

Observations of cetaceans in the Maldives, 1990-2002

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ABSTRACT

Cetaceans observed in Maldivian waters were recorded during the period August 1990 to June 2002, from both vessels-of-opportunity and dedicated cetacean-watching cruises. A total of 1,829 cetacean sightings were recorded during 535 days at sea (equivalent to 261 standardised days). There were 83 multispecies sightings, plus a further 58 sightings without associated effort data and 129 strandings were recorded by the author and others, making a total of 2,108 cetacean records. In all, 20 different species were positively identified from sightings. Spinner dolphins were the most abundant species seen, accounting for 35% of sightings and 53% of numbers. This species showed a clear diurnal pattern of behaviour, with many schools entering the atolls in the early morning, and leaving in the late afternoon. Spinner dolphins regularly occurred with pantropical spotted dolphins and both species associated with yellowfin tuna. Bryde's whales also associated with yellowfin tuna and appeared to be most common in Maldivian waters during El Niño Southern Oscillation events. Blue whales were only recorded during November to April. Dwarf sperm whales were especially difficult to locate in rough weather but relatively common, making up one sixth of all sightings in flat-calm conditions. Melon-headed whales were particularly common in the south of the Maldives, but rare in the centre and north. Other species recorded were humpback whale, sperm whale, rough-toothed dolphin, Risso's dolphin, bottlenose dolphin, striped dolphin, Fraser's dolphin, pygmy killer whale, false killer whale, killer whale, short-finned pilot whale, Blainville's beaked whale, Longman's beaked whale and Cuvier's beaked whale.

KEYWORDS: INDIAN OCEAN; SANCTUARIES; INCIDENTAL SIGHTINGS; SCHOOL SIZE; MIGRATION; EL NIÑO; BRYDE'S WHALE; BLUE WHALE; DWARF SPERM WHALE; PANTROPICAL SPOTTED DOLPHIN; SPINNER DOLPHIN; MELON-HEADED WHALE

INTRODUCTION

The Republic of Maldives is a small island nation in the central Indian Ocean, to the southwest of India and Sri Lanka (Fig. 1). It lies at the heart of the International Whaling Commission's (IWC) Indian Ocean Sanctuary and has a particularly rich cetacean fauna. Until recently, however, it has received relatively little attention from cetologists.

Among those who made brief visits to the Maldives and left some record of their cetacean sightings were: the 19th century French merchant-shipowner and naturalist Jean-Jacques Dussumier (Arvy, 1972; Gilpatrick *et al.*, 1987); the Dutch sea captain Willem Mörzer Bruyns, who passed through or by the Maldives on several occasions in the 1950s and 1960s (Mörzer-Bruyns, 1971); Captain Jacques-Yves Cousteau, who visited the Maldives in 1967 (Cousteau and Diolé, 1971; 1972); Stephen Leatherwood and fisheries worker Charles Peters, who visited the Maldives separately in 1980-83 (Leatherwood *et al.*, 1984; with additional information on some sightings in: Leatherwood, 1986; Gilpatrick *et al.*, 1987; Wilson *et al.*, 1987; Leatherwood *et al.*, 1991); Japanese whaling researchers who passed through the Maldives on two scouting vessels in March 1982 (Kasuya and Wada, 1991); cetologists on the research yacht *Tulip* who visited the Maldives in late 1983 and early 1984 (Whitehead *et al.*, 1983; Alling *et al.*, 1984) during the course of their research elsewhere in the Indian Ocean Sanctuary (Alling, 1986; Whitehead, 1989; Gordon, 1991); and marine biologists Lisa Ballance and Robert Pitman who passed through Maldivian waters in April and June 1995 during the course of a cetacean survey of the western Indian Ocean (Ballance *et al.*, 1996; Ballance and Pitman, 1998).

Among reports by scientists based in the Maldives are those on: miscellaneous strandings and sightings (Anderson, 1990; 1996); the association of large yellowfin tuna (*Thunnus albacares*) with dolphins (Anderson and Shaan, 1998); all known cetacean strandings and specimens from the Maldives up to early 1999 (Anderson *et al.*, 1999); a 20-

day cetacean survey in the north-eastern part of the Maldives during April 1998 (Ballance *et al.*, 2001); and a stranded Longman's beaked whale, *Indopacetus pacificus* (Dalebout *et al.*, 2003).

These studies between them reported a total of 18 species of cetacean from sightings in the Maldives, with a further two species reported from strandings. The 20 species (listed in the species accounts, below) include all of the expected pantropical varieties and all of the locally abundant species. However, most earlier studies were of limited duration and scale, and provided only limited information on local distribution, abundance, behaviour and ecology.

The aim of this paper is to summarise sightings of cetaceans in the Maldives made by the author over the 12-year period August 1990 to June 2002. Although not uniformly distributed, these sightings cover every month and every atoll and most have been recorded with associated effort data. While not comprehensive, they provide a broad overview of the cetacean species occurring in Maldivian waters including: a first impression of their distribution and relative abundance; some initial information on their local behaviour and ecology; and indications of promising avenues for more focussed future research.

METHODS

Survey 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 50-60m but vary from about 10-100m. Outside the atolls the reef slopes drop steeply away to the ocean floor, at about 2-3,000m. An exception is found in the area between the double chain of atolls in the central Maldives, the 'inter-atoll sea', where bottom depths are of the order of 2-500m. While these general features of Maldivian bathymetry are well

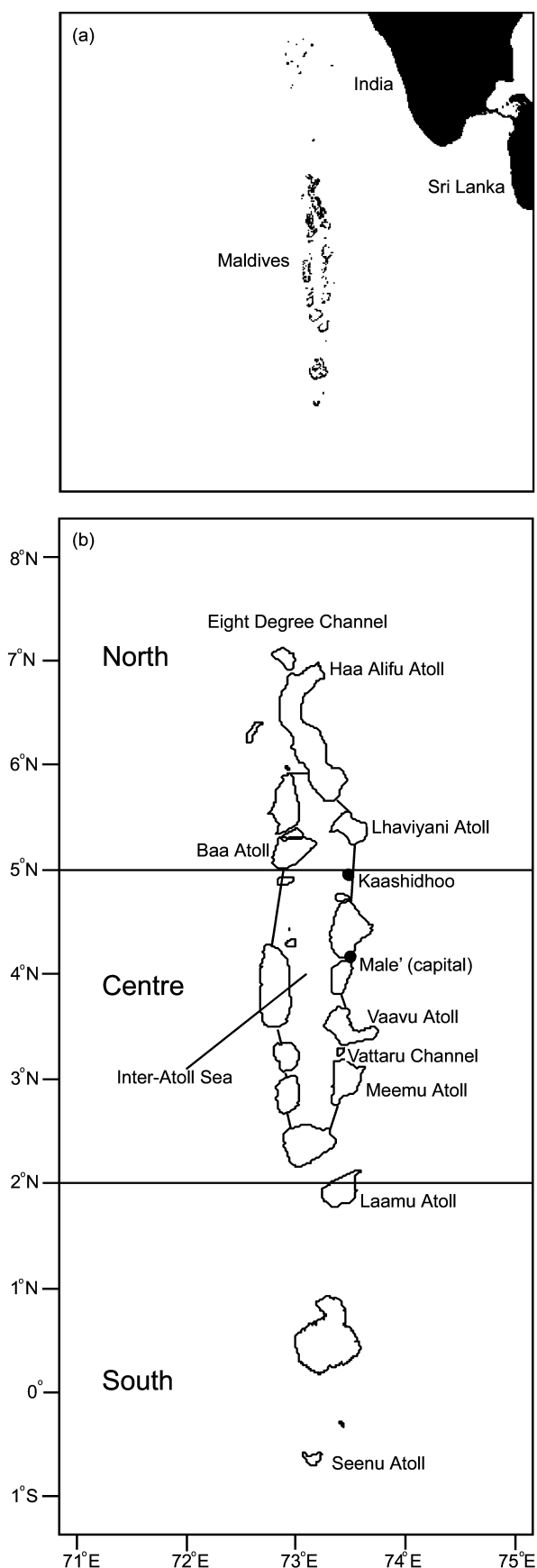


Fig. 1. The Maldives, showing location (a) and places and survey areas mentioned in the text (b).

established, there has been no detailed survey of the outer atoll slopes. As a result, discussion of this important cetacean habitat is restricted since bottom depths and gradients are not known accurately.

The Maldives is affected by the seasonal monsoons. The Northeast Monsoon lasts from about December to March, with winds and currents from the northeast or east. Winds can be quite strong in December and early January but are usually fairly calm in February and March. The Southwest Monsoon lasts from about May to October, with winds and currents mainly from the southwest and west. Winds can be particularly strong from late May to early August. April and November are inter-monsoon months, with variable but often light winds and currents. The south of the Maldives (south of about 2°30' or 2°00'N) is less affected by the monsoons than the north and centre of the country. Instead it is more under the influence of equatorial current systems.

Survey methodology

Between August 1990 and June 2002, 68 sea trips were undertaken, totalling 535 days at sea, during which cetacean sightings were systematically recorded. Observations were recorded from a wide variety of vessels (all mechanised), of lengths 10-45m (mostly 14-26m) with cruising speeds of 11-19km h⁻¹ (6-11 knots). These included both vessels-of-opportunity (mainly local fisheries-research and diving boats) and dedicated cetacean-watching vessels. The latter included the cetacean survey trip reported by Ballance *et al.* (2001). The overall strategy was to make use of existing opportunities to accumulate sightings records from numerous sea trips covering a wide area and a long duration, rather than to conduct a systematic survey. In all cases, searching for cetaceans was with a combination of handheld binoculars and naked eye. Different levels of observation effort were maintained during different sea trips, which can be grouped into four categories:

- (1) Early trips (1990-95), mostly undertaken for fisheries research but also for diving, during which only one observer was present and little effort was made to search for cetaceans. Eye height was about 2-4m above sea level.
- (2) Later fisheries and diving trips (1996-2002), during which 1-4 observers were present and some effort was made to search for cetaceans, although the main purpose of these trips was never cetacean observation. Eye height was 2-6m.
- (3) Fifteen trips (1998-2002), the main purpose of which was whale and dolphin watching, during which a dedicated watch was maintained by 1-3 experienced observers, assisted by 1-6 inexperienced observers, for an average of about 7-8 hours per day. Eye height was 3-10m.
- (4) One trip reported by Ballance *et al.* (2001), during which a dedicated watch was maintained by 5-8 experienced observers for an average of 7.8 hours per day 'on effort' with an additional average of about 2h d⁻¹ at sea. Eye height was 4m. A slight difference in total number of sightings reported for this one trip in Ballance *et al.* (2001) and in this paper is the result of subjective differences in recording some adjacent cetacean groups as associated or not associated.

Major details of these four trip types are summarised in Table 1. Each atoll in the Maldives was visited at least five times during 1990-2002 and at least three sea trips were undertaken in each calendar month. In total, 1,829 sightings were recorded (Fig. 2). The uneven distribution of sightings largely reflects the distribution of sighting effort rather than any major pattern of cetacean abundance. For example, Fig. 2 shows a concentration of sightings in the east-central

Table 1
Summary of cetacean sightings and sighting effort.

| Type of trip | No. sightings | No. trips | No. days | Sightings/ day | Raising factor | Std days |
|---------------------------|---------------|-----------|----------|-------------------|-------------------|----------|
| 1. General (1990-1995) | 195 | 27 | 197 | 1.0 | 0.141 | 27.8 |
| 2. General (1996-2002) | 380 | 25 | 176 | 2.2 | 0.308 | 54.2 |
| 3. Whalewatch (1998-2002) | 995 | 15 | 142 | 7.0 | 1.000 | 142.0 |
| 4. Cetacean survey (1998) | 259 | 1 | 20 | 13.0 | 1.848 | 37.0 |
| Sub-total | 1,829 | 68 | 535 | - | - | 261.0 |
| 5. No-effort sightings | 58 | | | | | |
| 6. Strandings | 129 | | | | | |
| Total | 2,016 | | | | | |

Maldives in the area closest to Malé (the capital and my home base near which most effort was concentrated) and a relative dearth of sightings on the west of the atoll chain (reflecting limited effort there). Each sighting was coded for certainty of identification (definite, probable, possible, unidentified). Weather conditions were not recorded systematically. However, wind conditions were recorded for most sightings from 1996 and 92% of all such sightings were recorded in Beaufort force 3 or less (Table 3).

In addition to the 1,829 on-effort sightings, a further 58 sightings, without associated effort data, and 129 strandings were recorded by the author and others, making a total of 2,016 cetacean records. Stranding records are from Anderson *et al.* (1999) and subsequent unpublished reports held by the Marine Research Centre, Malé. Sightings from other observers were only included when the observer was known personally to the author, was known to be experienced and reliable, and was able to supply sufficient details, notes or photographs to confirm their record. Note that a single sighting could include more than one species: there were 83 instances of sightings involving more than one species, with nine involving more than two species (see further discussion below). As a result, the 1,829 on-effort sightings produced 1,921 on-effort species records and 2,108 total records (Table 4).

Analyses

Standardisation of sighting effort

Sightings were collected during four types of trip during which levels of observation effort were very different. With the information available there is no entirely satisfactory means to standardise effort. Nevertheless, the aim of this paper is to summarise findings from all sightings, not just a subset. Effort was therefore standardised by raising the numbers of days in each trip category by the ratio of sighting rates, using the trip category with the most sightings (category 3 above) as the standard (Table 1). It is estimated that the equivalent of 261 standardised days was spent at sea. A summary of standardised sighting effort by month and major area is provided in Table 2. Standardised effort was clearly not distributed uniformly across calendar months or major areas. This method of standardisation may introduce some biases but they are unlikely to be particularly large in relation to other sources of error and it is not possible to estimate actual sighting effort for trip categories 1 and 2 in a more rigorous manner. One tendency of this approach to standardisation will be to dampen indications of seasonal variations in abundance; in view of this and the very limited sighting effort in several months (Table 2) discussion of seasonal variation is kept to a minimum.

Table 2
Summary of sighting effort (standard days) by region and month.

| Month | Inside atolls | Inter-atoll sea | Outside north | Outside centre | Outside south | Total |
|-------|---------------|-----------------|---------------|----------------|---------------|-------|
| Jan | 0.7 | 0.3 | 0.2 | 0.5 | 0.1 | 1.8 |
| Feb | 7.9 | 4.9 | 5.1 | 3.8 | 0.9 | 22.6 |
| Mar | 18.2 | 4.1 | 10.8 | 22.8 | 10.5 | 66.4 |
| Apr | 22.1 | 4.7 | 35.3 | 35.6 | 5.6 | 103.4 |
| May | 14.8 | 2.3 | | 7.3 | | 24.4 |
| Jun | 3.7 | 0.4 | 0.4 | 0.5 | | 5.0 |
| Jul | 2.1 | 0.3 | | 0.3 | 0.3 | 3.0 |
| Aug | 6.5 | 1.3 | 0.6 | 0.9 | 1.6 | 10.8 |
| Sep | 6.6 | 0.4 | | 0.3 | 1.2 | 8.4 |
| Oct | 4.7 | 0.6 | 0.3 | 0.8 | 0.5 | 6.9 |
| Nov | 3.6 | 0.1 | 0.9 | 0.2 | | 4.8 |
| Dec | 2.4 | 0.9 | | 0.1 | | 3.5 |
| Total | 93.3 | 20.1 | 53.6 | 73.2 | 20.7 | 261.0 |

Table 3
Cetacean sightings in relation to wind strength (for details of dwarf sperm whale see species account).

| Beaufort | Total sightings | Dwarf sperm whale |
|----------|-----------------|-------------------|
| 0 | 187 | 32 (17.1%) |
| 1 | 333 | 34 (10.2%) |
| 2 | 462 | 6 (1.3%) |
| 3 | 212 | 1 (0.5%) |
| 4 | 76 | 0 |
| 5 | 25 | 0 |
| 6 | 4 | 0 |
| Total | 1,299 | 73 (5.6%) |

Data limitations

Sightings from early trips (1990-95) were frequently unidentified and school-size estimates were erratic. Therefore these early data were not used in most analyses. For this study, all cetacean sightings recorded as 'identification possible' are treated as 'unidentified'. In most analyses, only data from 'identification definite' sightings are used, unless stated otherwise. Estimates of relative abundance were calculated simply as estimates of numbers actually seen. They do not take account of differences in sightability and therefore undoubtedly underestimate the relative abundance of the more cryptic species.

Regional analysis and scope

To facilitate analysis of regional differences in cetacean distribution and abundance, five 'major areas' (illustrated in Fig. 1) are defined for the purposes of this study as follows:

- (1) *Inside Atoll* – all waters inside all atolls, including reef channels into atolls;
- (2) *Inter-atoll Sea* – the relatively shallow area of water in the middle of the double row of atolls in the central Maldives;
- (3) *Outside North* – all waters outside the atolls north of 5°N, excluding the inter-atoll sea;
- (4) *Outside Centre* – all waters outside the atolls between 2°N and 5°N, excluding the inter-atoll sea; and
- (5) *Outside South* – all waters outside the atolls south of 2°N.

There are likely to be differences between the western and eastern portions of the offshore areas (Outside North, Centre and South), but the limited observation effort in the western portions (e.g. just 6.1 standard days in the west centre) precludes separate treatment. The Maldives claims a 200 n.mile Exclusive Economic Zone (EEZ) but has yet to formally declare all boundaries. As a result it is not clear if some published cetacean sightings lie within the Maldivian EEZ or not. This study was limited to sightings within about 50 n.miles (ca 90km) of the atolls. Most survey effort was actually carried out less than about 10 n.miles (ca 20km) from the atolls.

RESULTS AND DISCUSSION

Species accounts

A total of 20 species of cetacean were positively identified from sightings during 1990-2002 (Table 4). This included 19 of the 20 species previously recorded from the Maldives and one new record, the humpback whale (*Megaptera novaeangliae*).

Bryde's whale (*Balaenoptera edeni*)

Bryde's whales appear to be the most common baleen whale species in Maldivian waters (Tables 4, 6 and 7). The taxonomic status of this species in the north-central Indian Ocean remains uncertain but animals in Maldivian waters may be referable to *B. brydei* Olsen, 1913 (Rice, 1998; Ballance *et al.*, 2001; Wada *et al.*, 2003). One cow-calf pair was seen on 2 April 1999; the length of the calf was approximately one-third that of its mother.

For 17 dives by six individuals, mean dive time was 9.6min (SD=2.5min, range=6-12min). Blows varied considerably in strength, and exhalation sometimes took place underwater. Breaching was observed on two occasions. In four instances, Bryde's whales were observed lunge-feeding near the surface, sometimes on one side, sometimes vertically. Maldivian fishermen do not generally differentiate between different species of whale, calling them all *bodumas* (literally, big fish). However, they use the name *katterumas* (scissors fish) for whales that lunge through the surface with mouth agape; this name probably applies best to Bryde's whales.

Ballance *et al.* (2001) noted the presence of a concentration of Bryde's whales in the Vatteru Channel between Vaavu (=Felidhoo) and Meemu (=Mulaku) Atolls on 19-20 April 1998. Bryde's whales were actually present in this area from at least 26 March to 12 May 1998. A total of 77% of all on-effort sightings of Bryde's whales reported here ($n=53$ definite and probable identifications combined) were from this one concentration. As noted by Ballance *et al.* (2001) these whales appeared to be feeding: euphausiids were seen in the water near the whales on two days. On other occasions, Bryde's whales were seen feeding on anchovies (Engraulidae, once) and unidentified small red fish (three times).

Table 4
Summary of cetacean records by species (note that 'Other records' includes 129 strandings).

| Species | On-effort sightings | | | Other records | | Total |
|---------------------------|---------------------|-------------|------------------------------|---------------|-------------|-------|
| | ID definite | ID probable | % of all on effort sightings | ID definite | ID probable | |
| Spinner dolphin | 624 | 44 | 34.8 | 21 | 2 | 691 |
| Bottlenose dolphin | 226 | 27 | 13.2 | 6 | 1 | 260 |
| Risso's dolphin | 211 | 8 | 11.4 | 5 | 0 | 224 |
| Spotted dolphin | 63 | 4 | 3.5 | 2 | 0 | 69 |
| Striped dolphin | 43 | 3 | 2.4 | 0 | 0 | 46 |
| Fraser's dolphin | 17 | 0 | 0.9 | 1 | 1 | 19 |
| Rough-tooth dolphin | 6 | 0 | 0.3 | 0 | 0 | 6 |
| Short-finned pilot whale | 79 | 2 | 4.2 | 6 | 1 | 88 |
| Melon-headed whale | 12 | 0 | 0.6 | 7 | 1 | 20 |
| False killer whale | 10 | 0 | 0.5 | 4 | 0 | 14 |
| Killer whale | 9 | 0 | 0.5 | 2 | 0 | 11 |
| Pygmy killer whale | 4 | 0 | 0.2 | 2 | 0 | 6 |
| Melon-headed/pygmy killer | 0 | 0 | 0.0 | 0 | 2 | 2 |
| Cuvier's beaked whale | 17 | 6 | 1.2 | 0 | 0 | 23 |
| Blainville's beaked | 3 | 7 | 0.5 | 0 | 0 | 10 |
| Longman's beaked | 1 | 3 | 0.2 | 1 | 0 | 5 |
| Ginkgo-toothed beaked | 0 | 0 | 0.0 | 1 | 0 | 1 |
| UNID beaked whale | 0 | 37 | 1.9 | 0 | 1 | 38 |
| Bryde's whale | 36 | 17 | 2.8 | 2 | 0 | 55 |
| Blue whale | 12 | 2 | 0.7 | 8 | 5 | 27 |
| Humpback whale | 1 | 0 | 0.1 | 1 | 0 | 2 |
| UNID baleen whale | 0 | 4 | 0.2 | 0 | 5 | 9 |
| Dwarf sperm whale | 74 | 6 | 4.2 | 0 | 0 | 80 |
| Sperm whale | 9 | 1 | 0.5 | 51 | 0 | 61 |
| UNID dolphin | 0 | 216 | 11.2 | 0 | 13 | 229 |
| UNID cetacean | 0 | 57 | 3.0 | 0 | 6 | 63 |
| UNID whale | 0 | 20 | 1.0 | 0 | 29 | 49 |
| Total | 1,457 | 464 | 100 | 120 | 67 | 2,108 |

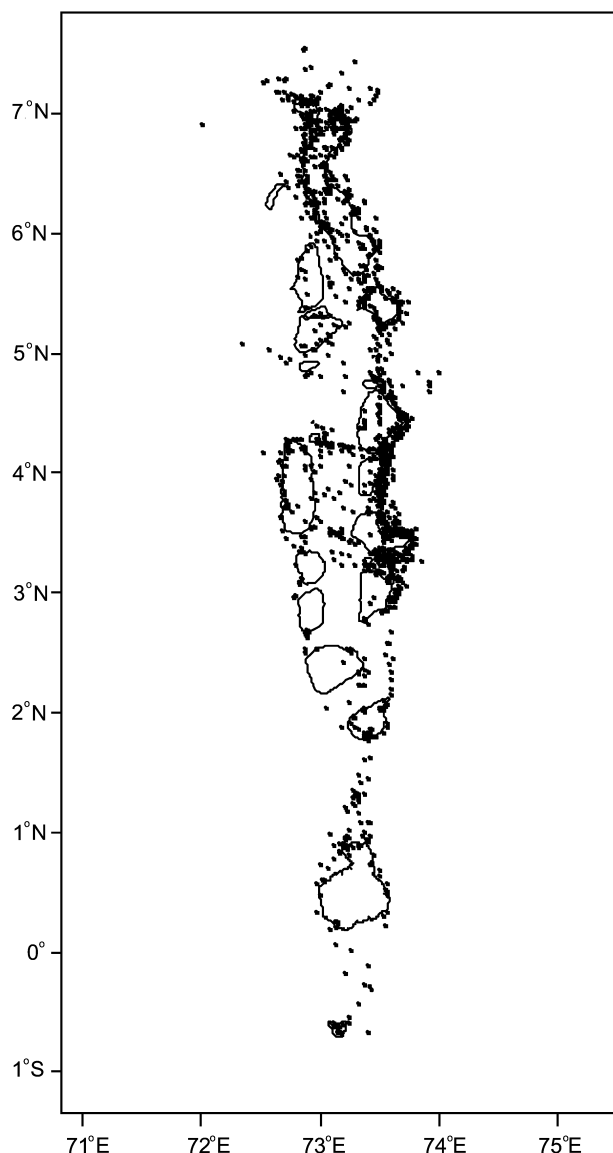


Fig. 2. Locations of cetacean sightings made during survey trips (n=1,829). The distribution of sightings largely reflects the distribution of sighting effort.

Anderson (1990) reported a baleen whale lunge-feeding off Lhaviyani Atoll in February 1988 which was tentatively identified as a Bryde's whale. Subsequent observations of this species confirm that sighting (from field notes) as a Bryde's whale. Anderson (1990) also reported sightings of many whales off Lhaviyani Atoll in 1972 (by N.T. Hasen Didi, formerly of Ministry of Fisheries, Maldives, pers. comm., 1990). Additional information (N.T. Hasen Didi, pers. comm., 1998) allows identification as probable Bryde's whales. As a result, and with further information from others, it appears that unusually large numbers of Bryde's whales (or probable Bryde's whales) were present in the following areas and years:

| | | |
|-----------------|-----------|--|
| Lhaviyani Atoll | 1972 | N.T. Hasen Didi (pers. comm.) |
| Vattaru Channel | c. 1977-8 | Meemu Atoll fishermen; Adam Hussein (pers. comm.) |
| Lhaviyani Atoll | 1988 | Lhaviyani Atoll fishermen; Anderson (1990) |
| Vattaru Channel | 1998 | Ballance <i>et al.</i> (2001); this study |

The Maldives is influenced by interannual variations in oceanographic conditions, notably El Niño Southern Oscillation (ENSO) events, which affect the distribution and

Table 5
Summary of cetacean school sizes by species.

| Species | N | Mean | 1.96 SE | Range | Mode |
|-----------------------------|-----|------|---------|----------|---------|
| Spinner dolphin | 466 | 58.2 | 6.6 | 6-750 | 20-30 |
| Bottlenose dolphin | 197 | 14.6 | 2.8 | 1-170 | 1-10 |
| Risso's dolphin | 184 | 33.3 | 5.1 | 2-300 | 2-15 |
| Pantropical spotted dolphin | 58 | 161 | 32.9 | 4-500 | 40-60 |
| Striped dolphin | 41 | 47.8 | 10.8 | 3-200 | 20-60 |
| Fraser's dolphin | 14 | 215 | 71 | 40-1,000 | 40-80 |
| Rough-tooth dolphin | 5 | 22.2 | 13.1 | 6-40 | |
| Short-finned pilot whale | 74 | 17.7 | 3.4 | 3-100 | 8-20 |
| Melon-headed whale | 12 | 412 | 218 | 30-1,200 | 100-120 |
| False killer whale | 12 | 36.0 | 15.3 | 1-100 | 40-50 |
| Killer whale | 9 | 6.3 | 1.2 | 5-11 | 5-7 |
| Pygmy killer whale | 4 | 16.5 | 9.1 | 9-30 | |
| Melon-headed/pygmy killer | 2 | 30 | | 30 | |
| Cuvier's beaked whale | 17 | 2.3 | 0.4 | 1-4 | 2 |
| Blainville's beaked | 3 | 3.7 | | 2-6 | |
| Longman's beaked | 4 | 6.5 | | 2-20 | 2 |
| UNID beaked | 36 | 2.5 | | 1-8 | 1-2 |
| Bryde's whale | 36 | 2.1 | 1.0 | 1-15 | 1 |
| Blue whale | 14 | 1.1 | 0.2 | 1-2 | 1 |
| Humpback whale | 2 | 2.0 | | 2 | 2 |
| UNID baleen whale | 4 | 1.0 | | 1 | 1 |
| Dwarf sperm whale | 74 | 1.7 | 0.2 | 1-6 | 1 |
| Sperm whale | 11 | 5.5 | 5.4 | 1-30 | 1 |
| UNID dolphin | 60 | 10.3 | 3.5 | 1-60 | 1-6 |
| UNID cetacean | 17 | 2.4 | 1.3 | 1-12 | 1-2 |
| UNID whale | 13 | 1.4 | 0.5 | 1-4 | 1 |

abundance of pelagic fishes (Anderson, 1993; Anderson *et al.*, 1998). Such ocean variability presumably also affects the distribution and abundance of at least some cetacean species in Maldivian waters. The years 1972, 1977, 1988 and 1998 were all ENSO years. It may be significant that anchovies appear to be more abundant than average during ENSO events and in the particular areas where Bryde's whale concentrations have been reported (Anderson and Saleem, 1994; 1995). In addition, yellowfin tuna (with which Bryde's whales often appear to associate, perhaps because they feed on the same prey) are most abundant in Maldivian waters during ENSO events (Anderson, 1993; Anderson *et al.*, 1998).

Blue whale (Balaenoptera musculus)

Blue whales in the northern Indian Ocean, including the Maldives, appear to be pygmy blues (*B. musculus breviceauda*) although their exact taxonomic status is uncertain and they may be referable to *B. m. indica* (*cf.* Yochem and Leatherwood, 1985; Mikhalev, 1996; Rice, 1998; Ballance *et al.*, 2001).

Blue whale dive times were distinctly bimodal: of 56 dives timed from eight whales (including those reported by Ballance *et al.*, 2001), 29 were short (range=5-9 min, mean=6.8min, SE=0.2min) while 25 were long (range=12-20min, mean=15.1min, SE=0.4min). Only two dives were of intermediate length (10 and 11min). The behaviour states associated with different dive times were not obvious, although the dive times of two whales did decrease when approached closely. Of 11 blue whales for which the information was recorded, 8 (73%) lifted their flukes high before diving, 1 (9%) barely lifted its flukes and 2 (18%) did not fluke at all.

Blue whale occurrence in Maldivian waters appears to be highly seasonal, with all sightings (not just those from this study) and strandings to date occurring between November and April. This is consistent with a hypothesis of a northern Indian Ocean stock (Yochem and Leatherwood, 1985;

Table 6

Estimated numbers of cetaceans seen by major areas within the Maldives. Note: Includes only sightings made during sea trips of categories 1-4 as defined in the Methods and summarised in Table 1.

| Species | Outside north | Outside centre | Outside south | Inside atolls | Inter-atoll sea | Total |
|--------------------------|---------------|----------------|---------------|---------------|-----------------|--------|
| Spinner dolphin | 5,304 | 5,996 | 2,181 | 20,924 | 3,518 | 37,923 |
| Spotted dolphin | 5,070 | 2,143 | 2,886 | 0 | 247 | 10,346 |
| Risso's dolphin | 2,190 | 2,452 | 15 | 32 | 299 | 4,988 |
| Fraser's dolphin | 1,110 | 1,520 | 610 | 0 | 300 | 3,540 |
| Bottlenose dolphin | 502 | 1,592 | 36 | 1,063 | 333 | 3,526 |
| Melon-headed whale | 100 | 650 | 2,588 | 0 | 0 | 3,338 |
| UNID dolphin | 772 | 552 | 306 | 684 | 383 | 2,697 |
| Striped dolphin | 879 | 1,138 | 0 | 0 | 55 | 2,072 |
| Short-finned pilot whale | 234 | 1,050 | 18 | 0 | 21 | 1,323 |
| False killer whale | 82 | 225 | 45 | 25 | 50 | 427 |
| UNID cetacean | 50 | 63 | 10 | 165 | 5 | 293 |
| Dwarf sperm whale | 61 | 69 | 0 | 0 | 2 | 132 |
| Rough-toothed dolphin | 101 | 18 | 0 | 0 | 0 | 119 |
| UNID beaked whale | 31 | 71 | 1 | 0 | 2 | 105 |
| Bryde's whale | 13 | 78 | 3 | 0 | 6 | 100 |
| Sperm whale | 60 | 10 | 0 | 0 | 0 | 70 |
| Pygmy killer whale | 45 | 21 | 0 | 0 | 0 | 66 |
| Killer whale | 21 | 31 | 5 | 0 | 0 | 57 |
| Cuvier's beaked whale | 22 | 24 | 6 | 0 | 0 | 52 |
| Dense-beaked whale | 5 | 22 | 0 | 0 | 0 | 27 |
| UNID whale | 10 | 4 | 11 | 0 | 1 | 26 |
| Longman's beaked whale | 2 | 22 | 2 | 0 | 0 | 26 |
| Blue whale | 12 | 2 | 2 | 1 | 0 | 17 |
| UNID baleen whale | 2 | 1 | 1 | 0 | 0 | 4 |
| Humpback whale | 0 | 0 | 0 | 2 | 0 | 2 |
| Total | 16,678 | 17,754 | 8,726 | 22,896 | 5,222 | 71,276 |

Table 7

Relative abundance of cetacean species by major areas within the Maldives (expressed as percentage of numbers of cetaceans seen in each area).

| Species | Outside north | Outside centre | Outside south | Inside atolls | Inter-atoll sea | Total |
|--------------------------|---------------|----------------|---------------|---------------|-----------------|-------|
| Spinner dolphin | 31.8 | 33.8 | 25.0 | 91.4 | 67.4 | 53.2 |
| Spotted dolphin | 30.4 | 12.1 | 33.1 | - | 4.7 | 14.5 |
| Risso's dolphin | 13.1 | 13.8 | 0.2 | 0.1 | 5.7 | 7.0 |
| Fraser's dolphin | 6.7 | 8.6 | 7.0 | - | 5.7 | 5.0 |
| Bottlenose dolphin | 3.0 | 9.0 | 0.4 | 4.6 | 6.4 | 4.9 |
| Melon-headed whale | 0.6 | 3.7 | 29.7 | - | - | 4.7 |
| UNID dolphin | 4.6 | 3.1 | 3.5 | 3.0 | 7.3 | 3.8 |
| Striped dolphin | 5.3 | 6.4 | - | - | 1.1 | 2.9 |
| Short-finned pilot whale | 1.4 | 5.9 | 0.2 | - | 0.4 | 1.9 |
| False killer whale | 0.5 | 1.3 | 0.5 | 0.1 | 1.0 | 0.6 |
| UNID cetacean | 0.3 | 0.4 | 0.1 | 0.7 | 0.1 | 0.4 |
| Dwarf sperm whale | 0.4 | 0.4 | - | - | 0.0 | 0.2 |
| Rough-toothed dolphin | 0.6 | 0.1 | - | - | - | 0.2 |
| UNID beaked whale | 0.2 | 0.4 | 0.0 | - | 0.0 | 0.1 |
| Bryde's whale | 0.1 | 0.4 | 0.0 | - | 0.1 | 0.1 |
| Sperm whale | 0.4 | 0.1 | - | - | - | 0.1 |
| Pygmy killer whale | 0.3 | 0.1 | - | - | - | 0.1 |
| Killer whale | 0.1 | 0.2 | 0.1 | - | - | 0.1 |
| Cuvier's beaked whale | 0.1 | 0.1 | 0.1 | - | - | 0.1 |
| Dense-beaked whale | 0.0 | 0.1 | - | - | - | 0.0 |
| UNID whale | 0.1 | 0.0 | 0.1 | - | 0.0 | 0.0 |
| Longman's beaked whale | 0.0 | 0.1 | 0.0 | - | - | 0.0 |
| Blue whale | 0.1 | 0.0 | 0.0 | 0.0 | - | 0.0 |
| UNID baleen whale | 0.0 | 0.0 | 0.0 | - | - | 0.0 |
| Humpback whale | - | - | - | 0.0 | - | 0.0 |
| Total | 100 | 100 | 100 | 100 | 100 | 100 |

Mikhalev, 1996), which migrates seasonally to feed on plankton associated with monsoonal upwelling off the coasts of Somalia and Arabia in May to October and disperses more widely (at least as far as the Maldives and Sri Lanka) during the leaner months of November to April (Anderson *et al.*, 1999).

Three blue whales seen in the Maldives in April were decidedly thin, i.e. with vertebrae clearly visible. Leatherwood *et al.* (1984) noted that blue whales seen off Trincomalee, east Sri Lanka, on 28 February 1983 were also thin. Whitehead (1989) presented a photo of another thin-looking blue whale off Trincomalee; although undated, the photo was probably taken in February or March 1984 (Jonathan Gordon, pers. comm., 17 July 2003). In contrast, Mikhalev (1996) described blue whales caught in the northwest Indian Ocean by Soviet whalers in the 1960s during October to December (mostly November) as being of 'good fatness'. This suggests that during October–December the whales are well fed, but by February–April they may be coming towards the end of a period with relatively little feeding. Around Sri Lanka, blue whales are regularly seen off the northeast coast near Trincomalee during December to April; they are rare later in the year, at least during October–November (Leatherwood *et al.*, 1984; Leatherwood and Reeves, 1989; Alling *et al.*, 1991). In 1983, blue whales had left the Trincomalee area by 24 April (Alling *et al.*, 1991). If at least some of the blue whales that spend the early part of each year off northeast Sri Lanka feed off Somalia and Arabia in May–October, then they might be expected to migrate via the Maldives in April. During this study, most sightings were made in April, while Ballance and Pitman (1998) recorded at least 27 blue whales in the Eight Degree Channel immediately north of the Maldives and in the area between the Maldives and Sri Lanka in April 1995.

Humpback whale (Megaptera novaeangliae)

Humpback whales in the Arabian Sea are believed to belong to a resident stock (Reeves *et al.*, 1991; Mikhalev, 1997; Papastavrou and Van Waerebeek, 1997; Minton *et al.*, 2002; Rosenbaum *et al.*, 2002). They appear to be rare in Maldivian waters, with only a single sighting by the author. This was of a cow-calf pair seen inside Seenu (= Addu) Atoll (0°37'S) in September 2001. The stock affinity of these whales is unknown, although they might have been from a southern population. Evidence for this includes: the timing of the sighting (during the austral winter); its location south of the equator; and the presence of a small calf approximately one third of the mother's length (at a time when Southern Hemisphere humpbacks are breeding).

The second sighting (Tables 4 and 6) was of another cow-calf pair, inside North Malé Atoll (4°14'N) in December probably of 1993 (Javier Martinez, Eurodivers Maldives, pers. comm., 1999). The timing of this sighting suggests that this pair might have been from the Arabian Sea stock.

These two sightings appear to be the first confirmed records of humpback whale from the Maldives although Brown (1957: fig. 4) recorded five sightings of humpback whales from merchant ship observers in the area immediately north of the Maldives and Slijper *et al.* (1964) also recorded several sightings of humpback whales in the general area of the Maldives. However, it is not clear how many, if any, of these records were made in what is now the Maldivian EEZ. Humpback whales were possibly not uncommon in the area of the Maldives prior to the mid-1960s. At that time (mostly in November 1966) Soviet whalers killed at least 242 humpback whales in the Arabian Sea (Mikhalev, 1997; 2000). Large numbers of blue,

Bryde's and sperm whales were taken at the same time, many of them in the vicinity of the Maldives (Mikhalev, 1996; 2000). Some older Maldivians in the northern atolls recall frequent sightings of whale blows in the 1950s and early 1960s, but few sightings thereafter. Humpback whales remain particularly rare in Maldivian waters.

Sperm whale (Physeter macrocephalus)

There were few sightings of sperm whales in this study (0.5% of all sightings). Most sightings (82%, $n=11$) of sperm whales were of 1–3 individuals. These animals were thought to be males in all cases where details were noted (5 out of 9). Two other sightings (of 15 and 30 animals) were of groups of presumed females and juveniles.

Although there were so few sightings, relatively little time was spent offshore (beyond a few miles from the atolls) where this species might be expected to be most abundant. In fact, the sperm whale is the species most commonly reported stranded in the Maldives (Anderson *et al.*, 1999). During the 19th century, Yankee whalers took sperm whales in the northern Maldives (Clark, 1887: plate 183, map of whaling grounds; Wray and Martin, 1983). Sperm whales were encountered and studied in the waters between the Maldives and Sri Lanka by the *Tulip* project (Whitehead *et al.*, 1983; Whitehead, 1989) and were also the most frequently sighted cetacean in a more recent survey of the western Indian Ocean (Ballance and Pitman, 1998).

Dwarf sperm whale (Kogia sima)

Dwarf sperm whales are not uncommon in the Maldives (Table 4), with only four species being sighted more frequently. Dwarf sperm whales were most easily seen in calm weathers and seas; one sixth of all sightings made in flat, calm conditions (Beaufort 0) were of this species (Table 3). Of 73 sightings positively identified as dwarf sperm whale for which wind conditions were recorded, 90% were made in Beaufort 0–1. No sightings were made in winds stronger than Beaufort 3. The frequency distribution of sightings in relation to wind strength was significantly different from expectations based on sightings for all cetaceans (chi-squared=87.3, $df=2$, $p<0.001$). This is a reflection of this animal's undemonstrative behaviour (Caldwell and Caldwell, 1989; Chantrapornsy et al., 1991; Willis and Baird, 1998). During calm conditions, slicks or current lines were frequently seen. Dwarf sperm whales were regularly observed lying at the surface in these lines. The reason(s) for this apparent association are unknown.

All dwarf sperm whales were observed over the outer atoll slopes. No sightings were identified as pygmy sperm whale (*Kogia breviceps*). These two species have broadly overlapping ranges and both have been reported from the tropical Indian Ocean, although the details of their distributions are not well known. Nevertheless, these observations are consistent with suggestions that dwarf sperm whales are more common over slopes and in warm seas (Ross, 1979; Caldwell and Caldwell, 1989; Chantrapornsy et al., 1991; Rice, 1998; Willis and Baird, 1998; Wang *et al.*, 2002), although this species has also been recorded from the open western Indian Ocean (Ballance and Pitman, 1998).

Rough-toothed dolphin (Steno bredanensis)

Rough-toothed dolphins are relatively rare in the Maldives, with just six sightings recorded (Table 4). Four of these sightings were off Haa Alifu Atoll in the far north. In two instances rough-toothed dolphins appeared to be associated with bottlenose dolphins, a taxon with which they have

previously been recorded interacting (Miyazaki and Perrin, 1994; Ritter, 2002). On one occasion, rough-toothed dolphins were seen diving near a fish aggregating device (FAD) and apparently feeding; on another occasion they were seen near some floating wood. The relatively frequent association of rough-toothed dolphins with floating objects has been noted by Pitman and Stinchcomb (2002). In one sighting, several rough-toothed dolphins were observed at the surface apparently playing with a pufferfish (*Arothron hispidus*) repeatedly pushing it with their snouts and flukes, and finally leaving it dead. Ritter (2002) recorded rough-toothed dolphins 'mistreating' a loggerhead turtle (*Caretta caretta*). The colour pattern observed was similar to that described by Miyazaki and Perrin (1994), but lips and bellies were often pink rather than white.

Moutou (1984) suggested that dolphins seen regularly between the islands of Malé and Vilingili in North Malé Atoll might have been rough-toothed dolphins. However, this seems most unlikely as rough-toothed dolphins were not recorded in this area during this survey; spinner dolphins occurred there regularly.

Risso's dolphin (Grampus griseus)

Risso's dolphins were the third most frequently recorded cetacean species, accounting for 11.4% of sightings and 7.0% of individuals seen (Tables 4 and 7). Risso's dolphins were nearly always seen outside the atolls, over the outer atoll slopes. Association with steep bottom topography appears typical for this species (Baumgartner, 1997; Kruse *et al.*, 1999). Several small groups were seen close to the outer atoll reefs, but only three groups were recorded inside an atoll.

Risso's dolphins were most frequently seen in small schools. Some 79% ($n=184$) of groups were of 30 or fewer animals. However, large groups did occur, with 9% of sightings of 60 or more animals. In these cases the group was usually spread in sub-groups over a large area, making determination of school boundaries somewhat subjective and estimation of school sizes particularly difficult.

Several types of behaviour were recorded for Risso's dolphins, but the most distinctive was holding the flukes high out of the water while maintaining a head-down position. This was noted in 15.6% of sightings for which some additional notes were made ($n=154$), and was not noted for any other dolphin species in the Maldives. The significance of this behaviour is not known. It was seen in schools of all sizes (range=4-200, mean=39.3, $n=23$, 1.96SE=22.6) and it occurred in schools demonstrating all other recorded types of behaviour.

Bottlenose dolphin (Tursiops sp.)

Most bottlenose dolphins seen in the Maldives appeared (on the basis of external morphology) to be *Tursiops truncatus*. However, the possibility that some *Tursiops* in Maldivian waters are Indo-Pacific bottlenose dolphins, *T. aduncus* (*cf.* Ross and Cockcroft, 1990; Rice, 1998; Hale *et al.*, 2000; Wang *et al.*, 2000), cannot be discounted. Bottlenose dolphins were the second most frequently sighted species (Table 4), but with a relatively low mean school size (Table 5) ranked only fifth in relative abundance (Table 7).

Bottlenose dolphin groups inside the atolls were smaller (mean=7.7, $n=98$, range=1-80, 1.96SE=1.8) than groups outside the atolls (mean=21.9, $n=97$, range=1-170, 1.96SE=4.9). This difference is statistically significant ($t=5.3$, $df=193$, $p<0.001$).

There were also differences in behaviour between bottlenose dolphins inside and outside the atolls. Inside the atolls they tended to avoid boats, did not readily bowride (only in 14% of sightings, $n=101$) and showed little aerial activity. In contrast, bottlenose dolphins outside the atolls bowrode more readily (in 37% of encounters, $n=104$) and were often active aerially. However, these differences might simply be a function of the larger school sizes outside the atolls. Although bottlenose dolphins inside the atolls did not associate with other species (apart from one group recorded with spinner dolphins), this may simply reflect the lack of other species inside the atolls. In comparison, 34% ($n=105$) of bottlenose dolphin groups outside the atolls were associated with another species.

In addition, there was some suggestion of colour differences between bottlenose dolphins in the two areas: those outside the atolls sometimes appearing darker with a more obvious diffuse pale patch behind the dorsal fin, while those inside the atolls appeared to show a more distinct white tip to the snout and at least one showed distinct ventral spotting. However, these differences were not always discernable. The underlying nature of the differences between bottlenose dolphins inside and outside atolls is not clear at this stage. In particular it is not known how these relate to the specific or sub-specific differences (e.g. *truncatus* versus *aduncus*) or ecomorphotypic differences (e.g. 'inshore' versus 'offshore') seen elsewhere.

Bottlenose dolphins were seen feeding, or apparently feeding, on 19 occasions, all except once inside the atolls. The single exception outside the atolls was adjacent to an anchored FAD. Inside the atolls, bottlenose dolphins were seen chasing bigeye scad (*Selar crumenophthalmus*, Carangidae), halfbeaks (Hemirhamphidae) and needlefish (Belonidae). Other possible prey items included swimming crabs (Portunidae), flying fish (Exocoetidae) and small jacks (Carangidae). A diving instructor (Carl Nichols, pers. comm.) filmed two large giant jacks (*Caranx ignobilis*, Carangidae) buzzing and then head-butting a single bottlenose dolphin in Baa Atoll. On seven occasions, bottlenose dolphins were seen feeding at night near anchored fish collection vessels. These ships regularly anchor at set locations within atolls to purchase fresh tuna from local fishermen. They have strong lights to facilitate transferring fish after sunset. These lights also attract numerous fish under the vessels. Local bottlenose dolphins appear to have learnt to hunt at these locations, as they can be seen regularly near particular collection vessels (e.g. in Haa Alifu and Laamu Atolls). On three occasions, bottlenose dolphins were noted feeding in atoll channels (where strong tidal currents promote fish concentrations).

Pantropical spotted dolphin (Stenella attenuata)

Pantropical spotted dolphins (referred to hereafter as spotted dolphins) were the second most abundant cetacean recorded (Tables 6, 7 and 8). They appeared to be particularly abundant in the north and south of the Maldives, in both areas making up over 30% of all cetaceans by number. In contrast, they contributed just 12% of cetaceans by number seen outside the atolls in the central Maldives. Spotted dolphins were not seen inside the atolls and they were uncommon in the inter-atoll sea between the central atolls. This distribution pattern is similar to that of large (>70cm fork length) yellowfin tuna, which are rare inside the atolls and in the inter-atoll sea and are commonest in the north and south of the country (Anderson and Shaan, 1998; Anderson *et al.*, 1998). Spotted dolphins were regularly associated with yellowfin tuna, seabirds and spinner dolphins (see

below). The modal size of spotted dolphin schools was 40-60 individuals (Table 5), although a secondary mode was also apparent, with school sizes of 150-300 individuals. Schools associated with spinner dolphins had on average 50% more spotted dolphins (mean=182 individuals, $n=35$, $1.96SE=41$) than those without (mean=122, $n=26$, $1.96SE=48$).

Spinner dolphin (Stenella longirostris)

The spinner dolphin was the most common species recorded during this study. It accounted for 35% of all sightings and 53% of estimated numbers (Tables 4 and 7), and was ubiquitous in the areas studied.

Spinner dolphins regularly enter the atolls through reef channels (Maldivian = *kanduoli*) in the morning and leave in the afternoon (Fig. 3). Sunrise varies from about 05:50 to 06:20h and is at about 06:00h during March-April when most sightings were recorded. Sunset varies from about 17:50 to 18:25h and is at about 18:15h in March-April. The peak time for entering was between 06:40 and 07:20h, when 39% of all entering spinner schools ($n=95$) were recorded. Excluding one school recorded leaving at 08:45h, there was no overlap in times of entering and departing the atolls. The peak time for leaving the atolls was between 16:15 and 17:50h, when 60% of all leaving schools ($n=117$) were recorded. Note that early entries (before 06:30h) were probably under-recorded, for the obvious reason. Some late departures may also have been missed in the rapidly falling darkness after sunset; there were two records of spinner dolphin schools inside an atoll heading towards a channel after dark, at 18:20 and 19:00h. Elsewhere around tropical oceanic islands spinner dolphins are known to move inshore to rest in shallow, sheltered areas by day and to move

offshore into deep water to feed on mesopelagic fishes at night (e.g. Norris *et al.*, 1994). The diurnal behaviour of Maldivian spinner dolphins thus appears typical for this species in this type of habitat.

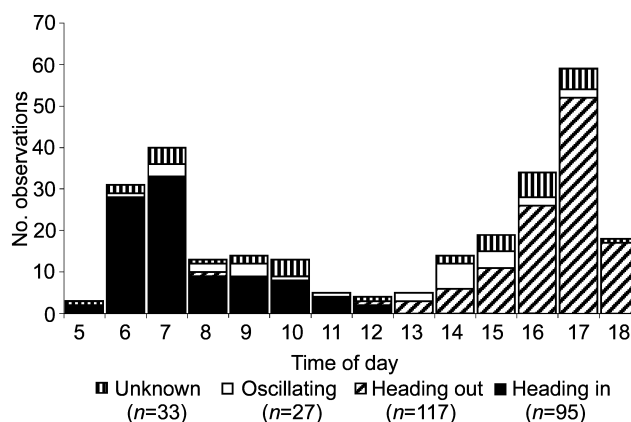


Fig. 3. Occurrence and direction of travel of spinner dolphin schools in atoll channels by time of day.

Reef channels break the atoll rim into a series of reefs, which vary considerably in length (from just a few metres to about 45km). Spinner dolphins use channels adjacent to long reefs more frequently than channels adjacent to short reefs. While this is partly because the longer reefs tend to face offshore (rather than into the inter-atoll sea), the main reason seems to be that spinner dolphins heading inshore in the morning towards a stretch of atoll rim with many short

Table 8
Relative abundance of cetaceans by major area within the Maldives (expressed as numbers of individuals seen per standard day).

| Species | Outside north | Outside centre | Outside south | Inside atolls | Inter-atoll sea | Total |
|--------------------------|---------------|----------------|---------------|---------------|-----------------|-------|
| Spinner dolphin | 99.0 | 81.9 | 105.4 | 224.3 | 175.0 | 145.3 |
| Spotted dolphin | 94.6 | 29.3 | 139.4 | - | 12.3 | 39.6 |
| Risso's dolphin | 40.9 | 33.5 | 0.7 | 0.3 | 14.9 | 19.1 |
| Fraser's dolphin | 20.7 | 20.8 | 29.5 | - | 14.9 | 13.6 |
| Bottlenose dolphin | 9.4 | 21.7 | 1.7 | 11.4 | 16.6 | 13.5 |
| Melon-headed whale | 1.9 | 8.9 | 125.0 | - | - | 12.8 |
| UNID dolphin | 14.4 | 7.5 | 14.8 | 7.3 | 19.1 | 10.3 |
| Striped dolphin | 16.4 | 15.5 | - | - | 2.7 | 7.9 |
| Short-finned pilot whale | 4.4 | 14.3 | 0.9 | - | 1.0 | 5.1 |
| False killer whale | 1.5 | 3.1 | 2.2 | 0.3 | 2.5 | 1.6 |
| UNID cetacean | 0.9 | 0.9 | 0.5 | 1.8 | 0.2 | 1.1 |
| Dwarf sperm whale | 1.1 | 0.9 | - | - | 0.1 | 0.5 |
| Rough-toothed dolphin | 1.9 | 0.2 | - | - | - | 0.5 |
| UNID beaked whale | 0.6 | 1.0 | 0.0 | - | 0.1 | 0.4 |
| Bryde's whale | 0.2 | 1.1 | 0.1 | - | 0.3 | 0.4 |
| Sperm whale | 1.1 | 0.1 | - | - | - | 0.3 |
| Pygmy killer whale | 0.8 | 0.3 | - | - | - | 0.3 |
| Killer whale | 0.4 | 0.4 | 0.2 | - | - | 0.2 |
| Cuvier's beaked whale | 0.4 | 0.3 | 0.3 | - | - | 0.2 |
| Dense-beaked whale | 0.1 | 0.3 | - | - | - | 0.1 |
| UNID whale | 0.2 | 0.1 | 0.5 | - | 0.0 | 0.1 |
| Longman's beaked whale | 0.0 | 0.3 | 0.1 | - | - | 0.1 |
| Blue whale | 0.2 | 0.0 | 0.1 | 0.0 | - | 0.1 |
| UNID baleen whale | 0.0 | 0.0 | 0.0 | - | - | 0.0 |
| Humpback whale | - | - | - | 0.0 | - | 0.0 |
| Total | 311.2 | 242.5 | 421.5 | 245.4 | 259.8 | 273.1 |

reef segments have many atoll channels to enter through, so any one channel receives relatively few entrants. In contrast, spinner dolphins approaching a long reef have to turn one way or the other and follow the reef along to the nearest entrance channel, which consequently receives dolphins from a wider area.

Spinner dolphin group size was highly variable (range=6-750). Mean school size was estimated at 58 ± 7 individuals, but there were major variations in mean size in different situations (Table 9). For example, there was a trend for mean school size to increase with distance offshore (inside atoll < channel < near offshore < further offshore). At a greater average distance offshore, in the wider western Indian Ocean, Ballance and Pitman (1998) estimated a still larger mean school size, of 170. These observations are consistent with a hypothesis of larger school size being an important anti-predation mechanism when offshore. However, it should be noted that spinner schools associated with spotted dolphins tended to be larger than those not associated with spotted dolphins (Table 9), since spotted dolphins are found offshore. The associations of spinner dolphins with spotted dolphins, tuna and seabirds are discussed below.

Most Maldivian spinner dolphins showed the tripartite colour pattern typical for the nominate sub-species (Perrin, 1990). Van Waerebeek *et al.* (1999) described a second 'colour morph' from Oman, which showed a dark stripe between the lateral medium grey field and the belly, which was pink rather than white or pale grey. A very similar colour pattern was noted on six occasions in the Maldives. However, the two main components of this 'colour morph' were also seen separately on a number of occasions. Several otherwise typically tripartite spinner dolphins were seen with pink bellies. Such a 'flushed' appearance has been noted for other dolphins in warm waters, and is related to thermoregulation (Perrin, 2002). On other occasions, animals with a dark lateral stripe were seen with pale, not pink, bellies; the significance of this striping is unknown.

Table 9

Spinner dolphin school size by major habitat and association.

| Habitat (subset) | Mean | 1.96 SE | Range | N |
|--|-------|---------|--------|-----|
| All | 58.2 | 6.6 | 6-750 | 466 |
| Inside atolls | 41.0 | 9.6 | 6-400 | 95 |
| Channels | 53.7 | 8.4 | 6-350 | 193 |
| Outside atolls (inter-atoll sea) | 60.6 | 26.4 | 6-400 | 31 |
| Outside atolls (offshore) | 74.8 | 15.2 | 6-750 | 147 |
| Outside atolls (≤ 1 nm offshore) | 56.8 | 13.0 | 6-250 | 76 |
| Outside atolls (> 1 nm offshore) | 94.0 | 27.6 | 6-750 | 71 |
| With spotted dolphins | 132.5 | 48.5 | 10-750 | 34 |
| Without spotted (offshore) | 57.4 | 11.7 | 6-400 | 113 |
| Without spotted (> 1 nm offshore) | 61.0 | 23.9 | 6-400 | 38 |
| Without spotted (all others) | 50.6 | 6.0 | 6-400 | 319 |

Striped dolphin (*Stenella coeruleoalba*)

Striped dolphins were moderately abundant, accounting for over 2% of sightings and individuals recorded, and ranking seventh in relative abundance (Tables 4 and 7). They only occurred outside the atolls and were not recorded in the south (Table 6). Striped dolphins were relatively less abundant around the Maldives than in the wider western tropical Indian Ocean, where they ranked second in abundance in a survey by Ballance and Pitman (1998). Even applying their sightability correction factor (Ballance and Pitman, 1998: table 2) would only raise striped dolphins to fifth ranking in the Maldives. This presumably reflects the striped dolphins' preference for an open oceanic habitat.

Striped dolphins were often extremely active, with much aerial activity. However, they alternated such frenetic outbursts with periods of apparent calm, with little aerial activity, during which it was very difficult to locate or follow schools. Striped dolphins often had pink (flushed) bellies; this was specifically recorded on six occasions, compared with only one record of white bellies.

Fraser's dolphin (*Lagenodelphis hosei*)

Fraser's dolphins are one of the commonest cetaceans in the Maldives, ranking fourth in abundance (Tables 7 and 8), even though it accounted for less than 1% of sightings on effort (Table 4). This is a reflection of this species' large mean school size (215 ± 71 individuals) (Table 5). Fraser's dolphin schools had a very characteristic appearance, which permitted identification even at a distance. The schools appeared tight and purposeful, with all individuals swimming in the same direction, often porpoising, and in calm conditions leaving a distinct wake. Some 53% of Fraser's dolphin schools were associated with other species, notably short-finned pilot whales and melon-headed whales (see below).

Melon-headed whale (*Peponocephala electra*)

Melon-headed whales had the largest estimated mean school size of any cetacean in the Maldives (412 ± 218 individuals) (Table 5). As a result, even though encounters were infrequent, just 0.6% of all sightings on effort (Table 4), this species ranked sixth in relative abundance (Tables 7 and 8). Melon-headed whales were much more common in the south of the Maldives than in the north and centre of the country (Fig. 4, Tables 7 and 8). This was the only species to show this pattern of regional distribution. Further afield, melon-headed whales appear to be rare in the Arabian Sea north of the Maldives (Leatherwood *et al.*, 1991; Ballance and Pitman, 1998; Van Waerebeek *et al.*, 1999).

Pygmy killer whale (*Feresa attenuata*)

Pygmy killer whales are one of the rarer cetaceans in the Maldives with just four on-effort sightings and two strandings records (Table 4). It is certainly uncommon, although these few sightings likely underestimate its true abundance, since it appeared to be relatively cryptic.

False killer whale (*Pseudorca crassidens*)

False killer whales accounted for just 0.5% of sightings and ranked ninth in relative abundance (Tables 4 and 7). There were several observations of false killer whales attacking or appearing to attack large prey, on one occasion a manta ray (*Manta birostris*) and on three occasions sailfish (*Istiophorus platypterus*). On another occasion, a pod of false killer whales was observed swimming out of an atoll channel as a school of spinner dolphins was entering. When the spinner dolphins were within about 400m of the false killer whales they abruptly changed course, increased speed and porpoised away from them. In contrast, two other schools of false killer whales were seen to swim through a group of Risso's dolphins and to pass by a group of pilot whales, without causing any apparent disturbance. False killer whales are believed to be predators of spinner dolphins, billfish and other large fish (Norris *et al.*, 1994; Odell and McClune, 1999; Strickland in Kiefner, 2002).

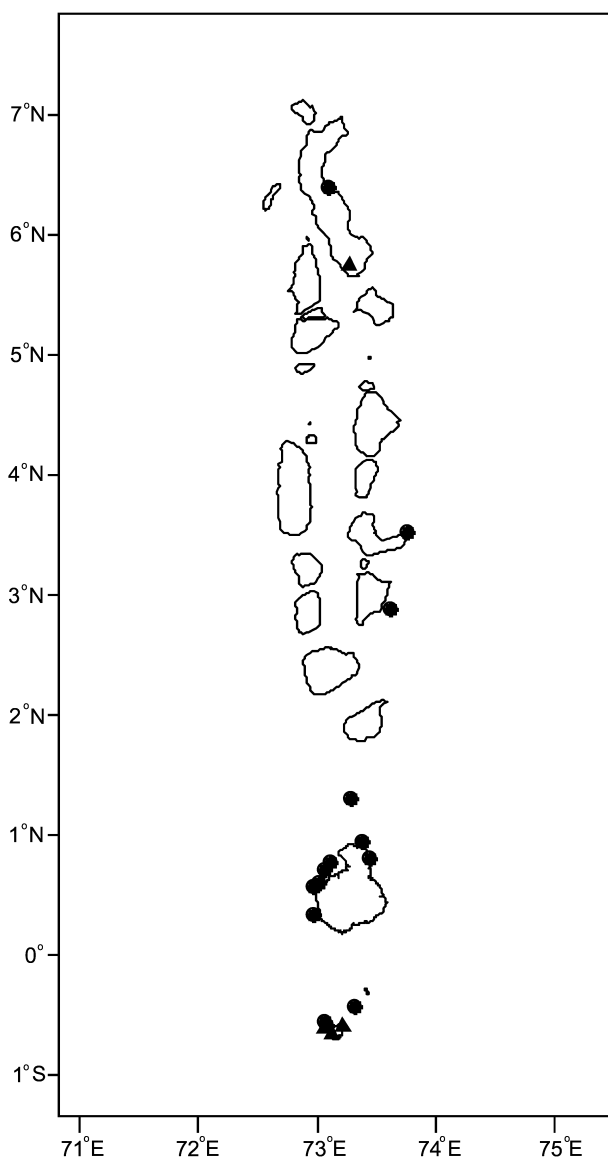


Fig. 4. Locations of sightings (circles, $n=14$) and strandings (triangles, $n=6$) of melon-headed whales. Note the concentration of observations in the south of the Maldives.

Killer whale (*Orcinus orca*)

Killer whales are not especially common in the Maldives (Tables 4, 6 and 7). School size ranged from 5–11 (Table 5). Eight of nine schools had 5–7 members; the ninth had 11 members. On one occasion the largest animal in a pod of about six was observed to have a large pink object in its mouth, probably the skinned carcass of a dolphin, shark or large tuna. On another occasion a pod of about six killer whales was observed apparently shadowing a school of spotted dolphins (which were associated with yellowfin tuna). There is also a report from a diving instructor of an underwater encounter with a pod of killer whales, which were seen toying with a manta ray, eventually leaving it dead (Tina Elgen, pers. comm.). Sivasubramaniam (1965) reviewed logbook records for damage to tuna longline catches by sharks and killer whales across the Indian Ocean, including the Maldives. He was not able to identify the 'killer whale' species implicated. Leatherwood *et al.* (1991) suggested that false killer whales were as likely as killer whales to have been involved.

Short-finned pilot whale (*Globicephala macrorhynchus*)

Pilot whales in the Maldives have been confirmed as short-finned pilot whales by: a pair of mandibles from a single stranding (Anderson *et al.*, 1999); close observation and photographs of live individuals (Ballance *et al.*, 2001; this study); and genetic analysis of biopsy samples collected by Ballance *et al.* (2001) (Susan Chivers, pers. comm.). They accounted for 4.2% of sightings and ranked eighth in relative abundance (Tables 4 and 6, Fig. 5). Pilot whales were usually observed over the outer atoll slope, most often just 1–2km offshore (see below). They were usually seen logging (apparently resting) or travelling. When travelling, most pilot whale groups (91% of groups for which direction of travel was recorded, $n=46$) tended to swim parallel to the atoll reef slope, presumably maintaining position over an appropriate feeding depth.

Pilot whales were rarely seen on the east side of the Maldives near Malé in the early part of the year. Indeed there were only two sightings off the east-central Maldives earlier than 29 March. Before that date the average sightings rate in the eastern central zone was 0.12 pilot whale sightings per day ($n=16$ days), whereas from that date the average sightings rate was 1.19 pilot whale sightings per day ($n=48$ days). This difference is statistically significant (chi-squared=14.7, $df=1$, $p<0.01$). The sudden arrival of pilot whales in that area at the end of March or in the first few days of April was noted each year from 1999 to 2002. It is not clear why pilot whales arrive in that area at that time; a possible explanation would be an increase in squid abundance, but there is no information on squid abundance in the Maldives. It is also not clear where the pilot whales come from, although they may come from the south. Among pilot whale groups encountered between 22 March and 21 April inclusive for which directions of movement were recorded ($n=21$), 76% were heading north, while only 24% were heading south. In contrast, for encounters from 30 April to 12 May inclusive, four pilot whale groups were heading south, while none were heading north.

One individual short-finned pilot whale, recognised by a distinctive cut on its dorsal fin, was seen three times over a 20-day period in 1998. On all three occasions it was recorded as being in a school of about ten individuals. It was first seen on 29 March off northeast Vaavu Atoll. On 13 April it was seen off northwest Lhaviyani Atoll (approximately 200km north). On 17 April it was seen near Kaashidhoo, an isolated island between Lhaviyani and North Malé Atolls (over 60km south of the second sighting). This pattern of individual movement is consistent with the pattern of school movement noted above, suggesting that pilot whales enter the area near Malé from the south in late March.

Beaked whales, *Ziphiidae*

Four species of beaked whale are known from the Maldives (Anderson *et al.*, 1999; Ballance *et al.*, 2001; Dalebout *et al.*, 2003): Cuvier's beaked whale (*Ziphius cavirostris*), Blainville's beaked whale (*Mesoplodon densirostris*), ginkgo-toothed beaked whale (*Mesoplodon ginkgodens*) and Longman's beaked whale (*Indopacetus pacificus*). The ginkgo-toothed beaked whale is so far known only on the basis of a tooth from a mature male in the National Museum, Malé (Anderson *et al.*, 1999).

All species together made up 3.9% of on-effort sightings. However, such were the difficulties of identifying beaked whales at sea with current knowledge, that only 28% of these sightings ($n=75$) were identified to species with

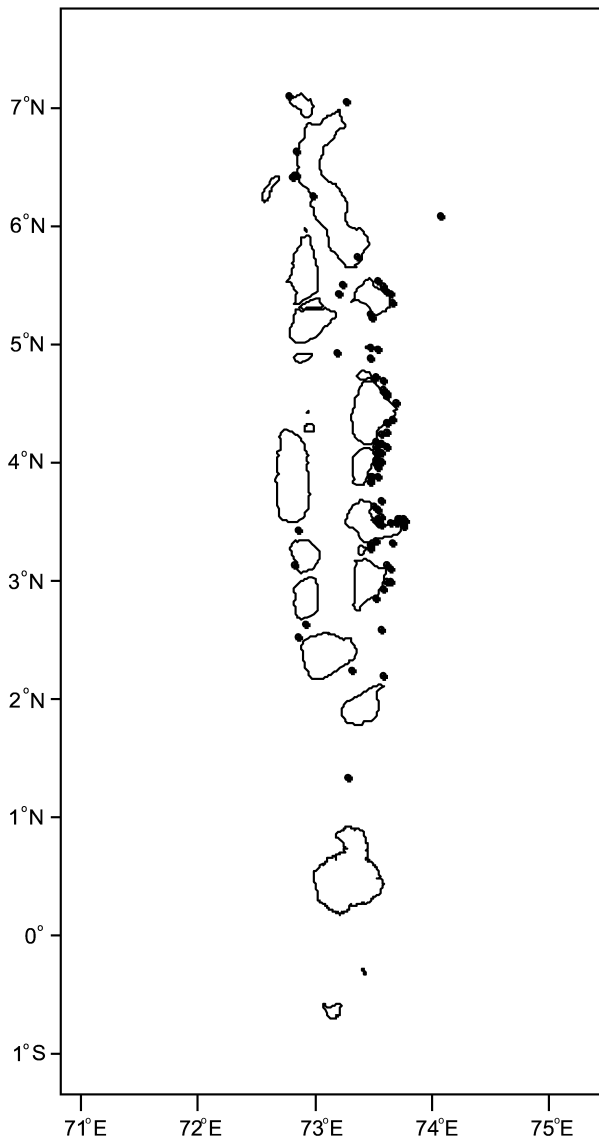


Fig. 5. Locations of sightings of short-finned pilot whales ($n=84$).

confidence. All beaked whales were seen in deep water outside the atolls, mostly over the outer atoll slopes. Only one was recorded from the rather flat-bottomed inter-atoll sea, and that was from the edge near the slope. The highest density of beaked whale sightings was off southeast Vaavu Atoll (Fig. 6), where the atoll reef juts out to form the most easterly point of the Maldives and where bottom topography is believed to be particularly steep.

Cuvier's beaked whale was the most frequently identified beaked whale (Table 4). Fourteen dives were timed for seven individuals. Mean duration of 13 dives was 26min (range=23-29min, SD=2.4min). One other dive, by a presumed mother and calf, was distinctly shorter at just 16min.

Blainville's beaked whale was difficult to identify positively at sea. The three definite sightings recorded here were all of (separate) groups containing a mature male with black barnacle tufts on their teeth (group size range=2-6 individuals). Nine dives by two individuals averaged 16min (range=13-22min, SD=3.8min).

Longman's beaked whale, long considered the least-known of all whales, was recorded from the Maldives by Dalebout *et al.* (2003) on the basis of a single stranding in 2000. There was one positive sighting of about 20

individuals, and three other sightings all of 2 individuals. Further details of these encounters will be published separately.

Other species

A total of 20 species of cetacean were positively identified at sea during the period 1990-2002. The only other species positively recorded from the Maldives so far is the ginkgo-toothed beaked whale, *Mesoplodon ginkgodens* (cf. Anderson *et al.*, 1999). There are as yet no confirmed live sightings of this species in the Maldives. The known cetacean fauna of the Maldives therefore currently stands at 21 species. A record of common dolphin (*Delphinus delphis*) from the Maldives by Deraniyagala (1956) is best regarded as unconfirmed (Anderson *et al.*, 1999; Jefferson and Van Waerbeek, 2002). A sighting tentatively identified as a fin whale (*Balaenoptera physalus*) by Anderson (1990) is now considered to have probably been a Bryde's whale. A photo of a minke whale (*Balaenoptera acutorostrata*) published by Kiefner (2002, p.30) was purportedly taken in the Maldives. According to the photographer (Helmut Debelius, pers. comm.) the photo was probably taken in the Maldives in the late 1970s, but the date and location cannot now be confirmed.

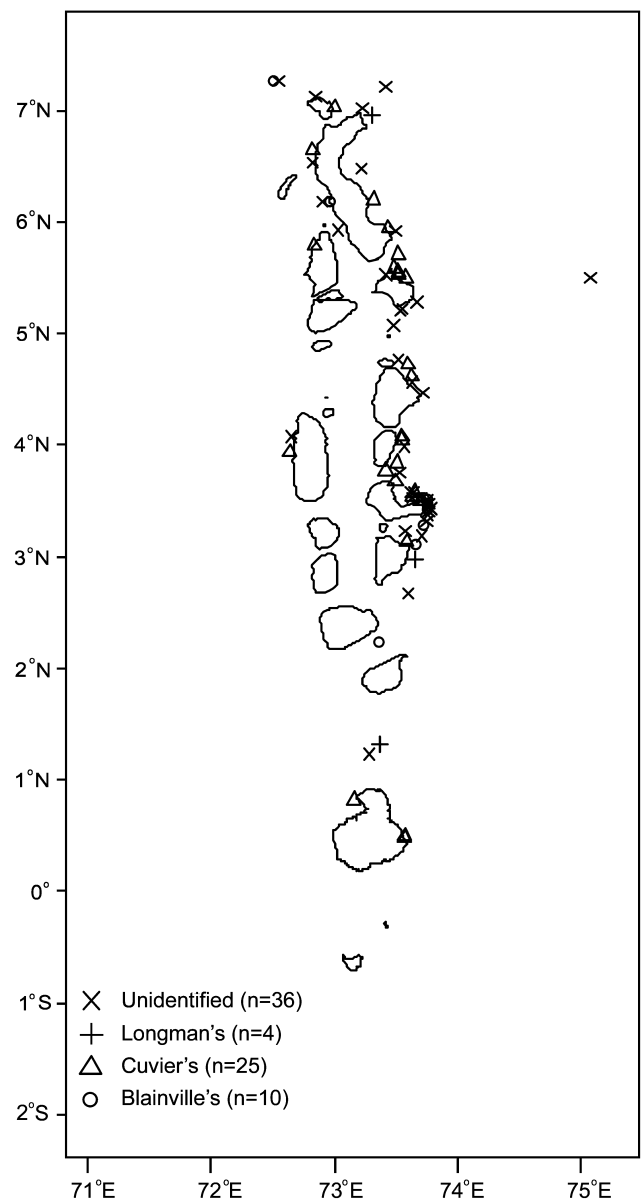


Fig. 6. Locations of sightings of beaked whales ($n=75$).

Inter-specific associations

A total of 83 sightings involved more than one species (Tables 10 and 11). Three or more species were associated in at least nine instances:

- 1 × spinner, spotted and striped dolphins;
- 1 × bottlenose dolphin, false killer whale and unidentified dolphin;
- 1 × bottlenose dolphin, pilot whale and Longman's beaked whale;
- 2 × bottlenose dolphin, pilot whale and Risso's dolphin;
- 3 × bottlenose dolphin, pilot whale and Fraser's dolphin;
- 1 × bottlenose dolphin, pilot whale, Fraser's dolphin and Risso's dolphin.

Spinner and spotted dolphins regularly associated only with each other, with 37 sightings of mixed schools. In 55% of sightings of spotted dolphins ($n=67$) they were associated with spinner dolphins. In contrast, in only 15% of sightings outside the atolls ($n=244$) were spinner dolphins associated with spotted dolphins. However, for spinner dolphins more than 1 n.mile (1.85km, the median distance of sightings) offshore, 46% ($n=71$) were associated with spotted dolphins. More than 2 n.miles (3.7km) offshore, 58% ($n=55$) of spinner dolphin sightings were associated with spotted dolphins.

Bottlenose dolphins associated with at least seven other cetacean species (six excluding a single observation with spinner dolphins), the largest number of associates for any cetacean in this survey. Bottlenose dolphins associated most frequently with pilot whales. Bottlenose dolphins were the only species associated with false killer whales, with which they were seen in four out of 10 on-effort false killer whale encounters.

Fraser's dolphins were associated with other cetacean species in 53% of sightings (Table 10). The species involved were melon-headed whales, short-finned pilot whales, Risso's dolphins and bottlenose dolphins (Table 11). While the association with melon-headed whales is well known, associations with other species appear to have been less frequently reported (Jefferson and Leatherwood, 1994; Perrin *et al.*, 1994; Perryman *et al.*, 1994; Dolar, 2002). In the south of the Maldives (where pilot whales appeared to be rare but melon-headed whales were common) 50% of Fraser's dolphin schools ($n=4$) were associated with melon-headed whales, whereas in the north and centre 42% ($n=12$) were associated with pilot whales. In addition to the five mixed groups recorded here, pilot whales were noted in the vicinity of Fraser's dolphin schools on another three occasions although they were not recorded as being associated at the time. Fraser's dolphins were often seen at some distance from associated pilot whales; the Fraser's dolphins usually moved faster than the pilot whales, but maintained contact by frequent changes of course, occasionally appearing to loiter while the pilot whales caught up. The significance of these observations is unclear but they might suggest that this association is more advantageous to the Fraser's dolphins than to the pilot whales. What that advantage might be and whether Fraser's dolphins reap a similar advantage from their association with melon-headed whales are matters for speculation at present.

Pilot whales and Risso's dolphins were the two most frequently sighted species associated with the outer atoll slopes (see below). Despite their relative abundance, and sharing a habitat of limited area, these two species were

recorded as being associated with each other on only four occasions (Table 10). In one case, the two species were travelling in the same direction but not in close proximity. In the other three cases, the Risso's dolphins displayed what could be interpreted as aggressive behaviour towards the pilot whales, including tail slapping and breaching. Shane (1995) suggested that Risso's dolphins and short-finned pilot whales compete for squid. She noted four instances of apparent aggression by Risso's dolphins towards pilot whales, and suggested that the former displaced the latter off Santa Catalina Island, California, when squid resources were limited.

Table 10
Occurrence of cetaceans in mixed schools.

| Species | No. mixed schools | Total sightings | % in mixed schools |
|--------------------------|-------------------|-----------------|--------------------|
| Spinner dolphin* | 38 | 244 | 15.6 |
| Spotted dolphin | 38 | 67 | 56.7 |
| Striped dolphin | 1 | 46 | 2.2 |
| Bottlenose dolphin* | 38 | 115 | 33.0 |
| Risso's dolphin | 9 | 219 | 4.1 |
| Fraser's dolphin | 9 | 17 | 52.9 |
| Rough-toothed dolphin | 1 | 6 | 16.7 |
| Short-finned pilot whale | 32 | 81 | 39.5 |
| False killer whale | 4 | 10 | 40.0 |
| Melon-headed whale | 2 | 12 | 16.7 |
| Longman's beaked | 1 | 3 | 33.3 |
| Sperm whale | 1 | 10 | 10.0 |
| Unidentified dolphin | 2 | | |
| Total | 176 | | |

*Note: for spinner and bottlenose dolphins, only sightings outside the atolls are included.

Associations with seabirds, tuna and other fishes

A summary of cetacean associations with seabirds and tuna is presented in Table 12. The spotted dolphin was the species most frequently seen with birds and tunas. Among 67 sightings of spotted dolphins, 64% were recorded as being associated with tunas. In all cases where it was possible to identify the tunas (54% of all sightings), they were identified as yellowfin tuna. Some 58% of spotted dolphin schools were associated with seabirds, of at least 15 different species, the most frequently recorded being Lesser Noddy (*Anous tenuirostris*) and Sooty Tern (*Sterna fuscata*). Overall, 76% of spotted dolphin schools were noted as associated with tuna and/or birds. Since it may not always be possible to detect the presence of tuna, and birds may not be present if the tuna are not feeding, it seems likely that 76% is an underestimate of the percentage of spotted dolphin schools associated with tuna. Spotted dolphins associated with yellowfin tuna were normally seen following the tuna, not vice versa. This behaviour is also reported by Maldivian pole and line tuna fishermen (Anderson and Shaan, 1998).

Spinner dolphins outside the atolls were associated with seabirds in 14% of sightings. At least 14 species of bird are involved, including Brown Noddy (*Anous stolidus*), Lesser Noddy, Sooty Tern, Bridled Tern (*Sterna anaethetus*) and Lesser Frigatebird (*Fregata ariel*). Spinner dolphins were recorded with tunas in 14% of sightings outside the atolls. In 26 cases the tunas were identified to species: 24 (9.8% of sightings) yellowfin tuna, 1 (0.4%) skipjack (*Katsuwonus pelamis*) and 1 (0.4%) kawakawa or little tuna (*Euthynnus affinis*). Spinner dolphins are known to associate regularly with yellowfin tuna, but not as frequently as spotted dolphins (Norris *et al.*, 1994). No bird or tuna associations with spinner dolphins were noted inside the atolls.

Table 11
Frequencies of inter-species associations.

| | Spinner dolphin | Spotted dolphin | Bottlenose dolphin | Risso's dolphin | Fraser's dolphin | Pilot whale | False killer | Total |
|--------------------|-----------------|-----------------|--------------------|-----------------|------------------|-------------|--------------|-------|
| Spotted dolphin | 37 | | | | | | | 37 |
| Striped dolphin | 1 | 1 | | | | | | 2 |
| Bottlenose dolphin | 1 | - | | | | | | 1 |
| Risso's dolphin | - | 1 | 5 | | | | | 6 |
| Fraser's dolphin | - | - | 5 | 2 | | | | 7 |
| Rough-toothed | - | - | 1 | - | - | | | 1 |
| Pilot whale | - | - | 29 | 4 | 5 | | | 38 |
| False killer | - | - | 4 | - | - | - | | 4 |
| Melon-headed | - | - | - | - | 2 | - | - | 2 |
| Longman's | - | - | 1 | - | - | 1 | - | 2 |
| Sperm whale | - | - | - | - | - | 1 | - | 1 |
| UNID | - | - | 1 | 1 | - | - | 1 | 3 |
| Total | 39 | 2 | 46 | 7 | 7 | 2 | 1 | (208) |

Note: totals in Tables 10 and 11 do not tally because some mixed schools contained more than two species.

Experienced Maldivian tuna fishermen report that dolphins (presumably spinner dolphins) with associated tunas leave the tunas if they enter an atoll.

Bryde's whales were associated with tunas in at least 15% of sightings. In every case the fish were identified as yellowfin tuna, although in two instances skipjack tuna were also present. Each time Bryde's whales were seen feeding ($n=6$), yellowfin tuna were seen feeding in the same area and apparently on the same prey. Seabirds were present in 9% of Bryde's whale sightings; the birds included Lesser Noddies, Brown Noddies, Sooty Terns, Bridled Terns and Great Crested Terns (*Sterna bergii*).

Seabirds were seen with killer whales and false killer whales on one occasion each. In both cases the birds (Swinhoe's Storm-petrels, *Oceanodroma monorhis*, in the case of the false killer whales, Flesh-footed Shearwaters, *Puffinus carneipes*, with the killer whales) were scavenging scraps (Anderson and Baldock, 2001).

On three occasions baleen whales were seen in close proximity to other plankton feeders. Once whale sharks (*Rhincodon typus*) were seen feeding on krill in the same area as Bryde's whales. Manta rays (*Mobula* sp.) were observed on two occasions, in close proximity to a blue whale and five feeding Bryde's whales.

Remoras (Echeneidae) were recorded on four different species. Unidentified remoras were seen on spinner, striped and bottlenose dolphins. What appeared to be whale-suckers (*Remora australis*) were regularly seen and photographed on blue whales. One shark-sucker (*Echeneis naucrates*) was clearly seen and photographed on a bowriding spinner dolphin. This remora species has recently been confirmed to associate with cetaceans (Fertl and Landry, 1999).

Regional distribution

The cetacean fauna inside the atolls was very different from that outside (Tables 6, 7 and 8). Only two species, spinner dolphin and bottlenose dolphin, occurred regularly inside the atolls. In addition, both records of humpback whale were from inside the atolls. In contrast, every other species occurred most frequently, or exclusively, outside the atolls.

Outside the atolls, the south of the Maldives showed several distinct differences in its cetacean fauna compared to the north and centre. Most obviously, melon-headed whales were common in the south, but rare in the north and centre. Spotted dolphins also appeared to be especially common in the south of the Maldives. In contrast, several species

Table 12
Occurrence of cetaceans with birds and tuna. Percent values are of total sightings for each species.

| Species | Total sightings | With birds | With tunas | With birds or tunas |
|-----------------------|-----------------|------------|------------|---------------------|
| Pantropical spotted | 67 | 39 (58.2%) | 43 (64.2%) | 51 (76.1%) |
| Spinner dolphin* | 244 | 33 (13.5%) | 34 (13.9%) | 43 (17.6%) |
| Bryde's whale | 53 | 5 (9.4%) | 8 (15.1%) | 8 (15.1%) |
| Striped dolphin | 46 | 7 (15.2%) | 3 (6.5%) | 7 (15.2%) |
| Dwarf sperm whale | 80 | 3 (3.8%) | 1 (1.3%) | 3 (3.8%) |
| Bottlenose dolphin* | 115 | 1 (0.9%) | 1 (0.9%) | 2 (1.7%) |
| Rough-toothed dolphin | 6 | 0 | 1 (16.7%) | 1 (16.7%) |
| Killer whale | 9 | 1 (11.1%) | 0 | 1 (11.1%) |
| False killer whale | 10 | 1 (10.0%) | 0 | 1 (10.0%) |
| Melon-headed whale | 12 | 1 (8.3%) | 0 | 1 (8.3%) |
| Risso's dolphin | 219 | 1 (0.5%) | 0 | 1 (0.5%) |
| Unidentified | | 5 | 5 | 8 |
| Total | | 97 | 96 | 127 |

*Note: for spinner and bottlenose dolphins, only sightings outside the atolls are included.

appeared to be less common in the south than in the north and centre, including Risso's dolphin, bottlenose dolphin, short-finned pilot whale and striped dolphin. The southern Maldives is less affected by the seasonal monsoon currents than the north and centre of the country, but is instead much influenced by equatorial currents and their associated upwellings (Molinari *et al.*, 1990; Anderson *et al.*, 1998). Within the Maldives, several pelagic fish species show distinct differences in abundance between the south and north-central Maldives (Anderson, 1992; Anderson and Saleem, 1994; Anderson *et al.*, 1998). Within the wider Indian Ocean, some other marine organisms are confined mainly to equatorial waters within about 5° of the equator. These include at least one seabird, Matsudaira's Storm-petrel *Oceanodroma matsudairae* (Bailey *et al.*, 1968), and a planktonic copepod (Meenakshikunjamma, 1974). In the Eastern Tropical Pacific, melon-headed whales are known to associate with equatorial upwellings (Au and Perryman, 1985).

Differences between the north and centre of the Maldives (outside the atolls) are much less obvious than those with the south (Tables 7 and 8). Spotted dolphins are less abundant in the centre than in the north (and south); as noted above, this is probably related to the abundance of large yellowfin tuna in these regions (Anderson and Shaan, 1998; Anderson *et al.*, 1998).

The cetacean fauna of the inter-atoll sea between the double chain of central atolls appears to be intermediate between that inside the atolls and that of the oceanic waters outside the atolls. Many species show intermediate levels of relative abundance (Tables 7 and 8). The inter-atoll sea shows intermediate oceanographic characteristics: much of it is relatively flat-bottomed and sheltered (like the inside of the atolls) while parts of it adjoin the steep slope of the Maldives ridge and are fully exposed to oceanic conditions.

Association with outer atoll slopes

Several species appeared to be closely associated with the steep outer atoll reef slopes. These included dwarf sperm whale, Risso's dolphin, short-finned pilot whale, Cuvier's beaked whale and Blainville's beaked whale (see individual species accounts above). All of these species feed heavily on squid, and their association with outer atoll slopes likely reflects a concentration of squid in this habitat. Despite the apparent importance of this habitat for some cetaceans, the outer atoll slopes have not been considered in detail in this study, because lack of detailed bathymetric information from outside the atolls hinders analysis. For example, while it is clear that these species are seen most frequently over the general area of the slopes, it has not been possible to relate sightings to precise bottom depths or gradients. Nevertheless, the association of some species with the outer atoll slopes did influence the distribution of sighting effort. During most whalewatching cruises (sea trip category 3 as defined previously), one aim was to maximise cetacean sightings. This was best achieved by cruising over the atoll slopes.

CONCLUSIONS

The Maldives has a high diversity of cetaceans, with all the expected pantropical species being represented. Numbers of small delphinids were particularly high, and beaked whales also appeared to be relatively abundant. The Maldives undoubtedly offers considerable scope for both whalewatching tourism and cetacean research. Studies within the northwest Indian Ocean Sanctuary should illuminate the recovery, or otherwise, of stocks of large whale following exploitation in the 1960s. The northern Indian Ocean, including the Maldives, is oceanographically unique and cetacean studies here might therefore be expected to produce fresh insights into cetacean behaviour and ecology. Variations in cetacean distribution and abundance between the eastern and western sides of the atoll chain, and within regions between the northeast and southwest monsoons, were not dealt with here but warrant further study. In addition, there is scope for more detailed studies of any of the commoner species, of ecological interactions between slope-associated teuthivores, of baleen whale migrations and of the two forms of bottlenose dolphins.

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REFERENCES

- Alling, A. 1986. Records of odontocetes in the northern Indian Ocean (1981-1982) and off the coast of Sri Lanka (1982-1984). *J. Bombay Nat. Hist. Soc.* 83(2):376-94.
- Alling, A., Gilligan, P.R., Gordon, J.C.D. and Papastravrou, V. 1984. Report to WWF/IUCN Indian Ocean Sperm Whale Project, Interim Rep., Jan-May 1984. Unpublished. [Available from the author].
- Alling, A., Dorsey, E.M. and Gordon, J.C.D. 1991. Blue whales *Balaenoptera musculus* off the northeast coast of Sri Lanka: Distribution, feeding and individual identification. *UNEP Mar. Mamm. Tech. Rep.* 3:247-58.
- Anderson, R.C. 1990. Report of a pygmy killer whale from Maldivian waters with notes on other whales. *Rasain* 10:148-56.
- Anderson, R.C. 1992. North-south variation in the distribution of fishes in the Maldives. *Rasain* 12:210-26.
- Anderson, R.C. 1993. Oceanographic variations and Maldivian tuna catches. *Rasain* 13:215-24.
- Anderson, R.C. 1996. First records of Fraser's dolphin (*Lagenodelphis hosei*) from the Maldives. *J. South Asian Nat. Hist.* 2:75-80.
- Anderson, R.C. and Baldock, M. 2001. New records of birds from the Maldives, with notes on other species. *Forktail* 17:67-73.
- Anderson, R.C. and Saleem, M.R. 1994. Seasonal and regional variation in the utilization of livebait in the Maldives. *Rasain* 14:162-82.
- Anderson, R.C. and Saleem, M.R. 1995. Inter-annual variations in the utilization of livebait in the Maldives. *Rasain* 15:193-216.
- Anderson, R.C. and Shaan, A. 1998. Association of yellowfin tuna and dolphins in Maldivian waters. *Rasain* 18:149-58.
- Anderson, R.C., Waheed, Z. and Adam, M.S. 1998. The tuna fishery resources of the Maldives. *Maldives Marine Research Bulletin* 3:1-180.
- Anderson, R.C., Shaan, A. and Waheed, Z. 1999. Records of cetacean 'strandings' from the Maldives. *J. South Asian Nat. Hist.* 4(2):187-202.
- Arvy, L. 1972. Jean-Jacques Dussumier, master mariner and cetologist (1792-1883). *Invest. Cetacea* 4:263-9.
- Au, D.W.K. and Perryman, W.L. 1985. Dolphin habitats in the eastern tropical Pacific. *Fish. Bull.* 83(4):623-43.
- Bailey, R.S., Pocklington, R. and Willis, P.R. 1968. Storm petrels *Oceanodroma* spp. in the Indian Ocean. *Ibis* 110:27-34.
- Ballance, L.T. and Pitman, R.L. 1998. Cetaceans of the Western Tropical Indian Ocean: distribution, relative abundance, and comparisons with cetacean communities of two other tropical ecosystems. *Mar. Mammal Sci.* 14(3):429-59.
- Ballance, L.T., Pitman, R.L., Reilly, S.B. and Force, M.P. 1996. Report of a cetacean, seabird, marine turtle and flying fish survey of the western tropical Indian Ocean aboard the research vessel *Malcolm Baldrige*, March 21-July 26, 1995. *NOAA Technical Memorandum NMFS NOAA-TM-NMFS-SWFSC-224*:132.
- Ballance, L.T., Anderson, R.C., Pitman, R.L., Stafford, K., Shaan, A., Waheed, Z. and Brownell, R.L. 2001. Cetacean sightings around the Republic of the Maldives, April 2001. *J. Cetacean Res. Manage.* 3(2):213-8.

- Baumgartner, M.F. 1997. The distribution of Risso's dolphin (*Grampus griseus*) with respect to the physiography of the northern Gulf of Mexico. *Mar. Mammal Sci.* 13(4):614-38.
- Brown, S.G. 1957. Whales observed in the Indian Ocean. Notes on their distribution. *Mar. Obs.* 27(177):157-65.
- Caldwell, D.K. and Caldwell, M.C. 1989. Pygmy sperm whale, *Kogia breviceps* (de Blainville, 1838); dwarf sperm whale, *Kogia simus* (Owen, 1866). pp. 235-60. In: S.H. Ridgway and R. Harrison (eds.) *Handbook of Marine Mammals*. Vol. 4. *River Dolphins and the Larger Toothed Whales*. Academic Press, London and San Diego. 442pp.
- Chantrapornsyil, S., Kinze, C.C., Leatherwood, S. and Prematunga, W.P. 1991. Notes on the genus *Kogia* in the northern Indian Ocean. *UNEP Mar. Mamm. Tech. Rep.* 3:79-88.
- Clark, A.H. 1887. The whale fishery. Part XV. In: G.B. Goode (ed.) *The Fisheries and Fishery Industries of the United States. Section V. History and methods of the fisheries. Vol. II*. Prepared through the co-operation of the Commissioner of the Fisheries and the Superintendent of the Tenth Census. Government Printing Office, Washington DC. 2 vols, with an atlas of 225 plates.
- Cousteau, J.-Y. and Diolé, P. 1971. *Life and Death in a Coral Sea*. Doubleday and Co, New York. 302pp. [English translation from the French].
- Cousteau, J.-Y. and Diolé, P. 1972. *The Whale*. Doubleday and Co, New York. 304pp. [English translation from the French].
- Dalebout, M.L., Ross, G.J.B., Scott Baker, C., Anderson, R.C., Best, P.B., Cockcroft, V.G., Hinsz, H.L., Peddemors, V. and Pitman, R.L. 2003. Appearance, distribution and genetic distinctiveness of Longman's beaked whale, *Indopacetus pacificus*. *Mar. Mammal Sci.* 19(3):421-61.
- Deraniyagala, P.E.P. 1956. Zoological collecting in the Maldives. *Spolia Zeylan.* 28:79-85.
- Dolar, L. 2002. Fraser's dolphin, *Lagenodelphis hosei*. pp. 485-7. In: W.F. Perrin, B. Würsig and J.G.M. Thewissen (eds.) *Encyclopedia of Marine Mammals*. Academic Press, San Diego. 1,414pp.
- Fertl, D. and Landry, A.M. 1999. Sharksucker (*Echeneis naucrates*) on a bottlenose dolphin (*Tursiops truncatus*) and a review of other cetacean-remora associations. *Mar. Mammal Sci.* 15(3):859-63. In Notes.
- Gilpatrick, J.W., Perrin, W.F., Leatherwood, S. and Shiroma, L. 1987. Summary of distribution records of the spinner dolphin, *Stenella longirostris*, and the pantropical spotted dolphin, *S. attenuata*, from the western Pacific Ocean, Indian Ocean and Red Sea. *NOAA Technical Memorandum NMFS NOAA-TM-NMFS-SWFC-89:42pp*.
- Gordon, J.C.D. 1991. The World Wildlife Fund's Indian Ocean sperm whale project: an example of cetacean research within the Indian Ocean Sanctuary. *UNEP Mar. Mamm. Tech. Rep.* 3:219-39.
- Hale, P.T., Barreto, A.S. and Ross, G.J.B. 2000. Comparative morphology and distribution of the *aduncus* and *truncatus* forms of bottlenose dolphin *Tursiops* in the Indian and Western Pacific Oceans. *Aquat. Mamm.* 26(2):101-10.
- Jefferson, T.A. and Leatherwood, S. 1994. *Lagenodelphis hosei*. *Mamm. Species* 470:1-5.
- Jefferson, T.A. and Van Waerebeek, K. 2002. The taxonomic status of the nominal dolphin species *Delphinus tropicalis* Van Bree, 1971. *Mar. Mammal Sci.* 18(4):787-818.
- Kasuya, T. and Wada, S. 1991. Distribution of large cetaceans in the Indian Ocean: data from Japanese sightings records, November-March. *UNEP Mar. Mamm. Tech. Rep.* 3:139-70.
- Kiefner, R. 2002. *Whales and Dolphins: Cetacean World Guide*. IKAN Unterwasserarchiv, Frankfurt. 305pp.
- Kruse, S., Caldwell, D.K. and Caldwell, M.C. 1999. Risso's dolphin *Grampus griseus* (G. Cuvier, 1812). pp. 183-212. In: S. Ridgway and R. Harrison (eds.) *Handbook of Marine Mammals*. Vol. 6. *The Second Book of Dolphins and the Porpoises*. Academic Press, London and San Diego. i-xix+486pp.
- Leatherwood, S. (ed.). 1986. *Whales, Dolphins and Porpoises of the Indian Ocean Cetacean Sanctuary: A Summary of Available Information*. UNEP, Nairobi. 264pp.
- Leatherwood, S. and Reeves, R.R. 1989. Marine mammal research and conservation in Sri Lanka 1985-1986. *UNEP Mar. Mamm. Tech. Rep.* 1:[vi],1-138.
- Leatherwood, S., Peters, C.B., Santerre, R., Santerre, M. and Clarke, J.T. 1984. Observations of cetaceans in the northern Indian Ocean Sanctuary, November 1980-May 1983. *Rep. int. Whal. Commn* 34:509-20.
- Leatherwood, S., McDonald, D., Prematunga, W.P., Girton, P., Ilangakoon, A. and McBrearty, D. 1991. Records of the 'Blackfish' (killer, false killer, pilot, pygmy killer and melon-headed whales) in the Indian Ocean, 1772-1986. *UNEP Mar. Mamm. Tech. Rep.* 3:33-65.
- Meenakshikunjamma, P.P. 1974. The distribution of species of subgenus *Urocorycaeus* (genus *Corycaeus*, Corycaeidae, Copepoda) in the Indian Ocean. *J. Mar. Biol. Assoc. India* 16(3):769-74.
- Mikhalev, Y.A. 1996. Pygmy blue whales of the northern-western Indian Ocean. Paper SC/48/SH30 presented to IWC Scientific Committee, June 1996, Aberdeen, UK (unpublished). 30pp. [Paper available from the Office of this Journal].
- Mikhalev, Y.A. 1997. Humpback whales, *Megaptera novaeangliae* in the Arabian Sea. *Mar. Ecol. Prog. Ser.* 149:13-21.
- Mikhalev, Y.A. 2000. Whaling in the Arabian Sea by the whaling fleets *Slava* and *Sovetskaya Ukraina*. pp. 141-81. In: A.V. Yablokov, V.A. Zemsky and D.D. Tormosov (eds.) *Soviet Whaling Data (1949-1979)*. Centre for Russian Environmental Policy, Moscow. 408pp.
- Minton, G., Collins, T., Findlay, K., Baldwin, R., Rosenbaum, H., Kennedy, F. and Cockcroft, V. 2002. Preliminary investigations of humpback whale (*Megaptera novaeangliae*) distribution and habitat use off the coast of Oman. Paper SC/54/H3 presented to the IWC Scientific Committee, April 2002, Shimonoseki, Japan (unpublished). 19pp. [Paper available from the Office of this Journal].
- Miyazaki, N. and Perrin, W.F. 1994. Rough-toothed dolphin – *Steno bredanensis* (Lesson, 1828). pp. 1-21. In: S.H. Ridgway and R. Harrison (eds.) *Handbook of Marine Mammals*. Vol. 5. *The First Book of Dolphins*. Academic Press, London and San Diego. 416pp.
- Mörzer-Bruyns, W.F.J. 1971. *Field Guide of Whales and Dolphins*. C.A. Meese, Amsterdam. 258pp.
- Molinari, R.L., Olsen, D. and Reverdin, G. 1990. Surface current distribution in the tropical Indian Ocean derived from compilations of surface buoy trajectories. *J. Geophys. Res.* 95(C):7217-38.
- Moutou, F. 1984. Les Iles Maldives. *Info-Nature Ile de la Réunion* 21:53-73.
- Norris, K.S., Würsig, B., Wells, R.S. and Würsig, M. 1994. *The Hawaiian Spinner Dolphin*. University of California Press, Berkeley, California. 408pp.
- Odell, D.K. and McClune, K.M. 1999. False killer whale, *Pseudorca crassidens* (Owen, 1846). pp. 213-43. In: S.H. Ridgway and R. Harrison (eds.) *The Second Book of Dolphins*. Vol. 6. *Handbook of Marine Mammals*. Academic Press, London and San Diego. 486pp.
- Papastavrou, V. and Van Waerebeek, K. 1997. A note on the occurrence of humpback whales (*Megaptera novaeangliae*) in tropical and subtropical areas: the upwelling link. *Rep. int. Whal. Commn* 47:945-47.
- Perrin, W.F. 1990. Subspecies of *Stenella longirostris* (Mammalia: Cetacea, Delphinidae). *Proc. Biol. Soc. Wash.* 103(2):453-63.
- Perrin, W.F. 2002. Coloration. pp. 236-45. In: W.F. Perrin, B. Würsig and J.G.M. Thewissen (eds.) *Encyclopedia of Marine Mammals*. Academic Press, San Diego. 1,414pp.
- Perrin, W.F., Leatherwood, S. and Collet, A. 1994. Fraser's dolphin *Lagenodelphis hosei* Fraser, 1956. pp. 223-40. In: S.H. Ridgway and R. Harrison (eds.) *Handbook of Marine Mammals*. Vol. 5. *The First Book of Dolphins*. Academic Press, London and San Diego. 416pp.
- Perryman, W.L., Au, D.W.K., Leatherwood, S. and Jefferson, T.A. 1994. Melon-headed whale, *Peponocephala electra* Gray, 1846. pp. 363-86. In: S.H. Ridgway and R.J. Harrison (eds.) *Handbook of Marine Mammals*. Vol. 5. *The First Book of Dolphins*. Academic Press, London and San Diego. 416pp.
- Pitman, R.L. and Stinchcomb, C. 2002. Rough-toothed dolphins (*Steno bredanensis*) as predators of mahimahi (*Coryphaena hippurus*). *Pac. Sci.* 56(4):447-50.
- Reeves, R.R., Leatherwood, S. and Papastavrou, V. 1991. Possible stock affinities of humpback whales in the northern Indian Ocean. *UNEP Mar. Mamm. Tech. Rep.* 3:259-69.
- Rice, D.W. 1998. *Marine Mammals of the World. Systematics and Distribution*. Special Publication No. 4. The Society for Marine Mammalogy, Allen Press Inc., Lawrence, Kansas. v-ix+231pp.
- Ritter, F. 2002. Behavioural observations of rough-toothed dolphins (*Steno bredanensis*) off La Gomera, Canary Islands (1995-2000) with special reference to their interactions with humans. *Aquat. Mamm.* 28:46-59.
- Rosenbaum, H.C., Collins, T., Minton, G., Baldwin, R., Glaberman, S., Findlay, K.P. and Best, P. 2002. Preliminary analysis of mtDNA variation among humpback whales off the coast of Oman and their relationship to whales from wintering grounds in the southwestern Indian Ocean. Paper SC/54/H4 presented to the IWC Scientific Committee, April 2002, Shimonoseki, Japan (unpublished). 10pp. [Paper available from the Office of this Journal].
- Ross, G.J.B. 1979. Records of pygmy and dwarf sperm whales, genus *Kogia*, from Southern Africa, with biological notes and some comparisons. *Ann. Cape Prov. Mus. (nat. Hist.)* 11(14):259-327.
- Ross, G.J.B. and Cockcroft, V.G. 1990. Comments on Australian bottlenose dolphins and taxonomic status of *Tursiops aduncus* (Ehrenburg 1832). pp. 101-28. In: S. Leatherwood and R.R. Reeves

- (eds.) *The Bottlenose Dolphin*. Academic Press, San Diego. i-xviii+653pp.
- Shane, S.H. 1995. Relationship between pilot whales and Risso's dolphins at Santa Catalina Island, California, USA. *Mar. Ecol. Prog. Ser.* 123:5-11.
- Sivasubramaniam, K. 1965. Predation of tuna longline catches in the Indian Ocean by killer whales and sharks. *Bull. Fish. Res. Stn., Ceylon* 17(2):93-6.
- Slijper, E.J., van Utrecht, W.L. and Naaktgeboren, C. 1964. Remarks on the distribution and migration of whales, based on observations from Netherlands ships. *Bijdr. Dierkd.* 34:3-93.
- Van Waerebeek, K., Gallagher, M., Baldwin, R., Papastavrou, V. and Al-Lawati, S.M. 1999. Morphology and distribution of the spinner dolphin, *Stenella longirostris*, rough-toothed dolphin, *Stenella bredanensis* and melon-headed whale, *Peponocephala electra*, from waters off the Sultanate of Oman. *J. Cetacean Res. Manage.* 1(2):167-77.
- Wada, S., Oishi, M. and Yamada, T.K. 2003. A newly discovered species of living baleen whale. *Nature, Lond.* 426:278-81.
- Wang, J.Y., Chou, L.S. and White, B.N. 2000. Differences in the external morphology of two sympatric species of bottlenose dolphins (genus *Tursiops*) in the waters of China. *J. Mammal.* 81(4):1157-65.
- Wang, M.-C., Walker, W.A., Shao, K.-T. and Chou, L.-S. 2002. Comparative analysis of the diets of pygmy sperm whales and dwarf sperm whales in Taiwanese waters. *Acta Zoologica Taiwanica* 13(2):53-62.
- Whitehead, H. 1989. *Voyage to the Whales*. Robert Hale, London. xi+195pp.
- Whitehead, H., Gilligan, P., Smyth, C., Weilgart, L. and Converse, C. 1983. WWF/IUCN Indian Ocean Whale Project. Interim Report, Oct-Dec. 1983. (Unpublished.) 34pp. [Available from the author].
- Willis, P.M. and Baird, R.W. 1998. Status of dwarf sperm whale, *Kogia simus*, with special reference to Canada. *Can. Field-Nat.* 112(1):114-25.
- Wilson, C.E., Perrin, W.F., Gilpatrick, J.W., Jr. and Leatherwood, J.S. 1987. Summary of worldwide locality records of the striped dolphin, *Stenella coeruleoalba*. *NOAA Tech. Mem. NMFS SWFSC* 90 65pp.
- Wray, P. and Martin, K.R. 1983. Historical whaling records from the western Indian Ocean. *Rep. int. Whal. Commn* (special issue) (5):213-41.
- Yochem, P.K. and Leatherwood, S. 1985. Blue whale – *Balaenoptera musculus* (Linnaeus, 1758). pp. 193-240. In: S.H. Ridgway and R. Harrison (eds.) *Handbook of Marine Mammals*. Vol. 3. *The Sirenians and Baleen Whales*. Academic Press, London and Orlando. xviii+362pp.

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