

Feeding Habits of Indo-Pacific Humpback Dolphins (*Sousa chinensis*) Stranded in Hong Kong

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Abstract

Dietary information derived from the examination of stomach contents of 29 Indo-Pacific humpback dolphins (*Sousa chinensis*) stranded in Hong Kong waters is presented in this study. Humpback dolphins in this area have a diet comprised nearly exclusively of fish. Prey spectrum from the 15 dolphins with contents includes a minimum of 24 species of fish, and one species of cephalopod. The croaker (*Johnius* sp.) was the most frequent and numerically most important prey, followed by the lionhead (*Collichthys lucida*) and anchovies (*Thryssa* spp.). The fish families Sciaenidae, Engraulidae, Trichiuridae, and Clupeidae accounted for over 93% of all prey consumed. Most of these prey are common in murky, brackish waters of estuaries and often occur in large shoals. There is some dietary overlap with finless porpoises (*Neophocaena phocaenoides*); the two species share some 13 fish species, but only anchovies figure among the top five prey for both species. In addition, finless porpoises rely more heavily on cephalopods (squids, cuttlefishes, and octopus) and may venture into deeper, clearer waters during foraging, whereas humpback dolphins seem to exploit demersal and shoaling fish of productive estuaries. The stocks of some fish species important in the diet of humpback dolphins may have been subjected to heavy exploitation by the fisheries in Hong Kong waters. Behavioral observations of dolphins feeding in association with pair trawlers suggest a somewhat different prey preference for some dolphins from the results of this study.

Key Words: Feeding habits, stomach contents, prey, humpback dolphin, *Sousa chinensis*, Hong Kong, South China Sea

Introduction

Indo-Pacific humpback dolphins (*Sousa chinensis*) are found in the tropical to temperate waters of the Indian and western Pacific Oceans (Jefferson & Karczmarski, 2001; Ross, 2002). This species typically has a nearshore distribution throughout its range, often found within the 20 m isobath (Corkeron, 1990; Karczmarski, 1996; Parsons, 2004a; Ross, 2002). In the waters of Hong Kong, humpback dolphins co-occur with finless porpoises (*Neophocaena phocaenoides*) year-round throughout some of the islands comprising the territory. Although the two species may appear sympatric, there is spatial and temporal segregation in the habitats they occupy. Thus, humpback dolphins prefer murky, brackish waters of the Pearl River Estuary, while finless porpoises typically are found in clear, more saline waters, often around reefs, less influenced by the freshwater input from the Pearl River (Jefferson, 2000; Parsons, 1997, 1998b). The area north of Lantau Island has been identified as the most important habitat for Hong Kong humpback dolphins (Jefferson, 2000; Jefferson et al., 2002b; Leatherwood & Jefferson, 1997; Parsons, 1998b). There is concern that pollution, loss of habitat, and interactions with fisheries may adversely impact the populations of resident cetaceans of Hong Kong (Jefferson, 2000; Jefferson, Curry, & Kinoshita, 2002a; Leatherwood & Jefferson, 1997; Minh et al., 1999; Parsons, 1997, 1998a,

1999a, 1999b, 2004a; Parsons & Chan, 1998; Smith & Jefferson, 2002).

This study provides insights into the feeding ecology of humpback dolphins in Hong Kong waters. We hope that these data will be useful in the interpretation of patterns of habitat use, competition with other cetacean species, interactions with fisheries, analyses of body burdens of pollutants accumulated through the food chain, and the ultimate conservation and management of this species in Hong Kong waters.

Materials and Methods

Specimens for this study were collected as strandings in Hong Kong (see Jefferson, 2000; Jefferson et al., 2002a; Parsons 1997, 1998a, 1999a; Parsons & Jefferson, 2000). Entire stomachs were removed from carcasses and examined in the laboratory for presence of food matter. We followed the methods outlined in a previous study (Barros et al., 2002) to allow for direct comparisons with similar data obtained for finless porpoises. Wet weight of stomach contents was recorded in grams, and fish earbones (otoliths) were the primary structures used in prey identification, using comparative material from a local reference collection and published pictorial guides (e.g., Härkönen, 1986; Shen, 1993; Smale et al., 1995; Zheng, 1981). Whenever possible, prey was identified to the level of species or genus. Undigested fish retrieved from stomachs were measured to the nearest millimeter. The numerical contribution of each fish species was calculated, assuming that the highest number of either left or right otoliths represented the total number of specimens consumed of each particular prey. The biomass of prey consumed could not be estimated, due to the lack of appropriate allometric equations relating prey hard structures to prey dimensions (Parsons, 1997). We re-analyzed data examined in Parsons and incorporated them into this study. A preliminary analysis of a subset of the present sample has been recently presented in Jefferson (2000). Calculations of taxa diversity (terminology used in Barros et al., 2002) were made using the Shannon-Wiener index (Krebs, 1999). Statistical analyses (Zar, 1999) were performed using SYSTAT (version 8.0 for Windows).

Results

The stomachs of 29 humpback dolphins stranded from 1994 to 2000 were examined. Of these, 13 were empty (SC95-02/04, 234 cm; SC95-03/05, 210 cm; SC96-26/05, 107 cm; SC96-09/08, 107 cm; SC96-29/08, 102 cm; SC96-31/08, 105 cm; SC97-10/02, 207 cm; SC97-10/09, 110 cm; SC98-

17/01, 238 cm; SC99-04/05, 114 cm; SC99-30/05, 113.3 cm; SC99-27/06, 107 cm; SC00-15/02, 183 cm). Because length at birth is estimated at 100 cm (Jefferson, 2000), eight of these dolphins were likely neonates. Milk was discovered in the stomach of one of these neonates (SC96-26/05). Subsequent analyses showed high concentrations of organic pollutants, notably PCBs and DDT (Parsons & Chan, 1998).

An additional dolphin (SC00-04/05, female, 220 cm) had a massive ball of fine-mesh net occupying most of its forestomach chamber. This "net ball" was about 15 cm in diameter, and the net had a mesh size of approximately 2 cm. The stomach was otherwise devoid of any other material or food remnants. The remaining 15 humpback dolphins (9 males, 4 females, and 2 of unconfirmed sex) had food matter in their stomachs and comprise the present analyses. These animals ranged from 144 to 265 cm in total length (Table 1).

Humpback dolphins inhabiting Hong Kong waters are nearly exclusively piscivorous. From a total of 1,885 prey items retrieved from all 15 stomachs, only one cephalopod beak was found (unidentified, but possibly belonging to the squid, *Loligo* sp.); all other items were teleosts. The fish-only category was thus observed in 14 of the 15 cases (93.3%), a disproportionate occurrence (chi-square test, $p < 0.001$). The average number of different prey taxa per stomach was 5.8 (\pm SD 3.26), and the number of prey items found per stomach ranged from 1 to 910 (mean=125.7 \pm SD 231.12). Excluding one sample containing 910 prey items, the latter figures are considerably lower (mean=69.6, \pm SD 82.61, $n=14$). There was considerable variation in the wet weight of stomach contents (range=1-821 g, $n=11$), with an average value of 264.7 g (\pm SD 300.24).

A minimum of 24 species of fish (within 14 families, 20 genera) and one cephalopod species were identified (Figure 1). The most important prey families in numerical terms were the fish families Sciaenidae (croakers), Engraulidae (anchovies), Trichiuridae (cutlassfishes), and Clupeidae (sardines), which accounted for 93.3% of all prey consumed. The most frequent and numerically important prey was the croaker (*Johnius* sp.), which occurred in 11 of 15 stomachs examined (73.3%), accounting for nearly a third (31.5%) of all prey taken. The lionhead, *Collichthys lucida*, and anchovies, *Thryssa* spp., also were important prey, being present in 60% and 53.3% of the samples, and representing 29.5% and 20.6% of the total consumed, respectively. Otolith morphology and dimensions suggest that at least two species of *Thryssa* may be present, one resembling *T. vitrirostris* (Smale et

Table 1. Stomach content data from humpback dolphins stranded in Hong Kong waters, 1994-2000

Field #	Stranding season	Dolphin sex	Dolphin length (cm)	Carcass decomposition code ²	Wet Weight ³ of stomach contents (g)	Prey type ⁴	No. prey taxa ⁵	No. prey items	Shannon-Wiener diversity index (H)
SC94-27/01 ⁶	W	M	144	2	<10	F,C	2	2	0.693
SC94-28/04 ⁶	Sp	M	>250	2	39	F	9	54	1.795
SC94-23/12 ⁶	W	M	222	¾	--	F	7	43	1.434
SC95-11/02 ⁶	W	M	247	3	--	F	5	141	1.297
SC95-02/04 ⁶	Sp	M	234	3	E	--	--	--	--
SC95-03/05 ⁶	Sp	U	210	2	E	--	--	--	--
SC95-28/05 ^{6,7}	Sp	M	205	4	<100	F	2	48	0.173
SC96-26/05 ⁷	Sp	F	107	3	E ⁸	--	--	--	--
SC96-31/05 ⁷	Sp	M	207	2	821	F	8	284	0.825
SC96-09/08	Su	F	107	4	E	--	--	--	--
SC96-29/08	Su	M	102	3	E	--	--	--	--
SC96-31/08	Sp	M	105	4	E	--	--	--	--
SC97-10/02	W	M	207	4	E	--	--	--	--
SC97-27/03	SP	F	>>200	3	187	F	10	125	1.300
SC97-31/5B ⁷	Sp	F	235	2	379	F	8	173	1.630
SC97-03/09	Fa	M	265	4	1	F	3	6	1.244
SC97-10/09	Fa	M?	110	3	E	--	--	--	--
SC98-17/01	W	U	238	4	E	--	--	--	--
SC98-17/04	Sp	M?	>233	3	759	F	3	20	0.394
SC98-07/08	Su	M	221	4	200	F	7	910	0.817
SC99-04/05	Sp	M	114	3	E	--	--	--	--
SC99-30/05 ⁷	Sp	M	113.3	3	E	--	--	--	--
SC99-03/06	Su	F	252	3	E	--	--	--	--
SC99-27/06	Su	U	107	4	<1	F	1	1	0.000
SC99-16/07 ⁷	Su	F?	226	4	E	--	--	--	--
SC99-24/12	W	M	234.5	4	76	F	11	50	1.974
SC00-14/02	W	F	251.5	4	443	F	8	22	1.934
SC00-15/02	W	M	183	4	6	F	3	6	1.011
SC00-04/05	Sp	F	220	4	E ⁹	--	--	--	--

¹ Fa= Fall (Sept.-Nov.), W= Winter (Dec.-Feb.), Sp= Spring (March-May), Su= Summer (June-Aug.).² 2= fresh; 3= moderately decomposed; 4= advanced decomposition³ E= stomach empty⁴ F= Fish, C= Cephalopod, K= Crustacean⁵ Lowest taxonomic level (See text for details.)⁶ Samples from Parsons (1997)⁷ Suspected fisheries' by-catches⁸ Milk remains⁹ Mass of fishing net occupied most of forestomach

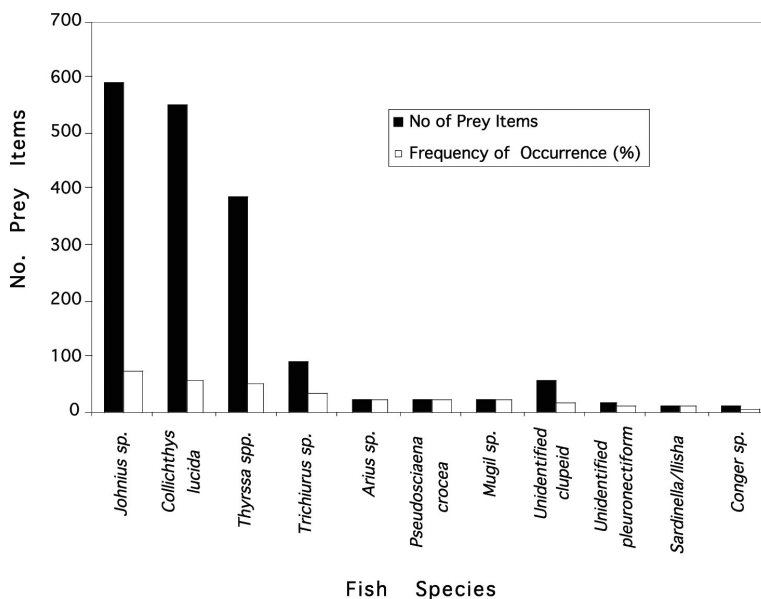


Figure 1. Prey of Indo-Pacific humpback dolphins (n=15 stomachs with prey remains) from Hong Kong waters. Presented in decreasing order of frequency of occurrence. Only prey species represented by ten or more individuals are shown.

al., 1995), seen in samples of humpback dolphins from South Africa (Barros & Cockcroft, 1999). The cutlassfish (hairtail), *Trichiurus sp.*, followed by the sea catfish, *Arius sp.*; the large yellow croaker, *Pseudosciaena crocea*; and the mullet, *Mugil sp.*, occurred in 5 and 4 of the 15 samples, respectively. The numerical contribution of *Johnius sp.*, *Collichthys lucida*, *Thryssa spp.*, and *Trichiurus sp.* amounted to nearly 87% (1,634 of 1,885) of all observed prey. In addition, they often occurred in large numbers in each stomach [e.g., *Johnius*: 46 specimens [dolphin, SC95-28/05], 479 specimens [dolphin, SC98-07/08]; *Thryssa*: 38 [SC95-11/02], 104 [SC97-31/5B], and 221 [SC96-31/05]; *Collichthys*: 22 [SC94-23/12], 40 [SC97-31/5B], 70 [SC97-27/03], and 409 [SC98-07/08]], suggesting they might have been taken when forming schools.

Most of the undigested fish were retrieved from a single stomach (SC96-31/05) and measured: *Trichiurus sp.*: 21.8 cm \pm 4.8 SD (range: 12-31 cm, n=48); *Thryssa sp.*: 8.3 cm \pm 1.1 (range: 7.5-9 cm, n=2); and *Collichthys lucida*: 9.0 cm (n=1). Sea catfish (*Arius sp.*) typically were represented in dolphin stomachs by their lapilli otoliths (the largest of the three pairs in this group, as opposed to the sagittal otoliths of other fish species (Gregory, 2002, p. 199; Rojo, 1991, p. 102); however, in one case (SC98-17/01), a total of 50 dorsal and pectoral spines (Figure 2) were also retrieved.

These spines were on average 44.5 mm long (\pm 4.1 SD, range: 34-52 mm, n=48).

The seasonality of humpback dolphin dietary consumption is shown in Tables 2 and 3. Sample sizes were too small for any statistical analyses. Due to the considerable variability in these data, no obvious trends related to seasonality could be detected; however, the most important prey (*Johnius*, *Collichthys*, *Thryssa*, *Trichiurus*) were consumed in nearly all seasons (a single sample was available during fall). Interestingly, croakers (*Johnius*) and anchovies (*Thryssa*) were present in nearly all dolphins examined during the spring.

Considerably more male dolphins (n=9) had stomachs with contents than female dolphins (n=4) (Table 4), but sample sizes were too small for statistical analyses. Although males seem to prey on more items and to strand with more food matter in their stomachs, there was considerable variation associated with those data. Important prey species were represented in similar proportions in male and female humpback dolphin stomachs (Table 5).

At least six of the samples analyzed were suspected to have resulted from fisheries' by-catches (Table 1). Using evidence gathered at necropsies (net marks; presence of undigested fish remains in stomachs, which was suggestive of a recent meal) and circumstantial observations of free-swimming behavior of a known animal around trawlers several days prior to death, Jefferson (2000)



Figure 2. Catfish spines retrieved from the stomach of a humpback dolphin from Hong Kong

speculated that two of these dolphins (SC95-31/05 and SC96-31/05) could have been caught in pair trawl nets. These dolphins had moderate to full stomachs ($293.4 \text{ g} \pm 327.12$, range: 76-821 g), and had preyed on *Johnius* and *Collichthys lucida* in large numbers.

Discussion

Feeding Associated with Estuaries

Humpback dolphins off Hong Kong appear to rely almost exclusively on fish for food. Important prey included bottom-dwelling species (e.g., catfish, sciaenid croakers), as well as typically pelagic groups (e.g., anchovies, cutlassfishes, sardines). Many of these prey are associated with the productive waters of estuaries and are found in large shoals (Smith & Heemstra, 1986; Van der

Table 2. Seasonality of stomach contents from Hong Kong humpback dolphins, 1994-2000

Stranding season ¹	Mean (\pm SD) prey taxa	Mean (\pm SD) prey items	Mean wet weight (\pm SD) of contents (g)	Mean (\pm SD) H	Sample size
Spring	6.7 ± 3.3	117.3 ± 99.2	437.0 ± 344.7^2	1.0 ± 0.5	6
Summer	6.3 ± 5.0	320.3 ± 511.3	92.3 ± 100.5	0.9 ± 0.7	3
Fall	3.0	6.0	1.0	1.2 ± 1.0	1
Winter	5.0 ± 2.5	42.8 ± 57.2	224.5 ± 309.0^3	1.3	5

¹ Spring = March-May, Summer = June-August, Fall = September-November, Winter = December-February

² n=5

³ n=2

Table 3. Seasonality of important prey species consumed by Hong Kong humpback dolphins, 1994-2000

Prey	Season							
	Winter (n=5)		Spring (n=6)		Summer (n=3)		Fall (n=1)	
	N.F.O. (%)		N.F.O. (%)		N.F.O. (%)		N.F.O. (%)	
<i>Johnius</i> sp.	4	60	94	100	496	67	--	--
<i>Collichthys lucida</i>	34	80	111	50	409	33	--	--
<i>Thryssa</i> spp.	44	60	332	83	13	33	--	--
<i>Trichiurus</i> sp.	38	20	52	33	5	67	--	--

Table 4. Stomach content data of male and female humpback dolphins from Hong Kong, 1994-2000

Dolphin sex	Mean no. (\pm SD) of prey taxa	Mean no. (\pm SD) of prey items	Mean (\pm SD) wet weight of contents (g)		Sample size
			Mean (\pm SD) H		
Male	5.7 \pm 2.7	167.8 \pm 292.2	296.1 \pm 268.7 ¹	1.1 \pm s.d. 1.4	9
Female	5.5 \pm 4.2	76.3 \pm 86.3	143.3 \pm 179.4	1.0 \pm s.d. 0.7	4

¹ n=7**Table 5.** Important prey species consumed by male and female humpback dolphins from Hong Kong

Prey	Dolphins			
	Males (n=9)		Females (n=4)	
	N.F.O. (%)		N.F.O. (%)	
<i>Johnius</i> sp.	532	67	44	75
<i>Collichthys lucida</i>	446	78	110	50
<i>Thryssa</i> spp.	280	67	108	75
<i>Trichiurus</i> sp.	88	33	4	25

Elst, 1981). Parsons (1998b) noted dolphins often feed at or near seawater/freshwater mixing zones in the North Lantau area. *Thryssa vitirostris*, *Collichthys lucida*, *Johnius belengerii*, *Trichiurus haumela*, and *T. brevis* were among the estuarine species contributing to the main fishery resources of the Pearl River Estuary during trawls (Li et al., 2000). *Johnius belengerii*¹ is a demersal fish with a preference for fine sediment of bays and estuaries (Lee, 1993; Wang et al., 1994; Zhang, 1996). *Thryssa*, *Johnius*, and *Collichthys* are all considered "small estuarine species," generally reaching about 20 cm in length (Anonymous, 1997a; Li et al., 2000). The preference for *sciaenid* croakers, mullet, anchovies, sardines, and porgies (Sparidae), among others, was noted in several feeding studies of humpback dolphins throughout their range (Salm, 1991, in Baldwin, Collins, Van Waerebeek, & Minton, 2004; Barros & Cockcroft, 1991, 1999; Burton, 1964; Jefferson, 2000; Parsons, 1997; Robineau & Rose, 1984; Ross, 1984; Saayman & Tayler, 1979; Wang &

Sun, 1982; Wang, 1995). Stocks of at least a few of the prey species of humpback dolphins (e.g., *Collichthys lucida*, *Trichiurus lepturus*, and the large yellow croaker, *Pseudosciaena crocea*) may have been subjected to heavy exploitation by the fisheries operating in Hong Kong (Anonymous, 1997b; He & Li, 1988; Huang & Walters, 1983; Lin, 1987).

Finding catfish as prey of humpback dolphins is of particular interest. These are bottom-dwelling species possessing dangerous, hard-fin spines covered by a venomous mucus, capable of inflicting painful lacerating wounds (Smith & Heemstra, 1986). Perforation of stomach chambers and adjacent organs by sea catfish (*Arius felis*, *Bagre marinus*) spines has been implicated in the death of several bottlenose dolphins in Mexico and Florida (Barros & Odell, 1995; Gallo & Hugentobler, 1986).

Seasonality and Sex Differences in Prey Consumption

Dietary differences between the sexes and among seasons could not be addressed due to small sample sizes and large variability in these data. Seasonal shifts in dolphin distribution and abundance in North Lantau waters have been documented (Jefferson, 2000; Jefferson & Leatherwood, 1997; Jefferson et al., 2002b; Parsons, 1998b). Li et al. (2000) observed seasonal variation in species

¹ The taxonomic status of this croaker has been recently questioned by Sasaki (1990), who re-assigned it to *J. grypotus*.

composition of both pelagic and demersal fishes in waters of the Pearl River Estuary. Data from Hong Kong fishery assessments (Anonymous, 1997b) also suggested seasonal abundance of fisheries resources for all gear types (i.e., trawl, gill net, purse-seine) surveyed. Wang (1985) noted differences in the abundance of sciaenid croakers off Zhejiang related to spawning migrations and changes in water temperature. If dolphin distribution patterns reflect those of their preferred prey, their diet should vary accordingly. As with the lack of seasonality in finless porpoise data (Barros et al., 2002), a larger sample size is needed to properly examine trends in diet related to gender and seasons.

Interactions with Fisheries

Evidence of mortality due to interactions with fisheries has been reported for both humpback dolphins and finless porpoises in Hong Kong (Jefferson, 2000; Jefferson et al., 2002a; Parsons, 1997; Parsons & Jefferson, 2000). Finding a fishing net in the stomach of a dolphin (SC00-04/05) suggests that the magnitude of such mortality could be higher, as evidence of interactions with fisheries can be difficult to detect in extremely decomposed carcasses, as was the case for this and many of the other dolphins in this study (Table 1). It is, therefore, possible that a larger portion of the samples represented fisheries-related mortality and could not be identified as such. Two suspected trawler by-caught dolphins (SC96-31/05 and SC97-31/5B; see Parsons & Jefferson, 2000) had undigested fish remains and near full stomachs, in addition to large numbers of prey species (*Johnius*, *Collichthys lucida*) typically caught by trawlers (see discussion below).

Humpback dolphins have been observed in close association with pair trawlers (Jefferson, 2000; Leatherwood & Jefferson, 1997; Parsons, 1997, 1998b). Pair trawling is the most important method of fishing in Hong Kong. Fish survey assessments (Anonymous, 1997b) identified 188 species of fish, 32 species of crustaceans, and 20 species of mollusks (including squid, cuttlefishes, and octopus) captured in trawl operations. In western Hong Kong waters, an important area for the distribution of humpback dolphins (Jefferson, 2000; Parsons, 1998b), the highest biomasses in the catches of trawls were recorded for croakers (*Collichthys lucida*, *Johnius belengerii*), shrimp (Penaeidae), gobies (Gobiidae), rabbit fish (Siganidae) and cardinal fishes (Apogonidae). Although dolphins consume croakers, other abundant species retrieved from the trawls (e.g., cardinal fishes, shrimp, cephalopods, and other invertebrates) are nearly absent from their diet. We present the following arguments for possible explanations of this apparent contradiction:

- (1) not all humpback dolphins have been observed to feed behind pair trawlers. In fact, some of the known animals (from photo-identification efforts) have never been observed doing so (Jefferson, 2000). It is possible that this specialized feeding technique is used by only part of the population;
- (2) pair trawlers operate both in mid-water and on the sea floor in shallow waters. It is not known if dolphins feed on the fish caught in the net, the fish that are stirred up by bottom trawling, or those that escape the nets. Thus, even those animals that do feed behind trawlers may not necessarily consume the same prey species as caught by the trawlers; or
- (3) pair trawling is a fairly seasonal and localized fishing operation in Hong Kong, occurring primarily in western waters, and this type of fishing operation has decreased dramatically in recent years.

In Moreton Bay, Australia, Corkeron et al. (1990) studied bottlenose dolphins feeding behind prawn trawlers (shrimp boats). They noticed that, whereas dolphins had access to a variety of food items, many of them were selective in their choice of food. Analyses of stomach contents of two dolphins entangled in trawl nets revealed that, in addition to several fish species, they also consumed squid (*Loligo* spp.) and small crabs (*Polydactylus plebejus*)—common organisms in the by-catch of trawlers. Curiously enough, finless porpoises in Hong Kong waters have shown prey composition suggestive of feeding in association with trawlers (Barros et al., 2002), in addition to the presence of undigested fish, squid, and shrimp in their stomachs. Because this behavior is far less documented for Hong Kong finless porpoises than for humpback dolphins (Jefferson & Braulik, 1999; Jefferson et al., 2002b; Parsons, 1997; Parsons & Wang, 1998; also see Torey, 2000, for anecdotal data collected through interviews with local fishermen), we suspect that porpoises may be more difficult to detect than dolphins when following pair trawlers (Barros et al., 2002).

Interspecific Competition with Other Cetaceans

Because humpback dolphins and finless porpoises share demersal and pelagic prey species (e.g., *Collichthys*, *Thryssa*, *Trichiurus*), they present some degree of dietary overlap in Hong Kong waters. Comparisons with similar dietary data obtained for finless porpoises (Barros et al., 2002) indicate, however, that humpback dolphins consume primarily fish, whereas finless porpoises prey disproportionately on cephalopods (chi-square test, $p < 0.001$). In addition, humpback dolphins appear to strand with more food in their stomachs than do finless porpoises (two-sample t -test, $p < 0.01$), possibly a result of the larger body sizes they attain. There were, however, no differences in prey richness and taxa diversity

(H) between the two species (two-sample *t*-test, $p > 0.05$) (finless porpoise data from Barros et al., 2002; humpback dolphin data from this study).

Because humpback dolphins prefer murky, brackish waters of estuaries, and finless porpoises occur more frequently in clear, more saline and colder waters (Jefferson, 2000; Jefferson & Braulik, 1999; Jefferson et al., 2002b; Parsons, 1998b), we suspect that spatial segregation may largely alleviate interspecific competition. Where the distribution of humpback dolphins overlaps finless porpoises, they show temporal segregation in habitat use (Parsons, 1998b). These results are remarkably similar to those obtained for bottlenose and humpback dolphins co-occurring off South Africa (Barros & Cockcroft, 1999). In that area, the two species show substantial dietary overlap (31 prey species are shared, primarily grunts, croakers, and anchovies), but spatial segregation and behavioral displacement were thought to explain, at least in part, how they are able to share the habitats they occupy. Those authors speculated that humpback dolphins may explore the "acoustic visibility" of their preferred prey, well-known sound producers of estuaries (Fish & Mowbray, 1970; Pilleri et al., 1982; Tavalga, 1977; Zbinden et al., 1977).

Humpback dolphins and finless porpoises are the only "resident" cetacean species in Hong Kong (Jefferson, 2000; Jefferson & Braulik, 1999; Parsons, 1997). They are also the two most abundant species in the stranding records, bottlenose dolphins being a distant third among some twelve different species recorded for Hong Kong (Parsons, 1998c). Bottlenose dolphins occasionally venture into shallow, nearshore waters, and in the process often feed on more neritic prey (Barros et al., 2000). Among these three cetacean species, finless porpoises show intermediate spatial distribution and habitat use around Hong Kong, as humpback dolphins are generally found in estuarine waters and bottlenose dolphins are typically found offshore. Not surprisingly, finless porpoises show overlap in prey consumed with both humpback and bottlenose dolphins (13 and 8 species are shared, respectively), suggesting they may compete in very nearshore (e.g., estuaries) and deeper (e.g., outer continental shelf) habitats. The cutlassfish (*Trichiurus*) is consumed by humpback dolphins (this study), finless porpoises (Barros et al., 2002), and bottlenose dolphins (Barros et al., 2000), implying they may constitute an important resource for resident and transient cetaceans occurring in Hong Kong waters.

With the continuation of the stranding program in Hong Kong, and the development of an onboard fishery observer program, we hope to elucidate the intricate relationships between Hong Kong

cetaceans and pair trawlers. For future studies, we recommend applying the techniques of stable isotopes and fatty acid signatures (using tissues obtained from free-ranging animals through biopsy darting) to address aspects of trophic ecology, habitat use, and resource partitioning among these animals. As more detailed dietary data on humpback dolphins and finless porpoises become available, studies correlating the contaminant burdens of Hong Kong cetaceans (e.g., Jefferson et al., 2000a; Minh et al., 1999; Parsons 1998a, 1999a; Parsons & Chan, 1998) to that of their preferred prey, as well as the monitoring of resulting impacts, are of particular importance to the health, conservation, and management of the local populations of these cetaceans.

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Literature Cited

- Anonymous. (1997a). *Fishbase 97 CD-ROM*. Manilla: ICLARM.
- Anonymous. (1997b). *Fisheries resources and fishing operations in Hong Kong waters*. Draft Final Report to the Agriculture & Fisheries Department, Hong Kong. 216 pp.
- Baldwin, R. M., Collins, M., Van Waerebeek, K., & Minton, G. (2004). The Indo-Pacific humpback dolphin of the Arabian region: A status review. *Aquatic Mammals*, 30(1), 111-124.
- Barros, N. B., & Cockcroft, V. G. (1991). Prey of humpback dolphins (*Sousa plumbea*) stranded in eastern Cape Province, South Africa. *Aquatic Mammals*, 17, 134-136.
- Barros, N. B., & Cockcroft, V. G. (1999). *Prey resource partitioning between Indo-Pacific humpback dolphins (Sousa chinensis) and bottlenose dolphins (Tursiops truncatus) off South Africa: Competitive exclusion or mutual tolerance?* In 13th Biennial Conference on the

- Biology of Marine Mammals, November 28-December 3, Maui, Hawaii.
- Barros, N. B., & Odell, D. K. (1995). *Prey-induced mortality in coastal bottlenose dolphins from the southeastern United States* (Abstract). 20th Reunión Internacional para el Estudio de los Mamíferos Marinos, April 18-22, La Paz, B.C.S., Mexico.
- Barros, N. B., Parsons, E. C. M., & Jefferson, T. A. (2000). Prey of offshore bottlenose dolphins from the South China Sea. *Aquatic Mammals*, 26(1), 2-6.
- Barros, N. B., Jefferson, T. A., & Parsons, E. C. M. (2002). Food habits of finless porpoises (*Neophocaena phocaenoides*) in Hong Kong waters. *Raffles Bulletin of Zoology, Supplement*, 10, 115-123.
- Burton, J. (1964). The grey dolphins of Djibouti Harbor. *Animals*, 3, 414-416.
- Corkeron, P. J. (1990). Aspects of the behavioral ecology of inshore dolphins *Tursiops truncatus* and *Sousa chinensis* in Moreton Bay, Australia. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 285-294). San Diego: Academic Press.
- Corkeron, P. J., Bryden, M. M., & Hedstrom, K. E. (1990). Feeding by bottlenose dolphins in association with trawling operations in Moreton Bay, Australia. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 329-336). San Diego: Academic Press.
- Fish, M. P., & Mowbray, W. H. (1970). *Sounds of Western North Atlantic fishes: A reference file for underwater biological sounds*. Baltimore: Johns Hopkins Press.
- Gallo, R. J. P., & Hugentobler, H. (1986). Un caso de muerte de tonina (*Tursiops truncatus*) por ingestión de bagre (*Bagre marinus*). *Veterinaria*, 17, 213-214.
- Gregory, W. K. (2002). *Fish skulls: A study of the evolution of natural mechanisms*. Malabar: Krieger Publishing Company. 481 pp.
- Härkönen, T. (1986). *Guide to the otoliths of the bony fish of the Northeast Atlantic*. Hellerrup, Denmark: Danbiu ApS. Biological Consultants. 256 pp.
- He, B., & Li, H. (1988). Stock assessment of *Collichthys lucidis* in the Pearl River Estuary. *Journal of Fisheries of China*, 12, 125-134.
- Huang, B., & Walters, C. J. (1983). Cohort analysis and population dynamics of large yellow croaker in the China Sea. *North American Journal of Fisheries Management*, 3, 295-305.
- Jefferson, T. A. (2000). Population biology of the Indo-Pacific hump-backed dolphin in Hong Kong waters. *Wildlife Monographs*, 144, 1-65.
- Jefferson, T. A., & Braulik, G. T. (1999). Preliminary report on the ecology of the finless porpoise in Hong Kong waters. *IBI Reports*, 9, 41-54.
- Jefferson, T. A., Curry, B. E., & Kinoshita, R. (2002a). Mortality and morbidity of Hong Kong finless porpoises, with emphasis on the role of environmental contaminants. *Raffles Bulletin of Zoology, Supplement*, 10, 161-171.
- Jefferson, T. A., Hung, S. K., Law, L., Torey, M., & Tregenza, N. (2002b). Distribution and abundance of finless porpoises in waters of Hong Kong and adjacent areas of China. *Raffles Bulletin of Zoology, Supplement*, 10, 43-55.
- Jefferson, T. A., & Karczmarski, L. (2001). *Sousa chinensis*. *Mammalian Species*, 655, 1-9.
- Jefferson, T. A., & Leatherwood, S. (1997). Distribution and abundance of Indo-Pacific hump-backed dolphins (*Sousa chinensis*, Osbeck, 1765) in Hong Kong waters. *Asian Marine Biology*, 14, 93-110.
- Karczmarski, L. (1996). *Ecological studies of humpback dolphins Sousa chinensis in the Algoa Bay region, eastern Cape, South Africa*. Ph.D. dissertation, University of Port Elizabeth, Port Elizabeth, South Africa. 202 pp.
- Krebs, C. J. (1999). *Ecological methodology*. Menlo Park, CA: Addison Wesley Longman, Inc. 620 pp.
- Leatherwood, S., & Jefferson, T. A. (1997). Dolphins and development in Hong Kong: A case study in conflict. *IBI Reports*, 7, 57-69.
- Lee, T. W. (1993). The demersal fishes of Asan Bay. 3. Spatial variation in abundance and species composition. *Bulletin of the Korean Fisheries Society*, 26, 438-445. (In Korean, English Abstract).
- Li, Y., Chen, G., & Sun, D. (2000). Analysis of the composition of fishes in the Pearl River estuarine waters. *Journal of Fisheries of China*, 24, 312-317. (In Chinese, English Abstract).
- Lin, X. (1987). Biological characteristics and resources status of three main commercial fishes in offshore waters of China. *Journal of Fisheries of China*, 11, 187-194.
- Minh, T. B., Watanabe, M., Nakata, H., Tanabe, S., & Jefferson, T. A. (1999). Contamination by persistent organochlorines in small cetaceans from Hong Kong coastal waters. *Marine Pollution Bulletin*, 39, 383-392.
- Parsons, E. C. M. (1997). *Hong Kong's cetaceans: The biology, ecology and behaviour of Sousa chinensis and Neophocaena phocaenoides*. Ph.D. dissertation, University of Hong Kong, Pokfulam, Hong Kong. 257 pp.
- Parsons, E. C. M. (1998a). Trace metal pollution in Hong Kong: Implications for the health of Hong Kong's Indo-Pacific hump-backed dolphins (*Sousa chinensis*). *Science of Total Environment*, 214, 175-184.
- Parsons, E. C. M. (1998b). The behaviour of Hong Kong's resident cetaceans: The Indo-Pacific hump-backed dolphins and the finless porpoise. *Aquatic Mammals*, 24(1), 91-110.
- Parsons, E. C. M. (1998c). Stranding of small cetaceans in Hong Kong territorial waters. *Journal of the Marine Biological Association of the United Kingdom*, 78, 1039-1042.
- Parsons, E. C. M. (1999a). Trace metal concentrations in tissues of cetaceans from Hong Kong's territorial waters. *Environmental Conservation*, 26, 30-40.
- Parsons, E. C. M. (1999b). Trace element concentrations in whole fish from North Lantau waters, Hong Kong. *ICES Journal of Marine Sciences*, 56, 791-794.

- Parsons, E. C. M. (2004a). The behaviour and ecology of the Indo-Pacific humpback dolphin (*Sousa chinensis*). *Aquatic Mammals*, 30(1), 38-55.
- Parsons, E. C. M. (2004b). The potential impacts of pollutants on humpback dolphins, with a case study on the Hong Kong population. *Aquatic Mammals*, 30(1), 18-37.
- Parsons, E. C. M., & Chan, H. M. (1998). Organochlorines in Indo-Pacific hump-backed dolphins (*Sousa chinensis*) and finless porpoises (*Neophocaena phocaenoides*) from Hong Kong. In B. Morton (Ed.), *The marine biology of the South China Sea III* (pp. 423-437). Hong Kong: Hong Kong University Press.
- Parsons, E. C. M., & Jefferson, T. A. (2000). Post-mortem investigations on stranded dolphins and porpoises from Hong Kong waters. *Journal of Wildlife Diseases*, 36, 342-356.
- Parsons, E. C. M., & Wang, J. Y. (1998). A review of finless porpoises (*Neophocaena phocaenoides*) from the South China Sea. In B. Morton (Ed.), *The marine biology of the South China Sea III* (pp. 287-306). Hong Kong: Hong Kong University Press.
- Pilleri, G., Kraus, C., & Gihl, M. (1982). The ambient noise in the environment of *Sousa plumbea* and *Neophocaena phocaenoides* with special reference to the sounds of *Johnius belangerii* (Pisces, Sciaenidae). In G. Pilleri (Ed.), *Investigations on cetacea, Volume 14* (pp. 95-128). Berne, Switzerland: Institute of Brain Anatomy, University of Berne.
- Robineau, D., & Rose, J-M. (1984). Les cétacés de Djibouti. Bilan des connaissances actuelles sur la faune cétologique de la mer Rouge et de Golfe d'Aden. *Bulletin de Musée Naturelle Histoire, Paris*, 6, 219-249.
- Rojo, A. L. (1991). *Dictionary of evolutionary fish osteology*. Boca Raton, FL: CRC Press. 273 pp.
- Ross, G. J. B. (1984). The smaller cetaceans of the southeast coast of Southern Africa. *Annals of the Cape Province Museum (Natural History)*, 15, 173-410.
- Ross, G. J. B. (2002). Humpback dolphins: *Sousa chinensis*, *S. plumbea* and *S. teuszii*. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (pp. 585-589). San Diego: Academic Press.
- Saayman, G. S., & Tayler, C. K. (1979). The socioecology of humpback dolphins (*Sousa* sp.). In H. E. Winn & B. L. Olla (Eds.), *The behaviour of marine animals. Volume 3: Cetaceans* (pp. 165-226). New York: Plenum Press.
- Sasaki, K. (1990). *Johnius grypotus* (Richardson, 1846), resurrection of a Chinese sciaenid species. *Japanese Journal of Ichthyology*, 37, 224-229. (In Japanese, English Abstract).
- Shen, S-C. (1993). *Fishes of Taiwan*. Taipei, Taiwan: Chu Ban Edition. 960 pp.
- Smale, M. J., Watson, G., & Hecht, T. (1995). Otolith atlas of southern African marine fishes. *Ichthyological Monographs of the J. L. B. Smith Institution of Ichthyology*, 1, 1-253.
- Smith, B. D., & Jefferson, T. A. (2002). Status and conservation of facultative freshwater cetaceans in Asia. *Raffles Bulletin of Zoology, Supplement*, 10, 173-187.
- Smith, M. M., & Heemstra, P. C. (1986). *Smith's sea fishes*. Grahamstown, South Africa: J. L. B. Smith Institute of Ichthyology. 1,047 pp.
- Tavolga, W. N. (Ed.). (1977). *Sound production in fishes. Benchmark papers in animal behaviour, Vol. 9*. Stroudsburg, PA: Dowden, Hutchinson & Ross, Inc.
- Torey, M. (2000). *Study on interactions between cetaceans and fisheries in Hong Kong waters: Final report*. Contract report to the Ocean Park Conservation Foundation, Hong Kong. 29 pp. + Appendices.
- Van der Elst, R. (1981). *A guide to the common sea fishes of southern Africa*. Cape Town, South Africa: Struik Publishers Ltd. 367 pp.
- Wang, C. (1985). Studies of the seasonal distribution of sciaenoid fishes of Zhejiang, China. *Studia Marina Sinica*, 25, 161-178.
- Wang, J., Su, Y., Liu, J., Qiu, X., & Yang, W. (1994). The feeding habits of five sciaenid fishes in Luoyuan Bay. *Journal of the Xiamen Fisheries College*, 16, 34-39.
- Wang, P., & Sun, J. Y. (1982). Studies on the Chinese white dolphin, *Sousa chinensis*, from the South China Sea. *Transactions of the Liaoning Zoological Society*, 3, 67-76. (In Chinese).
- Wang, W. (1995). Biology of *Sousa chinensis* in Xiamen harbor. In Z. G. Huang, S. Leatherwood, J. Woo, & W. Liu (Eds.), *Conference on Conservation of Marine Mammals by Fujian, Hongkong and Taiwan. Journal of Oceanography in the Taiwan Strait* (Specific Publication 4), 21-26. China: Xiamen District State Oceanic Administration. (In Chinese).
- Zar, J. H. (1999). *Biostatistical analysis*. Upper River Saddle, NJ: Prentice Hall. 663 pp.
- Zbinden, K., Pilleri, G., Kraus, C., & Bernath, O. (1977). Observations on the behaviour and underwater sounds of the plumbeous dolphin (*Sousa plumbea*, Cuvier, 1829) in the Indus Delta. In G. Pilleri (Ed.), *Investigations on Cetacea, Volume 8* (pp. 259-288). Berne, Switzerland: Institute of Brain Anatomy, University of Berne.
- Zhang, Y. (1996). Study on feeding habits of *Johnius belangerii* in Dongshan Bay. *Journal of the Xiamen Fisheries College*, 18, 25-32.
- Zheng, W. (1981). Comparative morphological studies of the otoliths of Chinese Carangidae and other fish families. *Transactions of the Chinese Ichthyological Society*, 2, 39-54.