

Fig. 1. (continued)

the Maldives (Figure 1). Geographic positions of strandings and observational details are presented in Supplementary Tables S1 and S2.

Charybdis smithii 2005–2011

SEYCHELLES

A stranding of crabs was recorded at North Island by the staff of Wilderness Safaris, which managed a large-scale island rehabilitation programme. Beach patrollers noticed and photographed unusual crab occurrences and reported areas of stranding, estimated numbers and associated data. A dive instructor reported in-water observation of crab behaviour, distribution and environmental conditions before stranding. The event was documented with a digital photo camera, but samples of crabs were not collected.

MALDIVES

Strandings of *C. smithii* were observed and documented in four islands of North Malé Atoll by co-author RCA. In 2005 seventeen crabs were sampled for identification and morphometric measurements. In 2009 and 2011 stranded crabs were photographed.

Natosquilla investigatoris 2002–2005

SOUTH-WEST INDIAN OCEAN

Strandings were observed on several islands located in the Mozambique Channel (Europa and the Glorieuses) and on Bird Island (Seychelles). Strandings were commonly preceded by dense swarms of mantis shrimps aggregated along the coastline or submerged shoals (Geyser Bank). Observations were documented by co-authors JPQ and FM and several French scientific teams with photo and video cameras. Eight fresh individuals were collected at Glorieuses Islands.

MALDIVES

Swarming associated with strandings was recorded by RCA around two islands in South-west Ari Atoll. A few days later a telephone survey was performed by SAS among administration offices of principal Maldivian atolls. Presence/absence of mantis shrimp swarms and stranding were documented throughout the archipelago.

All collected specimens of both species were measured to 0.1 mm: total length (TL) for mantis shrimps and carapace width (CW) for crabs.

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RESULTS

Charybdis smithii (Figure 1A, Supplementary Table S1)

SEYCHELLES

Charybdis smithii (Supplementary Figure S1A, Supplementary Table S1) stranded in August 2009 on western beaches of the North Island (Figure 1A). The crabs washed ashore were still alive but lethargic, dying shortly afterwards. An observer estimated that half of the beach edge was covered with crabs, amounting in total to 300–500 crabs (10–15 crabs per linear metre of beach). A week before the stranding, crabs were observed in the water by divers. Crabs were reported several times in large numbers, aggregated near the surface at 1 m depth. Surface water temperature was 26–27°C. Crabs were very active in the water, swimming energetically without obvious interaction. No mating, spawning or other specific behaviours were observed and females did not carry any eggs on their abdomen. On days following the mass stranding, only one individual swimming crab was encountered though dives were performed regularly.

MALDIVES

During the three stranding events observed in the Maldives Islands from 2005 to 2011 (Figure 1A, Supplementary Table S1), large numbers (hundreds to thousands) of *C. smithii* (Supplementary Figure S1B) were seen swimming in shallow waters (inside lagoons). No obvious signs of parasites or other epifauna were found on any of the sampled crabs. Some individuals exhibited signs of recent moulting. Size (CW) of stranded crabs ranged within 20–25 mm, corresponding to juvenile individuals.

Natosquilla investigatoris (Figure 1B, Supplementary Table S2)

GLORIEUSES ISLANDS

During the mass stranding event of *N. investigatoris* observed in November 2002 (Supplementary Figure S2), the abundance of stomatopods accumulated at the upper tide mark was estimated at about 500 ind m^{-2}. Individuals washed ashore were already dead. Before stranding, large dense swarms of *N. investigatoris* were observed three times from the deck of a vessel, and by divers over a wide area of sandy shoal (Supplementary Figure S3). After the stranding, no more swarms of stomatopods were observed in the vicinity of the islands.

Swarms were swimming in the water column from the surface to the bottom (~5 m depth). Swimming individuals were very active, and predation on a small flatfish (Pleuronectidae) was observed. Swarming mantis shrimps exhibited polarized swimming with a distance of around 15 cm between individuals. Over a sandy bottom mantis shrimps actively burrowed into the sand. Our records are the first documented observations of *N. investigatoris* burrowing behaviour in the natural environment. TL of live sampled mantis shrimps ranged from 51 to 63 mm. No egg was noticed on sampled individuals although developed cement glands and ventral telson with fused ovary (characteristic for reproductively active females) (Wortham-Neal, 2002a) were noted. Ovaries on advanced stage of maturation were found in one preserved sampled female dissected in January 2015.

In May 2003 and 2004 few stranded individuals (less than 100, i.e. no mass stranding) were observed (M. Le Corre, personal communication). No samples were collected, but TL was estimated between 30–40 mm.

GEYSER BANK

In November 2004 some *N. investigatoris* were observed swarming in the water column, and exhibited burrowing behaviour at the bottom. Sampled female individuals had developed cement glands and ventral telson with fused ovary. One year later (October 2005) a few small individuals (exact size unknown) were observed at the sea surface.

SEYCHELLES, BIRD ISLAND

A few stranded individuals of ~30–40 mm TL (less than 100, i.e. no mass stranding) were observed in June 2004 (M. Le Corre, personal communication). No samples were collected.

MALDIVES

Swarms and stranding were first recorded in shallow waters around two islands (Hanghghaameedhoo and Huvahendhoo) in South-west Ari Atoll in December 2002. Several swarms comprised thousands of individuals. A sample of mantis shrimps collected at Huvahendhoo was lost in transit; the size of the individuals collected was about 80 mm TL. No other information on size was recovered. A telephone survey within the Maldives produced reports of mantis shrimps swarming from islands throughout almost the entire length of the archipelago (from 7°N to the equator) (Figure 1B). These reports suggest that the swarming and stranding episode lasted from late November to late December (Supplementary Table S2). Mantis shrimps were observed mostly as freely swimming swarms in the ocean in close proximity to atolls but in several cases were reported swarming in lagoons and stranded on reefs and beaches. The numbers of mantis shrimps occurring in the Maldives was in the millions of individuals.

DISCUSSION

Strandings of pelagic and benthic crustaceans have been observed in upwelling systems sporadically (Branch, 1984; Stewart *et al.*, 1984; Gracia *et al.*, 1986) or on a regular basis (Aurioles-Gamboa *et al.*, 1994, Cockcroft *et al.*, 2008). However the reasons usually remain unknown.

In the Indian Ocean, mass mortality and strandings have been observed in several diverse groups including coelenterates (Billett *et al.*, 2006; Daryanabard & Dawson, 2008), crustaceans (Losse & Merrett, 1971a; this study), and fishes (Foxton, 1965; Panikkar & Jayaraman, 1966; Smith *et al.*, 2010). However, crustacean strandings in the Indian Ocean are rarely reported, even for such occasionally abundant species as *C. smithii* and *N. investigatoris*.

Charybdis smithii is present throughout the year in the pelagic environment of the equatorial Indian Ocean. Its biomass is highly variable, both on seasonal and annual scales, with densities exceeding 15,000 ind km^{-2} during abundance peaks (Romanov *et al.*, 2009). Nevertheless, mass strandings of *C. smithii* have previously only been reported on few occasions from the south-western periphery of the species' range, along the southern coast of South Africa

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from East London to Cape Town: in 1834–36, 1982–83 and 1993–1996 (MacLeay, 1838; Branch, 1984; van Couwelaar *et al.*, 1997). Although it has been suggested that crab strandings in South Africa are annual events (B. Newman in van Couwelaar *et al.*, 1997), no subsequent evidence of such periodicity appears to have been reported. Prior to this study, no stranding of *C. smithii* had been reported from its main pelagic distribution area, namely the western equatorial and northern Indian Ocean. This supports the hypothesis of Branch (1984) who attributed strandings along the South African coast to environmental anomalies. He reported mass mortalities of several species that are usually rare at the southern tip of Africa in association with a warm event in 1982–1983: *C. smithii*, Portuguese man of war (*Physalia* sp.) and blue button (*Porpita* sp.). In the equatorial Indian Ocean *C. smithii* inhabits waters within the temperature range of 30°C (at the surface) to 10°C (below the thermocline) (Romanov *et al.*, 2009). Thus warm oceanographic anomalies may facilitate the southward expatriation this species, with subsequent mortality apparently caused by recovering normal (relatively cold) conditions. However, pelagic swarms of *C. smithii* have never been reported from South Africa.

No reason was found for the crab strandings in Seychelles and Maldives reported here. No abnormality was reported, beyond the existence of daytime surface aggregations with relatively high swarm density (less than 1 m between crabs) and their advection into shallow waters. In normal conditions *C. smithii* are extremely rare in shallow waters (Apel & Spiridonov, 1998; Türkay & Spiridonov, 2006) and do not aggregate at the surface during daytime (Romanov *et al.*, 2009).

Crab 'swarms' observed at the surface during twilight and at night in the open ocean are always 'loose' aggregations of a density 0.1–0.2 ind m^{-2} (Della Croce & Holthuis, 1965; van Couwelaar *et al.*, 1997; Christiansen & Boetius, 2000). Maximum density reported earlier in the upper surface layer (0–150 m) reached 0.016 ind m^{-3} (van Couwelaar *et al.*, 1997) but much lower densities, about 0.0001 ind m^{-3} are usually found in the same stratum (Romanov *et al.*, 2009). The noticeably higher densities (about 1 ind m^{-3}) reported here before stranding suggest apparently unusual crab behaviour before they were washed ashore. Environmental stress or disease might alter crab behaviour. However, no major anomaly in sea temperature or in overall weather conditions was observed before or during our stranding observations. The recorded temperatures during stranding in Seychelles (26–27°C) do not exceed the range commonly observed in the crab's pelagic habitat (Romanov *et al.*, 2009). Observed temperature variations are much lower than the temperature gradient regularly crossed by the crabs during their diurnal vertical migrations in the open ocean, which can exceed 15°C (Romanov *et al.*, 2009). These crabs apparently also tolerate low oxygen concentrations (Karuppasamy *et al.*, 2007; Longhurst, 2007). The active swimming behaviour observed during stranding did not correspond to animals possibly incapacitated by stress. No external visible parasites were noted on stranded crabs.

Mass mortalities do not always result in stranding. In September–October 1995 mass sedimentation of immature (CW = 34–44 mm) dead individuals of *C. smithii* was observed at three deepwater stations (3190–4030 m depth) in the Arabian Sea (Christiansen & Boetius, 2000). Within a period of 15 days, fresh dead individuals of swimming crab were found at the stations separated by 250–370 nmi (station positions: 16°10′N 60°30′E; 14°30′N 64°30′E; 20°00′N 65°35′E. 1 nautical mile = 1.852 km.). The oceanic area inside the triangle formed by the stations where crab mortality was observed exceeded 40,000 nmi^2 (1 nmi^2 = 3.43 km^2) i.e. over 130,000 km^2. Christiansen & Boetius (2000) avoided the assumption of a single large-scale crab mortality episode, treating each observation as a non-connected event. Similar observations of large-scale mass mortality of jellyfish in the Arabian Sea were reported in 2002 (Billett *et al.*, 2006; Daryanabard & Dawson, 2008).

While no obvious natural factors responsible for the mortality of these pelagic organisms were identified (Christiansen & Boetius, 2000; Billett *et al.*, 2006, Daryanabard & Dawson, 2008) the scale and irregularity of such events, involving unrelated taxonomic groups, suggests the possibility of 'catastrophic' causes. Several factors may trigger mass mortalities of marine organisms, e.g. algal blooms, very high temperatures and/or oxygen depletion. The Arabian Sea is indeed known for anoxic conditions and the presence of hydrogen sulphide in subsurface waters (Longhurst, 2007).

In contrast to the swimming crab, strandings of the mantis shrimp *N. investigatoris* are always associated with recurrent 'bloom' episodes. These were reported in 1944, 1965–1967, 1971–1976 and 2000–2005, when dense swarms of thousands or even millions of individuals were observed swimming at the surface or stranded on beaches (Barnard, 1950; Losse & Merrett, 1971a, b; AzCherNIRO, 1972; Venema, 1975, 1976; Fonteneau *et al.*, 2004; Kamukuru & Mgaya, 2004; MBREMP, 2005; Asseid *et al.*, 2006). Strandings reported here coincide with the most recent mantis shrimps 'bloom', probably the strongest one ever observed, covering six contiguous years (2000–2005) (authors' unpublished data). During this period stomatopod swarms and strandings were spread from East African waters (Kamukuru & Mgaya, 2004; Asseid *et al.*, 2006) including the North Mozambique Channel (this paper), through the open ocean and islands of Seychelles archipelago (Anonymous, 2002; Potier *et al.*, 2004, 2007a, b; Malone *et al.*, 2011) to the Maldives (this paper) (Figure 1B). Swarms of *N. investigatoris* had never been reported from the Maldives before. The present observations considerably expand the known range of this species: previously the easternmost record was collected from the continental slope off the eastern tip of the Arabian Peninsula in ~60°E during the R/V 'Mabahiss' cruise (Chopra, 1939). During 2000–2005 event, active burrowing behaviour was observed on sandy shoals, and the presence of developed cement glands and ovaries on sampled individuals were both suggestive of active reproductive status of females in these abundant swarms (Hamano & Matsuura, 1984; Wortham-Neal, 2002a).

Mantis shrimps are bottom-dwellers inhabiting a wide range of habitats: from shallow waters to bathyal depths down to 1500 m, and from clear sandy shoals and coral reefs to turbid muddy estuaries (Reaka, 1980; Reaka & Manning, 1981; Kodama *et al.*, 2004). They also exhibit a diversity of lifestyles, behaviours and adaptations from solitary dispersed individuals (Ahyong, 2004) to abundant species supporting target fisheries (Kodama *et al.*, 2004; Maynou *et al.*, 2004). The Stomatopoda are divided into two broad functional and morphological groups relating to the manner of prey capture: 'smashers' and 'spearers' (Caldwell & Dingle, 1976). Most 'spearers' occur in dense aggregations inhabiting soft substrates (sand or mud) on the shelf and slope, living in self-excavated burrows where they lay their eggs (Caldwell & Dingle, 1976; Wortham-Neal, 2002a, b). Morphologically *N. investigatoris* is a typical 'spearer': burrowing in soft sediments may represent a natural attempt of reproductively active females to construct burrows and to reproduce.

While semelparity is rare among crustaceans and not previously reported for stomatopods (Thiel & Duffy, 2007), mass mortality observed immediately after swarming might indicate such a mode of reproduction in *N. investigatoris*.

These swimming crabs and mantis shrimps are common and abundant species in the western Indian Ocean, but their biology and life cycles are still poorly known. Mortality occurring in response to environmental variability or as a natural part of the life cycle, and sometimes resulting in strandings, is an important aspect of their natural history. Further studies, including meticulous registration of such events in combination with biological sampling and environmental observations should provide further information on the biology of both species, and further our understanding of their roles and interactions in the pelagic ecosystem of the tropical western Indian Ocean.

SUPPLEMENTARY MATERIAL

To view supplementary material for this article, please visit http://dx.doi.org/S002531541500096X

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