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Stomach contents of Australian snubfin (*Orcaella heinsohni*) and Indo-Pacific humpback dolphins (*Sousa chinensis*)

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In Australia, snubfin (*Orcaella heinsohni*) and Indo-Pacific humpback (*Sousa chinensis*, hereafter humpback dolphins) dolphins are found in coastal waters of Queensland, Northern Territory and north Western Australia (Parra *et al.* 2002, 2004). Interactions between dolphins and gillnet fisheries and shark nets set for swimmers protection have led to both bycatch and direct killing of snubfin and humpback dolphins in Australia (Harwood *et al.* 1984, Harwood and Hembree 1987, Paterson 1990, Hale 1997, Gribble *et al.* 1998). It is unknown if these interactions are, at least in part, due to dolphins foraging on prey that are targeted by commercial fisheries; however, their foraging ecology remains largely unknown. A comprehensive understanding of the feeding ecology of snubfin and humpback dolphins is needed as a first step towards establishing their role as consumers, their potential effects on ecosystem function, and identifying potential conflicts with fisheries.

Stomach content analyses of marine top predators are a valuable tool for identifying predator dietary needs and preferences (Gannon *et al.* 1997; Santos *et al.* 2001*b*, 2004, 2006), providing information on predator's distribution (MacLeod *et al.* 2003), detecting foraging behavior and diving capabilities (Clarke 1996), identifying resource partitioning (Dolar *et al.* 2003) and interspecific competition (Spitz *et al.* 2006), and assessing potential interactions with commercial fisheries (Santos and Pierce 2003, Pierce *et al.* 2004). The available information on the diet of Australian snubfin and humpback dolphins is limited to a qualitative assessment conducted in the late 1970s (Heinsohn 1979). This assessment was incomplete because of restricted diagnostic techniques available at the time for identifying hard parts (*e.g.*, otoliths,

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cephalopod beaks) from prey remains to the lowest taxonomic level.[4] Here we provide a quantitative analysis of the stomach contents of snubfin and humpback dolphins stranded or incidentally caught in shark nets along the Queensland coast between 1970 and 2008; including the stomach contents collected by Heinsohn during the 1970s. We use these data to gain insights into the feeding habits of Australian snubfin and humpback dolphins and provide preliminary estimates of their dietary breadth and overlap.

The stomachs of 14 snubfin dolphin (5 females, 7 males, and 2 of unconfirmed sex) and 9 humpback dolphin (4 females, 4 males, and 1 of unconfirmed sex) were collected opportunistically from animals incidentally caught in shark nets and stranded along the Queensland coast between 1970 and 2008. Whole stomachs were retained and either stored deep-frozen (−20°C) in polyethylene bags or in 95% ethanol. Most stomachs collected were from animals in the Townsville region, northeast Queensland (Table 1). Out of the 23 stomachs inspected, 19 (13 snubfin and 6 humpback dolphins) contained prey remains and 4 were empty (1 snubfin and 3 humpback dolphins, Table 1). The total length of the snubfin dolphins, for which data were available, ranged from 2.15 to 2.35 m long ($n = 9$) and for humpback dolphins from 1.5 to 2.3 m ($n = 4$). Both dolphin species reach adult sizes at around 2 m (Jefferson and Karczmarski 2001, Beasley *et al.* 2005). Therefore, most of the individuals examined were likely adults (Table 1).

Stomach contents were thawed and washed through a 1.0 and 0.5 mm mesh sieve to separate prey remains. Recognizable fish otoliths and bones were stored dry while cephalopod beaks and large undigested prey were stored in 95% ethanol. Otoliths, cephalopod beaks, undigested fish and crustaceans were identified to the lowest taxonomic group, using reference collections held at the Museum of Queensland, Museum Victoria and James Cook University, published guides (Clarke 1986, Smale *et al.* 1995), and expert advice from Jeffrey Johnson and Dr. Peter Davie (The Museum of Queensland), and Dr. Mark Norman (Museum Victoria).

Estimates of the minimum number of individual fish and cephalopods ingested were determined by the highest number of left or right otoliths and upper or lower beaks (Pierce and Boyle 1991). The relative importance of prey items in the overall diet of snubfin and humpback dolphins was evaluated in terms of: (1) frequency of occurrence (F_i), (2) percentage of the total number of prey ($\%N_i$), and (3) prey specific abundance (P_i), defined as the percentage of a prey taxon in only those stomachs in which the actual prey occurs (Hyslop 1980, Pierce and Boyle 1991, Pierce *et al.* 1993, Amundsen *et al.* 1996):

$$F_i = (n_i/N) \times 100,$$

$$N_i = (x_i/X) \times 100,$$

$$P_i = (\Sigma S_i/\Sigma St_i) \times 100,$$

where n_i is the number of stomachs in which prey i was found, N is the total number of stomachs that contained prey remains, x_i is the total number of prey i, X is the total number of prey across the whole sample; S_i is the total number of prey items comprised of prey i and St_i is the total number of prey items in those stomachs containing prey i.

[4]Personal communication from Dr. George Heinsohn, James Cook University, Townsville, Queensland, Australia, July 2003.

Table 1. Australian snubfin and humpback dolphins specimens stranded or incidentally caught in shark nets along the Queensland coast between 1970 and 2008 and for which stomach contents were analyzed ($n = 23$). Approximate locations of specimens collected are indicated in decimal degrees.

Species	Date	Location	Latitude S	Longitude E	Found	Sex	Length (cm)	No. prey items	Prey type[a]
Snubfin dolphins	23 April 1970	Townsville	−19.218°	146.922°	Shark net	M	2,350	209	F
	23 April 1970	Townsville	−19.218°	146.922°	Shark net	M	2,150	22	F, C, D
	23 April 1970	Townsville	−19.218°	146.922°	Shark net	M	2,190	162	C
	3 October 1970	Townsville	−19.218°	146.922°	Shark net	F	2,260	77	F, C
	23 January 1971	Townsville	−19.218°	146.922°	Shark net	F	2,200	84	F, C, D
	10 June 1971	Townsville	−19.218°	146.922°	Shark net	F	2,150	57	F, C
	4 September 1971	Townsville	−19.218°	146.922°	Stranding	F		37	F, C
	18 March 1972	Townsville	−19.218°	146.922°	Shark net	M	2,150	43	F
	21 April 1972	Townsville	−19.218°	146.922°	Stranding	M		333	F, C
	28 March 1975	Townsville	−19.218°	146.922°	Shark net	F	2,250	101	F, C, D, B
	24 August 1975	Townsville	−19.218°	146.922°	Shark net	M	2,120	95	F, C
	11 May 1986	Balgal Beach	−19.042°	146.413°	Stranding	UN		64	F, C
	21 June 1986	Unknown			Stranding	M		69	F, C
	9 August 2007	Gladstone	−23.843°	151.256°	Stranding	UN		0	E
Humpback dolphins	25 May 1971	Townsville	−19.218°	146.922°	Shark net	M	1,510	3	F
	24 October 1971	Townsville	−19.218°	146.922°	Shark net	M	1,950	38	F
	21 July 1985	Unknown			Stranded	UN		1	F
	18 July 2001	Townsville	−19.218°	146.922°	Stranded	M		203	F, B
	1 February 2002	Unknown			Stranded	F		0	E
	20 June 2002	Bribie Island	−26.950°	153.117°	Stranded	M	1,760	12	F, C
	6 November 2005	Townsville	−19.218°	146.922°	Stranded	F		2	F
	9 April 2008	Brisbane River	−27.373°	153.165°	Stranded	F	2,350	0	E
	11 April 2008	Mackay	−21.166°	149.235°	Stranded	F		0	E

[a]F = fish, C = cephalopods, D = decapoda, B = bivalves, E = empty.

We used the graphical method of Amundsen *et al*. (1996) to gain insights into the feeding strategy of snubfin and humpback dolphins. This method is based on the examination of the distributions of prey points along a two-dimensional graphical representation of the relationship between prey specific abundance (P_i) and their frequency of occurrence (F_i). In this graph, information on prey importance is provided by the diagonal axis running from the lower-left to the upper-right corner of the graph with rare and unimportant prey at the lower-left corner and dominant prey at the upper-right corner. The vertical axis provides information on generalization or specialization in regards to feeding strategy. Prey points in the lower part of the graph have been ingested occasionally and indicate generalization, whereas specialists have most prey points in the upper part of the graph. Points located in the upper left indicate specialization by subgroups of the predator population, whereas points in the upper right indicate specialization by the whole predator population on given prey. Hence, a predator population with a narrow niche width would be characterized by one or a few points located in the upper right corner of the graph, whereas a predator population with a broader niche width will lack prey points in this part of the graph. The diagonal axis running from the lower-right to the upper-left corner of the graph provides a measure of between and within individual variability in prey preference. Prey points located in the upper left corner have been consumed in high quantities but only by a few individuals displaying specialization, whereas prey points in the lower right corner have a low specific abundance and a high occurrence indicating they have been eaten occasionally by most individuals. For an explanatory diagram for interpretation of prey importance, feeding strategy, and niche width from this graph see Amundsen *et al.* (1996).

Dietary breadth of each dolphin species was calculated using the standardized form (B_{standard}) of the Levins Index (B) (Colwell and Futuyma 1971):

$$B = \left(\sum_{i=1}^{n} p_i^2 \right)^{-1},$$

$$B_{\text{standard}} = \frac{(B-1)}{(B_{\max}-1)},$$

where n is the number of prey categories, p_i is the proportion of records of prey category i, and $B_{\max}$ is the total number of prey categories. B_{standard} values can range between 0 (minimum diet breadth) and 1 (maximum diet breadth). We considered a food category any taxon that could be distinguished to genus within the stomach contents of either dolphin species. The degree of dietary overlap between snubfin and humpback dolphins was calculated using Pianka's index of dietary overlap (O_{jk}) (Pianka 1973, 1974):

$$O_{jk} = \sum_{i=1}^{n} (p_{ij} \times p_{ik}) / \sqrt{\sum_{i=1}^{n} p_{ij^2} \times \sum_{i=1}^{n} p_{ik^2}}.$$

Here p_{ij} is the proportion of food item i in the diet of predator *j and* p_{ik} is the proportion of food item i in the diet of predator k. The index of dietary overlap ranges from 0 (complete dissimilarity) to 1 (complete similarity). We calculated dietary overlap for prey items identified to genus, this included prey items in 13 snubfin and 5 humpback dolphin stomachs.

A total of 1,353 prey items comprising four major taxonomic groups (fish, cephalopods, decapods, and bivalves) were retrieved from the 13 stomachs of snubfin dolphins that contained prey remains (Table 2). The number of prey items found per stomach ranged from 22 to 333 (mean = 104.08 ± SD 85.6) and the average number of different prey taxa per stomach was 8.7 (± SD 4.3). We found undigested fish in 69% (n = 9) of the stomachs examined. Most stomachs included fish and cephalopods (n = 10), two contained only fish prey and one only cephalopods. Teleost fish were the most important food item (F_i = 92.3; N_i = 64.6% and P_i = 73.4%), followed by cephalopods (F_i = 84.6%, N_i = 34.7% and P_i = 42.7%), decapods (F_i = 23.1%, N_i = 0.6% and P_i = 3.9%) and bivalves (F_i = 7.7%, N_i = 0.1% and P_i = 1.0%).

We were able to identify a minimum of 24 different fish taxa (3 to species, 17 to genus, and 4 to family), 5 cephalopods (1 to species, 3 to genus, and 1 to order) and 4 decapods (1 to species, 1 to genus, 1 to family and 1 to order; Table 2). Unidentified fish remains accounted for 6.4 % of the number of prey examined. Overall, the cardinal fish (*Apogon* sp.) was the most important prey in numerical terms (N_i = 23.4%) followed by the cuttlefish (*Sepia* sp., N_i = 16.6%), the squid (*Uroteuthis (Photololigo* sp.), N_i = 15.3%), and the toothpony fish (*Gazza* sp., N_i = 9.6%) (Fig. 1). Fish belonging to 18 different families were encountered in the stomachs of snubfin dolphins (Table 2). The most frequently encountered fish families in the stomachs of snubfin dolphins were the Sciaenidae (69.2%), Leiognathidae (61.5%), Apogonidae, Haemulidae, Sillaginidae, and Synodontidae (53.8%). Cephalopods were represented by at least two families: Sepiidae (cuttlefish, 76.9%) and Loliginidae (squid, 53.8%). The few decapoda identified, the prawn *Metapenaeopsis* sp. and the Indian prawn (*Penaeus indicus*), belong to the family Penaeidae.

A total of 259 prey items were retrieved from the stomach contents of six humpback dolphins (Table 1). The number of prey items found per stomach ranged from 1 to 203 (mean = 43.2, SD = ± 79.5), and the mean number of different prey taxa per stomach was 4.2 (± SD 2.3). Undigested fish was found in 50% of the stomachs. The majority and most important prey items were teleost fish (F_i = 100%; N_i = 99.2% and P_i = 99.2%, Table 3). Cephalopods (F_i = 16.7%; N_i = 0.4% and P_i = 8.3%) and bivalves (F_i = 16.7%; N_i = 0.4% and P_i = 0.5%) were only found in one stomach and in very low numbers (Table 3). Grunt fish (*Pomadasys* sp.) were the most numerically important prey (Fig. 1) accounting for more than half (52.9%) of all prey items, followed by the cardinal fish (*Apogon* sp., 10.4%) and smelt-whiting (*Sillago* sp., 9.7%).

From the otoliths and undigested fish remains we were able to identify 16 different fish taxa: 2 to species, 11 to genus, and 3 only to family (Table 3). We were unable to identify 5.8% of the fish remains. The most frequent fish families found in the stomachs of humpback dolphins were the Apogonidae (50%), Clupeidae, Haemulidae, and Sciaenidae (33%).

Visual examination of the prey-specific abundance (P_i) against the frequency of occurrence (F_i) plots indicated that most prey species found in stomachs of snubfin and humpback dolphins showed low prey-specific abundances with low to medium levels in frequency of occurrence (Fig. 2). The majority of prey are located in the lower half of the plot suggesting that snubfin and humpback dolphins have a generalized feeding strategy and a broad niche width. Sepiid cuttlefishes *Sepia* spp., and fishes of the genus *Apogon* sp., *Sillago* sp., *Gazza* sp., *Pomadasys* sp., *Johnius* sp., and *Saurida* sp. showed high values in terms of their frequency of occurrence but low specific

Table 2. Overall importance of prey species identified in the stomachs of Australian snubfin dolphins stranded and bycaught in Queensland, Australia ($n = 13$). Importance is expressed as frequency of occurrence (F_i), percentage of the total number of prey N_i) and prey specific abundance (P_i).

Prey Taxa				F_i		N_i		P_i	
Order	Family	Genera/species	Common Names	No.	%	No.	%	No.	%
Beloniformes	Hemiramphidae	*Hyporhampus* sp.	Halfbeaks	1	7.7	2	0.1	333	0.6
Clupeiformes	Chirocentridae	*Chirocentrus* sp.	Wolf herrings	1	7.7	1	0.1	95	1.1
	Clupeidae	*Nematalosa* sp.	Shads	3	23.1	8	0.6	361	2.2
		Unidentified	Herrings, shads, sardines	2	15.4	3	0.2	428	0.7
	Synodontidae	*Saurida* sp.	Lizardfishes	7	53.8	19	1.4	907	2.1
	Engraulidae	*Stolephorus* sp.	Anchovies	1	7.7	2	0.1	333	0.6
		Thryssa sp.	Anchovies	4	30.8	35	2.6	322	10.9
Mugiliformes	Mugilidae	Unidentified	Mullets	1	7.7	1	0.1	95	1.1
Perciformes	Apogonidae	*Apogon* sp.	Cardinalfishes	7	53.8	317	23.4	904	35.1
	Leiognathidae	*Gazza* sp.	Toothponyfishes	7	53.8	130	9.6	968	13.4
		Leiognathus sp.	Pony fishes	2	15.4	22	1.6	106	20.8
		Unidentified	Slimys, slipmouths, ponyfishes	1	7.7	6	0.4	84	7.1
	Gerreidae	*Gerres* sp.	Mojarras	1	7.7	2	0.1	69	2.9
	Sciaenidae	*Johnius* sp.	Croakers	7	53.8	29	2.1	782	3.7
		Otolithes ruber	Tiger-toothed croaker	6	46.2	30	2.2	660	4.5
	Lactariidae	*Lactarius lactarius*	False trevally	1	7.7	3	0.2	57	5.3
	Haemulidae	*Pomadasys* sp.	Grunts	7	53.8	64	4.7	968	6.6
		Pomadasys trifaciatus	Black-ear javelin	1	7.7	16	1.2	84	19.0
	Sillaginidae	*Sillago* sp.	Smelt-whitings	7	53.8	74	5.5	500	14.8
	Sphyraenidae	*Sphyraena* sp.	Barracudas	3	23.1	3	0.2	201	1.5
	Trichiuridae	*Trichinurus* sp.	Cutlassfishes	2	15.4	2	0.1	390	0.5
	Mullidae	Unidentified	Goat fishes	1	7.7	3	0.2	333	0.9
Scorpaeniformes	Platycephidae	*Platycephalus* sp.	Flatheads	5	38.5	14	1.0	727	1.9
Siluriformes	Ariidae	*Arius* sp.	Sea catfishes	1	7.7	1	0.1	84	1.2
Unidentified fish				10	76.9	87	6.4	1,090	8.0

(Continued)

Table 2. (Continued)

	Prey Taxa			F_i		N_i		P_i	
Order	Family	Genera/species	Common Names	No.	%	No.	%	No.	%
All fish				12	92.3	874	64.6	1191	73.4
Sepiia	Sepiidae	*Sepia* sp.	Cuttlefish	10	76.9	225	16.6	1,079	20.9
Teuthida	Loliginidae	*Uroteuthis (Photoligo)* sp.	Squid	4	30.8	207	15.3	554	37.4
		Loliolus sp.	Squid	3	23.1	11	0.8	465	2.4
		Sepioteuthis lessoniana	Bigfin reef squid	4	30.8	5	0.4	369	1.4
	Unidentified			3	23.1	22	1.6	498	4.4
All Cephalopoda				11	84.6	470	34.7	1101	42.7
Decapoda	Penaeidae	*Penaeus indicus*	Indian prawns	1	7.7	2	0.1	84	2.4
		Metapenaeopsis sp.	Prawns	1	7.7	3	0.2	84	3.6
		Unidentified		1	7.7	2	0.1	22	9.1
	Unidentified crab remains			1	7.7	1	0.1	101	1.0
All Decapoda				3	23.1	8	0.6	207	3.9
Class Bivalvia (Unidentified order)	Unidentified mollusc			1	7.7	1	0.1	101	1.0
All Bivalvia				1	7.7	1	0.1	101	1.0
Total						1,353			

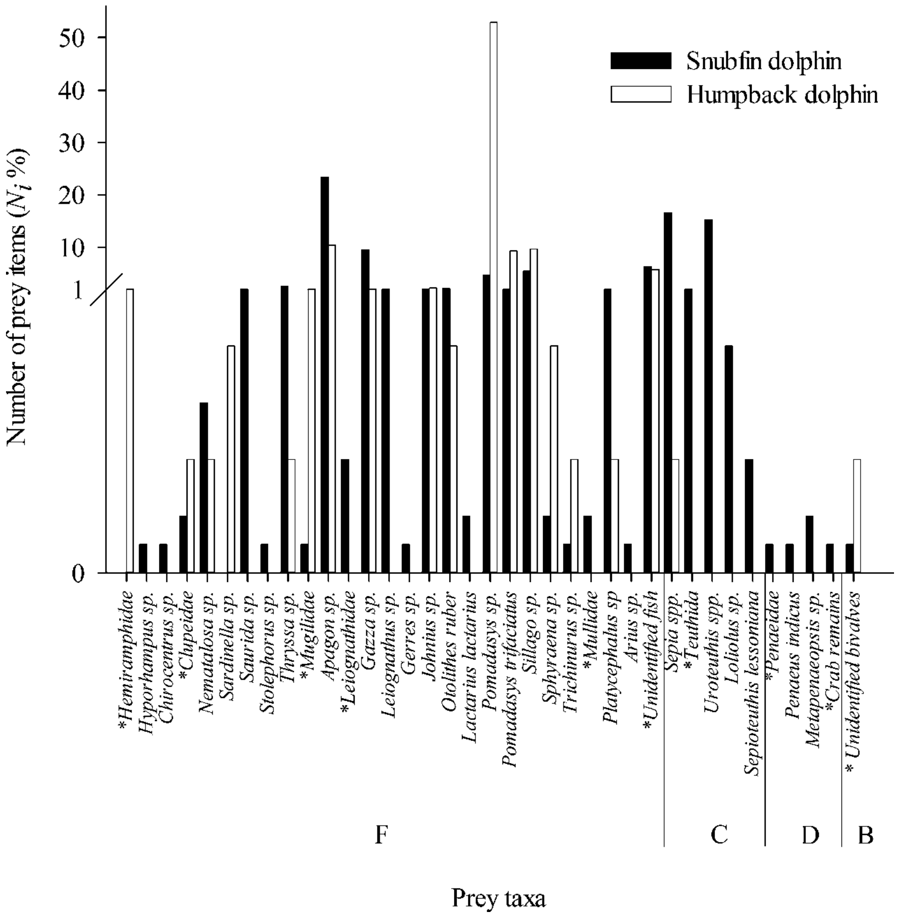

Figure 1. Percentage of the total number of prey items (N_i) found in the stomach contents of snubfin (n = 13) and humpback dolphins (n = 6) from Queensland waters. F = Fishes, C = Cephalopods, and D = Decapoda. Prey taxa with an (*) were only identified to order or family level.

abundance, suggesting these items are eaten occasionally by most snubfin dolphins (Fig. 2a). Loliginid squids (*Uroteuthis (Photololigo)* sp.) showed high specific abundance with relatively low frequency of occurrence, which suggested some degree of individual specialization in snubfin dolphins (Fig. 2a). In the case of humpback dolphins, *Apogon* sp. *w*ere the dominant prey species in terms of their frequency of occurrence (Fig. 2b). The high prey-specific abundance of *Sardinella* sp., *Pomadasys* sp. and *Trichiurus* sp. suggests that when they are consumed, they constitute a large proportion of humpback dolphin diet (Fig. 2b).

Snubfin dolphins showed a larger dietary breadth (B = 0.22) than humpback dolphins (B = 0.13). Despite these differences the diet of snubfin and humpback dolphins overlapped partially (O_{jk} = 0.30). All fish taxa identified to genus in the stomachs of humpback dolphins were also consumed by snubfin dolphins (Fig. 1). The most numerically important prey item in the stomach contents of each dolphin

Table 3. Overall importance of prey species identified in the stomachs of humpback dolphins stranded and bycaught in Queensland, Australia (n = 6). Importance is expressed as frequency of occurrence and percentage of the total number of prey (summed across all stomachs).

	Prey Taxa			F_i		N_i		P_i	
Order	Family	Genera/species	Common Names	No.	%	No.	%	No.	%
Beloniformes	Hemiramphidae	Unidentified	Halfbeaks	1	16.7	3	1.2	12	25.0
Clupeiformes	Clupeidae	*Nematalosa* sp.	Gizzard shads	1	16.7	1	0.4	12	8.3
		Sardinella sp.	Sardines	1	16.7	2	0.8	3	66.7
		Unidentified	Herrings, shads, sardines	1	16.7	1	0.4	3	33.3
	Engraulidae	*Thryssa* sp.	Anchovies	1	16.7	1	0.4	203	0.5
Mugiliformes	Mugilidae	Unidentified	Mullets	2	33.3	5	1.9	215	2.3
Perciformes	Apogonidae	*Apogon* sp.	Cardinal fishes	3	50.0	27	10.4	253	10.7
	Leiognathidae	*Gazza* sp.	Toothpony fishes	1	16.7	4	1.5	38	10.5
	Sciaenidae	*Johnius* sp.	Croakers	1	16.7	6	2.3	203	3.0
		Otolithes ruber	Tiger-toothed croaker	2	33.3	2	0.8	205	1.0
	Haemulidae	*Pomadasys* sp.	Grunts	2	33.3	137	52.9	241	56.8
		Pomadasys trifaciatus	Black-ear javelin	1	16.7	24	9.3	203	11.8
	Sillaginidae	*Sillago* sp.	Smelt-whitings	1	16.7	25	9.7	203	12.3
	Sphyraenidae	*Sphyraena* sp.	Barracudas	1	16.7	2	0.8	38	5.3
	Trichiuridae	*Trichinurus* sp.	Cutlassfishes	1	16.7	1	0.4	2	50.0
Scorpaeniformes	Platycephidae	*Platycephalus* sp.	Flatheads	1	16.7	1	0.4	12	8.3
Unidentified fish				4	66.7	15	5.8	254	5.9
All fish				6	100.0	257	99.2	257	100.0
Sepiia	Sepiidae	*Sepia* sp.	Cuttlefish	1	16.7	1	0.4	12	8.3
All Cephalopoda				1	16.7	1	0.4	12	8.3
Class Bivalvia (Unidentified order)	Unidentified mollusc			1	16.7	1	0.4	203	0.5
All Bivalvia				1	16.7	1	0.4	203	0.5
Total						259			

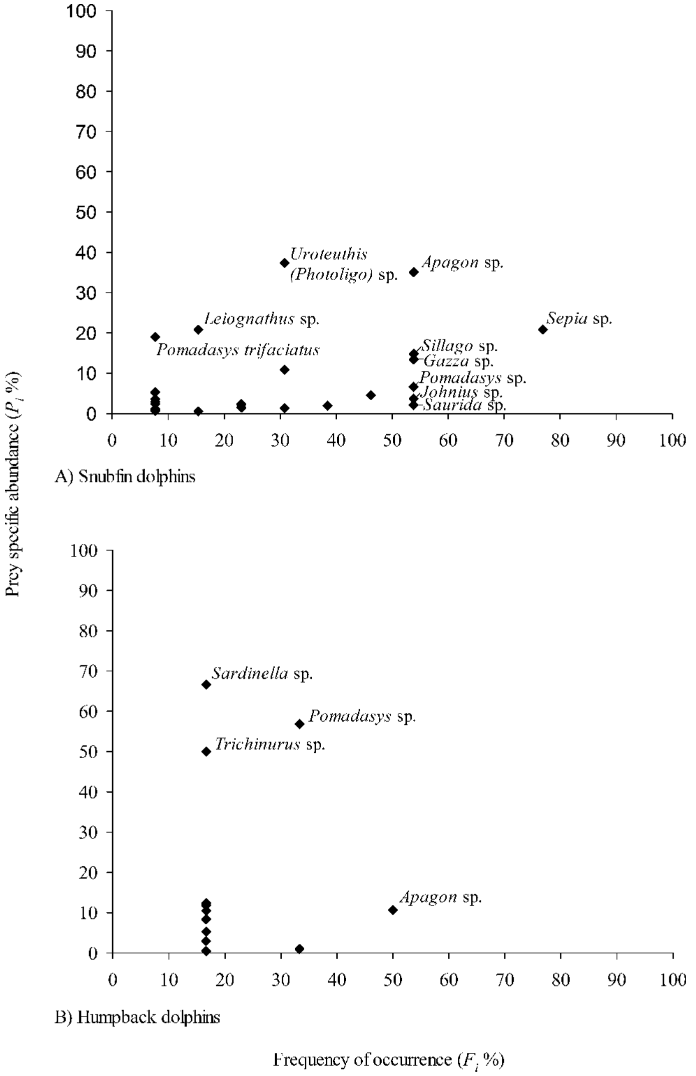

Figure 2. Prey-specific abundance (P_i) in number plotted against frequency of occurrence (F_i) of prey items found in the stomachs of Australian (A) snubfin and (B) humpback dolphins. The lowest taxonomic level identified is shown for some of the most important prey items in specific abundance and frequency of occurrence.

species was also consumed by the other (Fig. 1). The main dietary difference between snubfin and humpback dolphins appears to be cephalopods, which were only found in large quantities in the stomachs of snubfin dolphins.

Our analyses are constrained by small sample sizes and should be treated with caution; nevertheless, they provided useful insights into the feeding habits of snubfin and humpback dolphins and serve as a platform for future investigations into their feeding ecology. Our results suggest that snubfin and humpback dolphins are opportunistic-generalist feeders, preying on a wide variety of fish and cephalopods that are readily available in shallow coastal-estuarine environments.

The fish in the stomachs revealed that both dolphin species feed on schooling, bottom-dwelling fish (*e.g.*, grunts, toothponyfishes, croakers, flatheads, and whitings) as well as pelagic fish (*e.g.*, cardinalfishes, gizzard shads, anchovies, and barracudas). The cuttlefishes and squids found in the stomachs of snubfin dolphins can be found mid-water as well as on or near the bottom. Most of the fish and cephalopod taxa identified are associated with shallow coastal-estuarine environments. These features indicate that snubfin and humpback dolphins capture their prey throughout the water column and tend to feed in waters close to the coast and river mouths. Decapoda and bivalves represented only a small fraction of the prey items identified in the stomach contents and were presumably incidentally ingested when feeding or represent prey of prey. These feeding habits are in accordance with the habitat preference of snubfin and humpback dolphins for shallow, coastal-estuarine habitats where animals are often seen foraging (Parra 2006).

Humpback dolphins appear to rely mainly on fish for food and rarely include cephalopods in their diet compared to snubfin dolphins. The lack of cephalopods in the diet of humpback dolphins might be an effect of the lower sample size obtained for humpback dolphins ($n = 5$). However, these feeding habits are consistent with studies elsewhere that showed humpback dolphins preyed almost exclusively on fishes and very rarely on cephalopods (Barros *et al.* 2004). Similarly, some of the fish families identified as important prey for humpback dolphins in this study (Clupeidae and Sciaenidae) also accounted for a large proportion of humpback dolphins diet in Hong Kong (Barros *et al.* 2004).

Interspecific differences in consumption of cephalopods may be partly explained by slight differences in habitat preferences between snubfin and humpback dolphins. In coastal waters off the Townsville coast, northeast Queensland, where most of the samples for this study originated, snubfin and humpback dolphins occur in sympatry and their use of space overlaps considerably (Parra 2006). Nevertheless, snubfin dolphins prefer slightly shallower (1–2 m) waters, seagrass meadows, and occur closer to river mouths than humpback dolphins (Parra 2006). Several species of cephalopods are abundant in shallow water (≤1 m deep) close to the coast, and along breakwaters of Cleveland Bay (Jackson 1991) and this may help explain the inclusion of cephalopod prey in larger amounts in snubfin dolphins than humpback dolphins.

In addition, to habitat partitioning; morphological differentiation could also function as another mechanism for differences in the feeding habits between these sympatric species. Facial morphological differences in cetaceans are related to differences in diet and method of food capture (Heyning and Mead 1996; Werth 2000, 2006*a*, *b*). Snubfin and humpback dolphins differ substantially in their facial morphology. Snubfin dolphins have a short-blunt rostrum, their teeth have an expanded crown but are not compressed and are reduced in number varying from 11 to 22 teeth in the upper row and from 14 to 19 teeth in the lower row (Robertson and Arnold 2009). In contrast, humpback dolphins have a long-narrow rostrum; their teeth are conical, pointed and vary from 29 to 38 in upper and lower row (Jefferson and Karczmarski 2001). Odontocetes with long-narrow rostrums, catch their prey with their long jaw and transport the prey *via* suction to the posterior of the oral cavity for swallowing (Werth 2006*a*). The long rostrum with many teeth of humpback dolphins resembles the typical morphology of other delphinids that appear to rely on grasp for catching their prey before suction and which are known to feed mainly on fish but may also include cephalopods in their diet; common dolphins, *Delphinus delphis* (Pusineri *et al.* 2007), spotted dolphins, *Stenella attenuata* (Wang *et al.* 2003), and spinner dolphins, *S. longirostris* (Dolar *et al.* 2003). Odontocetes with a short-blunt rostrum, reduced dentition and small mouth openings however, suck their prey directly into the oral cavity eliminating the transport step (Werth 2006*a*, *b*). Suction feeding has been shown to be of particularly use for teuthophagous (cephalopod-eating) species, such as long-finned pilot whales, *Globicephala melas* (Werth 2000, 2006*a*). Such morphological characters allows predators to generate greater negative pressures to draw prey into their mouths, helping them to capture and hold the fast, small and presumably less manageable slippery-bodied prey of cephalopods (Heyning and Mead 1996; Werth 2000, 2006*a*). Thus the apparent consumption of cephalopods by snubfin dolphins in large numbers and almost lack thereof in humpback dolphins appears to be closely related to differences in their facial morphology.

Although stomach contents are valuable in studies of diet composition it is difficult to ensure they are representative of the population and of their actual diet due to inherent problems in sampling regime and prey identification (see reviews in Pierce and Boyle 1991, Santos *et al.* 2001*a*). Stranded animals may include sick animals that will not have been feeding normally or may not have been feeding at all. Similarly, the diet of individuals incidentally caught in commercial fisheries could be biased towards the targeted species of that specific fishery. Out of the 23 stomachs collected in this study 11 (snubfin dolphins = 9; humpback dolphins = 2) were from animals incidentally caught in shark nets set for swimmers protection. As these dolphins drowned incidentally and this fishery targets none of the dolphin prey items, the prey composition shown here should be representative of "healthy animals" and not biased towards the target species of the shark net fishery.

Additionally, not all ingested preys are equally likely to be identified. For example, the beaks of cephalopods tend to be more resistant to digestion than otoliths and sometimes accumulate in the stomach (Santos *et al.* 2001*a*). This could lead to an overestimation of the importance of cephalopods in the diet and underestimation of number and diversity of fish prey consumed. This may account for the high level of importance given to cuttlefish and squid in the diet of snubfin dolphins and the less diversity of fish found in humpback dolphins. Nevertheless, the facial morphology of snubfin dolphins suggests a teuthophagous diet and the general dietary composition of humpback dolphins is similar to the one reported in studies elsewhere (Barros *et al.* 2004).

Most of the fish and cephalopods identified in the stomachs of humpback and snubfin dolphins appear to be widespread along the Queensland coast and are associated with coastal-estuarine environments. Behavioral observations (Parra 2006) together with the data presented here on feeding habits indicate coastal-estuarine waters are important foraging habitats for snubfin and humpback dolphins. The coastal distribution and feeding ecology of snubfin and humpback dolphins indicates they are at a greater risk of directly or indirectly interacting with commercial fisheries operating in coastal waters. Dolphins, prey items included fish (*Pomadasys* sp., *Platycephalus* sp., *Sillago* sp.) and cephalopods (*Uroteuthis* sp.) that are targeted by net and trawling fisheries in Queensland. Future studies aimed at assessing the spatial and temporal extent to which foraging grounds of snubfin and humpback dolphins overlap with inshore gill nets and trawlers fishing effort will help elucidate the potential magnitude for interactions and manage areas of conflict.

Despite constraints and limitations of the presented dietary data, the stomach contents examined here represent the entire sample currently available from stranded and fishery bycatches of these species in Australian waters. It is apparent from our results that Australian snubfin and humpback dolphins rely strongly on coastal and estuarine waters for food. The maintenance and improvement of current stranding programs in retrieving stranded specimens will be critical in incrementing current sample sizes that will allow investigations on individual, interspecific, and seasonal variations in diet composition. This together with trophic studies using stable isotopes and fatty acid analyses of tissue samples from wild animals and prey will lead to a better understanding of the feeding ecology of these animals and their potential interaction with local fisheries.

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Literature Cited

Amundsen, P. A., H. M. Gabler and F. J. Staldvik. 1996. A new approach to graphical analysis of feeding strategy from stomach contents data—modification of the Costello (1990) method. Journal of Fish Biology 48:607–614.

Barros, N. B., T. A. Jefferson and E. C. M. Parsons. 2004. Feeding habits of Indo-Pacific humpback dolphins (*Sousa chinensis*) stranded in Hong Kong. Aquatic Mammals 30:179–188.

Beasley, I., K. M. Robertson and P. Arnold. 2005. Description of a new dolphin, the Australian snubfin dolphin *Orcaella heinsohni* sp. n. (Cetacea, Delphinidae). Marine Mammal Science 21:365–400.

Clarke, M. R. 1986. A handbook for the identification of cephalopod beaks. Oxford University Press, Oxford, U.K.

Clarke, M. R. 1996. Cephalopods as prey. III. Cetaceans. Philosophical Transactions of the Royal Society B: Biological Sciences 351:1053–1065.

Colwell, R. K., and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52:567–576.

Dolar, M. L. L., W. A. Walker, G. L. Kooyman and W. F. Perrin. 2003. Comparative feeding ecology of spinner dolphins (*Stenella longirostris*) and Fraser's dolphins (*Lagenodelphis hosei*) in the Sulu Sea. Marine Mammal Science 19:1–19.

Gannon, D. P., A. J. Read, J. E. Craddock and J. G. Mead. 1997. Stomach contents of long-finned pilot whales (*Globicephala melas*) stranded on the U.S. mid-Atlantic coast. Marine Mammal Science 13:405–418.

Gribble, N. A., G. McPherson and B. Lane. 1998. Effect of the Queensland Shark Control Program on non-target species: whale, dugong, turtle and dolphin: a review. Marine and Freshwater Research 49:645–651.

Hale, P. 1997. Conservation of inshore dolphins in Australia. Asian Marine Biology 14:83–91.

Harwood, M. B., and D. Hembree. 1987. Incidental catch of small cetaceans in the offshore gillnet fishery in northern Australian waters: 1981–1985. Report of the International Whaling Commission 37:363–367.

Harwood, M. B., K. J. McNamara, G. R. V. Anderson and D. G. Walter. 1984. Incidental catch of small cetaceans in a gillnet fishery in northern Australian waters. Report of the International Whaling Commission 34:555–559.

Heinsohn, G. E. 1979. Biology of small cetaceans in north Queensland Waters. Unpublished report to the Great Barrier Reef Marine Park Authority, The Great Barrier Reef Marine Park Authority. 23 pp.

Heyning, J. E., and J. G. Mead. 1996. Suction feeding beaked whales: Morphological and observational evidence. Natural History Museum of Los Angeles County Contributions in Science 464:1–12.

Hyslop, E. J. 1980. Stomach contents analysis—a review of methods and their application. Journal of Fish Biology 17:411–429.

Jackson, G. D. 1991. Age, growth, and population dynamics of tropical squid and sepioid populations in waters off Townsville, North Queensland, Australia. Ph.D. thesis, James Cook University, Townsville, Queensland, Australia. 221 pp.

Jefferson, T. A., and L. Karczmarski. 2001. *Sousa chinensis*. Mammalian Species 655:1–9.

MacLeod, C. D., M. B. Santos and G. J. Pierce. 2003. Review of data on diets of beaked whales: Evidence of niche separation and geographic segregation. Journal of the Marine Biological Association of the United Kingdom 83:651–665.

Parra, G. J. 2006. Resource partitioning in sympatric delphinids: Space use and habitat preferences of Australian snubfin and Indo-Pacific humpback dolphins. Journal of Animal Ecology 75:862–874.

Parra, G. J., C. Azuma, A. R. Preen, P. J. Corkeron and H. Marsh. 2002. Distribution of Irrawaddy dolphins, *Orcaella brevirostris*, in Australian waters. Raffles Bulletin of Zoology Supplement 10:141–154.

Parra, G. J., P. J. Corkeron and H. Marsh. 2004. The Indo-Pacific humpback dolphin, *Sousa chinensis* (Osbeck, 1765), in Australian waters: A summary of current knowledge. Aquatic Mammals 30:197–206.

Paterson, R. A. 1990. Effects of long-term anti-shark measures on target and non-target species in Queensland Australia. Biological Conservation 52:147–159.

Pianka, E. R. 1973. The structure of lizard communities. Annual Review of Ecology and Systematics 4:53–74.

Pianka, E. R. 1974. Niche overlap and diffuse competition. Proceedings of the National Academy of Sciences 71:2141–2145.

Pierce, G. J., and P. R. Boyle. 1991. A review of methods for diet analysis in piscivorous marine mammals. Oceanography and Marine Biology: An Annual Review 29:409–486.

Pierce, G. J., P. R. Boyle, J. Watt and M. Grisley. 1993. Recent advances in diet analysis of marine mammals. Symposium of the Zoolological Society of London 66:214–261.

Pierce, G. J., M. B. Santos, R. J. Reid, I. A. P. Patterson and H. M. Ross. 2004. Diet of minke whales *Balaenoptera acutorostrata* in Scottish (UK) waters with notes on strandings of this species in Scotland 1992–2002. Journal of the Marine Biological Association of the United Kingdom 84:1241–1244.

Pusineri, C., V. Magnin, L. Meynier, J. Spitz, S. Hassani and V. Ridoux. 2007. Food and feeding ecology of the common dolphin (*Delphinus delphis*) in the oceanic Northeast Atlantic and comparison with its diet in neritic areas. Marine Mammal Science 23:30–47.

Robertson, K. M., and P. A. Arnold. 2009. Australian snubfin dolphin: *Orcaella heinsohni*. Pages 62–64 *in* W. F. Perrin, B. H. Würsig and H. Thewissen, eds. Encyclopedia of marine mammals. Second edition. Academic Press, San Diego, CA.

Santos, M. B., and G. J. Pierce. 2003. The diet of harbour porpoise (*Phocoena phocoena*) in the Northeast Atlantic. Oceanography and Marine Biology: An Annual Review 41:355–390.

Santos, M. B., M. R. Clarke and G. J. Pierce. 2001*a*. Assessing the importance of cephalopods in the diets of marine mammals and other top predators: Problems and solutions. Fisheries Research 52:121–139.

Santos, M. B., G. J. Pierce, I. a. P. Patterson, R. J. Reid, H. M. Ross and E. Mente. 2001*b*. Stomach contents of bottlenose dolphins (*Tursiops truncatus*) in Scottish waters. Journal of the Marine Biological Association of the United Kingdom 81:873–878.

Santos, M. B., G. J. Pierce, J. A. Learmonth, *et al*. 2004. Variability in the diet of harbor porpoises (*Phocoena phocoena*) in Scottish waters 1992–2003. Marine Mammal Science 20:1–27.

Santos, M. B., G. J. Pierce, A. Lopez, R. J. Reid, V. Ridoux and E. Mente. 2006. Pygmy sperm whales *Kogia breviceps* in the Northeast Atlantic: New information on stomach contents and strandings. Marine Mammal Science 22:600–616.

Smale, M. J., G. Watson and T. Hecht. 1995. Otoliths atlas of southern African marine fishes. Ichthyological Monographs of the. J. L. B. Smith Institute of Ichthyology 1:1–253.

Spitz, J., Y. Rousseau and V. Ridoux. 2006. Diet overlap between harbour porpoise and bottlenose dolphin: An argument in favour of interference competition for food? Estuarine Coastal and Shelf Science 70:259–270.

Wang, M.-C., W. A. Walker, K.-T. Shao and L.-S. Chou. 2003. Feeding habits of the pantropical spotted dolphin, *Stenella attenuata*, off the eastern coast of Taiwan. Zoological Studies 42:368–378.

Werth, A. 2000. A kinematic study of suction feeding and associated behavior in the long-finned pilot whale, *Globicephala melas* (Traill). Marine Mammal Science 16:299–314.

Werth, A. J. 2006*a*. Odontocete suction feeding: Experimental analysis of water flow and head shape. Journal of Morphology 267:1415–1428.

Werth, A. J. 2006*b*. Mandibular and dental variation and the evolution of suction feeding in Odontoceti. Journal of Mammalogy 87:579–588.

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