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From monsoons to mantas: seasonal distribution of *Manta alfredi* in the Maldives

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ABSTRACT

The Republic of Maldives in the central Indian Ocean is home to large numbers of manta rays, *Manta alfredi*. They are known to undertake seasonal migrations within the Maldives, but these movements have not been well documented. The aims of this study were to map the seasonal distribution of manta rays within the Maldives, and to provide some indications of the physical and biological oceanographic processes affecting their distribution. The seasonal distribution of mantas was determined from a national survey of fishermen, interviews with experienced divers and personal observations. The data demonstrate that the distribution of mantas is strongly influenced by the seasonally reversing monsoon currents. Mantas occur on the downstream sides of the atolls, and are rare on the upstream sides, switching sides biannually as the monsoon currents change direction. These seasonally alternating currents are driven by monsoon winds which also alternate according to the season, and bring clear oceanic water to the upstream sides of the atolls. As the currents pass over the Maldives ridge, nutrient-rich waters are lifted to the surface, promoting phytoplankton blooms (as demonstrated by the distribution of chlorophyll-*a*) on the downstream sides of the atolls. This manifestation of the island mass effect supports an abundance of zooplankton, which in turn supports the manta rays.

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INTRODUCTION

Manta rays *Manta alfredi* (formerly *Manta birostris*, see Marshall *et al.*, 2009) are a conspicuous and charismatic component of tropical marine ecosystems. They are fished throughout much of their range (Notobartolo-di-Sciara, 1995; Homma *et al.*, 1999; White *et al.*, 2006). Several local populations have been particularly heavily exploited (Camhi *et al.*, 1998; Ishihara, 2005; IUCN, 2007) and are now judged to be vulnerable to extinction (Camhi *et al.*, 2009).

Manta rays feed almost exclusively on zooplankton, and although relatively little is known about their ecology, it is assumed that their distribution is influenced by the availability of suitable planktonic food (Notarbartolo-di-Sciara and Hillyer, 1989; Homma *et al.*, 1999; Lobel, 2003; Dewar *et al.*, 2008; Luiz *et al.*, 2009). As with other large marine planktivores (Sims and Quayle, 1998; Croll *et al.*, 2005), it is likely that mantas actively seek out and congregate in areas of high zooplankton abundance.

The Republic of Maldives is a small island nation in the tropical Indian Ocean, southwest of India. Mantas are not fished in the Maldives, where they occur in large numbers (many thousands) (R.C. Anderson, pers. obs.). Their seasonal occurrence at some sites is well known to local fishermen and divers (R.C. Anderson and M.S. Adam, pers. obs.), and is noted in diving guidebooks (Amsler, 1994; Godfrey, 1996; Harwood and Bryning, 1998), but there has been no attempt to compile and synthesize this knowledge. The improved understanding from such a synthesis should be of use to marine resource managers and conservationists as well as tour operators, and should also provide researchers with further insights into the ecology of both manta rays and Maldivian nearshore waters. Indeed, the physical setting of the Maldives, with its north–south atoll chain lying across the east–west flow of the seasonal monsoon currents, and the

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marked seasonality in plankton productivity that this causes, makes this archipelago a unique location for the study of manta distribution and movements.

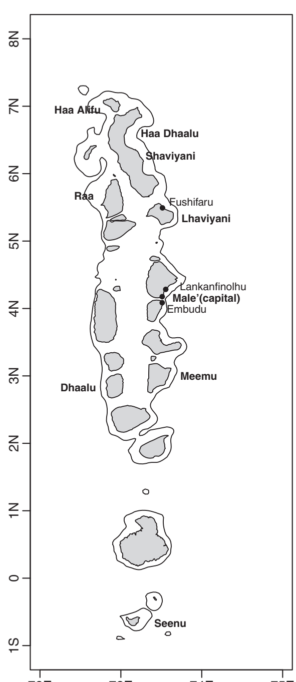
The aims of this paper are to present a first nationwide overview of the seasonal distribution of manta rays within the Maldives, and to provide some indications of the physical and biological ocean processes influencing this seasonal distribution.

METHODS

Study area

The Maldives is composed entirely of coral atolls, which form a chain running north–south from about 7°N to about 0.5°S (Fig. 1). The atoll chain is single in the north and south but double in the central part of the archipelago. Maximum depths within the atolls are typically 50–60 m but vary from about 10–100 m. Outside the atolls, the reef slopes drop steeply away to the ocean floor, at about 2000–3000 m. An exception is found in the area between the double chain of atolls in the central Maldives, where bottom depths are of the order of 200–500 m.

Figure 1. Map of the Maldives, showing locations mentioned in the text. Atoll names are indicated in bold; island locations are marked with dots. The outer line marks the position of the 1000-m depth contour. 1° latitude = 60 nautical miles = 111 km.



The waters of the northern Indian Ocean surrounding the Maldives are strongly influenced by the monsoons. The southwest monsoon (SW or boreal summer monsoon) extends from about May to October, while the northeast monsoon (NE or boreal winter monsoon) lasts from about December to March. Under the influence of the SW monsoon, ocean currents flow predominantly to the east, while during the NE monsoon they flow predominantly to the west (Wyrtki, 1973; Molinari *et al.*, 1990; Shankar *et al.*, 2002; Hydrographic Office, 2007). The southern Maldives (south of about 2–3°N) is less affected by the monsoons, and more influenced by equatorial currents. Ocean currents in the south still alternate between eastward and westward, but not with such a distinct biannual pattern.

Because of these regional differences in topography and oceanography, there are regional differences in the seasonal distribution of manta rays within the Maldives. For this reason, and for ease of discussion, the country is divided into three main regions for some analyses: the northern single-chain atolls (north of 6°00′N), the central double chain atolls (2°35′N to 6°00′N) and the southern atolls (south of 2°35′N).

Manta distribution

For this study, information on the seasonal distribution of mantas was obtained from interviews with two separate sets of informants, local fishermen and divers, in both cases supported by the authors' own personal observations. Traditional and other local knowledge has proved to be a valuable source of information on many aspects of the ecology of marine organisms, including the seasonality of fishes (e.g., Johannes, 1981; Johannes *et al.*, 2000), providing, among other things, that due care is taken in the choice of knowledgeable informants (Davis and Wagner, 2003).

To obtain information from fishermen, printed questionnaires were sent to the government office on each of the 200 inhabited islands. Each island chief was requested to ask experienced fishermen if mantas were seen near their island and, if so, in which season they occurred most commonly. For some islands from which ambiguous replies, or no replies, were received, follow-up telephone calls (N = 15) were made. In addition, during the course of other fisheries research activities (by R.C.A. and M.S.A.), fishermen were interviewed on over 60 islands. In total, reports were received from 163 inhabited islands. Note that inhabited islands are found in every atoll, but they are not evenly distributed. In particular, in the central double-chain atolls, inhabited islands are scarce on the western sides of the atolls.

To obtain information from divers, interviews were conducted with experienced resort dive centre leaders and safari boat dive guides (N = 51), who between them had knowledge of every atoll open to tourism. Interviews were conducted with base leaders, or the next most experienced person available; interviewees had between 4 and 30 yr of full-time diving experience in the Maldives, with most having between 8 and 15 yr. Most interviews were conducted in person (N = 37), but some were conducted by phone (N = 14). Divers were asked to identify manta diving sites and the months during which mantas were present. Published reports in diving guidebooks (Amsler, 1994; Godfrey, 1996; Harwood and Bryning, 1998) were also noted. Until very recently, tourism was confined to a central tourism zone (southern Raa and Lhaviyani in the north to Dhaalu and Meemu in the south) plus Haa Alifu Atoll in the far north and Seenu Atoll in the far south; the distribution of manta diving sites was therefore limited to these areas.

Manta seasonality

Manta occurrence at dive sites *within* seasons was quantified with a simple scoring system. Dive instructors were asked to confirm the months in which mantas were present at the manta sites they visited most frequently and with which they were therefore most familiar. Manta presence at a dive site on the eastern side of the atolls during any month was scored 1.0; if mantas were said to be particularly abundant during 1 or 2 months, those months were scored 1.5; if mantas were present in some years but not in others during months at the beginning and end of the manta season, those months were scored 0.5; absences were scored 0.0. Manta occurrence at dive sites on the western side of the atolls was scored in the same way, but with negative numbers (to highlight seasonal differences). Monthly totals were summed for eastern and western dive sites for which information was available (from 76 responses for 45 dive sites). As total scores depended not only upon occurrence of mantas but also on number of interviews, scores were normalized to remove the effect of sample size.

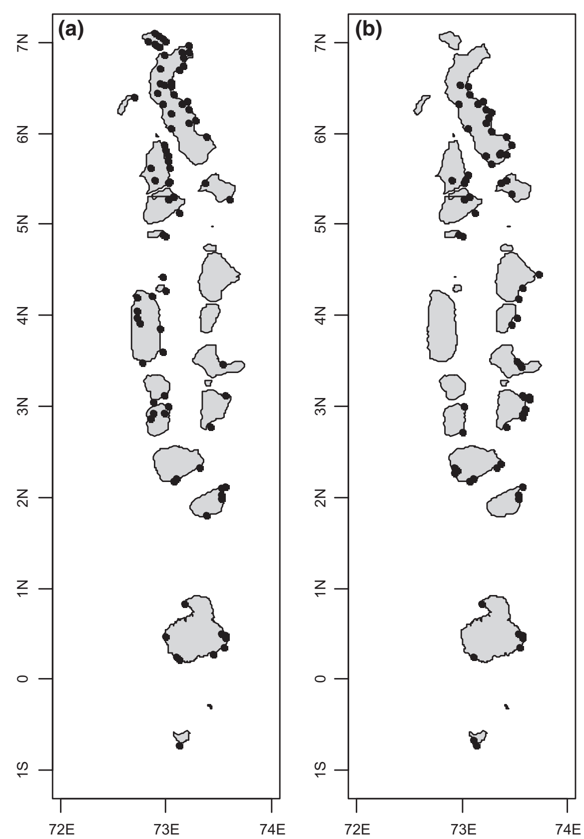
Winds

Daily average wind direction data for Malé for the years 1987–2006 were obtained from the Maldives Meteorological Service. Monthly wind direction frequencies were calculated for two sectors representing the NE and SW monsoons: N-E (0–90°) and SSW-NW (202.5–315°). NE wind frequencies were transformed by multiplying by −1 to emphasize the differences between the two seasons.

Chlorophyll-a concentrations

Chlorophyll-*a* concentrations (hereafter Chl-*a*) were estimated from remote sensing data obtained from NASA's ocean colour satellite SeaWiFS. The data sets used for our study were 9 km, monthly global area coverage (GAC) standard mapped images for the period September 1997 to December 2007. These data sets are available from the Distributed Active Archive Center of NASA's Goddard Space Flight Center and can be downloaded from http://oceancolor.gsfc.nasa.gov/. Mean monthly estimates of Chl-*a* were obtained for two areas, one to the west of the central atolls (2–6°N and 70–73°E) and one to the east (2–6°N and 73.5–76.5°E). A transformed ratio of these estimates [(Chl-*a*-east/Chl-*a*-west)-1] was used to highlight the *relative* productivity of the two sides of the central Maldives. Monthly fields of Chl-*a* were binned to generate seasonal maps of Chl-*a* for the NE monsoon (December–March), and SW monsoon (June–September).

Figure 2. Seasonal distribution of manta rays as reported by Maldivian fishermen (each dot represents one fishing island, near which mantas are reported to be present in that season). (a) Northeast monsoon season; currents flow predominantly east to west. (b) Southwest monsoon season; currents flow predominantly west to east.



RESULTS

The seasonal distribution of mantas in the Maldives as reported by local fishermen from 163 islands is summarized in Fig. 2. Each dot marks the position of one island near which mantas were reported to be present in that season. Throughout much of the Maldives, mantas are present on the downstream side of the atoll chain. However, this simple pattern does not hold true in the north and south of the archipelago.

The seasonal distribution of mantas as reported by experienced divers for 86 separate dive sites is summarized in Fig. 3. Each dot marks the position of one dive site at which mantas were reported to be present in that season. In the central Maldives, mantas are present on the downstream sides of the individual atolls. Again, this simple pattern does not apply in the far north and far south of the country.

Figure 3. Seasonal distribution of manta rays as reported by divers (each dot represents one dive site at which mantas are reported to be present in that season). (a) Northeast monsoon season; the two triangles indicate locations where mantas occur 'out of season'. (b) Southwest monsoon season.

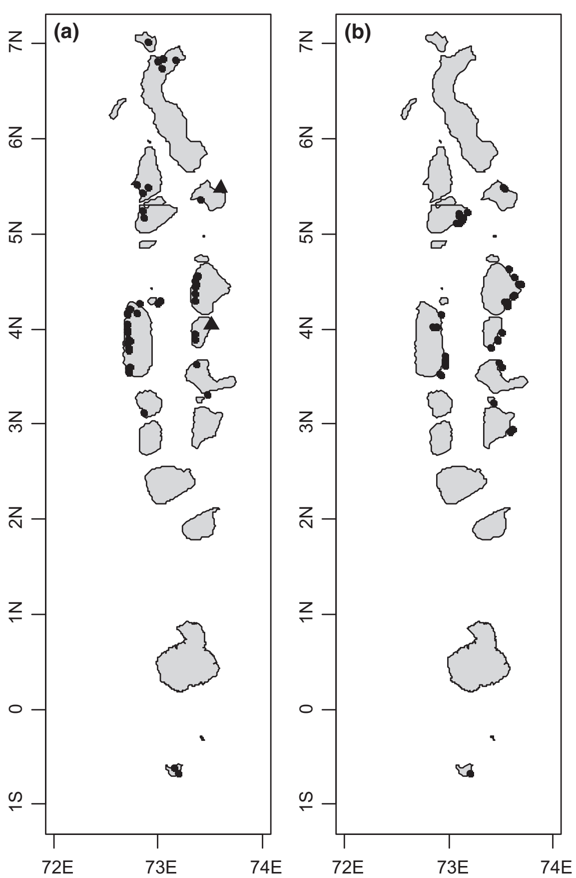
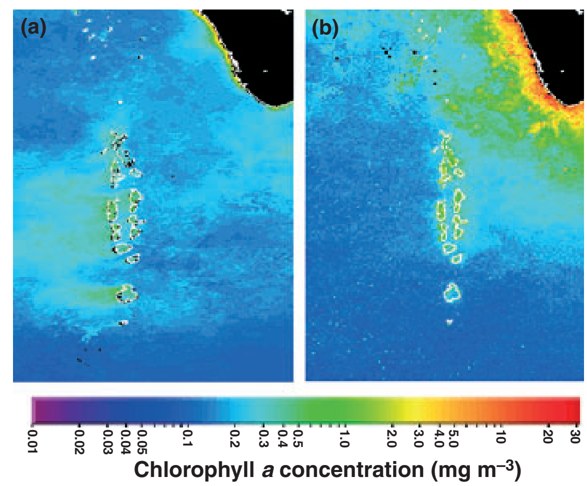


Figure 4. Seasonal distribution of Chl-*a* in the waters around the Maldives, as revealed by composite SeaWiFS satellite images. (a) Northeast monsoon season (21 December 2006 to 20 March 2007). (b) Southwest monsoon season (22 June 2006 to 21 September 2006).



Representative composite satellite images showing the distribution of Chl-*a* in the waters around the Maldives are given in Fig. 4. Consistent patterns that emerge from these composites are the higher Chl-*a* on the downstream side of the atolls, and the change of sides with the change of monsoon season. During the NE monsoon, mean Chl-*a* was of the order of 0.16 mg m^{-3} on the upstream (eastern) side of the central atolls in March and about 0.34 mg m^{-3} on the downstream (western) side of the atolls in January. The situation was reversed during the SW monsoon, with mean Chl-*a* of the order of 0.30 mg m^{-3} on the downstream (eastern) side of the central atolls in September and about 0.18 mg m^{-3} on the upstream (western) side of the atolls in May. These are maximum and minimum *monthly* means; *seasonal* mean Chl-*a* was about 40% higher on the downstream side of the Maldives ridge than on the upstream side.

Wind direction data are summarized in Fig. 5a. Winds are mainly from the NE during December to March, and predominantly from the W-SW during April to November. The ratio of Chl-*a* by month on the two sides of the central Maldives is presented in Fig. 5b. The occurrence of mantas by month at dive sites on the western and eastern sides of the central double-chain atolls is summarized in Fig. 5c and Table 1.

The relationship between Chl-*a* distribution and the occurrence of manta rays on the two sides of the central Maldives is summarized in Fig. 6. When Chl-*a* concentrations are at their highest on the eastern side of the central Maldives, mantas are most abundant on the east of the atolls and absent on the west, and vice versa.

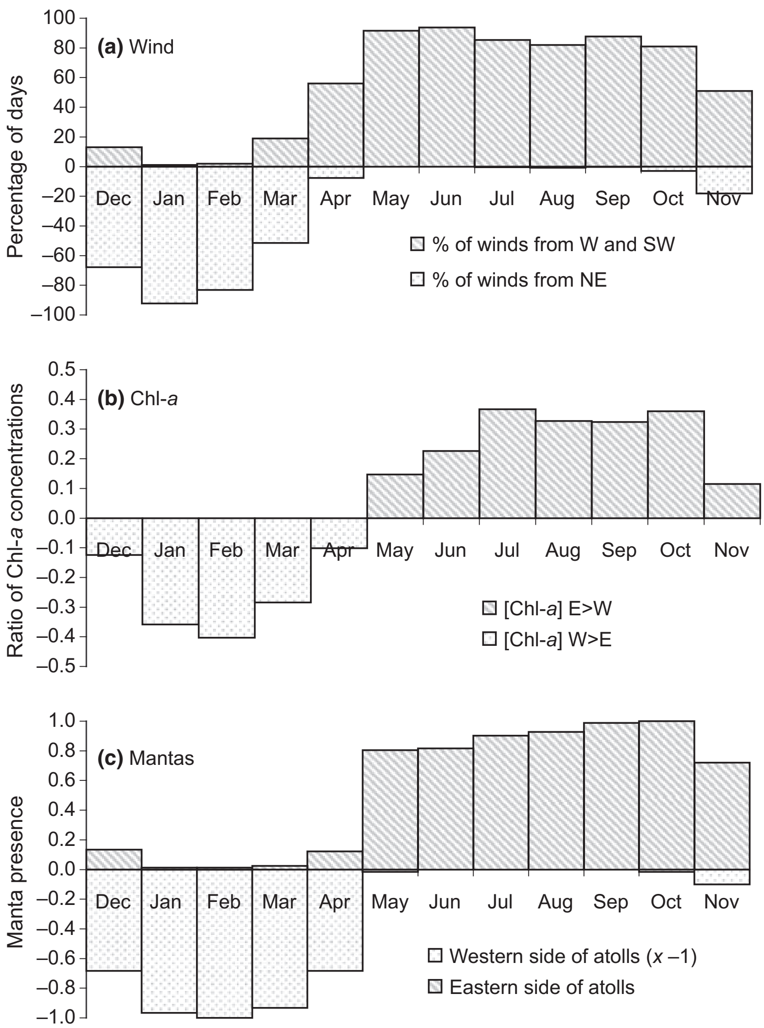


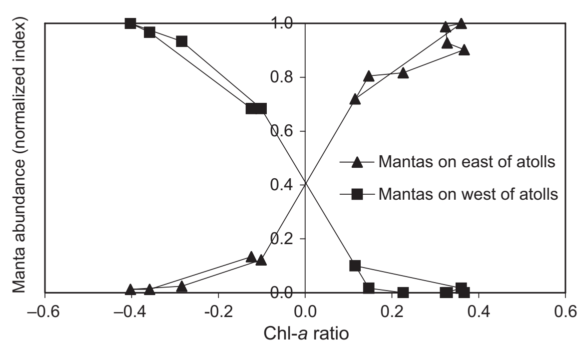
Figure 5. Seasonal variations in wind direction, Chl-*a* and manta distribution in the Maldives. (a) Monthly percentage of winds from two directions (W to SW and NE) at Malé, from average daily wind data 1987–2006. (b) Mean monthly ratios of Chl-*a* on the two sides of the central Maldives – [(Chl-*a*)E/(Chl-*a*)W]−1. Positive values indicate higher Chl-*a* on the eastern side of central Maldives, while negative values indicate higher Chl-*a* on the western side. (c) Normalized monthly distribution of mantas on the two sides of the central Maldives, as indicated by reports of presence or absence at eastern and western dive sites; positive values indicate manta presence on the eastern side of central Maldives, while negative values indicate manta presence on the western side.

Table 1. Number of dive sites (in the central double-chain atolls) at which manta rays occur reliably, by season and side of atoll.

	W side of atolls	E side of atolls	Total
SW monsoon	0	38	38
NE monsoon	33	2	35
Total	33	40	73

For the central double-chain atolls, 79 manta dive sites were documented. The distribution of manta rays according to side of atoll and season is summarized in Table 1 (seven sites were in mid-atoll and could not be assigned to E or W objectively, so are excluded from this analysis; one site had mantas present in both seasons). It is clear that manta rays are not distributed randomly with respect to season (χ^2 = 65.4, df = 1,

Figure 6. Relationship between Chl-*a* distribution around the central Maldives and the distribution of manta rays. Each data point represents one month. When Chl-*a* ratio is positive, i.e., Chl-*a* concentrations are greatest on the eastern side of the central Maldives, mantas are commonest on the east of the atolls and absent on the west, and vice versa.



$P < 0.001$), and that they are almost exclusively found on the downstream sides of the atolls.

DISCUSSION

The oceanography and pelagic ecology of the Maldives is dominated by the monsoons, with the seasonally reversing winds driving seasonally alternating ocean currents. These currents bring clear oceanic water to the upstream side of the Maldives. As the monsoon current passes over the Maldives ridge, mixing and upwelling entrain nutrients from below the mixed layer up into the euphotic zone. Additionally, benthic nitrogen fixation in the atolls might also play some role in the enrichment process (e.g., Charpy-Roubaud *et al.*, 2001). These processes result in a phytoplankton bloom on the downstream side of the atoll chain (Figs 4 and 5b). Consequently, underwater visibility is much reduced on the downstream side: anecdotal evidence from experienced divers (and pers. obs. by R. C. Anderson) suggests that horizontal underwater visibility at manta dive sites in the central atolls is mostly in the range 5–15 m (mean about 12 m) during the manta season and 20–40 m (mean about 25 m) during the non-manta season.

This enhancement of chlorophyll in the vicinity of the Maldives is a manifestation of the island mass effect (Doty and Oguri, 1956; Gilmartin and Revelante, 1974; Sengupta and Desa, 2001; Bakker *et al.*, 2007): nutrient enrichment of the surface waters and consequently increased production in the vicinity of oceanic islands as a result of the interaction between ocean circulation and island topography. An earlier brief report by Longhurst (1998), using data from the Coastal Zone Color Scanner (CZCS), provided indications of seasonally increased Chl-*a* on the downstream side of the Maldives chain, but the extent of that variability was not quantified.

Seasonally high primary production is believed to support high zooplankton biomass, providing food for many planktivores on the downstream side of the Maldives. These include mantas, which, as demonstrated here, are more common on the downstream side of the atolls than on the upstream side (Figs 2, 3 and 5c). There is thus a series of trophic links from monsoons to mantas, comparable to those linking wind to whales off the California coast (Croll *et al.*, 2005). In the Maldives, the seasonal distribution of mantas is similar to that previously described for both the zooplankton- and micronekton-eating whale shark *Rhincodon typus* (Anderson and Ahmed, 1993) and the planktivorous silver sprat *Spratelloides gracilis* (Anderson and Saleem, 1994). The silver sprat is the most important species of small fish used as livebait in the commercially significant Maldivian tuna pole and line fishery (Anderson, 1997). Manta rays are widely known in Dhivehi (Maldivian language) by the name *en-madi* (=baitfish-ray). This is a reference to their frequent occurrence with and supposed feeding on small baitfishes.

When diving with mantas, the water often appears greenish, and underwater visibility is reduced, as noted above. Certainly, manta occurrence does correlate well with Chl-*a* (Fig. 6). However, mantas eat zooplankton not phytoplankton, and the water rarely appears to contain much zooplankton (R. C. Anderson, pers. obs.). In addition, divers only occasionally see mantas feeding; most manta dives are at cleaning stations, usually near the rim of the atoll, where mantas are typically seen when tidal and ocean currents combine to produce outgoing currents. There appear to be many thousands of mantas in Maldivian waters (R. C. Anderson, pers. obs.), so the question arises, where is all their food?

While zooplankton surveys are lacking in the Maldives, some insights can be obtained from our observations at manta dive sites where feeding does occur. At one particular site for example, on the SE side of North Malé Atoll, just north of Malé, mantas are often seen during the SW monsoon at a cleaning station on the outer reef near Lankanfinolhu Island. During this season the prevailing current is to the east, and passes from the inside of the atoll to the ocean outside through the channel just south of Lankanfinolhu. On most days, any incoming tidal current is insufficient to overcome the out-flowing monsoon current, and the net flow remains outward. However, during the strongest spring tides, the incoming tide is sufficient to overcome the outgoing monsoon current, and there can be a strong net inward flow. At these times, the incoming water often contains large quantities of zooplankton, particularly copepods (R.C. Anderson, pers. obs). Strong tidal currents in reef passages are known to induce upwelling of deep water from outside the reef by Bernoulli suction (Wolanski and Hamner, 1988). This provides opportunities for mantas to feed on concentrated streams of plankton in the atoll channel, and more than 100 can be seen together at such times (R. C. Anderson, pers.obs).

More generally though, this provides evidence of large quantities of zooplankton at (unknown) depth outside the atolls on the downstream side of the atolls. We speculate that mantas often feed on this deep zooplankton, perhaps at night when the zooplankton migrates up into shallower water. Dewar *et al.* (2008) noted that mantas were absent from shallow reef sites in Indonesia at night, and speculated that they were feeding in deeper water on the deep-scattering layer. If these speculations are correct, mantas might be considered transient members of the mesopelagic boundary community (c.f., Reid *et al.*, 1991; Benoit-Bird and Au, 2004).

As noted above, whale sharks, which feed on micronekton as well as zooplankton (Colman, 1997), have a broadly similar seasonal distribution to manta rays in the Maldives, also being found more often on the downstream than upstream sides of the atolls (Anderson and Ahmed, 1993). However, there are differences in their distributions. For example, dive locations offering the most reliable encounters for the two species are often separated by a few kilometers. A contributing factor may be the differences in local distribution of their preferred prey within the mesopelagic boundary community (c.f., Benoit-Bird and Au, 2006).

The Maldives has a unique physical setting, with the north–south chain of atolls lying perpendicular to the east–west flow of the monsoon currents. This likely provides optimal conditions for the enhancement of primary productivity and the development of zooplankton biomass. The presence of a double chain of atolls might further enhance total primary productivity, by providing additional opportunities for nutrient enrichment of surface waters. This may go some way to explaining the particularly large numbers of mantas found in the Maldives. More generally, it may explain the relatively high pelagic productivity around these oceanic islands, which supports, for example, the highest catch of skipjack tuna *Katsuwonus pelamis* per unit area in the world (Fonteneau, 1997).

A notable feature of Fig. 5a,c is the rapid shift in distribution of mantas with the change of wind direction. There is relatively little lag between physical forcing and this component of biological response. One likely reason for this is that monsoons are a basin-wide phenomenon, with winds changing elsewhere over the Indian Ocean before they change over the Maldives, and currents responding to this remote forcing. According to Maldivian tradition, NE monsoon currents start on 16 November, whereas light NE winds do not begin until 27 November, and stronger NE winds only commence on 10 December (Maniku, 1989). A similar phenomenon occurs off the neighbouring southwest coast of India, where geostrophic shoaling occurs in April, at the start of the SW monsoon, weeks before local wind stress is able to force upwelling (McCreary *et al.*, 1993; Longhurst, 1998). A second reason for the very short delay between physical forcing and biological response may be that plankton on the downstream side of the atolls may provide a ready source of immigrants (to the new downstream side) when the currents do change direction.

While the discussion so far has been general, there are, as mentioned above, significant regional differences in the topography and oceanography within the Maldives. These have an impact on the seasonal distribution of mantas. In this context, the central double-chain atolls form the largest region.

In the central atolls, there are differences in some details between the pattern of seasonal distribution of manta rays obtained from reports by fishermen (Fig. 2) and that obtained from reports by divers (Fig. 3). This is because fishermen reported manta presence within general areas and divers at specific sites. Figure 3 therefore gives a more precise picture of manta ray seasonal distribution compared with Fig. 2. Nevertheless, both data sets demonstrate that manta rays are found on the downstream side of atolls. We know of only two exceptions to this general pattern (both marked with triangles in Fig. 3). One of these is in Lhaviyani Atoll, near Fushifaru Island, where mantas are seen in most years for a short period during February-March. The reason(s) for this regular occurrence of mantas on the upstream side of Lhaviyani Atoll are unknown, but the possibility of a local plankton bloom, perhaps associated with a local spawning event, should be investigated. The other exception is near Embudu Island in the NE corner of South Malé Atoll, where small numbers of manta rays are seen during the NE monsoon. The reason(s) for the occurrence of manta rays on the upstream side of this atoll are again unknown, but their proximity to an atoll channel again suggests the possibility of localized feeding opportunities.

In the southern, single-chain atolls (south of 2°35′N), mantas are present year-round and show no obvious seasonality, at least on the temporal and spatial scales considered here. This is probably a reflection of the oceanography of this region being less clearly demarcated into two seasons: in addition to the monsoon currents, the southern atolls are also under the influence of equatorial currents. Indeed, southern fishermen divide the year into four seasons, not just two. However, both fishermen and divers in the southern Maldives report that mantas show changes in abundance in relation to lunar phase. Fishermen report that mantas are most frequently seen on full moon nights, whereas divers in Seenu Atoll report that mantas are most frequently seen during spring tidal periods.

The northern single-chain atolls (north of 6°00′N) can best be considered in two parts. In the southern section, comprising Shaviyani Atoll and the southern part of Haa Dhaalu Atoll (between 6°00′N and 6°33′N), mantas are present in both seasons. There is some evidence of seasonal shifts, with more fishermen on eastern islands reporting mantas during the SW monsoon, and more fishermen on western islands reporting mantas during the NE monsoon. This area might thus be regarded as a longitudinally compressed extension of the central double-atoll chain.

The northern part of this region (north of 6°33′N) comprises most of Haa Dhaalu Atoll and all of Haa Alifu Atoll, and shows a very distinct seasonal pattern of manta distribution. Mantas are present here during the NE monsoon, but absent or rare in the SW monsoon. Fishermen from 17 islands all reported that mantas occur only in the NE monsoon. Divers noted that mantas are common on five dive sites during the NE monsoon season, but are only rarely seen during the SW monsoon season (and then usually at greater depths). This strong seasonal signal in manta occurrence is not easily explained by the available ocean colour data. In addition, underwater visibility, as reported by divers, is greatest during the NE season, when mantas are present, and least during the SW monsoon. This is something of a paradox, as some increase in productivity during the NE monsoon might be expected. Not only are mantas more abundant here in the NE monsoon than in the SW monsoon, but so, too, are large-sized skipjack tuna *Katsuwonus pelamis* (Rochepeau and Hafiz, 1990; Anderson *et al*., 1998), large yellowfin tuna *Thunnus albacares* (Adam and Anderson, 1996; Anderson and Shaan, 1998), Lesser Noddies *Anous minutus* (Anderson, 2007) and spotted dolphins *Stenella attenuata* (Anderson, 2005). It is possible that there may be some seasonal increase in primary productivity associated with a deep chlorophyll maximum which is not visible to SeaWiFS. In addition, the proximity of the Indian subcontinent may play some role in modulating seasonal productivity. These possibilities deserve further investigation.

CONCLUSIONS

The tropics are sometimes thought of as showing little seasonality, but this is certainly not the case in regions such the Maldives which are under the influence of the monsoons. In the Maldives, the distinct seasonality in the oceanographic environment results in marked seasonality in the distribution and abundance of many organisms, including, as demonstrated here, manta rays. The interaction of the seasonally alternating monsoon currents with the Maldives ridge produces nutrient enrichment of the surface waters, and a consequent increase in phytoplankton biomass on the downstream side of the ridge. This in turn supports a zooplankton bloom, on which the mantas feed. This study is the first to describe such a series of links between physical forcing and biological response in the nearshore waters of the Maldives, which are of enormous economic importance for both fisheries and marine tourism. This study is also the first to suggest the existence of a mesopelagic boundary community in Maldivian waters, reinforcing the notion that such communities are a widespread phenomenon.

Much, however, remains unknown. Photo-identification studies currently underway in the Maldives (using unique ventral spotting patterns), plus the use of electronic tags, should shed much further light on the movements of individual mantas over a variety of temporal and spatial scales. Plankton studies are also required to improve understanding of manta feeding ecology.

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