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The Behavior and Ecology of the Indo-Pacific Humpback Dolphin (*Sousa chinensis*)

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Abstract

The Indo-Pacific humpback dolphin (*Sousa chinensis*) can be divided into two morphological types: (1) west of India, *plumbea*-type humpback dolphins are dark gray or almost black in color, with a defined "hump" and (2) east of India, in Southeast Asia and Australia, *chinensis*-type humpback dolphins do not possess a "hump" and are often white or very light in color, with or without blue-gray spots and freckles.

Plumbea-type humpback dolphins inhabit coastal waters, bays, and estuaries typically within 0.5 km of the coast, in waters less than 15 m deep. School sizes are small (< 25), although schools of up to 100 have been sighted off Oman. Diurnal patterns and seasonal and tide-related changes in behavior are observed, which have been attributed to changes in seawater temperature and, ultimately, the availability of prey. Feeding behavior tends to be correlated with rocky reefs and rocky shores. Social and sexual behavior, as well as births, occur year-round, but with seasonal peaks (October-May).

The acoustic behavior of the *plumbea*-type humpback dolphin is little known although clicks of 20-25 kHz, "screams" from 3 to 20 kHz, and whistles from 3 to 25 kHz have been reported. Interactions between *plumbea*-type humpback dolphins and a variety of non-cetacean species have been reported, and in Zanzibar mixed groups of humpback and bottlenose dolphins are common. *Plumbea*-type humpback dolphins typically display aversive reactions to boat traffic.

Chinensis-type humpback dolphins are primarily coastal and estuarine, almost exclusively estuarine in the northern parts of their range. Australian dolphins off the Great Barrier Reef were observed at considerable distances offshore (up to 55 km), but always close to shallow water. Inhabited water depth is usually less than 10 m.

School sizes resemble those of *plumbea*-type humpback dolphins, although groups of up to 44 have been observed. The home ranges of individual animals are more compact and less coastal than *plumbea*-type humpback dolphins, varying both by season and year. Seasonal changes in distribution observed in Hong Kong are linked to changes in hydrography of the Pearl River. Diurnal and tide-related changes in behavior also have been noted. Feeding is the predominant behavior noted for *chinensis*-type humpback dolphins in Hong Kong, which is frequently associated with estuarine mixing zones and trawling activities.

Social behavior occurs year-round, but peaks during the same period as calf conception. Calves primarily are born between January and August, with peaks in April/May and August. Epimeletic behavior has been reported in *chinensis*-type humpback dolphins.

Chinensis-type humpback dolphins have been recorded producing whistles of between 1.2 and 16 kHz, and broadband harmonic pulses and low frequency, narrow band "grunts." The spectra of broadband click pulses ranged from 30 to 200 kHz. The sounds produced by these humpback dolphins can be as low as 600 Hz and coincide with frequencies produced by many types of boat traffic.

In Moreton Bay, Australia, humpback dolphins often are observed in mixed groups with bottlenose dolphins (*Tursiops truncatus*), although humpback dolphins do not associate with finless porpoises (*Neophocaena phocaenoides*) in Hong Kong. Associations with fishing trawlers have been noted in China and Australia. Increased dive durations as a result of increased shipping density and avoidance of high-speed vessels have been recorded in Hong Kong. In addition ship-strikes have been a documented cause of mortality in this area. *Chinensis*-type humpback dolphins often are present in areas of high shipping traffic densities and, thus, impacts of boat traffic on this species are a cause for concern.

Despite some very detailed studies in discrete areas (e.g., South Africa and Hong Kong), little is known about the ecology and behavior of either

form of *S. chinensis*. An understanding of their behavior and ecology is essential to any initiative to conserve this species.

Key Words: Indo-Pacific humpback dolphin, *Sousa*, *chinensis*, *plumbea*, behavior, ecology, habitat, feeding, interactions, boat traffic

Introduction

Humpback dolphins are distributed throughout the African and Indo-Pacific region. The exact taxonomic designation of the humpback dolphin is currently under review. Rice (1998) split humpback dolphins into three tentative species: (1) the Atlantic humpback dolphin (*Sousa teuszi*), (2) the Indian humpback dolphin (*Sousa plumbea*), and (3) the Pacific humpback dolphin (*Sousa chinensis*); however, others considered Indian and Pacific humpback dolphins to belong to the same species (i.e., *S. chinensis*), the Indo-Pacific humpback dolphin (Jefferson & Karczmarski, 2001; Ross et al., 1995). In 2002, this single species classification was adopted by the International Whaling Commission (IWC) (2003) and, therefore, this paper uses this latter taxonomic classification.

Indo-Pacific humpback dolphins can be divided into two distinct morphological types: (1) west of India to southern South Africa—*plumbea* type are dark gray in color, with a defined "hump" after which the dolphins are named and (2) east of India, in Southeast Asia, eastern China, and northern Australia—*chinensis*-type humpback dolphins do not possess a "hump" and are often white or very light in color, with or without blue-gray spots and freckles (Jefferson & Karczmarski, 2001; Ross et al., 1995). This paper, therefore, distinguishes between the *plumbea* and *chinensis* types of Indo-Pacific humpback dolphin.

The distribution of Indo-Pacific humpback dolphins, regardless of morphological type, coincides with some of the greatest densities of human population and, as such, these dolphins are exposed to a high number of anthropogenic threats such as fisheries by-catch, pollution, coastal development, and boat traffic. Because of this, there is concern about the status of humpback dolphins (e.g., IWC, 2003; Jefferson, 2000; Karczmarski, 2000; Karczmarski et al., 1998, 2000a; Parsons, 1997, 1998a, 1998c, 1998d, 1999a, 1999b; Parsons & Chan, 1998; Parsons & Jefferson, 2000; Parsons et al., 1999); however, information about the biology, behavior, and ecology of this species is extremely limited and dispersed, although several studies in discrete areas (such as Hong Kong and South Africa) have added considerably to current knowledge.

The above threats must be addressed through conservation actions, but any initiatives to manage and conserve populations ultimately need to be based upon information on the behavior and ecological requirements of a species. To assist in the compilation of this information, this paper reviews and summarizes the current understanding of the behavior and ecology of the Indo-Pacific humpback dolphin, *S. chinensis*.

Habitat Use

Findlay et al. (1992) recorded that all sightings of *plumbea*-type humpback dolphins obtained in dedicated surveys and incidental sightings in South African waters occurred in waters less than 50 m in depth. Saayman & Tayler (1979) described other South African humpback dolphins occupying coastal waters in Plettenberg Bay as being within 250 m of land, just seawards of breaking waves. Karczmarski et al. (1998, 2000a) stated that the Algoa Bay population primarily inhabited waters less than 15 m deep (91.3% of sightings), from 150 m to 400 m from the shore (58.6% of sightings). A small percentage of sighted animals (5.3%) were more than 0.5 km from the coastline, with two groups traveling 1-1.5 km from the coast, but all sightings were in depths of less than 25 m. The distribution of these dolphins was correlated with the presence of natural, rocky, or human-made reefs. Saayman & Tayler (1973) also noted that South African humpback dolphins in Plettenberg Bay associated with isolated reefs and rocky feeding grounds. They also occasionally lingered in the vicinity of sandy gullies caused by localized rip tides, where fish aggregate (Saayman & Tayler, 1979). In Natal, South Africa, most humpback dolphins by-caught in gill nets were captured either at the mouths of large rivers or adjacent to bays, suggesting that these areas are primary habitats for humpback dolphins in this part of South Africa (Cockcroft, 1990).

There was also some suggestion of site fidelity for South African populations. A small number (n=7) of identifiable individuals were repeatedly sighted over a three-year period in Algoa Bay, over a period of nine to 17 months, and approximately half of the identifiable animals were resighted in periods of two to seven months (Karczmarski, 1999). Of the former, more resident animals, 71.6% were adults, of which 80% were female. The remainder of the animals were sighted only once or only within a one month period. Saayman et al. (1972) and Saayman & Tayler (1979) also reported residency in South African humpback dolphins, with specific animals being sighted in Plettenberg Bay year-round and over a period of three years, despite fluctuations in environmental factors such as sea surface temperature.

Karczmarski (2000) hypothesized that humpback dolphin site fidelity may be greater in areas where prey density is greater. Moreover, because site fidelity appeared to be linked to the reproductive stage of females, Karczmarski (1999) suggested that site fidelity or "residency," at least in the context of Algoa Bay, is the result of calves limiting their mothers' movements and activities to a small area which were dubbed "nurseries" (Karczmarski, 2000).

Outside of South Africa, information on habitat use is sparser. In Matupu Bay, Mozambique, humpback dolphins are observed in shallow waters, with animals moving along tidal channels and feeding over coral reefs and seagrass beds, or sheltered areas where they can use the bottom topography to increase their feeding efficiency (Guissamulo & Cockcroft, 2004). Karczmarski (2000) stated that similar patterns of habitat use also are exhibited by humpback dolphins in the lagoon systems of Lamu in Kenya.

Humpback dolphins in Djibouti inhabited waters less than 35 m deep, typically with marine vegetation-covered sandy seabed (Robineau & Rose, 1984). Pilleri & Gihr (1974) encountered the species 800 m to 1.6 km offshore in the Strait of Hormuz (Arabian Gulf) in waters <10 m deep, and in shallower waters (*ca* 2-4 m) adjacent to Hormuz and Qishm Islands. Also in the Arabian Gulf, Keith (2002) noted that humpback dolphins in Saudi Arabian waters were confined to similar depths (< 10 m) and within 1 km of the shore.

Baldwin et al. (2004) highlighted that although elsewhere in the Arabian region humpback dolphins are associated with a soft-sediment seabed, shallow waters, and a low energy shoreline, in parts of Oman, humpback dolphin distribution coincides with rocky, high-energy shorelines, and animals have been encountered in waters greater than 40 m in depth.

Pilleri & Gihr (1974) described *plumbea*-type dolphins in the Indus Delta, Pakistan, inhabiting waters adjacent to mangroves (i.e., as close as 0.5 m), at a depth of 1.5 m; however, the species were not observed by the same authors associating with mangroves in the Arabian Gulf. Although many species reviews and summaries mention *Sousa* spp. inhabiting mangrove areas (e.g., Klinowska, 1991), the Pilleri & Gihr (1974) reference to the Indus Delta is the only actual published example of this type of habitat use.

All *plumbea*-type humpback dolphins observed by Parsons (1998a) in Goa, India, were coastal or associated with an estuary. Coastal animals were within 3-4 km from the coast or within 8 km of the mouth of a river, and all animals were sighted in waters less than 10 m deep.

In China, Wang (1984) described *chinensis*-type humpback dolphins as associated with river mouths, with examples of animals swimming tens of kilometres upstream in the Jiulong and Pearl Rivers. Moreover, Zhou et al. (1997) recorded *S. chinensis* stranded on a sandbank several kilometres upstream in the Yangtze River, and there are records of animals from Hensha Island and Rugao County, near the mouth of the Yangtze (Jefferson, 2000). Hershkovitz (1966) recorded the species "750 miles up the Yangtze at least as far as Hankow," but this is a mistake dating from an earlier misidentification of the baiji or Yangtze River dolphin (*Lipotes vexillifer*) as a humpback dolphin (see Jefferson & Hung, 2004). Wang & Han (1996) reported a specimen being captured in Zhaoqing City more than 300 km from the mouth of the Pearl River Estuary, although the reliability of this information cannot be confirmed.

The comprehensive surveys by Jefferson (2000) on humpback dolphin distribution in Hong Kong and neighbouring Lingding Bay demonstrated that the dolphin occurred in areas that were influenced by the freshwater output of the Pearl River and emphasised that no dolphins were observed in areas that had no estuarine influence. This pattern of estuarine habitat use appears to be typical of Chinese humpback dolphins (Zhou et al., 1995) and in neighbouring *chinensis*-type populations, as sightings of humpback dolphins in Vietnam in an estuarine area at the mouth of the Nam Trieu River reinforces (Smith et al., 2003), although this latter study did note a dolphin encounter in shallow waters (< 20 m) several km more offshore than their typical distribution.

Parsons (1998b) suggested that *chinensis*-type humpback dolphins' pattern of estuarine habitat use may be due to aggregations of prey species in the estuaries' freshwater/saltwater mixing zones or possibly to avoid predation by certain species of shark that are unable to inhabit freshwater.

Jefferson (2000) noted that humpback dolphins in Hong Kong did not use any specific part of their range for particular class of behavior; socializing was equally likely in any part of the species habitat. Even so, the research conducted in Jefferson (2000) did not specifically involve behavioral studies on habitat use, and use of specific areas by dolphins was not tested for. It was noted, however, that humpback dolphin density was higher in deep water channels, which unfortunately also are major shipping routes; the dolphins were consequently exposed to high levels of shipping traffic.

Individual Hong Kong dolphins have different ranges; some animals were only sighted in Hong Kong waters north of Lantau Island, some only in the Chinese waters of Lingding Bay adjacent to Hong Kong, whereas others were much more wide-roaming (Jefferson, 2000). Hung & Jefferson (2004) calculated that individual humpback dolphins in Hong Kong occupied home ranges of 24-304 km^2 (with a mean range size of 99.5 $km^2 \pm 61.04$ km^2), with these home ranges consisting of irregular polygons with linear ranges of only a few tens of kilometres. This is in stark contrast to the habitat use and home range patterns of South African humpback dolphins, which are more coastal, occupying home ranges consisting of narrow strips of coastal waters with linear distances of over 100 km (Karczmarski, 1999; Karczmarski et al., 1999). Hung & Jefferson (2004) also stated that there were annual and seasonal variations in home ranges of individuals and, although not statistically significant, the ranges of sub-adult animals tended to be smaller (80.7 $km^2 \pm 61.04$ km^2) than those of adults.

Corkeron (1990) described Australian humpback dolphins inhabiting waters of a mean depth of 9 m at an average distance of 6 km offshore. Humpback dolphins also were encountered associating with bottlenose dolphins *(Tursiops truncatus)* in slightly deeper waters closer to shore, in habitats more normally utilized by bottlenose dolphins. Lear & Bryden (1980) also noted Australian humpback dolphins present in waters 5 km from the coastline.

Corkeron et al. (1997), from surveys of the Great Barrier Reef, reported humpback dolphins ranging up to 55.6 km from the Australian coast, with a mean distance of 6.6 km (± 1.26 SD). Despite these distances from the coast, the mean distance of these dolphins to the nearest shallow area (either land or a reef) was only 2.6 km, with a maximum distance of 8.1 km away from one of these shallow areas.

School Size

A high proportion of *plumbea*-type humpback dolphins encountered in South Africa are solitary animals. For example, Karczmarski (1999) reported 15.4% of animals to be solitary in Algoa Bay. This degree of solitary behavior is much more common than in other coastal small cetacean species (e.g., Wells et al., 1980, 1987). This is reinforced by sightings of humpback dolphins from Goa, India, where solitary animals accounted for 40.7% of dolphin sightings (Parsons, 1998a).

The size of *plumbea*-type humpback dolphin schools tends to be small in the several locations studied to date, typically less than 20 animals and often a dozen or less (Table 1). In Maputo Bay, Mozambique, mean school sizes were slightly larger than documented in South Africa, which was attributed to smaller groups coalescing in deeper waters during periods of low tide (Guissamulo & Cockcroft, 2004). Despite the majority of schools being less than 20 animals off of Oman (Table 1), more than ten humpback dolphin schools have been sighted off the Arabian Sea coast of the country containing 30 or more animals, including three schools of over 50, and one school of approximately 100 animals. Large schools of more than 30 animals also have been sighted off northern Oman (Baldwin et al., 2004) and in the offshore waters of the United Arab Emirates (Baldwin, 1995). These large schools may form as the result of several smaller groups coalescing for breeding (Baldwin et al., 2004). Large schools of humpback dolphins such as those described above are, to date, unique to the Arabian region.

In Plettenberg Bay, South African school sizes varied seasonally from 3.91 (± 1.07 SE) to 13.6 (± 2.11 SE), with significantly larger groups in the winter than in the spring (Saayman & Tayler, 1979). Conversely, in Algoa Bay, significant increases in group size were observed in the summer and late winter, which in turn were correlated with increases in sea surface temperature (Karczmarski et al., 1999); however, school sizes in Mozambique did not change significantly throughout the day, between months, nor between seasons (Guissamulo & Cockcroft, 2004).

Up to a third of school members in Algoa Bay, South Africa, were considered to be calves (range: 0% to 33%; mean: 14%) and, furthermore, schools containing calves were significantly larger (mean size: 10) than schools without calves (mean size: 4.7) (Karczmarski, 1999).

Karczmarski (1999) described associations between pairs of dolphins as frequently changing, with one animal associating with 55 different affiliates, although there were certain possible combinations and associations between animals that never were observed during the three-year study period. To date, this is the only published study to investigate the dynamics of *plumbea*-type dolphin groups.

As with *plumbea*-type humpback dolphins, *chinensis*-type dolphins are predominantly sighted in small schools (Table 1), with researchers noting that most encounters were with solitary or pairs of animals (Huang & Chou, 1995; Jefferson, 2000; Parsons, 1998b). Larger schools of up to 44 animals were sighted by Jefferson (2000) when boat surveys were conducted in Lingding Bay, adjacent to Hong Kong.

No significant seasonal changes in *chinensis*-type dolphin school size have been observed (Jefferson, 2000); however, researchers in Hong Kong noted that schools of dolphins pursuing

Table 1. Indo-Pacific humpback dolphin school sizes

Location		Range	Mean	Reference
S. plumbea				
South Africa	Algoa Bay	1-24	7.0 ± 2.52 SE	Karczmarski, 1999
				Karczmarski et al., 1998
	Plettenberg Bay	1-25	6.0 ± 1.40 SE	Saayman & Tayler, 1973
			6.5 ± 0.38 SE	Saayman & Tayler, 1979
	coast		6.8 ± 1.94 SD*	Findlay et al., 1992
			4.8 ± 3.04 SD**	
Mozambique			14.0 ± 7.32 SD	Guissamulo & Cockcroft, 2004
Saudi Arabia		1-15	-	Keith, 2002
Oman		1-20 +	11.0 ± 14.40 SD	Baldwin et al., 2004
Djibouti	Djibouti Harbor	<6	-	Robineau & Rose, 1984
Persian Gulf		4-20	-	Mörzer Bruyns, 1960
		<16	5-6	Pilleri, 1973
India	coast	4-20	-	Mörzer Bruyns, 1960
India	Goa	1-9	2.6 ± 2.12 SD	Parsons, 1998a
Sri Lanka		30 [#]	-	Leatherwood et al., 1984
S. chinensis				
China	Fujian Province	-	3-5	Wang, 1984
	Xiamen	1-9		Huang & Chou, 1995
	Hong Kong	1-13[†]	2.6 ± 2.55 SD[†]	Parsons, 1998b
		1-7[‡]	3.1 ± 1.46 SD[‡]	Parsons, 1998b
		1-23+	3.1 ± 12.29 SD	Jefferson, 2000
Australia	Moreton Bay	1-9	2.4 ± 1.13 SD	Corkeron, 1990
	Amity Point	1-10	5.0 ± 1.00 SD	Van Parijs & Corkeron, 2001a

* Value for dedicated surveys
** Value for incidental sightings
+ NB schools of up to 100 (Oman) and 44 (China) animals have been sighted (see text)
[#] Approximate estimate for one sighting
[†] Values from land-based surveys of northern Hong Kong waters
[‡] Values from land-based surveys of southern Hong Kong waters

fishing trawlers were significantly larger than schools engaged in any other kind of behavior (Jefferson, 2000; Parsons, 1998b). Jefferson (2000) also noted that group compositions varied significantly in different areas of Hong Kong, with high proportions of juveniles being recorded in Deep Bay and south of Lantau Island (i.e., in Hong Kong, juvenile humpback dolphins tended to occur more in the periphery of the humpback dolphins' habitat) (Jefferson, 2000).

In terms of school structures, Jefferson (2000) is the only published research for *chinensis*-type dolphins. In Hong Kong, dolphins exhibited very fluid, fission/fusion group dynamics, with most individuals never, or rarely, appearing in the same group (except for mothers and calves).

In summary, school sizes for both types of Indo-Pacific humpback dolphin are similar, although this seems to vary according to habitat, behavior, and the abundance of food sources (Shane et al., 1986). The fact that Indo-Pacific humpback dolphin group size is similar to that of other dolphins species inhabiting a coastal and estuarine environment (e.g., 5-7 animals in *Tursiops truncatus*) (Wells, 2003; Wells et al., 1987) emphasizes this.

Diurnal and Tide-Related Behavior Patterns

Plumbea-type humpback dolphins in Algoa Bay, South Africa, frequently were sighted in the morning, with occurrence decreasing at midday, then increasing in the evening during winter months (Karczmarski & Cockcroft, 1999; Karczmarski et al., 1998, 2000b). This diurnal pattern was suggested to follow cycles of occurrence of prey species (Karczmarski, 1996), and it was noted that the observed frequency of feeding behavior followed a similar pattern to changes in abundance (Karczmarski et al., 1998). Incidence of traveling behavior was highest in the afternoon (Karczmarski & Cockcroft, 1999). There was no observed diurnal pattern to the size of humpback dolphin groups, however. Karczmarski & Cockcroft noted that there was a tendency towards an increase in feeding behavior at high tide, but there was no effect of tidal state on the other behavior, nor group size, of these dolphins (Karczmarski et al., 1998, 2000a).

Saayman & Tayler (1979) noticed that in Plettenberg Bay, feeding periods tended to be longer in the early part of the day. In addition, they noted an increase in feeding activity and resting periods and a decrease in traveling during the flood tide, continuing until two hours after high tide, a period they associated with a greater abundance of prey. All activities other than traveling decreased with the ebbing tide, with traveling behavior at a peak and all other behaviors at a minimum at low tide.

In Hong Kong, the tidal cycle affected *chinensis*-type humpback dolphin abundance near shore, with sighting frequency being significantly greater during the ebb tide: 70-75% of sightings occurred during the ebb tide. Different diurnal patterns of abundance also were noticed at different survey sites. Humpback dolphin sightings were greatest in the morning at a northern, more estuarine site, whereas they were greatest in the afternoon in more southern, less estuarine waters (Parsons, 1998b).

Diurnal and tidal changes in group size, occurrence, and behavior likely reflect changes in food resources, and diurnal variations in cetacean behavior and distribution are commonly observed in a variety of species (e.g., Sekiguchi, 1995; Shane et al., 1986; Wells et al., 1980) into which Indo-Pacific humpback dolphins can be included.

Seasonal Behavior Patterns

Ross et al. (1994), in their review of humpback dolphins, stated that there was no evidence of them showing any seasonal migrations; however, subsequent research has demonstrated that populations of this species do in fact show seasonal changes in distribution and behavior. For example, in Algoa Bay (South Africa), *plumbea*-type humpback dolphin abundance increases in the summer (October-April) and late winter (August-September) (Karczmarski, 1999; Karczmarski et al., 1998, 1999). This reinforces the findings of earlier studies in the area, which also noted an increase in the rate of sightings in the bay during this period (Ross, 1984). These changes in abundance were linked with fluctuations in seawater temperature (Karczmarski et al., 1998, 1999). Moreover, feeding behavior was more frequently observed in the winter months (May-July) and social behavior increased in the summer (October-December) (Karczmarski & Cockcroft, 1999).

Another South African humpback dolphin population in Plettenberg Bay did not display any significant seasonal changes in abundance, although dolphins stayed within the bay for significantly longer periods in the winter (May-July) than in the spring (August-September), with animals being less restricted to the bay in spring. Moreover, as mentioned above, group sizes were significantly larger in the winter than in the spring (Saayman & Tayler, 1979). There appears to be a slight increase in humpback dolphins in Kwazulu-Natal (South Africa) in the summer/autumn months based on incidences of humpback dolphin by-catch in shark nets, although catches occur year-round, demonstrating a year-round residence of this species in the Natal inshore zone (Cockcroft, 1990).

Guissamulo & Cockcroft (2004) suggested summer influxes of humpback dolphins into areas of Maputo Bay, Mozambique, which was linked to seasonal changes in river discharges and salinity, and, hence, increased availabilities of humpback dolphin prey species in part of the bay.

Lal Mohan (1988) reported on a peak in by-catches of *plumbea*-type humpback dolphins off the west coast of India between the months of October and December, which accounted for 63.6% of the annual catch of this type of dolphin. Although these data should be treated with caution because the total number of by-caught dolphins included in the dataset was low (n=11), it still represents the only data on possible seasonal changes in abundance for *plumbea*-type dolphins in the eastern Indian Ocean.

Wang (1984) stated that *chinensis*-type humpback dolphins occur seasonally in Fujian Province, China, from February to May, at the mouth of the Min River in the Mei Zhou, Quan Zhou and Tong Shan Bays. Wang also mentioned the species occurring in Xiamen Harbor year-round, which was affirmed by Huang & Chou (1995).

In Hong Kong waters, humpback dolphins are present year-round (Parsons et al., 1995), although Parsons (1998b) reported changes in their abundance throughout the year, with the frequency of dolphin sightings from southern Lantau Island, Hong Kong, being significantly greater during the summer (May-September). These changes were significantly correlated with water temperature and salinity; however, there was no significant seasonal change in abundance recorded in a more northern, more estuarine survey site. Data gathered from boat surveys in Hong Kong and the adjacent waters of Lingding Bay also indicated seasonal changes in dolphin abundance (Jefferson, 2000); in the winter, animals were more evenly spread;

in the spring and autumn, there was a slight shift to the east (the Hong Kong side of the Pearl River estuary), but in the summer there was a dramatic southward shift in Lingding Bay, with areas of previously high dolphin density in the winter (i.e., Neilingding Island) becoming relatively devoid of dolphins.

Photo-identification data gathered by Jefferson (2000) also showed that dolphins observed south of Lantau Island in the summer shifted out of Hong Kong territorial waters, presumably into Lingding Bay, for the rest of the year (when the seasonal increase in sightings subsided), rather than into other parts of Hong Kong.

The Pearl River, the largest in southern China, has a dramatic effect on the hydrography of the region, notably with regard to turbidity, salinity, pH, tides, currents, and temperature of the waters of Hong Kong and Lingding Bay (Shen, 1983); consequently, the dramatic increase in its freshwater output during the summer also changes fish distribution, which in turn influences the abundant distribution of Hong Kong's humpback dolphins.

Diving and Surfacing Behavior

Plumbea-type humpback dolphins surface in a characteristic rolling manner, often hitting the water with their rostrum, particularly in young animals. Karczmarski et al. (1997) described their surfacing behavior as stereotypical, with the rostrum rising steeply above the water before the melon broke the surface of the water, and with most of the rest of the body remaining submerged when the blowhole was open barring a small proportion of the anterior dorsal surface and the anterior portion of the animal's hump. This stereotypical behavior is common to humpback dolphins everywhere, although Parsons (1998a) noted that humpback dolphins off Calangute, India, rolled slightly to one side when diving, so that when the dorsal fin first entered the water it was approximately 45° to the vertical. Mean inter-surfacing intervals for both types of humpback dolphins are summarized in Table 2.

Feeding Behavior

As would be expected, considering the habitat of *plumbea*-type humpback dolphins as described above, prey consumed tend to be coastal reef-dwelling or estuarine species (e.g., Barros & Cockcroft, 1991, 1999; Ross, 1984).

Feeding was the most commonly reported class of humpback dolphin behavior observed in Algoa Bay, South Africa: 46% of encountered animals

Table 2. Inter-surfacing intervals in Indo-Pacific humpback dolphins according to the category of behavior exhibited

Location	Behavior	Range (sec)	Mean duration (sec) ± SD	Reference
S. plumbea				
South Africa Algoa Bay	Feeding		25.6 ± 17.30	Karczmarski & Cockcroft, 1999
	Opportunistic feeding		30.1 ± 11.80	
	Slow traveling		23.3 ± 7.10	
	Fast traveling		8.6 ± 4.10*	
South Africa (Plettenburg Bay)	Diving on reefs	180+		Saayman & Tayler, 1979
S. chinensis				
China (Hong Kong)	Milling	2-434	49.4 ± 55.58	Parsons, 1998b
	Traveling	5-230	38.5 ± 33.43	
	Various	10-277	28.7 ± 32.23	Jefferson, 2000
	Various	6-124	20.8 ± 19.43	Ng & Leung, 2003
	Boat association			
	Close (< 200m)		30.2 ± 26.94	
	Intermediate (200-500 m)		23.1 ± 24.10	
	Far (500 m-1 km)		19.9 ± 13.77	
	No boat association		17.7 ± 15.29	

*Mean interval for 4-9 rapid ventilations, which was followed by a long period (101.3 sec. ± 20.90) of submergence were feeding, and a further 18% fed opportunistically (i.e., they interrupted their previous behavior to chase or dive for fish) (Karczmarski & Cockcroft, 1999). Their foraging behavior showed diurnal and seasonal patterns, as noted above, with increased feeding in the morning and the evening (Karczmarski, 1996) and more time spent feeding during the winter (Karczmarski & Cockcroft, 1999). Feeding behavior also was correlated with the presence of rocky reefs (Karczmarski et al., 1998). Large groups were widely dispersed when feeding with distances of 1-100 m between individuals (Karczmarski & Cockcroft, 1999), although individuals in smaller feeding groups (< 7 animals) remained fairly close to each other, 1-20 m. Cooperation between individuals when feeding was limited (Karczmarski et al., 1997).

Elsewhere in South Africa, Saayman & Tayler (1979) noted that humpback dolphins in Plettenberg Bay altered their feeding behavior after a drop in water temperature; animals started hunting in shallows (as opposed to around rocky reefs), and they exhibited more jumps and high-speed chasing, often swimming with their ventrum uppermost. This change in behavior was attributed to offshore cold water bodies driving pelagic, warm-water fish species into Plettenberg Bay.

Peddemors & Thompson (1994) described an interesting feeding behavior for humpback dolphins in the tidal channels of the Bazaruto Archipelago, Mozambique. Here, humpback dolphins chase fish into shallow waters and sandbanks, where opportunities for the fish to escape are restricted, with the animals beaching intentionally while in pursuit of the fish. To date, exhibition of this beaching behavior by humpback dolphins is unique to this area.

On the other side of the Indian Ocean, Parsons (1998a) reported that feeding dolphins in Goa, India, were associated with the freshwater/saltwater mixing zone that was clearly visible at the mouth of an estuary.

Tactics for catching fish species are little known, but Saayman & Tayler (1979) described humpback dolphins in South Africa seizing prey species behind the neck, manipulating the prey with their tongue, and swallowing the fish head first.

In Hong Kong, feeding was the most commonly observed behavior for *chinensis*-type humpback dolphins at Castle Peak, with 55% of encounters showing some aspect of this. Most foraging dolphin groups at Castle Peak (41.2%) were seen either at or adjacent to the seawater/freshwater mixing zone, which was clearly visible to the naked eye (Parsons, 1998b).

Moreover, 16% of encountered dolphin groups at this site were pursuing fishing trawlers (Parsons, 1998b). Jefferson (2000) also reported humpback dolphins following trawlers; 3.2% of sightings were associated with shrimp or small trawlers, and 12.1% of sightings were associated with pair trawlers. Pair trawler associations could last more than two hours, with the animals swimming at speeds of 1.99 m/s (± 1.1 SD) or 7.2 km/h, and both researchers noted that groups following these trawlers were significantly larger than other groups observed in Hong Kong (Jefferson, 2000; Parsons, 1998b).

Barros et al. (2004) noted that stomach content analyses have shown that although dolphins do consume some species of croaker (Sciaenidae) that commonly are caught by pair trawlers, many of the species harvested (e.g., cardinal fishes [Apogonidae], crustaceans, and cephalopods) are nearly absent from the diet of the Hong Kong dolphin population. One explanation for this possible contradiction was that not all humpback feed behind pair trawlers, and perhaps this behavior may be a specialized feeding technique that is only utilized by part of the population.

The dolphins in Hong Kong seemed actively to seek out the trawlers, and Jefferson (2000) noted that one animal was observed heading at high speed towards a pair trawler from a distance of about one km away. Photo-identification data, however, showed that some individual dolphins were more likely to engage in this behavior than others, with some animals never being observed chasing trawlers and others ("pair trawler junkies"), essentially always being associated. Associating with fishing trawlers also has been described for *chinensis*-type humpback dolphins elsewhere in the world, notably prawn trawlers in Moreton Bay in Australia (Corkeron, 1990; Hill & Wassenberg, 1990; Wassenberg & Hill, 1990).

Unsuprisingly, considering its habitat, prey species that have been reported to be consumed by humpback dolphins in Hong Kong are primarily estuarine, frequently demersal, fish (Barros et al., 2004); a pattern which is echoed in studies conducted in other parts of China (e.g., Wang & Sun, 1982; W. Wang, 1995).

Social Behavior

Karczmarski & Cockcroft (1999) noted that 6% of observed *plumbea*-type humpback dolphins in Algoa Bay, South Africa, were engaged in social behavior. These authors also noted that the frequency of social behavior was doubled in the summer (October-May). In step with this increase in social behavior, the incidence of sexually orientated behavior also increased in the summer months. Social behavior in these animals was not restricted to any particular area or habitat (Karczmarski et al., 2000a).

Saayman & Tayler (1973) described a variety of social behaviors exhibited by humpback dolphins in Plettenberg Bay, including leaping, airborne cartwheels, chasing, rubbing against and mouthing each other, and striking each other with their flukes. These behaviors were associated by the authors with courtship and "greetings," the latter because these social behaviors were often observed when groups and individuals first came together.

In Hong Kong, there also appeared to be a seasonal variation in the number of social interactions observed between *chinensis*-type humpback dolphins, with frequency of social behavior increasing between August and November (Parsons, 1998b). This increase in social behavior also was noted by Jefferson (2000). The peak in social behavior was not correlated with either season or changes in salinity and temperature; however, it was positively correlated with the level of dolphin abundance (i.e., socializing occurred when abundance increased) (Parsons, 1998b), and Jefferson (2000) linked the increase in social behavior with an increase in calf conception in August.

Play Behavior

Saayman & Tayler (1979) recounted an incident where a juvenile South African humpback dolphin was seen repeatedly holding a seashell in its mouth. The juvenile was surrounded by other, older animals, and the juvenile would repeatedly throw the shell with its rostrum. Then, all the dolphins present would be seen diving, presumably after the shell. When the animals resurfaced, the juvenile always would be seen holding the shell in its mouth.

Two dolphins also were observed "playing" with a fish (thought to be *Trachinotus blochi*). One animal held the fish midway across the body and took it 90 m from the rocky coastline then released it; the fish swam towards the rocks. As it neared them, the dolphins would accelerate, recapture the fish, take it out further, and repeat the process (Saayman & Tayler, 1979).

Although in an unnatural environment, a humpback dolphin from western India kept in captivity was observed playing with various items in its pool, including pieces of plastic and rope, flicking the items with its rostrum and taking them to the side of the pond in which it was being held (Lal Mohan, 1983).

Epimeletic Behavior

Epimeletic, or care-giving, behavior is frequently observed in cetaceans (Caldwell & Caldwell, 1966). The first mention of humpback dolphins exhibiting "succourant behavior," a subcategory of epimeletic behavior wherein care and attention is directed towards injured or distressed group members, appears in Huang et al. (1978), for *chinensis*-type humpback dolphins in China. There is one anecdotal report of this type of behavior in Hong Kong: a male humpback dolphin was attended by several other dolphins for a whole morning until the animal died and stranded (Parsons, 1998b). Parsons also recounted two other cases of epimeletic behavior in Hong Kong, and on both occasions, "nurturant" (Caldwell & Caldwell, 1966) behavior was exhibited: an adult, and group of adults, attending the corpses of dead calves. Fertl & Schiro (1994) commented on the carrying of dead calves by several cetacean species, although Dudzinski et al. (2003) noted that attending dead animals need not necessarily be reflective of epimeletic behavior. Nonetheless, the incidents described in Parsons (1998b) are the first examples of this attending behavior occurring in humpback dolphins.

Allomaternal care (the care of a calf by a female other than its mother) is another type of epimeletic behavior reported in cetaceans (e.g., Arnbom & Whitehead, 1989). Both Saayman & Tayler (1979) and Karczmarski et al. (1997) remarked upon South African humpback dolphins possibly engaging in allomaternal care of offspring, with Karczmarski et al. (1997) describing temporary groupings of females with mother-calf pairs, presumably to help nurture and protect humpback dolphin calves.

Traveling and Resting Behavior

A quarter (24%) of *plumbea*-type humpback dolphin schools in Algoa Bay, South Africa, were occupied in "traveling" behavior (Karczmarski & Cockcroft, 1999), that is to say, persistent directional movement, usually with group members surfacing synchronously. In Algoa Bay, individuals in a traveling school traveled in "single file" with a distance of up to 2.5 m between animals and the positions of animals within the school changing frequently. Traveling behavior in these dolphins was higher along open stretches of coastline, over sandy seabed, and in areas with extensive human activity (Karczmarski et al., 2000a).

As mentioned above, traveling behavior was more frequently observed in Algoa Bay animals in the afternoon (Karczmarski & Cockcroft, 1999), and these humpback dolphins traveled up to 110 km to the neighboring St. Francis Bay (Karczmarski et al., 1998). Traveling dolphins in Plettenberg Bay followed habitual routes close to the shore, just seaward of breaking waves (Saayman & Tayler, 1973) at speeds of 80.6 m/min (± 5.5) (Saayman & Tayler, 1979).

Dolphins were observed resting motionless in 2% of encounters in Algoa Bay (Karczmarski & Cockcroft, 1999) and 9% of encounters in Plettenberg Bay (Saayman & Tayler, 1979). Resting behavior varied significantly throughout the day and peaked in the early afternoon (Karczmarski & Cockcroft, 1999).

By comparison, 72% of Indian humpback dolphins observed off Goa were traveling (Parsons, 1998a). Indeed, all of the animals observed off Calangute Beach were engaged in this behavior, suggesting that the particular study site was an area that the animals merely transited on their way to feeding areas, such as the mouth of the estuary to the south of the site. Moreover, the traveling animals off Calangute were mainly observed in the morning, a pattern of occurrence which was supported by anecdotal information gathered from local fishermen (Parsons, 1998a).

A similar proportion of traveling *chinensis*-type dolphins, to Algoa Bay (*plumbea*-type) dolphins, was observed in one estuarine site in northern Hong Kong (21%); however, the proportion of traveling dolphins was much higher at a site situated in southern Hong Kong waters (41%). Traveling schools of humpback dolphins in Hong Kong ranged from one to six individuals with mean school sizes of 2.14 (± 1.37 SD) to 2.28 (± 0.58 SD) (Parsons, 1998b). Although there are periods of lower activity during which animals may be obtaining rest, humpback dolphins in Hong Kong have not yet been seen to exhibit obvious and distinct "resting" behavior (Jefferson, 2000; Parsons, 1998b).

Reproductive Behavior

Karczmarski (1999) noted that in Algoa Bay, South Africa, 70% of *plumbea*-type calves were born in the summer (October-May), although births occurred throughout the year. This peak in reproduction also coincided with an increase in school size. This pattern also was observed in Plettenberg Bay; they noted year-round births, but 65.3% of these occurred between December and February (Saayman & Tayler, 1979).

Mating behavior was observed in Plettenberg Bay year-round (Saayman & Tayler, 1979). In Algoa Bay, "courtship" and mating behavior occurred in varying school sizes (4-16), containing all age classes, and the number of animals actually involved in courtship activities ranged from two to six, and these individuals usually became isolated from the rest of the group and circled at high speed (Karczmarski et al., 1997). Despite several animals being involved in these courtships groups, only two animals were observed actually mating at one time. Juveniles also engaged in courtship and sexual behavior, although the bouts lasted only two or three minutes, with copulation lasting no longer than two or three seconds.

For the rest of the Indian Ocean, data on *plumbea*-type dolphin reproductive behavior is scarce. In Maputo Bay, Mozambique, as in South Africa, year-round births were also reported with no distinct breeding season observed (Guissamulo & Cockcroft, 2004).

In Djibouti, a newborn humpback dolphin was reported in October (Robineau & Rose, 1984), while Pilleri & Gihr (1974) and Zbinden et al. (1977) observed presumed mating behavior off of Qishm Island, Arabian Gulf, in January. The only other data comes from a *plumbea* foetus from the southwestern coast of India examined by Lal Mohan (1982), which was estimated to have been conceived in April.

Based on examinations of dead animals, W. Wang (1995) estimated that in China (*chinensis*-type), humpback dolphins from Xiamen gave birth between April and June, with a gestation period of 10 to 12 months. P. Wang & Sun (1982) reported most calves being born from March to April, although calves also were seen outside of this period. Jefferson (2000) stated that calves were observed throughout the year in Hong Kong, but few calves were seen during the winter months. A peak in observed social/sexual behavior also was reported in the late summer/autumn in this study area. Based on examination and extrapolation of birth dates of stranded calves and foetuses, 92% of calves were reported to be born between January and August, reinforcing the low incidence of calf observations outside this period, as mentioned above. Jefferson also noted that there was a peak in births of Hong Kong humpback dolphin calves in April/May and August.

Acoustic Behavior

Zbinden et al. (1977) described three types of underwater sounds from *plumbea*-type humpback dolphins in the Indus Delta:

1. *Clicks:* Single pulses with a main energy component at 20-25 kHz.
2. *Whistles:* Sinusoidal frequency-modulated sounds of varying length, with a frequency range of 3-25 kHz.
3. *Screams:* Unpulsed sounds with a harmonic structure, usually frequency-modulated, with a frequency range of 3-20 kHz.

The recording equipment used in Zbinden et al. (1977) was only capable of recording low frequency sounds and, thus, any higher frequency sounds that the dolphins may have produced would not have been documented. There are no other published data on the acoustic behavior of *plumbea*-type humpback dolphins.

Schultz & Corkeron (1994) reported *chinensis*-type humpback dolphins whistling in the frequency range of 1.2-16 kHz in Australian waters, and described these as similar to those produced by bottlenose dolphins, although of a shorter duration and higher overall frequency. Van Parijs & Corkeron (2001a, 2001b) described humpback dolphin acoustics in Australian waters in more detail, noting that they produced broadband click trains (12-22 kHz with a click rate of 23 clicks/sec. and a duration of 0.6-44.9 sec.), which were predominantly associated with foraging behavior (76% of occasions) and burst pulses. The latter were divided into "barks" and "quacks."

"Barks" ranged in frequency from a minimum of 0.6-11 kHz to more than 22 kHz, with a duration of 0.2 to 7.4 sec., and comprised 1-22 harmonics (Van Parijs & Corkeron, 2001a). These "barks" were primarily reported during foraging (44% of encounters) or socializing (47%) and were similar vocalizations to those described in other delphinids (e.g., Ford & Fisher, 1983; Herzing, 1996; Popper, 1980) albeit of a slightly higher frequency (Van Parijs & Corkeron, 2001a).

"Quacks" were low frequency (0.6-3.7 kHz) broadband harmonic sounds of slightly shorter duration than "barks" (0.08 to 2.7 sec.); they were primarily associated with socializing (63% of encounters), although they also were recorded during foraging behavior (37%) (Van Parijs & Corkeron, 2001a). In addition, "grunts" were also low frequency (0.9 ± 0.3 kHz to 1.4 ± 0.4 kHz), narrowband sounds of short duration (0.09 ± 0.03 sec), and seventeen types of whistles were recorded (Van Parijs & Corkeron 2001a, 2001b).

Two types of whistles were most predominant among seventeen whistles (Van Parijs & Corkeron, 2001a), and both of these in turn resembled the two most dominant whistle types reported from bottlenose dolphins (*Tursiops truncatus*) in McCowan & Reiss (1995a, 1995b). Furthermore, Van Parijs & Corkeron (2001a) noted that whistles were frequently produced in association with social behavior and in a context exactly the same as in other delphinid species, notably Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (Herzing, 1996; Tyack, 1999).

In addition to the data provided in the two studies mentioned above, a single Australian humpback dolphin was reported in Van Parijs & Corkeron (2001c) as producing whistles from 5.2 to 15.5 kHz and broadband clicks from 2 to 22 kHz. These whistles often were produced in response to the handling of the animal in question. Due to the nature of the calls, Van Parijs & Corkeron suggested that humpback dolphins may possess individual-specific calls or "signature whistles" (see Caldwell & Caldwell, 1965); however, due to a recent study that may throw doubt on the signature whistle hypothesis (i.e., McCowan & Reiss, 2001), the researchers subsequently expressed their reservations as to the role of these whistles (Corkeron & Van Parijs, 2002).

The characteristics of Hong Kong humpback dolphin echolocation clicks were described by Goold & Jefferson (2004). Clicks were produced as broadband pulses, similar to other dolphin species, with a spectrum of 30-200 kHz. To date, this is the only study to investigate the ultrasonic acoustic behavior of *chinensis*-type humpback dolphins.

The fact that humpback dolphins communicate in frequencies as low as 600 Hz suggests they have good hearing sensitivities at low frequencies. Shipping noise, which typically produces frequencies of 6 kHz or less (see Parsons et al., 2003) would, presumably, be clearly audible to both types of Indo-Pacific humpback dolphins.

Barros & Cockcroft (1999) suggested that humpback dolphins hunt their prey species by passively listening for the sounds that they make. The preferred prey of both types of humpback dolphins includes fish species that are quite soniferous, in particular croakers (Sciaenidae) and members of family Sparidae (e.g., Barros & Cockcroft, 1999; Barros et al., 2004). If this is indeed the case, high levels of low frequency noise (such as that produced by boat traffic) could seriously disrupt the ability of humpback dolphins to locate prey, reinforcing the potential impacts that the noise of shipping traffic could have on these cetaceans.

Interactions with Other Species

Saayman & Tayler (1979) recounted a variety of interactions between *plumbea*-type humpback dolphins and other species, including chasing birds such as cormorants (*Phalacrocorax capensis* and *P. carbo*) and a jackass penguin (*Spheniscus demersus*); feeding alongside black-backed gulls (*Larus dominicanus*); accompanying a southern right whale (*Eubalaena australis*) in Algoa Bay; pursuing and avoiding Cape fur seals (*Arctocepalus pusillus*); circumventing a hammerhead shark (*Sphryna zygaena*); and mobbing a great white shark (*Carcharodon carcharias*). The latter behaviors are not surprising because high levels of predation and injury of *plumbea*-

type humpback dolphins by sharks has been noted (Cockcroft, 1991).

When a school of killer whales (*Orcinus orca*) approached a school of dolphins, they were observed huddling close to shore and rocks and above reefs in waters too shallow to allow the whales egress. Several interactions with bottlenose dolphins also occurred, including aggression towards lone humpback dolphins by bottlenose dolphins; one instance of avoidance and one instance of ignoring a traveling bottlenose school; three instances of solitary humpback dolphins joining and integrating into bottlenose dolphin schools; and a social interaction in Algoa Bay wherein bottlenose and humpback dolphins swam together at high speed in the surf zone, engaging in aerial behaviors (Saayman & Tayler, 1979).

Also in Algoa Bay, Karczmarski et al. (1997) reported humpback dolphins occasionally forming mixed schools with bottlenose dolphins, although the humpback dolphins remained on the periphery of the school. Despite the fact that bottlenose and humpback dolphins used the same feeding area in Algoa Bay, it was not usual for them to be seen together, and when both species were present, they often stayed at opposition ends of the feeding area.

One interesting association in Algoa Bay between a bottlenose and humpback dolphin is of note: Karczmarski et al. (1997) observed a bottlenose dolphin calf following an adult humpback dolphin, which was one of three adults in a school also containing two calves and a juvenile. The bottlenose dolphin calf could have been a bottlenose/humpback dolphin hybrid (although it appeared to be morphologically a bottlenose dolphin) or perhaps an example of interspecies adoption of a calf.

Humpback dolphins often interacting with bottlenose dolphins elsewhere. Mixed schools of *plumbea*-type humpback dolphins with bottlenose dolphins accounted for 33% of sighted cetacean schools in Menai Bay, Zanzibar, Tanzania (Stensland et al., 2001). These mixed species schools were more frequently recorded traveling and resting than schools comprised of just one species and social behavior was also frequently observed in these mixed species schools, including bottlenose dolphins herding humpback dolphins (Stensland et al., 2001). These schools may form in response to predator threats or as a result of the two species competing for the same habitats or resources (Stensland et al., 2001).

Further to the north, Scheyler & Baldwin (1999) reported two encounters with mixed bottlenose/humpback dolphin schools off of Somalia. Furthermore, a single humpback dolphin was noted among a school of *Tursiops* with behavior resembling that of a bottlenose dolphin, rather than its own species.

Baldwin et al. (2004) also reported interactions in the waters of Oman, including aggressive action by bottlenose dolphins to a solitary humpback dolphin, as well as a school of bottlenose dolphins closely tailing another school of humpback dolphins. Finally, an association between humpback and tropical common dolphins (*Delphinus capensis tropicalis*) was observed in Oman waters: a single humpback dolphin accompanying a group of the former species.

Although elsewhere in the area single species are primarily observed, one study conducted in Moreton Bay, Australia, noted that 77.5% of *chinensis*-type humpback dolphins encountered were in mixed schools with bottlenose dolphins (Corkeron, 1990). The total number of animals in these mixed schools was significantly higher than single-species schools, and the mixed schools were encountered in deeper water (17.1 m vs. 9 m), but slightly closer to shore (5 km vs. 6 km) than single-species groups. The habitat used by these mixed schools was essentially the same as normally occupied by single-species schools of bottlenose dolphins; the humpback dolphins, therefore, were entering into the bottlenose dolphin habitat rather than the other way around. The mixed schools only occurred associated with trawlers and, thus, formed as a response to a food resource.

Contrary to this, Parsons (1998b) noted a significant relationship between the presence of *chinensis*-type humpback dolphins and the absence of finless porpoises in Hong Kong. In Hong Kong, humpback dolphins and finless porpoises may compete for food resources as they have a number of key prey species in common (Barros et al., 2002, 2004; Parsons, 1997). Barros et al. (2004) suggested that the need to reduce this competition may have led to the distributions of humpback dolphins and finless porpoises being largely separate, with the former occupying brackish estuarine waters and finless porpoises inhabiting cooler and more saline waters (Jefferson, 2000; Jefferson & Braulik, 1999; Jefferson et al., 2002; Parsons, 1998b), but when the distribution of humpback dolphins overlaps with porpoises, instead of spatially, their distribution is separated temporally (as seen in Parsons, 1998b). Barros et al. (2004) also suggested that competition might occur between humpback dolphins and other cetacean species, as shared prey species also have been documented with South China Sea bottlenose dolphins (Barros et al., 2000, 2004).

More unusual associations between humpback dolphins and other species have been reported in Tin Can Bay in Western Australia. In this area, humpback dolphins have associated with humans for several years and have approached humans to be hand-fed with fish.

Humpback dolphins being fed by humans also has been reported in Hong Kong; a mother and calf pair used to reside in the waters near Stanley, off the south of Hong Kong Island, where locals apparently threw them food to eat (T. A. Jefferson, pers. comm.).

Interactions with Boat Traffic

Karczmarski et al. (1997, 1998) reported that the behavior of *plumbea*-type humpback dolphins in Algoa Bay, South Africa, was not affected by the presence of bathers or surfboats; however, powerboats did cause change in behaviors, and when these vessels were present, avoidance reactions were observed by the dolphins in 95.3% of occasions (Karczmarski et al., 1998). The response to boat traffic involved the animals taking a long dive, changing their direction, and swimming away perpendicular to the route of the boat. Females with calves also were observed joining with other females when disturbed by boat traffic, the females interposing themselves between the approaching boat and calves in a protective fashion (Karczmarski et al., 1997). Nowacek et al. (2001) noted that bottlenose dolphin mothers accompanying calves may be more vulnerable to being struck by boat traffic, and experienced mothers displayed greater reactions to boat traffic, presumably having learned that avoiding boats is an important adaptive behavior. This also appears to be the case in *plumbea*-type humpback dolphin mothers.

Pilleri & Gihr (1974) described *plumbea*-type dolphins in the Arabian Gulf reacting negatively to the presence of an approaching boat—that is, diving deeply, the dispersing of the group, and movement away from the boat similar to the behavior exhibited by dolphins in Algoa Bay, South Africa. They also described animals in the same locale engaged in probable mating behavior in the vicinity of at least 20 active shrimp fishing boats. In the Indus Delta, they noted no reaction to the slow approach of a boat.

Mixed schools of *chinensis*-type humpback dolphins and bottlenose dolphins feeding in association with fishing trawlers in Moreton Bay, Australia, already have been described above (Corkeron, 1990). There are also several records of humpback dolphins following fishing trawlers in various parts of China (e.g., Jefferson, 2000; Parsons 1998b; P. Wang & Sun, 1982; W. Wang, 1995). This behavior is particularly common in Hong Kong (Jefferson, 2000; Parsons 1998b), with 95% of pair trawlers in some areas being followed by humpback dolphins (Jefferson, 2000).

Van Parijs & Corkeron (2001b) studied the acoustic behavior of *chinensis*-type dolphin schools in response to boat traffic in Queensland, Australia. They discovered that the rate of dolphin whistling significantly increased when boats entered an area. Although click train or burst pulse rates were not affected, whistling rates increased when boats came within 1.5 km of the dolphins. Moreover, they noted that groups with no calves produced significantly fewer whistles, and it was suggested that mother/calf pairs were most disturbed by transiting boat traffic.

Behavioral changes in response to boat traffic were also recorded by Ng & Leung (2003). This study monitored changes in diving behavior in Hong Kong dolphins exposed to boat traffic and noted that dive duration increased the closer animals were to vessels. Increased density of vessel traffic also was correlated with increased dive duration. In addition, responses to different types of shipping were noted. For example, dolphins generally responded positively to (i.e., approached) fishing vessels, did not respond to cargo vessels, but responded negatively to (i.e., avoided) high-speed vessels (e.g., high-speed turbo ferries, catamarans, and speed boats). Both positive and negative responses were noted towards passenger vessels and, although not quantified, Ng and Leung suggested that juvenile dolphins tended to approach dolphin-watching tourist vessels more frequently than adults. These positive responses by juveniles to certain vessels also was noted by Jefferson (2000), who observed juveniles riding the bow wave of vessels for short periods on three occasions, a behavior which is very rare for this species.

Hong Kong is one of the busiest ports in the world, approximately one-half million oceanic and river-going vessels travel through Hong Kong's waters every year, and 30 high-speed and hydrofoil ferries pass through the area of greatest humpback dolphin abundance daily (Parsons, 1997). In addition to changes in dolphin behavior, this boat traffic also has more direct impacts on the resident dolphin population. For example, between 1993 and 1998, three stranded humpback dolphins were diagnosed to have been killed by boat strikes, and another dolphin mortality was suspected to have been caused by a boat strike (Parsons & Jefferson, 2000). This represents 14% of all stranded humpback dolphin during this period. Moreover, six animals in Hong Kong, from a catalogue of 174 identifiable individuals, displayed healed lacerations consistent with those caused by a ship's propeller. Other *chinensis*-type dolphin populations also occur in areas of high boat traffic (e.g., Shanghai and Singapore), and the impact of shipping on humpback dolphins is a cause for concern for this species throughout its range.

Summary

The coastal and estuarine habitat and the behavior of humpback dolphins are presumably shaped by the spatial and temporal abundance of resources and, perhaps, the avoidance of predators. Humpback dolphin school sizes tend to be small and their group dynamics fluid, and, although mating tends to occur year-round, there are seasonal peaks in reproductive behavior. Interesting behaviors, such as nurturant and succourant epimeletic behavior, alloparenting, and playing with "toys," also have been observed in humpback dolphins; however, knowledge of their acoustic behavior is very limited. Finally, they coexist and interact with a variety of species—mainly bottlenose dolphins—and also interact with fishing vessels, although avoidance of boat traffic has been recorded in many areas of their range.

It should be noted that this review is largely limited to published information. There is more information on the behavior and ecology of humpback dolphins in some select areas, such as South Africa and Hong Kong, but for the majority of their wide geographic range, information is sketchy at best and nonexistent at worst.

Humpback dolphins have been highlighted by several international organizations, such as the International Union for the Conservation of Nature and Natural Resources (IUCN) (Perrin, 1989; Reeves & Leatherwood, 1994; Reeves et al., 2003) and the IWC (2003), as a species at risk. An understanding of their behavior and ecology, and the processes underlying these, is essential for the development of any conservation plans or strategies, and as this review indicates, although such information is detailed in some areas, there is much that needs to be discovered.

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