

CETACEANS OF THE WESTERN TROPICAL INDIAN OCEAN: DISTRIBUTION, RELATIVE ABUNDANCE, AND COMPARISONS WITH CETACEAN COMMUNITIES OF TWO OTHER TROPICAL ECOSYSTEMS

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ABSTRACT

We conducted a cetacean survey in the pelagic western tropical Indian Ocean (WTIO) aboard an 85-m research vessel from March to July 1995, covering 9,784 linear km. Using 25× binoculars and line-transect methods, we recorded 589 sightings of 21 species. *Stenella longirostris* was the most abundant cetacean, in terms of number of individuals sighted, by an order of magnitude above any other species, while *Physeter macrocephalus* was the most frequently sighted, in terms of number of schools. Twelve species were widespread, seven were rare, and two were localized; our sightings include new distributional records for 12 species. Significant observations included the following: (1) *Delphinus cf. tropicalis* was abundant off the coast of Oman (16 sightings) and readily distinguishable in the field from *D. delphis* and *D. capensis*, (2) *Balaenoptera musculus* was fairly common and localized in the area of the Maldives (17 sightings), and (3) three sightings were made of an unidentified bottlenose whale tentatively referred to as *Indopacetus* (i.e., *Mesoplodon pacificus*). We recorded 26 mixed-species cetacean schools, 43 schools with which seabirds associated, and 17 schools associated with tuna. Notable among these were mixed aggregations of *Stenella attenuata*, *S. longirostris*, yellowfin tuna, and seabirds.

The cetacean community of the WTIO was similar to that of the eastern tropical Pacific (ETP) and the Gulf of Mexico (GM) in several respects. First, differences in abundance rank of individual species were small, with the result that common species were common and rare species were rare, regardless of ocean. Second, these differences in abundance were due primarily to differences in encounter rate, which varied with ocean by as much as 3,000%, and less so to school size, which generally varied less than 100%. Third, regardless of ocean, three species comprised the majority of cetaceans in the community, *Stenella attenuata*, *S. longirostris*, and *S. coeruleoalba*, representing 62%–82% of all individuals for all species. However, the rank order of abundance for

these three species differed with ocean. Most notably, *S. attenuata* was abundant in the ETP and GM (abundance rank = 2 and 1, respectively) but much less common in the WTIO (abundance rank = 6). Although habitat preferences for *S. attenuata* appear to overlap considerably with those of *S. longirostris* in the ETP, our results suggest there may actually be significant differences between these two species. Detailed analysis of oceanographic correlates of distribution will be necessary in order to understand fully the habitat requirements of these pelagic dolphins, often the most conspicuous elements of tropical cetacean communities around the world.

Key words: Indian Ocean, Arabian Sea, tropical cetacean communities, eastern tropical Pacific, Gulf of Mexico, cetacean-seabird-tuna feeding interactions, *Balaenoptera musculus*, *Physeter macrocephalus*, *Indopacetus pacificus*, *Mesoplodon pacificus*, *Delphinus* cf. *tropicalis*, *Stenella attenuata*, *Stenella longirostris*, *Stenella coeruleoalba*.

In 1979 the Indian Ocean Cetacean Sanctuary was established, encompassing the entire Indian Ocean north of 55°S (IWC 1980). Although this designation served to prohibit commercial whaling, no provisions were made to protect smaller cetaceans or identify critical habitats. Subsequent to the designation, a program of monitoring and research in the Sanctuary was called for (Anonymous 1981), along with a review of the current state of knowledge of the cetaceans in the Indian Ocean (Leatherwood and Donovan 1990).

Despite this attention, the cetacean community of the Indian Ocean remains poorly known. With few exceptions (Leatherwood *et al.* 1984, Gordon 1990, Kasuya and Wada 1990), most research, both directed and opportunistic, has been conducted along the coast in localized areas, or around islands (van Bree and Gallagher 1978, Keller *et al.* 1982, Ross 1984, Frazier *et al.* 1987, de Silva 1987, Leatherwood and Reeves 1989, Cockcroft and Ross 1990, Leatherwood and Donovan 1990, Peddemors *et al.* 1990, Small and Small 1990, Smeenk *et al.* 1996). Thus, there is still much to be learned about the oceanic cetacean community. Which species occur there; where are they found and with what abundance; how do these patterns change over space and time?

In contrast to the Indian Ocean, cetacean communities in some tropical areas are relatively well known. For example, in the eastern tropical Pacific, the need to monitor the impact of incidental mortality of dolphins by the tuna purse-seine fishery has resulted in more than 20 yr of directed research over a vast spatial scale. The outcome has been a basic knowledge of the composition of the cetacean community, distribution and abundance patterns, species-specific habitat preferences and their seasonal and interannual variation, and foraging ecology and behavioral associations (Smith 1983, Au and Perryman 1985, Au and Pitman 1986, Holt and Sexton 1990, Reilly 1990, Gerrodette and Wade 1991, Wade and Gerrodette 1993, Fiedler and Reilly 1994, Reilly and Fiedler 1994). The cetaceans of the Gulf of Mexico have also been well studied relative to those of the Indian Ocean, resulting in a basic understanding of distribution and abundance (Mullin *et al.* 1994, Blaylock *et al.* 1995, Davis and Fargion 1996, Jefferson 1996, Jefferson and Schiro 1997). As knowledge of cetacean communities in different oceans accumulates, it

becomes possible to compare these communities in an attempt to better understand how variations in the ecosystem, be they natural or human induced, are manifested.

In 1995 we spent four months at sea in the western tropical Indian Ocean (WTIO), mostly in waters seaward of the continental shelf, surveying cetaceans and seabirds. In this paper we document species composition, distribution, and relative abundance of the WTIO cetacean community and compare them with those of the eastern Pacific and Gulf of Mexico.

METHODS

Survey Area

We conducted our survey aboard the 85-m National Oceanic and Atmospheric Administration research vessel *Malcolm Baldrige*, which was engaged in physical and biological oceanographic work during the cruise. We used the *Baldrige* as a ship of opportunity and, accordingly, our track lines were determined by other project needs (Fig. 1). The itinerary included four legs: (I) Durban, South Africa to Colombo, Sri Lanka (21 March–21 April 1995); (II) Colombo to Muscat, Oman (27 April–24 May 1995); (III) Muscat to Victoria, Seychelles (31 May–30 June 1995); (IV) Victoria to Muscat, Oman (12–24 July 1995), for a total of 105 sea days. During legs I and III, the ship stopped to conduct 2–3-h oceanographic stations every 2–5 h, around the clock. During leg II, the ship conducted sampling stations lasting from 1 h to 3 d on an irregular schedule. Leg IV was a transit leg. When not on station, ship's speed through the water averaged 25 km/h (14 kn).

The Indian Ocean has a marked seasonal monsoon, a strong atmospheric and oceanic phenomenon, causing striking changes in sea-surface current direction and strength, affecting movements of water masses both above and below the thermocline and resulting in intense localized upwelling (Wyrtki 1973). During the relatively gentle Northeast Monsoon, occurring from approximately November through April, water movement north of the equator is generally from east to west. During the more vigorous Southwest Monsoon, occurring from approximately May through October, water movement north of the equator is from west to east, and a strong western boundary current, the Somali Current, develops. Consequently, intense coastal upwelling occurs, especially along the coasts of Somalia and Oman.

In 1995 the Southwest Monsoon began in late May. Although the major oceanographic changes associated with the monsoon almost certainly affect cetacean distribution (*e.g.*, Reilly 1990), our ability to detect animals was adversely affected by the strong winds associated with this event (Table 1). Accordingly, we are unable to address seasonal patterns; we analyzed pre-monsoon (21 March–24 May) and Southwest Monsoon data (31 May–24 July) together.

Survey Methods

We used line-transect methods described by Holt (1987) to survey for cetaceans. Two observers scanned the ocean area in front of the ship from beam to beam and out to the horizon (*ca.* 15 km, total survey width of 30 km) or to the farthest limit of visibility. They used 25 × 150-power "Fujinon" binoculars, which were mounted on the deck to the port and starboard sides of the flying bridge, 15.5 m above water. A third observer used a 10 × 50 power hand-held binocular and unaided eye to search for animals closer to the vessel. We surveyed for cetaceans during all daylight hours when the ship was in transit, weather permitting, taking short breaks as necessary for meals or rest. Generally, we surveyed in sea conditions corresponding to Beauforts 0–6 (wind velocities up to 50 km/h = 27 kn) and suspended effort when the sea state was higher. In our estimates of relative abundance, however, we include only effort and sightings made during Beaufort 5 or less (wind velocities less than 40 km/h = 22 kn). We recorded observation conditions from the flying bridge; navigational and environmental data (*i.e.*, sea surface temperature and salinity, water depth, *etc.*) were automatically recorded continuously throughout the cruise.

With few exceptions, the ship did not divert from its course to approach animals for confirmation of species identifications or school size estimates. When a cetacean was detected, one observer focused on that individual or school while the other observer continued to scan for new sightings. Rarely, both observers focused on the sighting in order to confirm species identification or assist in making school size estimates. In the latter case we suspended survey effort until these data were obtained. We recorded identity to the lowest possible taxon, school size estimate, and behavior for all cetaceans sighted, as well as species identity, number, and behavior of any associated birds, marine turtles, or fish, and presence/absence of flotsam.

Relative Abundance

Because of uneven spatial coverage throughout the area (Fig. 1) and a small number of sightings for some species (Table 2), we did not attempt to estimate

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Figure 1. Sighting locations for all species recorded during the cruise and the portion of ship's track line that was visually surveyed. Sightings in areas where the species has not been previously recorded are represented by filled symbols. (a) *Balaenoptera musculus* (*n* = 17) and *Balaenoptera* sp. (*n* = 12); (b) *Balaenoptera edeni* (*n* = 8), *Physeter macrocephalus* (*n* = 99), and *Kogia breviceps* (*n* = 2); (c) *Kogia simus* (*n* = 20) and *Steno bredanensis* (*n* = 12); (d) "Unidentified Bottlenose Whale" (*n* = 3), *Ziphius cavirostris* (*n* = 1), and *Mesoplodon* sp. (*n* = 19); (e) *Peponocephala electra* (*n* = 3), *Feresa attenuata* (*n* = 5), and *Peponocephala/Feresa* (*n* = 2); (f) *Pseudorca crassidens* (*n* = 7), *Orcinus orca* (*n* = 2), and *Globicephala* sp. (*n* = 16); (g) *Delphinus cf. tropicalis* (*n* = 16) and *Delphinus* sp. (*n* = 5); (h) *Tursiops* sp. (*n* = 41); (i) *Lagenodelphis hosei* (*n* = 3) and *Grampus griseus* (*n* = 49); (j) *Stenella attenuata* (*n* = 12); (k) *Stenella coeruleoalba* (*n* = 37); (l) *Stenella longirostris* (*n* = 66).

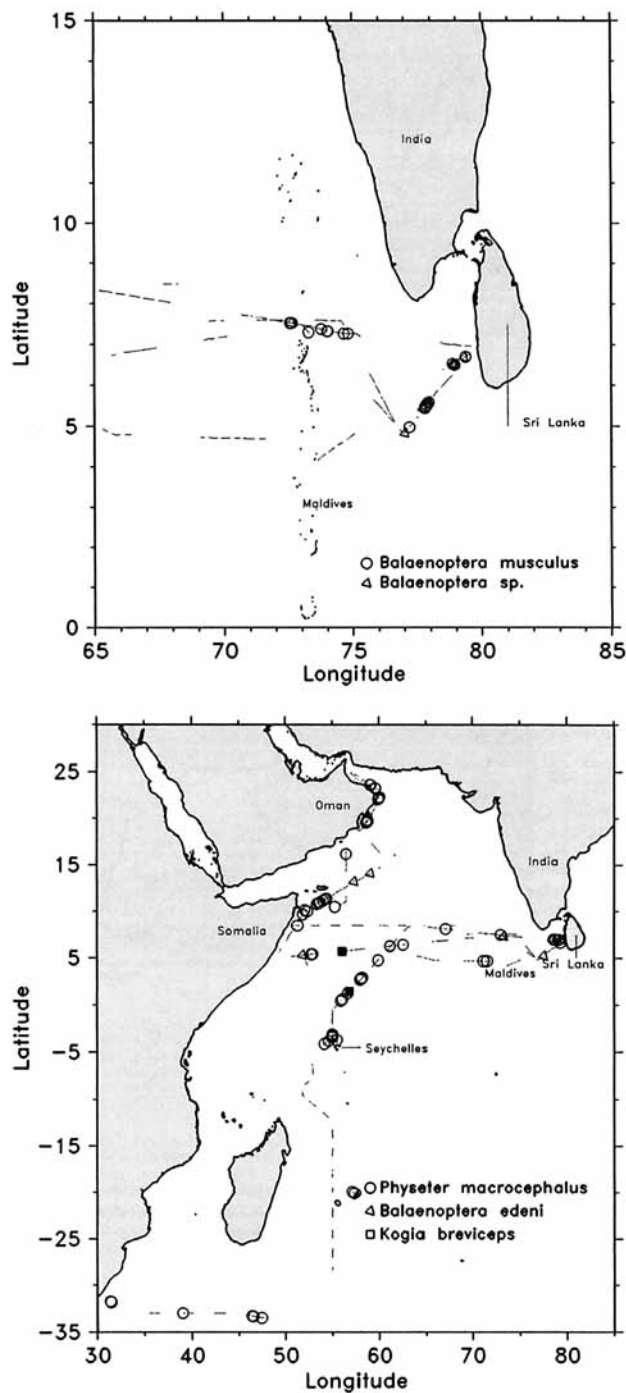


Figure 1. (a), (b)

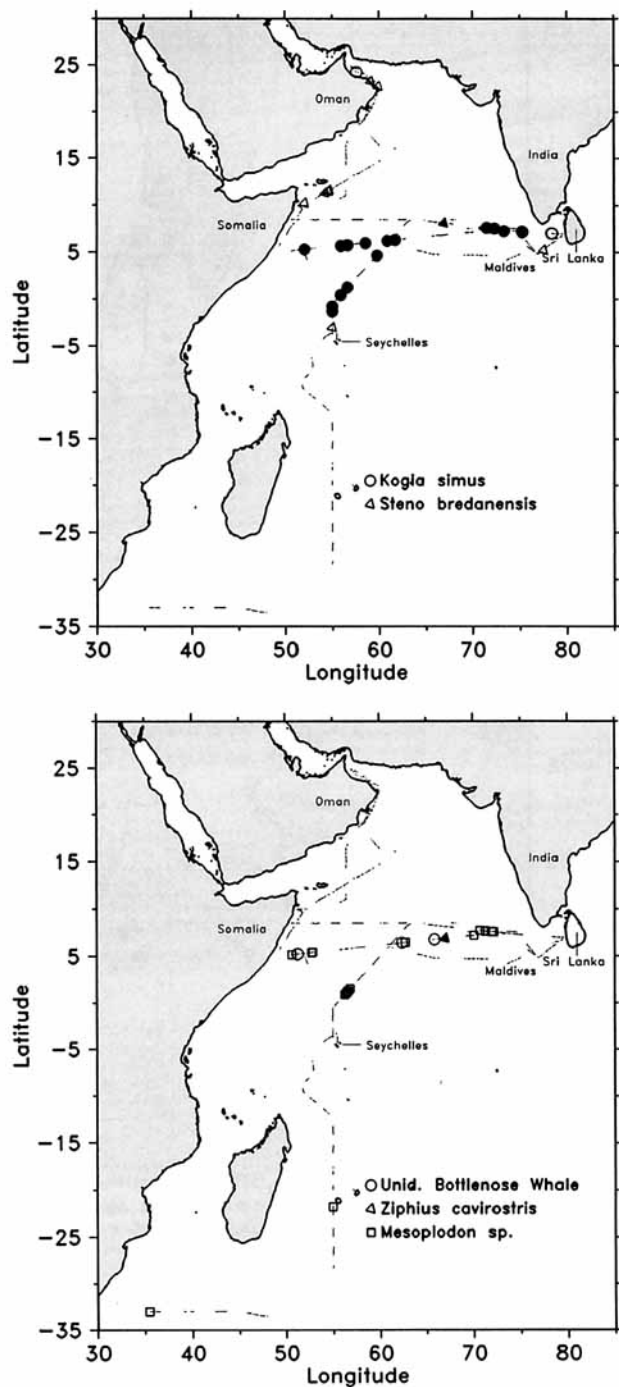
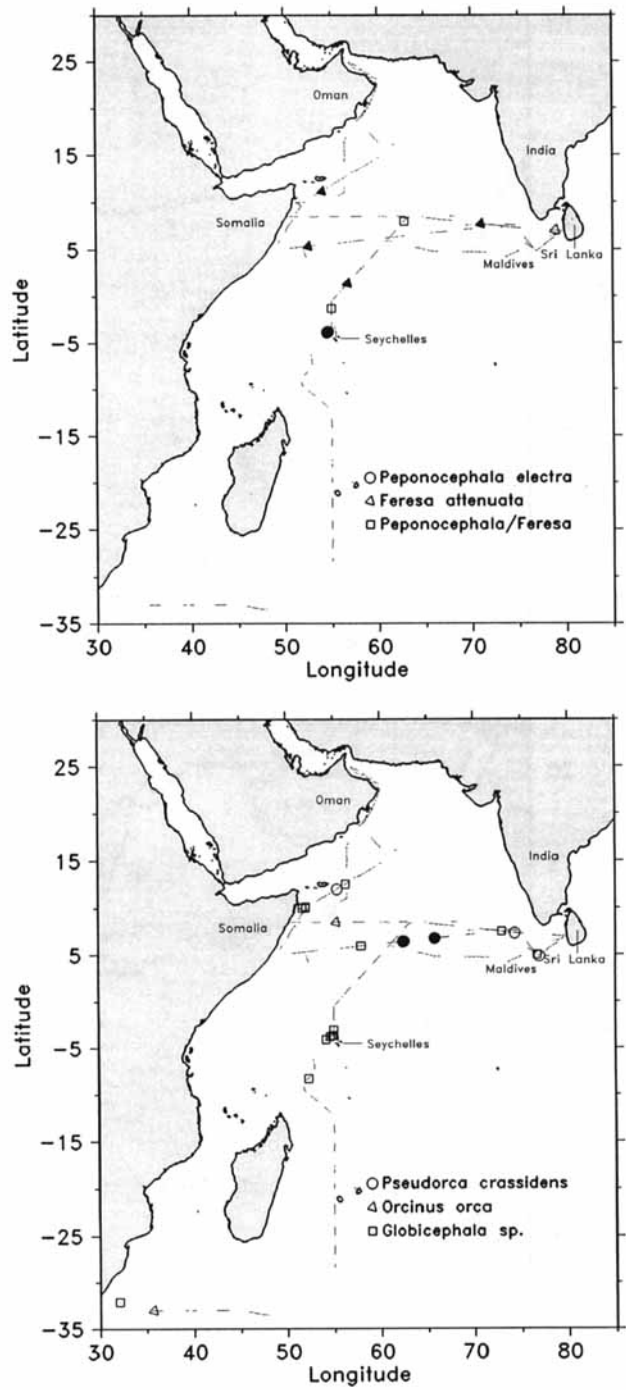


Figure 1. (c), (d)



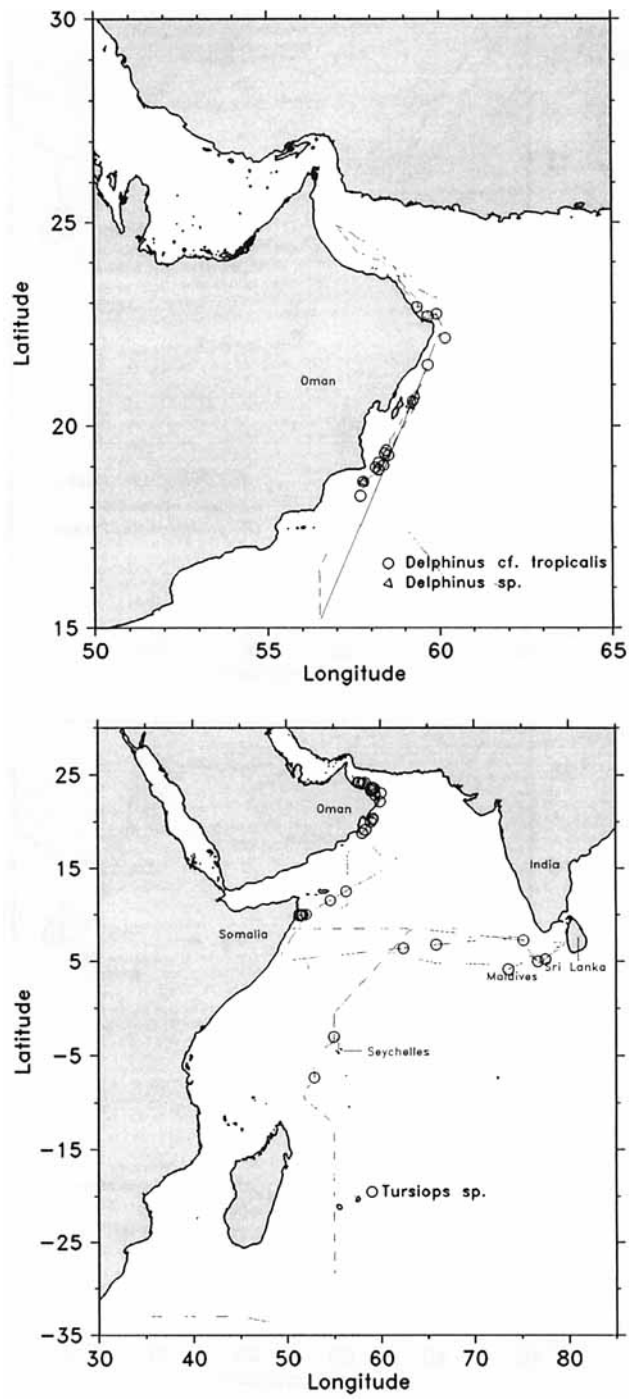
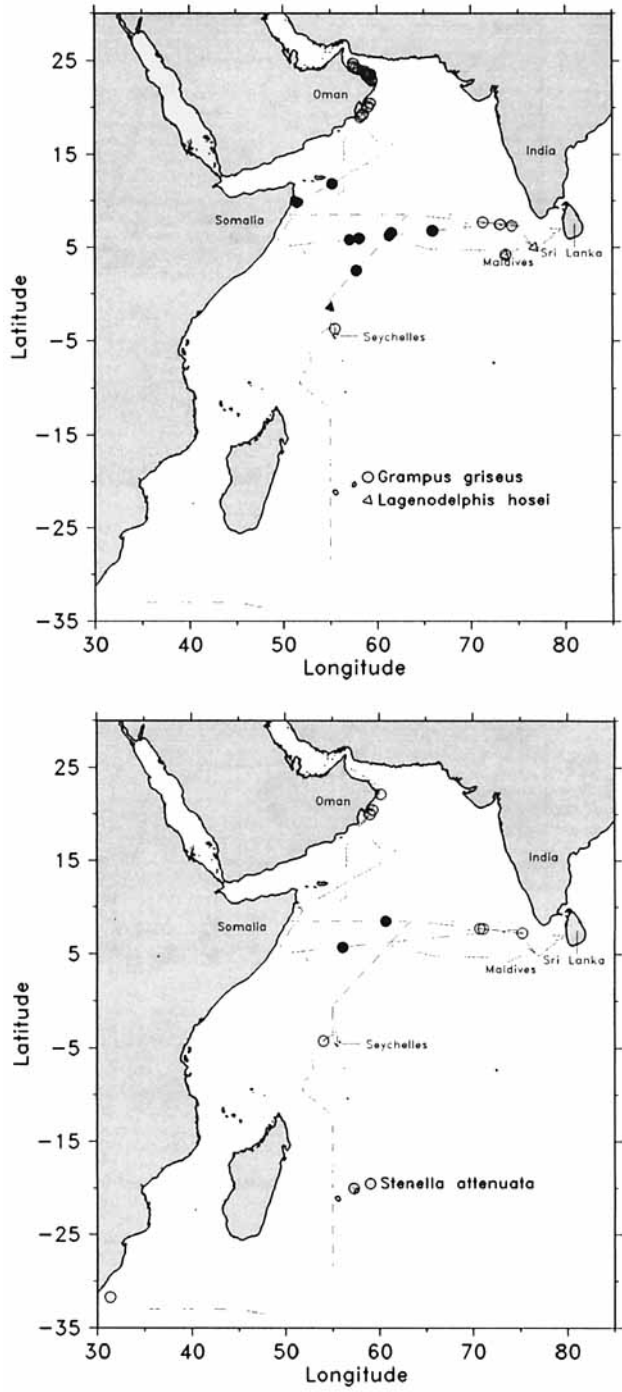


Figure 1. (g), (h)



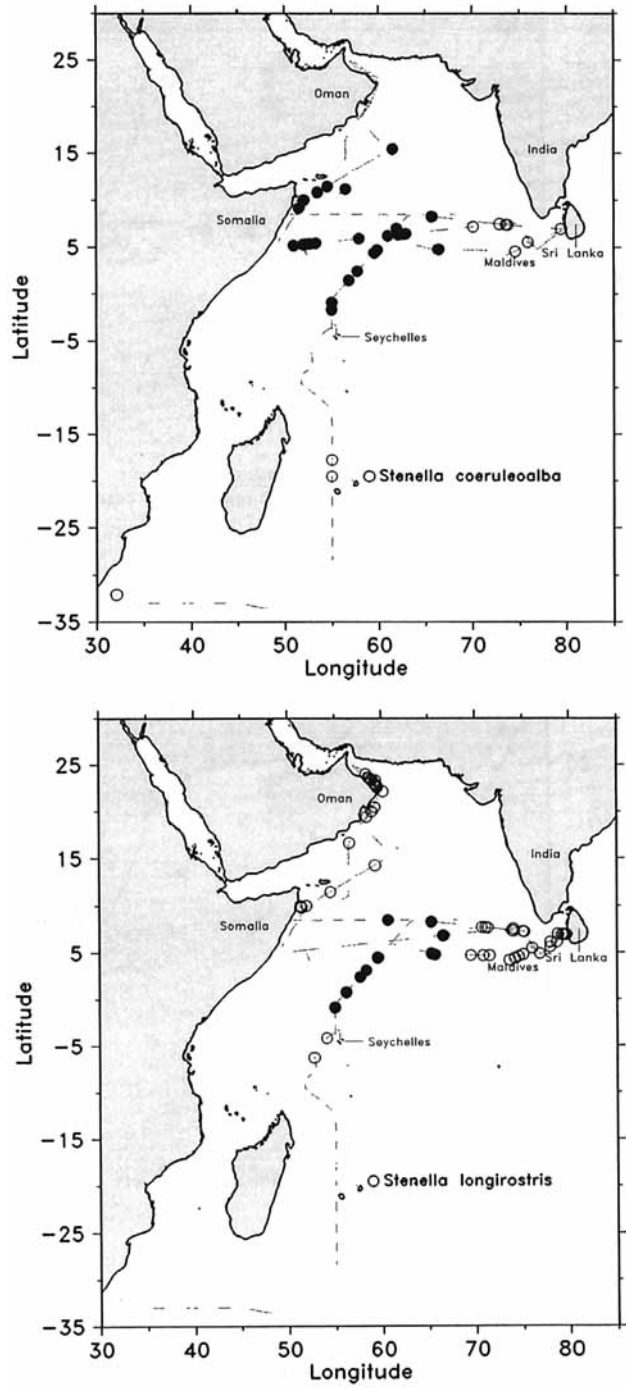


Figure 1. (k), (l)

Table 1. Observation conditions during survey.

Observation conditions	Pre-monsoon (21 March–24 May 1995)			Southwest monsoon (31 May–24 July 1995)			Total	
	h	% of condition	% of season	h	% of condition	% of season	h	% of condition
Excellent (Beaufort 0–2, winds 0–11 km/h)	114	87.8	45.5	16	12.2	10.4	129.9	32.2
Good–Fair (Beaufort 3–4, winds 12–30 km/h)	114.2	61.3	45.6	72.2	38.7	47.1	186.4	46.1
Poor (Beaufort 5+, winds >31 km/h)	22.4	25.6	8.9	65.1	74.4	42.5	87.6	21.7
Total	250.6	62	100	153.3	38	100	403.9	100

Table 2. Relative abundance of cetaceans sighted in the western tropical Indian Ocean. Species listed in descending order of corrected number of individuals sighted. Effective strip width = $1/f(0) \times 2$; correction factor standardizes effective strip widths to highest value (see Methods). * indicates high number of sightings due to effort in Gulf of Oman (see Methods).

Species	Sightings			Effective strip width (km)	Correction factor	Corrected number of on-effort sightings	Corrected number of individuals sighted
	Total	On effort (Beaufort 0-5)					
<i>Stenella longirostris</i>	66	58		5.70	1.10	63.80	10,833.2
<i>Tursiops</i> sp.*	41	31		3.03	2.06	63.86	3,391.0
<i>Stenella coeruleoalba</i>	37	36		3.03	2.06	74.16	3,174.0
<i>Delphinus</i>	21	13		5.70	1.10	14.30	3,038.0
<i>Delphinus</i> cf. <i>tropicalis</i>	16	9		5.70	1.10	9.90	2,326.5
<i>Delphinus</i> sp.	5	4		5.70	1.10	4.40	711.5
<i>Grampus griseus</i> *	49	41		4.26	1.47	60.27	2,911.0
<i>Stenella attenuata</i>	12	9		5.70	1.10	9.90	1,457.3
<i>Peponocephala electra</i>	3	3		5.70	1.10	3.30	934.9
<i>Globicephala</i> sp.	16	13		4.26	1.47	19.11	586.7
<i>Steno bredanensis</i>	12	11		3.03	2.06	22.66	484.9
<i>Lagenodelphis hosei</i>	3	2		5.70	1.10	2.20	403.3
<i>Pseudorca crassidens</i>	7	5		4.26	1.47	7.35	303.6
<i>Physeter macrocephalus</i>	99	86		6.25	1.00	86.00	240.8
<i>Feresa attenuata</i>	5	5		3.03	2.06	10.30	162.7
<i>Mesoplodon</i> sp.	19	19		4.48	1.40	26.60	53.2
<i>Kogia simus</i>	20	20		4.48	1.40	28.00	44.8
<i>Balaenoptera musculus</i>	17	17		6.25	1.00	17.00	27.2
<i>Orcinus orca</i>	2	2		4.26	1.47	2.94	23.5
"Unidentified bottlenose whale"	3	1		4.48	1.40	1.40	21.0
<i>Balaenoptera edeni</i>	8	8		6.25	1.00	8.00	9.6
<i>Ziphius cavirostris</i>	1	1		4.48	1.40	1.40	4.2
<i>Kogia breviceps</i>	2	2		4.48	1.40	2.80	2.8

absolute abundance. Instead, we present an estimate of *relative* abundance, with respect to number of schools, and number of individuals, based on a correction factor to account for differences in sightability between species. This correction factor and relative abundance were calculated as follows.

First, we calculated effective strip width (ESW), a parameter used in line-transect analysis that directly estimates the difficulty of sighting animals under field conditions (Buckland *et al.* 1993). ESW values are dependent upon sighting conditions (*e.g.*, sea state, sun glare) and behavioral characteristics of the animals (*e.g.*, school size, aerial activity). However, due to sample size constraints, we could not stratify our data to calculate separate ESW values for each sighting condition and each species. Instead, we calculated a single ESW, using data collected during all sighting conditions, for each of five species categories based on groupings of species with similar behavioral characteristics (*e.g.*, Barlow 1995). These include Large Whales: *Balaenoptera musculus*, *Balaenoptera edeni*, *Balaenoptera* sp., *Physeter macrocephalus*; Large-school Dolphins: *Peponocephala electra*, *Lagenodelphis hosei*, *Delphinus* cf. *tropicalis*, *Delphinus* sp., *Stenella attenuata*, *Stenella longirostris*, *Stenella* sp.; Small Whales: *Feresa attenuata*, *Feresa/Peponocephala*, *Pseudorca crassidens*, *Orcinus orca*, *Globicephala* sp., *Grampus griseus*; Small-school Dolphins: *Steno bredanensis*, *Tursiops* sp., *Stenella coeruleoalba*; and Cryptic Species: *Kogia breviceps*, *Kogia simus*, *Ziphius cavirostris*, "Unidentified Bottlenose Whale" (see Species Accounts below), *Mesoplodon* sp.

We used the program DISTANCE (Laake *et al.* 1994) to calculate ESW. Perpendicular distance from the track line to each sighting was calculated with bearing and radial distance estimates made in the field, using the equation from Lerczak and Hobbs (in press). Data were truncated so that 15% of sightings for each species group was eliminated; this corresponded to truncation distances ranging from 2.7 to 6.2 km. The parameter $f(0)$ (defined as the sighting probability density at zero perpendicular distance, Buckland *et al.* 1993) was estimated by fitting the model which minimized Akaike's Information Criteria to the distribution of ungrouped perpendicular sighting distances; in every case, this was the half-normal key function model with cosine adjustment. Our ESW values represent $2 \times 1/f(0)$.

Next, we calculated a correction factor, which standardized our ESW values to the highest value, that for Large Whales (Table 2). This correction factor was then multiplied by the total number of on-effort sightings for each species to obtain a "corrected" number of on-effort sightings representing relative abundance with respect to number of schools. We also report corrected encounter rate, equal to the corrected number of sightings divided by the total linear distance surveyed on effort. Finally, this corrected number of sightings was multiplied by mean school size to obtain a relative measure of abundance of individuals.

Comparison with Other Cetacean Communities

We compared three aspects of the cetacean community of the WTIO with those of the eastern tropical Pacific (ETP) and the Gulf of Mexico (GM):

relative abundance, mean school size, and encounter rate. We used results from Wade and Gerrodette (1993) based on surveys during 1986–1990 for the ETP and Hansen *et al.* (1995) based on surveys during 1991–1994 for the GM.

We compared relative abundance by ranking species within each ocean according to number of individuals. We used our estimate for relative number of individuals sighted for the WTIO and absolute abundance estimates for the ETP and GM. In the WTIO a large proportion of the total *Tursiops* sp. and *Grampus griseus* sightings (41% and 33%, respectively) was made during the last six days of our survey, when we intensively covered the southern portion of the Gulf of Oman (Fig. 1h, 1i), a neritic habitat. When comparing cetacean communities between oceans, we did not want to artificially bias our data toward neritic composition. So, for this comparison only, we did not include the *Tursiops* and *Grampus* sightings that were recorded during this period.

We compared encounter rate by calculating “corrected encounter rates” for the ETP and GM, so as to be comparable to those for the WTIO. For each of these other two oceans, we used published species-specific ESW values [representing $2 \times 1/f(0)$], calculated a correction factor by standardizing each ESW to the highest value within that ocean, multiplied the number of on-effort sightings (from the published data) by this correction factor to obtain the “corrected number of sightings” for each species, and finally, divided this number by the linear distance surveyed on effort (also from the published data).

RESULTS

We surveyed a total of 403.9 h during 92 d; this represents a linear distance of 9,784 km, 8,795 km (90%) of which were surveyed during Beaufort 5 conditions or better (Fig. 1). The majority of our survey time (78%) occurred during fair to excellent conditions (sea states of Beaufort 0–4, wind velocities below 31 km/h; Table 1). These conditions occurred primarily before the onset of the Southwest Monsoon, after which observation conditions were generally poor.

Community Composition

We recorded 589 cetacean sightings, comprising a minimum of 21 different species (Table 2). We identified 480 sightings (81.5%) to the genus or species level; the remaining 109 sightings were recorded at higher taxonomic categories (unidentified dolphin, unidentified large/small whale, unidentified odontocete, unidentified cetacean).

Stenella longirostris was the most abundant cetacean by far, with the corrected number of individuals sighted an order of magnitude greater than for any other species (Table 2). Also abundant were *Tursiops* sp., *Stenella coeruleoalba*, *Delphinus* sp., and *Grampus griseus*. *Physeter macrocephalus* was the most fre-

quently sighted species (Table 2), but groups were much smaller than for the abundant small dolphins.

As expected, species classified as Cryptic were relatively rare (Table 2); their relative abundance is likely to be biased low. ESW values were greater for Cryptic species than for Small Whales, or Small School Dolphins (Table 2), undoubtedly due to the fact that we sighted Cryptic species only under the best of sighting conditions, suggesting that they are more cryptic than rare. Therefore, even the corrected number of sightings for this group is low. Further, because most of these are deep divers, their relative abundance should be further negatively biased relative to shallow-diving species.

Distribution

Sighting locations are plotted in Figures 1a–l (see Ballance *et al.* 1996a for exact latitude and longitude coordinates). Our data include sightings from areas where the species have not been previously recorded for *Kogia breviceps* (Fig. 1b, Caldwell and Caldwell 1989), *K. simus* (Fig. 1c, Caldwell and Caldwell 1989), *Ziphius cavirostris* (Fig. 1d, Heyning 1989), *Peponocephala electra* (Fig. 1e, Perryman *et al.* 1994), *Feresa attenuata* (Fig. 1e, Ross and Leatherwood 1994), *Pseudorca crassidens* (Fig. 1f, Leatherwood *et al.* 1990), *Steno bredanensis* (Fig. 1c, Miyazaki and Perrin 1994), *Lagenodelphis hosei* (Fig. 1i, Perrin *et al.* 1994b), *Grampus griseus* (Fig. 1i, Kruse *et al.* 1990), *Stenella attenuata* (Fig. 1j, Perrin and Hohn 1994), *Stenella coeruleoalba* (Fig. 1k, Perrin *et al.* 1994a), and *Stenella longirostris* (Fig. 1l, Perrin and Gilpatrick 1994).

With the caveat that our survey was not spatially complete, the distributions can provisionally be grouped into three basic patterns. Twelve taxa were widespread: *Physeter macrocephalus*, *Kogia simus*, *Mesoplodon* sp., *Feresa attenuata*, *Pseudorca crassidens*, *Globicephala* sp., *Steno bredanensis*, *Grampus griseus*, *Tursiops* sp., *Stenella attenuata*, *S. coeruleoalba*, and *S. longirostris* (Fig. 1b–f, h–l). Seven taxa were rare: *Balaenoptera edeni*, *Kogia breviceps*, “unidentified bottlenose whale,” *Ziphius cavirostris*, *Peponocephala electra*, *Orcinus orca*, and *Lagenodelphis hosei* (Fig. 1b, d–f, and i). Two taxa were localized: *Balaenoptera musculus* and *Delphinus cf. tropicalis/Delphinus* sp. (Fig. 1a and g).

Interspecific Associations

Although most sightings (96%) were of single-species schools, we recorded 26 mixed-species schools, comprising a total of nine species (Table 3, 4). The most frequent associations occurred between *Tursiops* sp. and either *Grampus griseus* or *Globicephala* sp. and between *Stenella attenuata* and *S. longirostris*. The only school comprised of more than two species contained *Tursiops* sp., *Globicephala* sp., *Stenella longirostris*, *S. coeruleoalba*, and possibly *S. attenuata*.

Mixed-species associations occurred most frequently for *Stenella attenuata*: in more than half of this species' sightings (Table 3). In every case the associated species was *S. longirostris* (although only 15% of *S. longirostris* schools was associated with other species, Table 3). *Tursiops* sp. was also recorded in

Table 3. School composition and foraging associations for cetaceans sighted in the western tropical Indian Ocean. Species listed in order as in Table 2. Percent values represent % of total sightings of each species.

Species	Single species		Mixed species		With birds		With tuna	
	No. sightings	%	No. sightings	%	No. sightings	%	No. sightings	%
<i>Stenella longirostris</i>	56	84.8	10	15.2	20	30.3	6	9.1
<i>Tursiops</i> sp.	24	58.5	17	41.5	2	4.9	2	4.9
<i>Stenella coeruleoalba</i>	36	97.3	1	2.7	1	2.7		
<i>Delphinus</i>								
<i>Delphinus cf. tropicalis</i>	14	87.5	2	12.5	6	37.5	4	25.0
<i>Delphinus</i> sp.					3	60.0	2	40.0
<i>Grampus griseus</i>	40	81.6	9	18.4	0	0.0	1	2.0
<i>Stenella attenuata</i>	5	41.7	7	58.3	7	58.3	5	41.7
<i>Peponocephala electra</i>	3	100.0	0	0.0	0	0.0		
<i>Globicephala</i> sp.	10	62.5	6	37.5	0	0.0		
<i>Steno bredanensis</i>	12	100.0	0	0.0	1	8.3		
<i>Lagenodelphis hosei</i>	3	100.0	0	0.0	0	0.0		
<i>Pseudorca crassidens</i>	6	85.7	1	14.3	4	57.1		
<i>Physeter macrocephalus</i>	98	99.0	1	1.0	0	0.0		
<i>Feresa attenuata</i>	5	100.0	0	0.0	0	0.0		
<i>Mesoplodon</i> sp.	19	100.0	0	0.0	0	0.0		
<i>Kogia simus</i>	20	100.0	0	0.0	0	0.0		
<i>Balaenoptera musculus</i>	17	100.0	0	0.0	0	0.0		
<i>Orcinus orca</i>	2	100.0	0	0.0	0	0.0		
"Unidentified bottlenose whale"	3	100.0	0	0.0	0	0.0		
<i>Balaenoptera edeni</i>	8	100.0	0	0.0	0	0.0		
<i>Ziphius cavirostris</i>	1	100.0	0	0.0	1	100.0	1	100.0
<i>Kogia breviceps</i>	2	100.0	0	0.0	0	0.0		

Table 4. Number and species components of mixed-species schools of cetaceans. Includes one school composed of *Globicephala*, *Tursiops*, *Stenella coerulealba*, and *Stenella longirostris*.

	<i>Physeter macrocephalus</i>	<i>Pseudorca crassidens</i>	<i>Globicephala</i> sp.	<i>Delphinus</i> cf. <i>tropicalis</i>	<i>Tursiops</i> sp.	<i>Stenella attenuata</i>	<i>Stenella coerulealba</i>
<i>Tursiops</i> sp.	1	1	6				
<i>Grampus griseus</i>					6		
<i>Stenella coerulealba</i>			1		1		
<i>Stenella longirostris</i>			1	2	1	7	1

mixed-species schools frequently and with more species than any other cetacean.

We recorded seabird flocks in association with nine species of cetaceans on 43 occasions (7% of all sightings, Table 3). Seabirds associated most frequently with *Delphinus*, *Stenella attenuata*, *Pseudorca crassidens*, and *S. longirostris*, in declining order. The bird species most frequently recorded in flocks were terns (Laridae), especially sooty tern *Sterna fuscata* and noddies *Anous* sp., and shearwaters (Procellariidae), especially Persian shearwater *Puffinus lherminieri persicus*, Audubon's shearwater *Puffinus lherminieri*, flesh-footed shearwater *Puffinus carneipes*, and Jouanin's petrel *Bulweria fallax* (see Ballance *et al.* 1996a for data).

We also recorded associations between seven species of cetaceans and schools of tuna (17 [3%] sightings, Table 3). When we were able to identify the tuna (8 sightings) they were always yellowfin tuna (*Thunnus albacares*). Tuna association was most prevalent for *Stenella attenuata*; for this species 80% of these tuna-associated schools (4 sightings) also contained *S. longirostris*, and 60% (3 sightings) were accompanied by seabird flocks. *Delphinus* sp. was also frequently associated with tuna; all but one of these tuna-associated schools were accompanied by flocks of seabirds.

Comparison of Cetacean Communities between Tropical Oceans

Abundance rank, mean school size, and corrected encounter rate for the species or species groups found in the WTIO, ETP, and GM are given in Table 5. Note that CVs for school size estimates in the GM are particularly high, so conclusions based on school size must be made with caution. Nevertheless, from these comparisons, we can draw several immediate conclusions.

First, common species are common, and rare species are rare, regardless of the tropical ocean in which they are found (Table 5). The abundance rank for a particular species almost always differed between oceans, but, with few exceptions, these differences were generally restricted to a value of ± 3 or less.

Second, these differences in abundance rank are due primarily to differences in encounter rate, not to differences in school size (Table 5). For all but four species (*Lagenodelphis hosei*, *Physeter macrocephalus*, *Balaenoptera edeni*, and *Kogia breviceps*), school size in the ETP and GM differed by less than 100% relative to that in the WTIO, and ETP *Physeter macrocephalus* schools, 182% larger than schools of the same species in the WTIO, were those with the largest relative difference. In contrast, differences in encounter rate were one to two orders of magnitude greater. In fact, for all but 7 of the 18 species common to all three oceans, encounter rates differed by more than 100%, and they differed by more than 1,000% for four species.

Third, regardless of ocean, the majority of cetaceans comprise three species: *Stenella attenuata*, *S. longirostris*, and *S. coeruleoalba* (Fig. 2). These three total an estimated 5.5 million individuals in the ETP (from Wade and Gerrodette 1993), an estimated 42.5 thousand in the GM (from Hansen *et al.* 1995), and a relative total sighted of 15,500 in the WTIO (Table 2). These abundances

Table 5. Comparison of relative abundance of cetaceans in three tropical oceans: WTIO = western tropical Indian Ocean, ETP = eastern tropical Pacific, GM = Gulf of Mexico. See Methods for data sources and calculation of corrected encounter rate. Species marked with * were corrected for high effort in Gulf of Oman (see Methods).

Species	Abundance rank			Mean school size (CV)			Corrected encounter rate (sightings/1,000 km)		
	WTIO	ETP	GM	WTIO	ETP	GM	WTIO	ETP	GM
<i>Stenella longirostris</i>	1	4	2	169.8 (1.37)	120.5	70.8 (24.62)	7.39	5.19	14.28
eastern stock					111.7 (0.09)				
whitebelly stock					134.1 (0.16)				
<i>Stenella coeruleoalba</i>	2	3	5	42.8 (0.99)	60.9 (0.05)	36.1 (11.63)	8.44	14.34	1.79
<i>Delphinus</i>	3	1	—	221.2 (1.32)	380.1	—	1.63	3.02	—
northern stock					385.9 (0.23)				
central stock					254.4 (0.13)				
southern stock					472.8 (0.11)				
<i>Tursiops</i> sp.*	4	6	3	53.1 (2.39)	22.7 (0.22)	14.0 (11.81)	4.92	4.72	10.16
<i>Grampus griseus</i> *	5	7	8	48.3 (2.29)	11.8 (0.08)	10.7 (9.44)	4.85	6.27	3.49
<i>Stenella attenuata</i>	6	2	1	147.2 (1.52)	127.9	57.7 (7.67)	1.13	5.97	9.68
northeastern stock					115.9 (0.09)				
western/southern stock					149.4 (0.08)				
<i>Peponocephala electra</i>	7	10	6	283.3 (0.97)	199.1 (0.20)	119.6 (22.50)	0.38	0.10	8.36
<i>Globicephala</i> sp.	8	8	13	30.7 (0.66)	18.3 (0.08)	16.6 (21.16)	2.17	3.66	3.87
<i>Sieno bredanensis</i>	9	9	9	21.4 (0.70)	14.7 (0.18)	14.4 (12.18)	2.58	4.63	19.09
<i>Lagenodelphis hosei</i>	10	5	16	183.3 (0.57)	394.9 (0.20)	34.0 (—)	0.25	0.25	8.48
<i>Pseudorca crassidens</i>	11	11	12	41.3 (0.88)	11.4 (0.12)	20.4 (42.07)	0.84	1.21	4.98
<i>Physeter macrocephalus</i>	12	14	10	2.8 (0.96)	7.9 (0.17)	2.6 (7.87)	9.78	1.24	3.57
<i>Feresa attenuata</i>	13	12	11	15.8 (0.44)	27.9 (0.12)	29.2 (62.44)	1.17	0.63	5.73
<i>Mesoplodon</i> sp.	14	13	17	2.0 (0.53)	3.0 (0.11)	1.9 (13.56)	3.03	3.10	4.82
<i>Kogia simus</i>	15	17	14	1.6 (0.55)	1.7 (0.07)	2.2 (13.77)	3.19	3.20	1.93
<i>Balaenoptera musculus</i>	16	19	—	1.6 (0.39)	1.5 (0.13)	—	1.93	0.36	—
<i>Orcinus orca</i>	17	18	15	8.0 (—)	5.4 (0.09)	10.0 (15.28)	0.33	0.66	4.09
<i>Balaenoptera edeni</i>	18	16	19	1.2 (0.37)	1.7 (0.07)	2.7 (45.07)	0.91	2.46	4.69
<i>Ziphius cavirostris</i>	19	15	20	3.0 (—)	2.2 (0.06)	1.2 (16.67)	0.16	3.25	4.73
<i>Kogia breviceps</i>	20	no data	18	1.0 (—)	no data	2.2 (11.75)	0.32	no data	3.32
<i>Stenella clymene</i>	—	—	4	—	—	63.7 (26.67)	—	—	14.13
<i>Stenella frontalis</i>	—	—	7	—	—	21.2 (15.89)	—	—	5.46

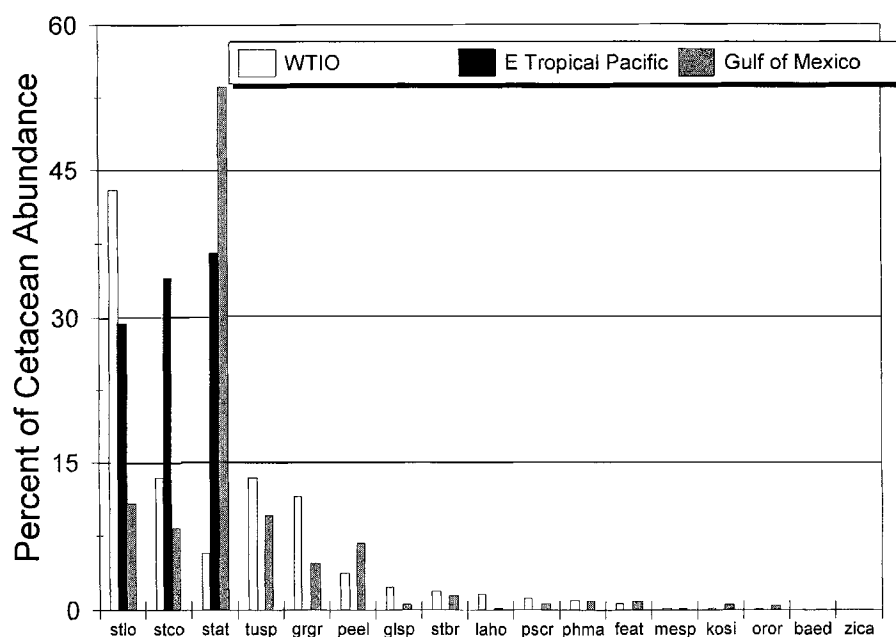


Figure 2. Percent of total cetacean abundance represented by species for three tropical oceans: the western tropical Indian Ocean (WTIO), the eastern tropical Pacific, and the Gulf of Mexico. (See Methods for data sources.) Only those species common to all three oceans are represented. Four-letter species codes as follows: stlo—*Stenella longirostris*, stco—*Stenella coeruleoalba*, stat—*Stenella attenuata*, tusp—*Tursiops* sp., grgr—*Grampus griseus*, peel—*Peponocephala electra*, glsp—*Globicephala* sp., stbr—*Steno bredanensis*, laho—*Lagenodelphis hosei*, pscr—*Pseudorca crassidens*, phma—*Physeter macrocephalus*, feat—*Feresa attenuata*, mesp—*Mesoplodon* sp., kosi—*Kogia simus*, oror—*Orcinus orca*, baed—*Balaenoptera edeni*, zica—*Ziphius cavirostris*.

represent from 62%–82% of the individuals for all cetacean species common to all three oceans.

However, the rank order of abundance for these three species varies by ocean. Most notably, *S. attenuata* was abundant in the ETP (abundance rank = 2), and the GM (abundance rank = 1), but much less common in the WTIO (abundance rank = 6, Table 5). And *S. longirostris* and *S. coeruleoalba* were less common in the other two oceans than in the WTIO, although the difference in abundance rank was less pronounced than for *S. attenuata* (Table 5).

As is the case for other species, this difference in abundance rank is due primarily to a difference in encounter rate, as opposed to a difference in school size (Table 5). School sizes in the ETP and GM differed from –61% to +42% relative to those for the same species in the WTIO. But encounter rates varied by an order of magnitude ranging from a 79% lower encounter rate, in the case of *S. coeruleoalba* in the GM, to a 757% higher encounter rate, in the case of *S. attenuata* in the GM. Especially for *S. attenuata* then, the higher abundance in the ETP and GM was due to the fact that there were more

schools in both of these systems relative to the WTIO, rather than to a difference in the size of these schools.

Annotated Species Accounts

Balaenoptera musculus—In addition to 17 confirmed sightings of 27 animals (Table 2), we recorded 7 sightings of 10 unidentified large *Balaenoptera* in the same localized area that likely were of this species (Fig. 1a). Of this total, 13 sightings appeared to be single animals, 9 were pairs, and the remaining 2 were sightings of three individuals. Thirty individuals (16 sightings, 67%) likely were feeding (the whales were sighted in the same areas as operating artisanal long liners, or they were surface lunging or fluking up on a terminal dive). Curiously, Kasuya and Wada (1990) sighted no *Balaenoptera musculus* in this area during the same season (March and April) of 1965–1966 and 1984–1985 but reported large numbers in localized distributions in the south-central Arabian Sea and off the coast of Somalia. Small and Small (1990) recorded them off the coast of Somalia only during October, November, and December, and Alling *et al.* (1990) sighted them off the northeast coast of Sri Lanka between February and April. This suggests a localized distribution, perhaps subject to seasonal and interannual variation.

The putative “pygmy blue whale,” *Balaenoptera musculus brevicauda*, is suspected to be resident in the northern Indian Ocean (Yochem and Leatherwood 1994, Zemsky and Sazhinov 1994) and it has been suggested that it is isolated from the nominate form (“true blue whales”) in the rest of the Indian Ocean (Kasuya and Wada 1990). However, we were unable to make subspecific determinations for any of our sightings.

Megaptera novaeangliae—Based on sightings data, comparison of songs from Arabian Sea animals with those from the North Pacific and North Atlantic, feeding behavior, and reproductive biology, several researchers have suggested that humpback whales in the Arabian Sea represent a northern population that is resident year-round (Whitehead 1985, Reeves *et al.* 1990, Mikhalev 1997). We did not see this species during our survey, despite the fact that there are sighting records from many coastal areas bordering the entire Arabian Sea, including the coast of Oman (Mikhalev 1997 and references therein), which we surveyed thoroughly in May, June, and July (Fig. 1).

Mesoplodont beaked whales—We were unable to identify any of the 19 sightings of *Mesoplodon* sp. to species, despite the fact that we often viewed these animals at close range and under good conditions. All had a nondescript color pattern, no visible teeth, and no prominent scarring. Known distributions suggest that four species of *Mesoplodon* are likely to occur in our survey area: *M. densirostris*, *M. grayii*, *M. layardii*, and *M. ginkgodens* (Jefferson *et al.* 1993). The animals we saw all had short beaks, eliminating *grayii* and *layardii*, and lacked the flat-headed profile of *densirostris* (R.L.P. has had extensive at-sea experience with all three of these species). Therefore we suspect that many of our *Mesoplodon* sightings were of *M. ginkgodens*.

Eight of our sightings (42%), representing 16 individuals (42%), were made

on a single day as we passed over a bank that shoaled at 135 m (1°15'N, 56°38'E; Fig. 1d).

"Unidentified bottlenose whale"—We recorded three separate sightings of a distinctive, but as yet unidentified ziphiid, (Table 2). All were in open ocean waters of the central Arabian Sea north of 5°N (Fig. 1d). One group was observed for over 2 h and passed within 500 m of our vessel as we drifted on station. This is a large beaked whale, approximately 7 m long, with a chunky build and tall, falcate dorsal fin. It has a large, rounded melon that drops perpendicular to the rostrum, or slightly overhangs the rostrum in some individuals. The rostrum is short to medium in length. Many, but not all, of the animals had a distinctive, cream-colored melon; the remainder of the body is dark to grayish-brown, with a pale ventrum and sides. Animals stayed close together in schools, diving and surfacing synchronously, even when group size was large (group sizes were 2, 8, and 45 individuals).

This species is easily discernable from the various species of *Mesoplodon* by its larger size (both in length and girth), its prominent dorsal fin, visible blow, and oversized melon with distinct beak. Animal size, school size, and swimming behavior are all suggestive of the two other genera of large ziphiids: *Berardius* and *Hyperoodon*, both known mainly from high latitudes. However, both *Berardius* species (*B. bairdii* and *B. arnouxii*) have a smaller, more rounded dorsal fin and a much longer rostrum than this unidentified whale. *Hyperoodon planifrons* has a larger, more bluff melon, a stubbier beak, and often has a whitish or tan coloration, frequently with heavy scarring.

Based on our field experience and the characteristics described above, the unidentified whale is clearly a bottlenose whale. Although possibly a distinct form of *Hyperoodon* (and identified as *H. cf. planifrons* in Ballance *et al.* 1996a, 1996b), we now believe that this animal may be *Indopacetus* (i.e., *Mesoplodon*) *pacificus* (R. L. Pitman, unpublished data). The type specimen of *Indopacetus pacificus* came from Queensland, and the only other known specimen is from Somalia, suggesting a tropical distribution that includes the Indian Ocean (Moore 1968). In fact, the school of eight animals we saw on 3 May 1995 was 268 km off the coast of Somalia.

Globicephala sp.—Although we did not confirm the species identification for any of our sightings, we assume all were *G. macrorhynchus*, as this species occurs in low latitudes (Leatherwood and Reeves 1983) and is the only *Globicephala* to have been previously recorded in the WTIO (Leatherwood *et al.* 1990).

Delphinus cf. tropicalis—We identified 16 of 21 *Delphinus* sightings as the extremely long-beaked form, *D. cf. tropicalis* (Table 2): the remaining five sightings were too distant to positively identify, but we suspect that all were also this form. All of our *Delphinus* sightings were highly localized and common off the coast of Oman (Fig. 1g), where they generally consisted of large schools (mean = 221, Table 5). However, *Delphinus* is more widely distributed in the WTIO than our records suggest. For example, Small and Small (1990) reported large numbers (including one confirmed *D. tropicalis*) off the coast of Somalia and found them especially concentrated near the Horn of Africa, where

Eyre (1995) also sighted them. Smeenk *et al.* (1996) recorded sightings of *Delphinus*, which they identified as *D. tropicalis*, in the Red Sea. Pilleri and Gahr (1972) documented the *tropicalis*-type along the coast of Pakistan and India, and there are records of an extremely long-beaked *tropicalis*-type *Delphinus* from as far east as Vietnam (Smith *et al.* 1995).

Two forms of *Delphinus* have previously been reported to occur off Oman, a short-beaked form *D. delphis*, and a long-beaked form that van Bree (1971a, b) designated *D. tropicalis* (van Bree and Gallagher 1978, Gallagher 1990). Subsequently, based on genetic and morphological analyses, *Delphinus* was split into two species: the short-beaked *D. delphis*, and the long-beaked *D. capensis* (Heyning and Perrin 1994, Rosel *et al.* 1994). Although Heyning and Perrin (1994) recognized that the putative *D. tropicalis* had a longer rostrum and higher tooth count than any of the *D. capensis* they analyzed, they deferred judgement on the validity of the species until more specimens became available. More recently, Smeenk *et al.* (1996) conducted a limited morphological analysis that suggested that the *tropicalis* type is, in fact, only a long-beaked form of *D. capensis*. In their review, Heyning and Perrin (1994) referred to as *D. capensis* a specimen from Oman that van Bree and Gallagher (1978) had reported as "clearly *Delphinus delphis*." This and our sightings data make the status of *D. delphis* off Oman questionable.

Although the taxonomic status of *D. tropicalis* is unclear, we found it clearly separable in the field from both *D. capensis* and *D. delphis*. Heyning and Perrin (1994) suggested that *D. tropicalis* may have a color pattern similar to that of *D. capensis*, but we found *D. tropicalis* lacked both the heavy black stripe coming forward on the sides from the vent and the black or smudgy face patterning often visible among individuals in large schools of *D. capensis*. (These latter features are common among *D. capensis* schools off southern California; Heyning and Perrin 1994; R. L. Pitman, unpublished data). *D. tropicalis* was separable from *D. delphis* by the extreme length of the rostrum alone (even longer than that of *D. capensis*). The overall impression was that *D. tropicalis* has a *D. capensis* body shape (but with a noticeably longer beak) and a *D. delphis* color pattern. These features are clearly evident in an excellent photograph of some live *D. tropicalis* off Oman in Baldwin and Salm (1994, p. 35) and in our photograph in Figure 3.

Tursiops sp.—All of the *Tursiops* that we observed closely appeared to be *T. truncatus*, but because we have little experience in distinguishing the *truncatus* type from the *aduncus* type, we recorded all sightings as *Tursiops* sp. We obtained biopsy samples from 13 individual bowriding *Tursiops* in 6 schools (see Ballance *et al.* 1996a for sampling locations). All were subsequently identified by genetic analysis as *T. truncatus* (Curry 1997).

Stenella longirostris—Most sightings of this species in all oceans have been associated with inshore waters, islands, or banks (Perrin and Gilpatrick 1994), including in the Indian Ocean, prior to our survey (Leatherwood 1985, Leatherwood and Reeves 1989, Small and Small 1990). The exception is the ETP, where large numbers of the two subspecies *S. l. orientalis* and *S. l. longirostris* occur hundreds of miles from the nearest land (Perrin and Gilpatrick 1994).



Figure 3. *Delphinus* cf. *tropicalis* photographed along the northeast coast of Oman, spring 1995.

Norris *et al.* (1985, 1994) suggested that the common association of these oceanic schools of *S. longirostris* with *S. attenuata* may be explained by the spinner dolphins taking advantage of the diurnal attentiveness of the spotted dolphins, thus using the latter species as surrogate islands or bays for protection. Although we occasionally recorded them in mixed-species schools in the WTIO (Table 3), spinner dolphins were recorded in single-species schools far more frequently. Thus, the association in the open ocean apparently is not obligatory.

DISCUSSION

While our survey has added considerably to knowledge of the cetacean community of the oceanic WTIO, the above results and species accounts, combined with previously published information, indicate the need for further research in many areas. The taxonomic status of the genus *Delphinus*, the distribution and taxonomic status of *Balaenoptera musculus brevicauda*, and the population status of *Megaptera* are just three examples. Despite this, it is possible to interpret results of our survey to a great extent through comparisons with other systems.

For example, we should expect that species found in pelagic areas in other tropical oceans will occur in the WTIO, and that they will occur with similar relative abundances. This, in fact, seems to be the general case, and, although we report sighting records in locations where species have not previously been

reported, these are not unexpected (see Jefferson *et al.* 1993) but simply a reflection of the paucity of survey effort in the pelagic WTIO.

We should expect that habitat preferences for a particular species will be fairly constant, regardless of the ocean in which it is found. This expectation is supported by our data on *Delphinus* sp., which, in the ETP, exhibits habitat preferences for "upwelling modified" waters, areas of highly variable oceanographic features where upwelling occurs seasonally (Au and Perryman 1985, Reilly 1990). That common dolphins were highly localized off the coast of Oman (Fig. 1g, Papastavrou and Salm 1990), where upwelling during the Southwest Monsoon is extremely intense in terms of volume and nutrient enrichment (Currie *et al.* 1973, Wyrcki 1973, Sheppard *et al.* 1992), supports the hypothesis that habitat preferences for *Delphinus* may be constant between these two oceans. A similar situation may exist for *Balaenoptera musculus*. In the ETP this species occurs in geographically restricted areas of relatively cool, upwelling-modified waters, high in productivity and standing stocks of euphausiids (Reilly and Thayer 1990), and because of this, it has been suggested that it selects habitats in tropical waters which permit foraging (Reilly and Thayer 1990). Although *B. musculus* has been reported to have a wide distribution in the WTIO (Kasuya and Wada 1990, Alling *et al.* 1990, Small and Small 1990, Yochem and Leatherwood 1994, Zemsky and Sazhinov 1994), there is little information regarding the seasonality of these patterns and, in fact, sightings were highly localized during the months of our survey. Because the WTIO exhibits such a striking seasonal pattern in productivity (Wyrcki 1973; predictable but patchy with respect to large spatial scale), *B. musculus* may track productive areas here just as it appears to do in the ETP.

Finally, we should expect that social behavior (as evidenced by school size and interspecific associations, for example) should be broadly similar across oceans. This too seems largely the case. School sizes vary with ocean but are almost always within the same order of magnitude, and species-specific interactions are largely the same. For example, *Tursiops*, *Grampus*, and *Globicephala* are recorded in mixed-species schools, not only in the WTIO, but in the ETP and GM (Fritts *et al.* 1983, Scott and Chivers 1990, Mullin *et al.* 1994).

These are all examples of how similarities in the ecology of a species that hold across different oceans can be used to infer characteristics of a lesser-known ecosystem, in this case the WTIO. But it is the differences that can lead to new insights. One of these that we believe significant pertains to the three most abundant dolphins.

These three, *Stenella attenuata*, *S. longirostris*, and *S. coeruleoalba* occur in all three systems reviewed here, yet there are intriguing differences in their relative abundance and behavior. Because our survey was conducted during a single year only, largely during the pre-monsoon season, these results could reflect some seasonal or interannual variation, both of which are known to affect dolphin distribution (Reilly 1990, Reilly and Fiedler 1994). We believe it equally likely, however, that these differences are an indication of something more.

Through analysis of an extensive dataset from the ETP, habitat preferences

for the abundant dolphins, the three *Stenella* spp. listed above, and *Delphinus* spp. have been clearly identified. Au and Perryman (1985) outlined a basic dichotomy: *S. attenuata* and *S. longirostris* occur primarily in tropical waters (temperature $>25^{\circ}\text{C}$, salinity $<34\text{‰}$) underlain by a sharp, shallow thermocline ($>2^{\circ}\text{C}/10\text{ m}$ at depths $<50\text{ m}$) with small annual variation in surface temperature, while *S. coeruleoalba* and *Delphinus* spp. occur in equatorial and subtropical waters with highly variable oceanographic features (large seasonal changes in surface temperature and thermocline depth) that are "upwelling modified." Reilly (1990) extended this analysis to find significant differences in habitat preferences for *S. coeruleoalba* versus *Delphinus* spp., with the latter occurring in waters of higher sigma- t values and shallower thermocline depth, but he confirmed that *S. attenuata* and *S. longirostris* had largely overlapping habitat preferences.

However, our results from the WTIO suggest that there may, in fact, be significant differences in the habitat requirements of *S. attenuata* and *S. longirostris*. While *S. attenuata* and *S. longirostris* have largely overlapping ranges in the ETP to the extent that they often co-occur in schools (Wade and Gerrodette 1993, Perrin and Gilpatrick 1994, Perrin and Hohn 1994), in the GM these two species do not form mixed schools, and they exhibit largely parapatric distributions (Jefferson and Schiro 1997; R. L. Pitman, unpublished data). In the WTIO *S. longirostris* is far more widespread and abundant than *S. attenuata*, although the few schools of *S. attenuata* that we recorded regularly mixed with schools of *S. longirostris*. These patterns clearly indicate that these two species have significantly different habitat requirements. We propose that detailed analysis of oceanographic correlates of distribution patterns for *S. attenuata* and *S. longirostris* in the WTIO may identify differences in habitat preferences for this pair.

Further, we believe that comparisons among all three oceans may offer some clues about behavioral differences in these species. Although *S. attenuata* is relatively rare in the WTIO, when it occurs, it behaves similarly to *S. attenuata* in the ETP. Specifically, in the WTIO it regularly schools with *S. longirostris*, regularly associates with surface tunas, and regularly is accompanied by seabirds (Table 3). Similarly, in the ETP it schools with *S. longirostris* in 33.5% of its sightings (Au and Perryman 1985), frequently associates with surface tunas (Perrin and Hohn 1994), and is accompanied by seabirds in 59% of its sightings (and in 96% of sightings of mixed *S. attenuata*-*S. longirostris* schools; Au and Pitman 1986). The situation in the GM is strikingly different. Here, although *S. attenuata* is the most common species, it does not school with *S. longirostris*, does not associate with surface tunas, and is not accompanied by seabirds (R. L. Pitman, unpublished data). We believe that investigation of the oceanographic correlates of these behavior states in the three separate oceans may provide some clues about the mechanisms underlying these associations.

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