

Feeding habits of Australian Snubfin (*Orcaella heinsohni*) and Indo-Pacific humpback dolphins (*Sousa chinensis*)

Guido J. Parra and Maria Jedensjö

School of Veterinary Science, The University of Queensland, St. Lucia



THE UNIVERSITY
OF QUEENSLAND
AUSTRALIA



Australian Government
Great Barrier Reef
Marine Park Authority



Funded by the Great Barrier Reef Marine Park Authority
Supported by the Reef & Rainforest Research Centre Ltd
Project 1.4.1(e) Condition, trends and projected futures of marine species of conservation concern:
Feeding habits of Australian snubfin and Indo-Pacific humpback dolphins

© The University of Queensland

Cover Image: Examining a dead stranded humpback dolphin in Moreton Bay, Queensland, prior to collecting the animal's stomach. Photograph: Maria Jedensjö.

This report should be cited as:

Parra, G. J. and Jedensjö, M. (2009) *Feeding habits of Australian Snubfin (Orcaella heinsohni) and Indo-Pacific humpback dolphins (Sousa chinensis)*. Project Report to the Great Barrier Reef Marine Park Authority, Townsville and Reef & Rainforest Research Centre Limited, Cairns (22pp.).

This publication is copyright. Apart from any use as permitted under the Copyright Act 1968, no part may be reproduced by any process without prior written permission from the authors.

March 2009

Contents

List of Figures.....	ii
List of Tables.....	ii
Acronyms and Abbreviations.....	ii
Acknowledgements.....	ii
Abstract.....	iii
Introduction.....	1
Materials and Methods.....	2
Sample collection and stomach contents analysis.....	2
Results.....	3
Diet of Australian Snubfin dolphins.....	5
Diet of Indo-Pacific humpback dolphins.....	7
Dietary breadth and overlap.....	9
Discussion.....	9
Potential interaction with commercial fisheries.....	10
References.....	12

List of Figures

Figure 1:	Percentage of the total number of prey items found in the stomach contents of snubfin (n = 13) and humpback dolphins (n = 6) from Queensland waters	7
------------------	---	---

List of Tables

Table 1:	List of snubfin and humpback dolphins specimens stranded or incidentally caught in shark nets along the Queensland coast between 1970-2008 and for which stomach contents were analysed (n = 23).....	4
Table 2:	Overall importance of prey species identified in the stomachs of Australian snubfin dolphins stranded and bycaught in Queensland, Australia (n = 13).....	6
Table 3:	Overall importance of prey species identified in the stomachs of humpback dolphins stranded and bycaught in Queensland, Australia (n = 6).....	8

Acronyms and Abbreviations

DPI&F	Queensland Department of Primary Industries and Fisheries
ECIFF	East Coast Inshore Fin Fish Fishery
ECTF	East Coast Trawl Fishery
IUCN	International Union for Conservation of Nature
Lat	Latitude
Long	Longitude
No	Number (of)
SD	Standard deviation

Acknowledgements

Funding for this project was provided by the Great Barrier Reef Marine Park Authority. We are thankful to Dr George Heinsohn for making the stomach samples he collected during the 1970s available to us. A special thanks to Jeffrey Johnson (The Museum of Queensland), Dr Peter Davie (The Museum of Queensland) and Dr Mark Norman (Museum Victoria), Aaron Ballagh and Saskia De Jong from James Cook University for their valuable help with the identification of fish and cephalopods. Many thanks as well to the numerous Queensland Parks and Wildlife Rangers who assisted in the collection of new samples from stranded animals.

Abstract

Little information exists on the feeding habits of Australian Snubfin (*Orcaella heinsohni*) and Indo-Pacific humpback dolphins (*Sousa chinensis*). In this study we provide quantitative analyses of the diet of both dolphin species in Queensland waters, based on the examination of stomachs (14 snubfins and nine humpbacks) collected from stranded and bycaught animals between 1970 and 2008. Snubfin and humpback dolphins appear to be opportunistic-generalist feeders, eating a wide variety of fish and cephalopods associated with coastal-estuarine waters. Bottom-dwelling and pelagic fishes were consumed by both species, indicating snubfin and humpback dolphins capture fish throughout the water column. Humpback dolphins appear to feed primarily on fish, while snubfin dolphins also included cephalopods in their diet. The most important prey in numerical terms for snubfin dolphins was the cardinal fish (*Apogon sp.*), followed by the cuttlefish (*Sepia sp.*), the squid *Uroteuthis (Photololigo) sp.* and the toothpony fish (*Gazza sp.*). Grunts (*Pomadasys sp.*), cardinal fishes (*Apogon sp.*) and smelt-whitings (*Sillago spp.*) were the most important fish prey for humpback dolphins. Several fish prey, including the most important, was common in the diet of both dolphin species indicating some partial dietary overlap. Differences in diet likely reflect some of the morphological and ecological differences between both species. The diet of snubfin and humpback dolphins included taxa that are targeted by net and trawling fisheries in Queensland. Interactions with these fisheries are expected, particularly in areas where fishing operations overlap with dolphins' high use areas.

Introduction

Coastal dolphins are among the most threatened species of cetaceans because of their close proximity to anthropogenic activities (Thompson *et al.* 2000, DeMaster *et al.* 2001). Australian populations of snubfin (*Orcaella heinsohni*) and Indo-Pacific humpback dolphins (*Sousa chinensis*) are found in coastal waters of Queensland, Northern Territory and Western Australia (Parra *et al.* 2002, Parra *et al.* 2004). Australian snubfin and Indo-Pacific humpback dolphins (hereafter humpback dolphins) together with bottlenose dolphins (*Tursiops aduncus*), are the only strictly coastal dolphin species found in northern Australia and as upper level predators are likely to have a quantitatively important role in the marine food web of coastal ecosystems. The Australian snubfin dolphin was only recently described as a new species and is the only cetacean endemic to Australian waters and possibly Papua New Guinea (Beasley *et al.* 2005). Recent genetic studies on Indo-Pacific humpback dolphins indicate Australian populations may also represent a different species only found in Australia (Frère *et al.* 2008). Both dolphin species are listed as *Rare* under the Queensland *Nature Conservation Act 1992* and are classified as *Near Threatened* by the IUCN (Reeves *et al.* 2008a, Reeves *et al.* 2008b).

Estimates of population size in local areas along the Queensland coast indicate that populations of both species are small making them particularly vulnerable to human-induced disturbances on coastal ecosystems (Corkeron *et al.* 1997, Parra *et al.* 2006). Photo-identification data also suggests moderate levels of site fidelity in both species making them potentially vulnerable to habitat degradation and loss given their restricted coastal distribution (Parra *et al.* 2006). Consequently there are concerns that human activities associated with coastal zones (fisheries, coastal zone development, boat traffic) may adversely affect local populations of snubfin and humpback dolphins (Parra *et al.* 2006).

Prey availability influences population dynamics, movement patterns, and habitat preferences of marine predators (Allen *et al.* 2001, Heithaus and Dill 2002, Benoit-Bird and Au 2003). For example, it has been suggested that snubfin and humpback dolphins' habitat preferences and movement patterns are influenced by the availability of their prey (Parra 2006). However, their foraging ecology remains largely unknown. In addition, there has been some history of interactions between coastal dolphins and gillnet fisheries and shark nets set for bathers protection leading to both by-catch and direct killing of 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. Thus, understanding snubfin and humpback dolphins feeding habits is an essential component to identifying potential conflicts with inshore fisheries.

Stomach contents analyses of marine top predators are a valuable tool for identifying the predator's dietary needs and preferences (Gannon *et al.* 1997, Santos *et al.* 2001b, Santos *et al.* 2004, Santos *et al.* 2006), can provide information on predator's distribution (MacLeod *et al.* 2003), foraging behaviour and diving capabilities (Clarke 1996), resource partitioning (Dolar *et al.* 2003), potential for interspecific competition (Spitz *et al.* 2006); and potential interactions with commercial fisheries (Santos and Pierce 2003, Pierce *et al.* 2004). The only data on stomach contents of Australian snubfin and humpback dolphins was limited to a qualitative assessment because of restricted diagnostic techniques available at the time for identifying hard parts from prey remains to the lowest taxonomic level (otoliths, cephalopod beaks) (Heinsohn 1979). In this study we provide quantitative analyses of the stomach contents collected by Heinsohn during the 1970s together with new samples collected from stranded animals over the last eight years. We use these data to provide a quantitative analysis of the diet of Australian snubfin and humpback dolphins, estimate their dietary breath and overlap, and assess potential interactions with commercial fisheries.

Materials and Methods

Sample collection and stomach contents analysis

The stomach contents of 14 snubfin dolphin (five females, seven males and two of unconfirmed sex) and nine humpback dolphin (four females, four males and one of unconfirmed sex) were collected opportunistically from animals incidentally caught in shark nets and stranded along the east coast of Queensland between 1970 and 2008 (Figure 1). Most stomach contents collected were from animals entangled in shark nets set for bather protection in the Townsville region, northeast Queensland. Stomach contents were washed through a 1.0 and 0.5mm mesh sieve in order to separate prey remains. Recognisable fish otoliths and bones were stored dry while cephalopod beaks and large undigested prey were stored in 95% ethanol. Otoliths, cephalopod beaks, and 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 (fish curator, The Museum of Queensland), Dr Peter Davie (crustacean curator, The Museum of Queensland) and Dr Mark Norman (mollusc curator, Museum Victoria).

Estimates of the minimum number of individual fish and cephalopods ingested were determined by the maximum number of left or right otoliths and upper or lower beaks. The relative importance of prey items in the overall diet of snubfin and humpback dolphins was evaluated using two standard indices: (1) frequency of occurrence, and (2) percentage of the total number of prey (summed across all stomachs), (Hyslop 1980, Pierce and Boyle 1991, Pierce *et al.* 1993). We used frequency of occurrence for calculation of dietary breadth and overlap (Reynolds and Aebischer 1991). Dietary breadth of each dolphin species was calculated using the standardized form (B_{standard}) of the Levins Index (B) (Colwell and Futuyma 1971):

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

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

where n is the number of food categories, p_i is the proportion of records of food category i , and B_{max} is the total number of food categories. B_{standard} values can range between 0 (minimum diet breadth) and 1 (maximum diet breadth). We considered a food category any taxon (to the lowest taxonomic level) that could be distinguished within the stomach contents of either dolphin species.

The degree of overlap between snubfin and humpback dolphins diet was calculated using Pianka's index of dietary overlap (O) (Pianka 1973, 1974):

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

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 five humpback dolphin stomachs.

Measures of dietary overlap were compared using the Mantel test (Mantel 1967) to determine whether diets were significantly different between species. The Mantel test is a non-parametric statistical procedure for comparing two distance matrices that has been used widely in dietary studies (Patterson 1986, Edwards *et al.* 1998, Jones and Barmuta 1998, Ray *et al.* 2001). The test calculates the correlation (r_M) between a matrix containing values for diet overlap between all individual dolphins examined and a species identity matrix representing the null hypothesis being tested (no differences in overall diet between species). In the species identity matrix each element was zero where the corresponding element in the diet overall matrix was a between species comparison or one for a within species comparison. As sample sizes were unequal (13 snubfin vs. five humpback dolphin) we weighted the species identity matrix by accounting for the sample size of each species as devised by Luo and Fox (1996). The significance of the test was evaluated through 10,000 random permutations. Random correlation values were then compared with the original observed correlation value to obtain the number of permuted correlation values that are as less than the observed (i.e. p value).

Results

We examined the stomach contents of 14 snubfin dolphins (seven males, five females and two of undetermined sex) and nine humpback dolphins (four males, four females and one of undetermined sex) (Table 1). Of the stomachs inspected, 19 (13 snubfin and six humpback dolphins) contained prey remains and four were empty (one snubfin and three humpback dolphins, Table 1). The size of the snubfin dolphins for which data was available, ranged from 2.15 to 2.35m long ($n = 9$) and for humpback dolphins from 1.5 to 2.3m ($n = 4$). Both species reach adult sizes at around two metres (Jefferson *et al.* 2008); therefore most of the individuals examined, for which size was known, were likely adults (Table 1).

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

Species	Date	Location	Lat S	Long E	Found	Sex	Length (cm)	No. Prey items	Prey type*
Snubfin dolphins	23-Apr-70	Townsville	-19.218°	146.922°	Shark net	M	2350	209	F
	23-Apr-70	Townsville	-19.218°	146.922°	Shark net	M	2150	22	F, C, D
	23-Apr-70	Townsville	-19.218°	146.922°	Shark net	M	2190	162	C
	03-Oct-70	Townsville	-19.218°	146.922°	Shark net	F	2260	77	F, C
	23-Jan-71	Townsville	-19.218°	146.922°	Shark net	F	2200	84	F, C, D
	10-Jun-71	Townsville	-19.218°	146.922°	Shark net	F	2150	57	F, C
	04-Sep-71	Townsville	-19.218°	146.922°	Stranding	F	?	37	F, C
	18-Mar-72	Townsville	-19.218°	146.922°	Shark net	M	2150	43	F
	21-Apr-72	Townsville	-19.218°	146.922°	Stranding	M	?	333	F, C
	28-Mar-75	Townsville	-19.218°	146.922°	Shark net	F	2250	101	F, C, D, B
	24-Aug-75	Townsville	-19.218°	146.922°	Shark net	M	2120	95	F, C
	11-May-86	Balgol Beach	-19.042°	146.413°	Stranding	?	?	64	F, C
	21-Jul-86	?	?	?	Stranding	M	?	69	F, C
09-Aug-07	Gladstone	-23.843°	151.256°	Stranding	?	?	0	E	
Humpback dolphins	25-May-71	Townsville	-19.218°	146.922°	Shark net	M	1510	3	F
	24-Oct-71	Townsville	-19.218°	146.922°	Shark net	M	1950	38	F
	21-Jul-85	?			Stranded	?	?	1	F
	18-Jul-01	Townsville	-19.218°	146.922°	Stranded	M	?	203	F, B
	01-Feb-02	?			Stranded	F	?	0	E
	20-Jun-02	Bribie Island	-26.950°	153.117°	Stranded	M	1760	12	F, C
	06-Nov-05	Townsville	-19.218°	146.922°	Stranded	F	?	2	F
	09-Apr-08	Brisbane River	-27.373°	153.165°	Stranded	F	2350	0	E
	11-Apr-08	Mackay	-21.166°	149.235°	Stranded	F	?	0	E

Diet of Australian Snubfin dolphins

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). Most stomachs included fish and cephalopods ($n = 10$), two contained only fish prey and one only cephalopods. In numerical terms, most of the prey items found in all stomachs were teleost fish ($n = 874$, 64.6%) followed by cephalopods ($n = 470$, 34.7%), decapods ($n = 8$, 0.6%) and bivalves ($n = 1$, 0.1%). The number of prey items found per stomach ranged from 22 to 333 (Mean=104.08, SD= \pm 85.6) and the average number of different prey taxa per stomach was 8.7 (\pm SD 4.3). We found undigested fish in 69% ($n = 9$) of all the stomachs.

We were able to identify a minimum of 24 different fish taxa (three to Species, 17 to Genus, and four to Family), five cephalopods (one to Species, three to Genus, and one to Order) and five decapods (one to Species, one to Genus, one to Family and one 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 followed by the cuttlefish (*Sepia sp.*), the squid *Uroteuthis (Photololigo) sp.* and the toothpony fish (*Gazza sp.*) (Figure 1). Fishes belonging to 19 different families were encountered in the stomachs of snubfin dolphins. The most frequently encountered fish families were the Sciaenidae (all stomachs), Leiognathidae (76.9%), Sillaginidae (61.5%), Haemulidae (61.5%), Apogonidae (53.8%) and Synodontidae (53.8%). The most important fish prey in numerical terms was the cardinal fish (*Apogon sp.* 23.4%), followed by the toothpony fish (*Gazza sp.*, 9.4%), Smelt-whiting (*Sillago spp.*, 5.3%), grunts (*Pomadasyss sp.*, 4.6%) and tiger-toothed croaker (*Otolithes ruber*, 2.2%) (Figure 1). Cephalopods were represented by at least two families: Sepiidae (cuttlefish) and Loliginidae (squid). The cuttlefish (*Sepia sp.*) was the most important cephalopod prey in numerical terms (Figure 1) accounting for 16.6% of all prey items, followed by the squids *Uroteuthis (Photololigo) sp.*(15.3%) and *Loliolus sp.* (0.8%). Among the few decapods identified, the prawn *Metapenaeopsis sp.* was the most numerous (0.2%) followed by the Indian prawn (*Penaeus indicus*, 0.1%).

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 and percentage of the total number of prey (summed across all stomachs).

Prey Taxa			Common Names	Occurrence		Number	
Order	Family	Genera/species		No.	%	No.	%
Beloniformes	Hemiramphidae	<i>Hyporhamphus sp.</i>	Halfbeaks	1	7.7	2	0.1
Clupeiformes	Chirocentridae	<i>Chirocentrus sp.</i>	Wolf herrings	1	7.7	1	0.1
	Clupeidae	<i>Nematalosa sp.</i>	Shads	3	23.1	8	0.6
		Unidentified	Herrings, shads, sardines	2	15.4	3	0.2
	Synodontidae	<i>Saurida sp.</i>	Lizardfishes	7	53.8	19	1.4
	Engraulidae	<i>Stolephorus sp.</i>	Anchovies	1	7.7	2	0.1
		<i>Thryssa sp.</i>	Anchovies	4	30.8	35	2.6
Mugiliformes	Mugilidae	Unidentified	Mulletts	1	7.7	1	0.1
Perciformes	Apogonidae	<i>Apogon sp.</i>	Cardinalfishes	7	53.8	317	23.4
	Leiognathidae	<i>Gazza sp.</i>	Toothponyfishes	7	53.8	130	9.6
		<i>Leiognathus sp.</i>	Pony fishes	2	15.4	22	1.6
		Unidentified	Slimys, slipmouths, ponyfishes	1	7.7	6	0.4
	Gerreidae	<i>Gerres sp.</i>	Mojarras	1	7.7	2	0.1
	Sciaenidae	<i>Johnius sp.</i>	Croakers	7	53.8	29	2.1
		<i>Otolithes ruber</i>	Tiger-toothed croaker	6	46.2	30	2.2
	Lactariidae	<i>Lactarius lactarius</i>	False trevally	3	23.1	3	0.2
	Haemulidae	<i>Pomadasys sp.</i>	Grunts	7	53.8	64	4.7
		<i>Pomadasys trifaciatius</i>	Black-ear javelin	1	7.7	16	1.2
	Sillaginidae	<i>Sillago sp.</i>	Smelt-whittings	8	61.5	74	5.5
	Sphyrnaeidae	<i>Sphyrna sp.</i>	Barracudas	3	23.1	3	0.2
	Trichiuridae	<i>Trichinurus sp.</i>	Cutlassfishes	2	15.4	2	0.1
	Mullidae	Unidentified	Goat fishes	2	15.4	3	0.2
Scorpaeniformes	Platycephidae	<i>Platycephalus sp.</i>	Flatheads	5	38.5	14	1.0
Siluriformes	Ariidae	<i>Arius sp.</i>	Sea catfishes	1	7.7	1	0.1
Unidentified fish				10	76.9	87	6.4
All Fish				12	92.3	874	64.6
Sepiia	Sepiidae	<i>Sepia sp.</i>	Cuttlefish	11	84.6	225	16.6
Teuthida	Loliginidae	<i>Uroteuthis (Photoligo) sp.</i>	Squid	4	30.8	207	15.3
		<i>Lololus sp.</i>	Squid	3	23.1	11	0.8
		<i>Sepioteuthis lessoniana</i>	Bigfin reef squid	4	30.8	5	0.4
	Unidentified			3	23.1	22	1.6
All Cephalopoda				11	84.6	470	34.7
Decapoda	Penaeidae	<i>Penaeus indicus</i>	Indian prawns	1	7.7	2	0.1
		<i>Metapenaeopsis sp.</i>	Prawns	1	7.7	3	0.2
		Unidentified		1	7.7	2	0.1
	Unidentified crab			1	7.7	1	0.1
All Decapoda				3	23.1	8	0.6
Class Bivalvia Unidentified order	Unidentified mollusc			1	7.7	1	0.1
All Bivalvia				1	7.7	1	0.1
TOTAL						1353	

Diet of Indo-Pacific humpback dolphins

A total of 259 prey items were retrieved from the stomach contents of six humpback dolphins (Table 1). The majority of these prey items were teleost fish ($n = 257$, Table 3). Fish remains were found in all stomachs, whereas cephalopods and bivalves were only found in one stomach and in very low numbers (Table 3). The number of prey items found per stomach ranged from 1 to 203 (Mean = 43.2, SD = ± 79.5), and the average number of different prey taxa per stomach was 4.2 (\pm SD 2.3). Undigested fish was found half of the stomachs.

From the otoliths and undigested fish remains we were able to identify 16 different fish taxa: two to Species, 13 to Genus, and three 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 (half of all stomachs), Mugilidae, Clupeidae, Sciaenidae and Haemulidae (33%) (Table 3). Grunt fish (*Pomadasys sp.*) were the most numerically important prey (Figure 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 spp.*, 9.7%).

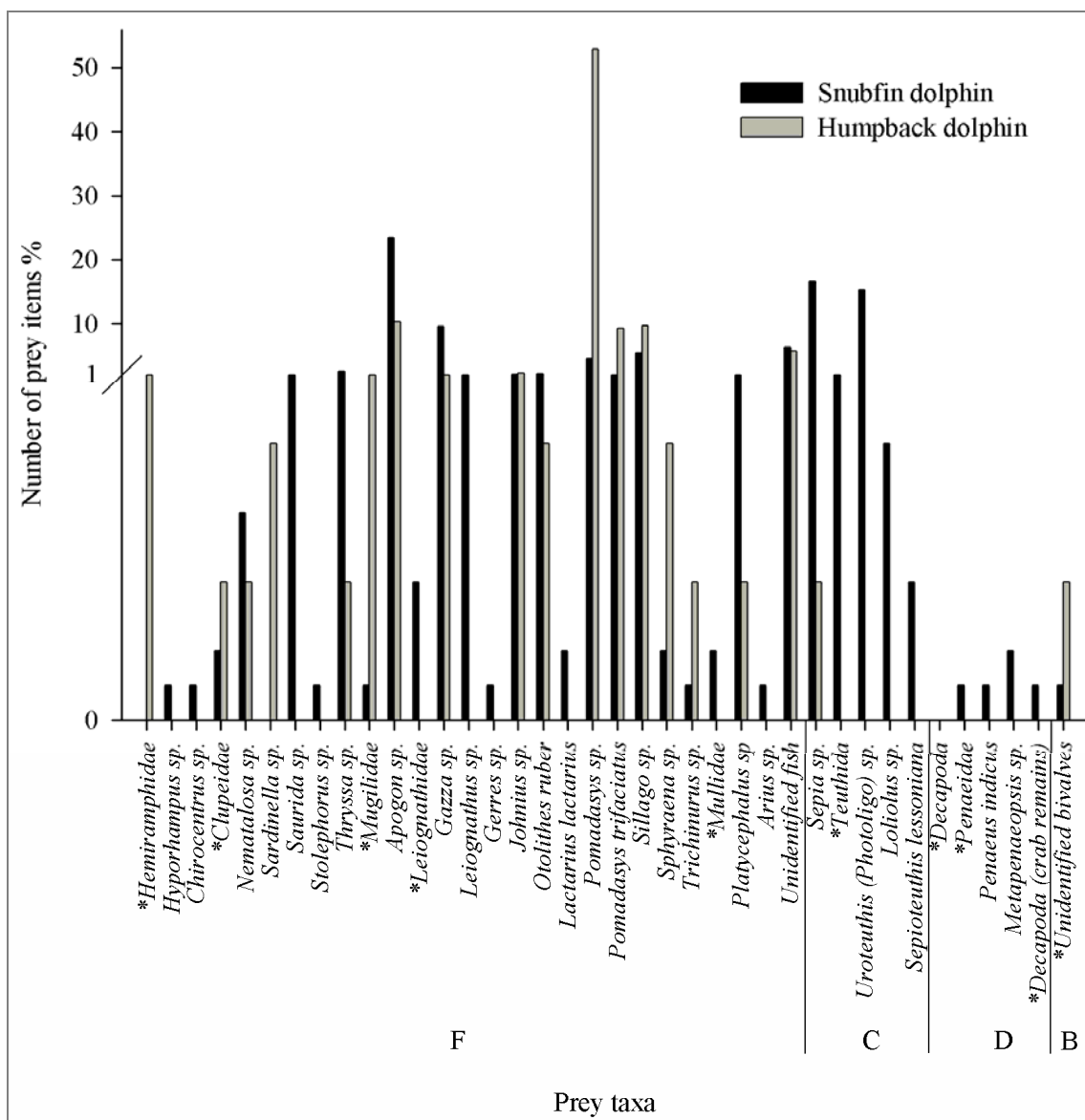


Figure 1. Percentage of the total number of prey items found in the stomach contents of snubfin ($n = 13$) and humpback dolphins ($n = 6$) from Queensland waters. F = Fishes; C = Cephalopods; D = Decapods. Prey taxa with an asterisk (*) were only identified to Order or Family level.

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			Common Names	Occurrence		Number	
Order	Family	Genera/species		No.	%	No.	%
Beloniformes	Hemiramphidae	Unidentified	Halfbeaks	1	16.7	3	1.2
Clupeiformes	Clupeidae	<i>Nematalosa sp.</i>	Gizzard shads	1	16.7	1	0.4
		<i>Sardinella sp.</i>	Sardines	1	16.7	2	0.8
		Unidentified	Herrings, shads, sardines	1	16.7	1	0.4
	Engraulidae	<i>Thryssa sp.</i>	Anchovies	1	16.7	1	0.4
Mugiliformes	Mugilidae	Unidentified	Mulletts	2	33.3	5	1.9
Perciformes	Apogonidae	<i>Apogon sp.</i>	Cardinal fishes	3	50.0	27	10.4
	Leiognathidae	<i>Gazza sp.</i>	Toothpony fishes	1	16.7	4	1.5
	Sciaenidae	<i>Johnius sp.</i>	Croakers	1	16.7	6	2.3
		<i>Otolithes ruber</i>	Tiger-toothed croaker	2	33.3	2	0.8
	Haemulidae	<i>Pomadasys sp.</i>	Grunts	2	33.3	137	52.9
<i>Pomadasys trifasciatus</i>		Black-ear javelin	1	16.7	24	9.3	
	Sillaginidae	<i>Sillago sp.</i>	Smelt-whittings	1	16.7	25	9.7
	Sphyraenidae	<i>Sphyraena sp.</i>	Barracudas	1	16.7	2	0.8
	Trichiuridae	<i>Trichinurus sp.</i>	Cutlassfishes	1	16.7	1	0.4
Scorpaeniformes	Platycephidae	<i>Platycephalus sp.</i>	Flatheads	1	16.7	1	0.4
Unidentified fish				5	83.3	15	5.8
All fish				6	100.0	257	99.2
Sepiia	Sepiidae	<i>Sepia sp.</i>	Cuttlefish	1	16.7	1	0.4
All Cephalopoda				1	16.7	1	0.4
Class Bivalvia Unidentified order	Unidentified mollusc			1	16.7	1	0.4
All Bivalvia				1	16.7	1	0.4
TOTAL						259	

Dietary breadth and overlap

Snubfin dolphins showed a larger dietary breadth ($B = 0.21$) than humpback dolphins ($B = 0.13$). Despite these differences there was some dietary overlap between both species ($Ojk = 0.30$) and the Mantel test revealed no significant interspecific differences in dietary composition ($r_M = -0.041$, $p = 0.328$). Of the 13 fish taxa identified to genus in the stomachs of humpback dolphins 12 were also consumed by snubfin dolphins (Figure 1). The most frequent and numerically important prey item of each dolphin species was also consumed by the other (Figure 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.

Discussion

This study represents the first quantitative assessment of the diet of Australian snubfin and humpback dolphins. Our results indicate that snubfin and humpback dolphins are opportunistic-generalist feeders preying on a wide variety of fish and cephalopods associated with shallow, inshore and estuarine habitats. Humpback dolphins appear to feed primarily on fish, while snubfin dolphins' also included cephalopods in their diet. Decapods and bivalves represented only a small fraction of the prey items identified in the stomach contents of both species.

The fish encountered in the stomachs revealed that both dolphins feed on schooling, bottom-dwelling fish (e.g. grunts, toothponyfishes, croakers, flatheads, whittings) as well as pelagic fish (e.g. cardinalfishes, gizzard shads, anchovies, barracudas). The cuttlefish and squid found in the stomachs of snubfin dolphins are typically mid-water swimmers. 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 through the water column and tend to feed in waters close to the coast and river mouths. These feeding habits are in accordance with snubfin and humpback dolphins habitat preferences and foraging behaviour: (1) high use areas by both species are typically located in shallow, coastal-estuarine habitats where animals are often seen foraging (Parra 2006); and (2) sediment clouds rising from the bottom are often observed during foraging activities indicating bottom feeding (Parra 2007, personal observations).

The comparison of snubfin and humpback dolphins' diet suggested snubfin dolphins have a wider dietary breadth including nine more species of fish as well as cephalopods (squid and cuttlefish). In Hong Kong Barros (2004) found humpback dolphins preyed almost exclusively on fishes and very rarely on cephalopods. Despite these differences, a number of fish prey were common in the diet of both dolphin species and the Mantel test revealed no significant interspecific differences in dietary composition. Most of the fish taxa consumed by humpback dolphins (12 out of 13), including their most important fish prey (Grunt fish, *Pomadasys sp.*), formed part of the diet of snubfin dolphins (Figure 1). Mantel tests are sensitive to small sample sizes and lose power for sample sizes below ten (Fortin and Gurevitch 1993). The lack of difference in diet between both species may be due to the small sample size of humpback dolphins ($n = 5$) in our analysis. Despite our potential lack of power to detect interspecific differences in diet, our data indicates snubfin and humpback dolphins diet partly overlap.

The partial overlap in dietary composition is likely due to the similar habitat preferences and ranging patterns between both species in coastal waters off the Townsville coast (Cleveland Bay); the origin of most of the samples analysed in this study. At the same time, the dietary differences found may also partly explain some of the slight differences in habitat

preferences between snubfin and humpback dolphins within their shared ranges in Cleveland Bay. In Cleveland Bay snubfin dolphins preferred slightly shallower (one to two metres) waters than humpback dolphins (two to five metres) (Parra 2006). Several species of cephalopods are abundant in shallow water ($\leq 1\text{m}$) close to the coast, and along breakwaters of Cleveland Bay (Jackson 1991). If the cuttlefish and squid species snubfin dolphins feed on are more abundant in shallow water this may help explain their preference for this type of habitats in comparison to humpback dolphins.

Facial morphological differences are likely related to differences in diet and method of food capture (Heyning and Mead 1996, Werth 2000, Werth 2006b, Werth 2006a). Snubfin and humpback dolphins differ substantially in their facial morphology. 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. Snubfin dolphins have a short-blunt rostrum, their teeth have an expanded crown but are not compressed and are reduced in number varying from 11-22 teeth in each half of the upper jaw and 14-19 teeth in each lower row (Robertson and Arnold 2008). In contrast, humpback dolphins have a long-narrow rostrum; their teeth are conical, pointed and vary from 29-38 in each tooth 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 2006b). 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 2006b, Werth 2006a). Suction feeding has been shown to be of particularly use for teuthophagous (cephalopod-eating) species, such as long-finned pilot whales, *Globicephala melas*, and harbour porpoises *Phocoena phocoena* (Werth 2000, Werth 2006b). 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, Werth 2006b).

Potential interaction with commercial fisheries

Depletion of local food resources is likely to negatively affect coastal populations of marine mammals over the next century (DeMaster *et al.* 2001). The majority of the Australian fisheries catch is taken close to the coast in waters less than fifty metres deep (Resource Assessment Commission, 1993), and commercial fisheries are at or near full exploitation (Kearney *et al.* 1996). 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. Behavioural observations (Parra 2006) together with the data presented here on diet composition indicate coastal-estuarine waters are important foraging habitats for snubfin and humpback dolphins. Because of their coastal distribution and feeding ecology snubfin and humpback dolphins are at greater risk of directly or indirectly interacting with commercial fisheries operating in coastal waters.

Of the different fisheries operating in Queensland waters net and trawling fisheries are the most likely to interact with coastal dolphins given their operations usually take place in inshore waters. Human-related mortality of humpback and snubfin dolphins in Australian waters is thought to be largely attributable to entanglements in inshore gillnets set across creeks, rivers, and shallow estuaries for fin fish species such as the barramundi (*Lates calcarifer*) and king and blue threadfins salmon (*Polydactylus sheridani* and *Eleutheronema tetradactylum*) (Hale 1997); and to shark nets set for bather protection (Paterson 1990).

The commercial East Coast Inshore Fin Fish Fishery (ECIFF) is the third most valuable fishery in Queensland. Commercial operations occur in inshore coastal and estuarine waters adjacent to Queensland's east coast and include over three hundred fishing vessels using a variety of different net fishing methods. The fishery targets a wide range of tropical and subtropical fin fish species including king and blue threadfins, barramundi, bream (*Acanthopagrus australis*), grey mackerel (*Scomberomorus semifasciatus*), spotted grunter bream (*Pomadasys kaakan*); mullet (*Mugil cephalus*), tailor (*Pomatomus saltatrix*), whiting (*Sillago sp.*), flathead (*Platycephalus sp.*), mulloway (*Argyrosomus hololepidotus*), and school mackerel (*Scomberomorus queenslandicus*) (DPI&F 2008). Among these species snubfin and humpback dolphins feed on mullets, grunters, whittings and flatheads. Although our analysis didn't allow us to identify most prey taxa to species level, it is clear that both dolphin prey on fish commonly targeted by the (ECIFF). As a result interactions with these fisheries are expected, particularly in areas where fishing operations overlap with dolphins' high use areas.

The East Coast Trawl Fishery (ECTF) is Queensland's largest commercial fishery, with about 600 vessels producing up to eight thousand tonnes of product a year (DPI&F 2007). The main targets of the ECTF are scallops, stout whiting, bugs and squid. The principal prawn species targeted are: tiger prawn (*Penaeus esculentus*, *P. semisulcatus* or *P. monodon*), endeavour prawn (*Metapenaeus endeavouri* and *M. ensis*), red spot king prawn (*Penaeus longistylus*), banana prawn (*Penaeus merguensis*), eastern king prawn (*Penaeus plebejus*) and bay prawn (*Metapenaeus bennettiae* and *M. macleayi*). The main squid species caught are; pencil squid (*Photololigo* – two species), tiger squid or northern calamari (*Sepioteuthis* – two species) and arrow squid (*Nototodarus* – two species, *Ommastrephes bartramii*, *Sthenoteuthis oualaniensis*). The key fish species targeted in the trawl fishery are the stout whiting (*Sillago robusta*) and red spot whiting (*Sillago flindersi*).

Prawns were only found in small proportions in the stomachs of snubfin dolphins (Figure 1) and do not appear to be a major prey item in their diet. However, squids (*Photololigo sp.*) were frequently found in the stomachs of snubfin dolphins (Figure 1) and whittings (*Sillago sp.*) were preyed by both humpback and snubfin dolphins (Figure 1). Thus some overlap and potential interactions between trawling fishing activities and snubfin and humpback dolphins is likely to occur. In fact, humpback dolphins have been observed foraging behind trawlers for several hours in different areas along the Queensland Coast and elsewhere throughout their range (Corkeron 1990, Jefferson 2000, Parra 2006). It is unclear if humpback dolphins feed on the fish caught in the trawler net, those that escape the net or those that are stirred up by the trawling. Thus humpback dolphins may not necessarily consume the same prey species as caught by the trawlers.

Most recent dietary studies of cetaceans rely on stomach contents from stranded and bycaught animals. Although these samples 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 and prey identification. Stranded animals may include sick animals that will not have been feeding normally or may not have been feeding at all. Additionally not all ingested preys are equally likely to be identified. The beaks of cephalopods tend to be more resistant to digestion than otoliths and sometimes accumulate in the stomach (Santos *et al.* 2001a). 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). 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 will lead to a better understanding of the feeding ecology of these animals and their potential interaction with local fisheries.

References

- Allen, M. C., A. J. Read, J. Gaudet, and L. S. Sayigh. 2001. Fine-scale habitat selection of foraging bottlenose dolphins *Tursiops truncatus* near Clearwater, Florida. *Marine Ecology Progress Series* 222: 253-264.
- 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.
- Benoit-Bird, K. J. and W. W. L. Au. 2003. Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. *Behavioral Ecology and Sociobiology* 53: 364-373.
- Clarke, M. R. 1986. *A handbook for the identification of cephalopod beaks*. Oxford University Press, USA
- 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.
- Corkeron, P. J. 1990. Aspects of the behavioural ecology of inshore dolphins *Tursiops truncatus* and *Sousa chinensis* in Moreton Bay, Australia. Pages 285-293 in S. Leatherwood and R. R. Reeves, editors. *The Bottlenose Dolphin*. Academic Press, London.
- Corkeron, P. J., N. M. Morissette, L. J. Porter, and H. Marsh. 1997. Distribution and status of hump-backed dolphins, *Sousa chinensis*, in Australian waters. *Asian Marine Biology* 14: 49-59.
- DeMaster, D. P., C. W. Fowler, S. L. Perry, and M. E. Richlen. 2001. Predation and competition: the impact of fisheries on marine-mammal populations over the next one hundred years. *Journal of Mammalogy* 82: 641-651.
- 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.
- DPI&F. 2007. *Annual status report 2007: East Coast Trawl Fishery*. Department of Primary Industries and Fisheries, Brisbane, Queensland.
- DPI&F. 2008. *Annual status report 2008: East Coast Inshore Fin Fish Fishery*. Department of Primary Industries and Fisheries, Brisbane, Queensland.

- Edwards, J. W., D. G. Heckel, and D. C. Guynn, Jr. 1998. Niche Overlap in Sympatric Populations of Fox and Gray Squirrels. *The Journal of Wildlife Management* 62: 354-363.
- Fortin, M. and J. Gurevitch. 1993. Mantel tests: spatial structure in field experiments. Pages 342-359 in S. M. Scheiner and J. Gurevitch, editors. *Design and analysis of ecological experiments*. Chapman & Hall, New York.
- Frère, C. H., P. T. Hale, L. Porter, V. G. Cockcroft, and M. L. Dalebout. 2008. Phylogenetic analysis of mtDNA sequences suggests revision of humpback dolphin (*Sousa* spp.) taxonomy is needed. *Marine and Freshwater Research* 59: 259-268.
- 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 us 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. *Reports 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. *Reports 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, Townsville, Queensland.
- Heithaus, M. R. and L. M. Dill. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology* 83: 480-491.
- 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.
- 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. and L. Karczmarski. 2001. *Sousa chinensis*. *Mammalian Species* 655: 1-9.
- Jones, M. E. and L. A. Barmuta. 1998. Diet overlap and relative abundance of sympatric dasyurid carnivores: A hypothesis of competition. *Journal of Animal Ecology* 67: 410-421.
- Luo, J. and B. Fox. 1996. A Review of the Mantel Test in Dietary Studies: Effect of Sample Size and Inequality of Sample Sizes. *Wildlife Research* 23: 267-288.

- 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.
- Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research* 27: 209-220.
- 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. 2007. Observation of an Indo-Pacific humpback dolphin carrying a sponge: object play or tool use? *Mammalia* 71: 147-149.
- 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.
- Parra, G. J., P. J. Corkeron, and H. Marsh. 2006. Population sizes, site fidelity and residence patterns of Australian snubfin and Indo-Pacific humpback dolphins: Implications for conservation. *Biological Conservation* 129: 167-180.
- 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.
- Patterson, G. B. 1986. A statistical method of testing for dietary differences. *New Zealand Journal of Zoology* 13: 113-115.
- 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. *Symp. Zool. Soc.* 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 UK* 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.
- Ray, J. Ray, Sunquist, and M. Sunquist. 2001. Trophic relations in a community of African rainforest carnivores. *Oecologia* 127: 395-408.

- Reeves, R. R., M. L. Dalebout, T. A. Jefferson, L. Karczmarski, K. Laidre, O'Corry-Crowe, R.-B. G., S. L., E.R., E. Slooten, B. D. Smith, J. Y. Wang, and K. Zhou. 2008a. *Sousa chinensis*. 2008 IUCN Red List of Threatened Species. .
- Reeves, R. R., T. A. Jefferson, L. Karczmarski, K. Laidre, O'Corry-Crowe, R.-B. G., S. L., E.R., E. Slooten, B. D. Smith, J. Y. Wang, and K. Zhou. 2008b. *Orcaella heinsohni*. 2008 IUCN Red List of Threatened Species.
- Reynolds, J. C. and N. J. Aebischer. 1991. Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the Fox *Vulpes vulpes*. *Mammal Review* 21: 97-122.
- Robertson, K. M. and P. A. Arnold. 2008. Australian Snubfin Dolphin: *Orcaella heinsohni*. Pages 62-64 in W. F. Perrin, B. H. Würsig, and H. Thewissen, editors. *Encyclopedia of Marine Mammals Second Edition*. Academic Press, San Diego, CA.
- Santos, M. B., M. R. Clarke, and G. J. Pierce. 2001a. 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. 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., G. J. Pierce, J. A. Learmonth, R. J. Reid, H. M. Ross, I. A. P. Patterson, D. G. Reid, and D. Beare. 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.
- Santos, M. B., G. J. Pierce, R. J. Reid, I. A. P. Patterson, H. M. Ross, and E. Mente. 2001b. Stomach contents of bottlenose dolphins (*Tursiops truncatus*) in Scottish waters. *Journal of the Marine Biological Association of the United Kingdom* 81: 873-878.
- 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.
- Thompson, P. M., B. Wilson, K. Grellier, and P. S. Hammond. 2000. Combining power analysis and population viability analysis to compare traditional and precautionary approaches to conservation of coastal cetaceans. *Conservation Biology* 14: 1253-1263.
- 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. 2006a. Mandibular and dental variation and the evolution of suction feeding in odontoceti. *Journal of Mammalogy* 87: 579-588.

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