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Predation by killer whales (*Orcinus orca*) and the evolution of whistle loss and narrow-band high frequency clicks in odontocetes

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predation;
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Abstract

A disparate selection of toothed whales (Odontoceti) share striking features of their acoustic repertoires including the absence of whistles and high frequency but weak (low peak-to-peak source level) clicks that have a relatively long duration and a narrow bandwidth. The non-whistling, high frequency click species include members of the family Phocoenidae, members of one genus of delphinids, *Cephalorhynchus*, the pygmy sperm whale, *Kogia breviceps*, and apparently the sole member of the family Pontoporiidae. Our review supports the 'acoustic crypsis' hypothesis that killer whale predation risk was the primary selective factor favouring an echolocation and communication system in cephalorhynchids, phocoenids and possibly Pontoporiidae and Kogiidae restricted to sounds that killer whales hear poorly or not at all (< 2 and > 100 kHz).

Introduction

The odontocetes, or toothed whales, are a diverse group of 71 species in 10 families ranging from the tropics to the polar ice-caps and inhabiting rivers on several continents. They range in size from the enormous male sperm whale at 18 m and 55 t, to the diminutive Hector's dolphin of the coastal waters of New Zealand, at 1.5 m. A striking puzzle in odontocete biology is the convergence of members of the porpoise family Phocoenidae and the delphinid genus *Cephalorhyncus*, in a number of traits. All four cephalorhynchids and most phocoenids are small odontocetes, ranging from 1.5 to 2 m in length and lack a definite beak. As groups, their distribution can be characterized as primarily coastal and cool temperate, found mostly from 30° to 60°. They are the only small odontocetes to occupy nearshore waters in the cool temperate regions of both hemispheres. Exceptions include three phocoenids, *Phocoenoides dalli* and *Australophocaena dioptrica*, that exceed 2 m in length and have a substantial offshore distribution, and *Neophocaena phocaenoides*, a riverine/coastal warm water species. Cephalorhynchids and phocoenids also share two characteristics of their acoustic repertoire: they do not whistle and they produce high frequency but weak (low peak-to-peak source level) clicks that have a relatively long duration and narrow bandwidth (Au, 1993). All of these shared traits may be primitive for the porpoise genera (but likely derived at the family level) and derived for the genus *Cephalorhynchus*, which is nestled within the delphinid subfamily Lissodelphininae (LeDuc *et al.*, 1999; Harlin-Cognato & Honeycutt, 2006; May-Collado & Agnarsson, 2006).

More recently, similar narrow-band high frequency (NBHF) clicks have been reported in the pygmy sperm whale (*Kogia breviceps*), a species that is ecologically and phylogenetically far removed from *Cephalorhynchus* and the Phocoenidae (Ridgway & Carder, 2001; Madsen *et al.*, 2005a). Furthermore, it appears that, *Pontoporia blainvillei*, another distant relative of porpoises and delphinids, produces phocoenid type clicks and does not whistle (Von Fersen *et al.*, 2000).

Andersen & Amundin (1976) first suggested that the NBHF clicks of harbour porpoises (*Phocoena phocoena*)

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might be an adaptation to evade acoustic detection by killer whales. Recently, Morisaka (2005) and Madsen *et al.* (2005a) linked the convergent evolution of whistle loss and NBHF click production in cephalorhynchid, phocoenids, *K. breviceps* and likely *P. brainvillei* (Morisaka, 2005) to predation risk from killer whales, which apparently cannot hear NBHF clicks.

Here we develop further the killer whale predation hypothesis for the evolution of whistle loss and high-frequency clicks in odontocetes and evaluate alternative hypotheses. Before presenting the hypotheses, we review briefly odontocete sounds and the evolution of whistles and NBHF clicks.

Sound production in odontocetes

Unlike most mammals, odontocetes do not produce sounds in the larynx but in the narial passages above the larynx (Ridgway *et al.*, 1980; Mackay & Liaw, 1981). The exact mechanism of sound production has been the focus of extensive study, mostly because of navy (both USA and USSR) interest in dolphin biosonar. More is known about sound production in the bottlenose dolphin than any other odontocete. Bottlenose dolphin sounds are rather easily dichotomized into two broad categories; whistles, which are relatively long duration (mean duration: 0.1–2.3 s; Matthews *et al.*, 1999) tonal sounds that are often frequency modulated (Fig. 1), and pulsed sounds, which are short duration and relatively broad band. Whistles and pulsed sounds can be emitted simultaneously (Lilly & Miller, 1961), suggesting they are produced by different sound production mechanisms. Whistles are thought to be for communication exclusively while pulsed sounds are used for echolocation and communication. Both whistles and clicks have been described in a large number of odontocetes (Tables 1 and 2).

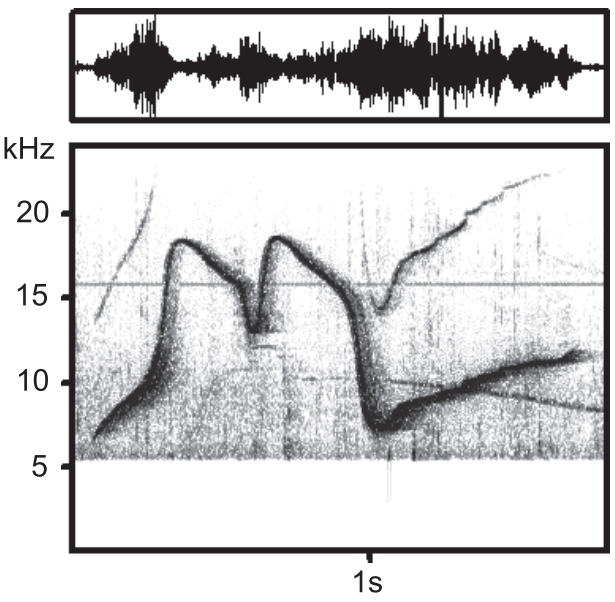

Fig. 1 Spectrogram of a whistle. The *x*-axis represents time (s), and the *y*-axis represents frequency (kHz).

Clicks

The click sounds of odontocetes can be divided into two general categories. Broadband clicks are short (40–70 μs) and intense pulses with bandwidths (−3 dB) of tens of kHz. Narrow-band high frequency clicks are relatively long (> 125 μs) and weak signals with one peak above 100 kHz and with bandwidths (−3 dB) typically < 10 kHz (Au, 1997, 2002; Fig. 2). The waveform of the weaker 'polycyclic' NBHF pulse exhibits an amplitude increase for the first five cycles and then decays exponentially (Nakamura & Akamatsu, 2004; Fig. 2a), whereas broadband clicks have one or two cycles with the first cycle achieving maximum amplitude (Fig. 2b; Evans, 1973; Au, 1993; Madsen *et al.*, 2004b).

All species of odontocetes for which there are published data on click structure and that produce whistle-like sounds produce broadband clicks with short durations. This includes the Delphinidae, except for members of the genus *Cephalorhyncus*, the Monodontidae, Iniidae, Lipotidae and may be some Ziphiids.

The clicks produced by Phocoenid species and members of the genus *Cephalorhynchus* are 'polycyclic' (Nakamura & Akamatsu, 2004); they last five to 10 times longer and have roughly half the bandwidth (−3 dB) of clicks produced by bottlenose dolphins. *Kogia breviceps* and *P. brainvillei* are the only two other odontocetes known to produce NBHF clicks (Von Fersen *et al.*, 2000; Madsen *et al.*, 2005a). Importantly, all NBHF species exhibit peak frequencies over 100 kHz (Table 1). NBHF species are also thought to exhibit peak-to-peak source levels several orders of magnitude less than clicks produced by bottlenose dolphins (see reviews in Au, 1993; Tyack & Clark, 2000). Recently, Villadsgaard *et al.* (2007) reported that wild harbour porpoises (*P. phocoena*) produce clicks with a mean peak-to-peak source level of 191 dB re 1 μPa at 1 m, which is stronger than previously reported. However, NBHF clicks are still an order of magnitude weaker than that of 'broadband' clicks. Further field research may reveal differences in peak-to-peak levels between 'broadband' and 'polycyclic' clicks.

To establish homology in odontocete sound production, one would ideally like a detailed understanding of sound structure, sound production mechanisms and, on a more refined level, how changes in mechanism impact the acoustic structure of sounds. The best evidence suggests that all odontocetes make echolocation clicks that are produced by the phonic lips and associated acoustic fat bodies, together called the 'monkey-lips and dorsal bursae complex', or MLDB (Cranford *et al.*, 1996; Fig. 3) and that the MLDB complex arose once in

Table 1 Echolocation clicks in odontocetes.

			Clicks (kHz; mean ± SD)							
Family	Latin name	Common name	LPF	HPF	CF	Frequency Range(kHz)	Structure	Condition	Data used	Reference
Physeteridae	*Physeter catodon*	Sperm whale			15	5–24 (–10 dB)	One peak	Sea	y	Madsen *et al.*, (2002)
Kogiidae	*Kogia brainvillei*	Pygmy sperm whale		130 ± 0.7	129 ± 0.6		One peak	Tank	y	Madsen *et al.*, (2005)
Platanistidae	*Platanista gangetica*	Susu				15–60 ?/20–100	?	Tank	n	Herald *et al.*, 1969/Pilleri *et al.*, (1971)
Ziphiidae	*Hyperoodon ampullatus*	Northern bottlenose whale			11, 24	2–26	Bimodal?	Sea	y	Hooker & Whitehead, (2002)
	Mesoplodon densirostris	Blainvilles beaked whale				25->43	One peak?	Sea	n	Johnson *et al.*, (2004)
	Mesoplodon carlhubbsi	Hubbs beaked whale				0.3->40	?	Tank	n	Lynn & Reiss, (1992)
	Barardius bairdii	Bairds beaked whale	23	42			Bimodal	Sea	y	Dawson *et al.*, (1998)
	Ziphius cavirostris	Cuviers beaked whale		40	42	15–80 (–30 dB)	One peak?	Sea	y	Zimmer *et al.*, (2005)
Lipotidae	*Lipotes vexillifer*	Baiji	71	112.1	78.9 ± 19.1		Bimodal	Tank	y	Nakamura, (1999)
Pontoporiidae	*Pontoporia blainvillei*	Franciscana		130			One peak?	Tank	y	Von Fersen *et al.*, (2000)
Iniidae	*Inia geoffrensis*	Boto				60–80/85–100	?	Tank/Lake	n	Evans, 1973/Kamminga *et al.*, (1993)
Monodontidae	*Delphinapterus leucas*	Beluga	71	112.6	82.5 ± 21.7	46.6–125.7	Bimodal	Tank	y	Nakamura, (1999)
	Monodon monoceros	Narwal			48 ± 10	24–95 (–10 dB)	?	Sea	y	Miller *et al.*, (1995)
Phocoenidae	*Phocoena phocoena*	Harbor porpoise		123.9 ± 2.2		118.9–128.4	One peak	Tank	y	Au *et al.*, (1999)
	Phocoena sinus	Vaquita		132.9 ± 3.9		128–139	One peak	Sea	y	Silber, (1991)
	Neophocoena phocaenoides	Finless porpoise		125 ± 2.3		117.2–130.2	One peak	Tank	y	Kamminga *et al.*, (1986)
	Phocoenoides dalli	Dalls porpoise		133			One peak	Tank	y	Kamminga *et al.*, (1996)
Delphinidae	*Orcaella brevirostris*	Irrawaddy dolphin				50–75	?	Tank	n	Kamminga *et al.*, (1983) in Richardson *et al.*, (1995)
	Orcinus orca	Killer whale	20–30	40–60	50	45–80	Bimodal	Sea	y	Au *et al.*, (2004)
	Pseudorca crassidens	False killer whale	45.7	110	62.3		Bimodal	Tank	y	Au *et al.*, (1995)
	Feresa attenuata	Pygmy killer whale	40	100	70–85	45–117	Bimodal	Sea	y	Madsen *et al.*, (2004a)
	Peponocephala electra	Melon-headed whale				20–40	?	Sea	n	Watkins *et al.*, (1997)
	Grampus griseus	Rissos dolphin	30–50	80–100	47.9		Bimodal	Tank	y	Philips *et al.*, (2003)
	Sotalia fluviatilis	Tucuxi			80–95		One peak?	River	y	Kamminga *et al.*, (1993)
	Stenella attenuata	Pantropical spotted dolphin	40–60	120–140	69.4 ± 31.3	40–140	Bimodal	Sea	y	Schotten *et al.*, (2004)
	Stenella longilostris	Spinner dolphin	40–60	120–140	69.7 ± 23.1	40–140	Bimodal	Sea	y	Schotten *et al.*. (2004)
	Tursiops truncatus	Bottlenose dolphin	67.3	114.3	94.1 ± 23.7	34.5–131.9	Bimodal	Tank	y	Nakamura, (1999)
	Stenella frontalis	Atlantic spotted dolphin	40–50	110–130	65		Bimodal	Sea	y	Au & Herzing, (2003)
	Delphinus delphis	Short-beaked common dolphin	81.4	114.8	112.1 ± 10.5	71.8–128.8	Bimodal	Tank	y	Nakamura, (1999)
	Lagenorhynchus obliquidens	Pacific white-sided dolphin	72.5	113.8	94.6 ± 23.6	30.5–129.5	Bimodal	Tank	y	Nakamura, (1999)
	Lagenorhynchus obscurus	Dusky dolphin	50–60	100–110	73.8 ± 27.3	30–130	Bimodal	Sea	y	Au & Würsig, (2004)
	Cephalorhynchus hectori	Hectors dolphin		125		115–135	One peak	Sea	y	Dawson & Thorpe, (1990)
	Cephalorhynchus commersonii	Commersons dolphin		125.4 ± 3.8		120.5–136.6	One peak	Tank	y	Nakamura, (1999)
	Lagenorhynchus albirostris	White-beaked dolphin	115	250	82 ± 4		Bimodal	Sea	y	Rasmussen & Miller, (2002), (2004)

Blanks indicate there are no published or satisfactory data. LPF, HPF and CF indicate low peak frequency, high peak frequency and centroid frequency of the clicks, respectively. In frequency range column, (–10 dB) and (–30 dB) indicate the frequency range for 10 and 30 dB below the maximum signal amplitude, respectively.

Condition indicates the recording location. In 'data used' column, 'n' indicates the data was not used for further regression analysis, whereas 'y' indicates the data was used in Fig. 8.

Table 2 Whistles in odontocetes.

			Whistle (kHz)								
Family	Latin name	Common name	y/n	Mini	Max	Min av	Max av	Centre	Number of analysis	Recording site	Reference
Physeteridae	*Physeter catodon*	Sperm whale	n								Watkins (1977) in Herman & Tavolga (1980)
Kogiidae	*Kogia breviceps*	Pygmy sperm whale	n								Ridgway & Carder (2001)
Platanistidae	*Platanista gangetica*	Susu	n								Andersen & Pilleri (1970); Pilleri *et al.* (1971); Takemura & Nishiwaki (1975); but Mizue *et al.* (1971)
Ziphiidae	*Hyperoodon ampullatus*	Northern bottlenose whale	y	3	16				?	Nova Scotia, Canada	Winn & Perkins (1970) in Matthews *et al.* (1999)
	Mesoplodon densirostris	Blainville's beaked whale	y	1	6				?	Stranded subadult male	Caldwell & Caldwell (1971a)
	Mesoplodon carlhubbsi	Hubb's beaked whale	y	0.3	18	4.2	7.7		6	captive juvenile males	Lynn & Reiss (1992)
	Berardius bairdii	Baird's beaked whale	y	4	8				4	Off Oregon, USA	Dawson *et al.* (1998)
	Berardius amuxii	Arnoux's beaked whale	y	2	6			4.90	24	Kemp Land, Antarctica	Roger & Brown (1999)
Lipotidae	*Lipotes vexillifer*	Baiji	y	3	18.4			6	?	Captive male	Jing *et al.* (1981)
				3.78	9.34	4.98	5.84		46	captive & Oxbow, China	Wang *et al.* (1999)
Pontoporiidae	*Pontoporia blainvillei*	Franciscana	n								Busnel *et al.* (1974); Nakasai & Takemura (1975); Von Fersen *et al.* (2000)
Iniidae	*Inia geoffrensis*	Boto	y	0.22	5.16	2.54	2.97		76	Maranon and Tigre rivers, Peru	Wang *et al.* (1995b, 2001)
				0.4	7.92	1.41	2.9		240	Mamiraua researve, Amazon river	Podos *et al.* (2002)
Monodontidae	*Delphinapterus leucas*	Beluga	y	0.26	20	3.38	4.33	3.89	807	Cunningham Inlet, NW Canada	Sjare & Smith (1986)
	Monodon monoceros	Narwal	y	0.3	18	0.3	10		503	Baffin Island, Canada	Ford & Fisher (1978)
Phocoenidae	*Phocoena phocoena*	Harbor porpoise	n								Schevill *et al.* (1969)
	Phocoena sinus	Vaquita	n								Silber (1991)
	Neophocaena phocaenoides	Finless porpoise	n								Kamminga *et al.* (1986)
	Phocoenoides dalli	Dall's porpoise	n								Evans (1967 in Herman & Tavolga (1980)
Delphinidae	*Orcaella brevirostris*	Irrawaddy dolphin	y	1.1	6	3.15	4.2		51	Queensland, Australia	Van Parijs *et al.* (2000), but no whistle in Asian riverine form: Kamminga *et al.* (1983)
	Orcinus orca	Killer whale	y	1.5	18	6	12		?	Vancouver	Ford (1989) in Thomsen *et al.* (2001)
				2.4	16.7	5.4	9.9		180	Vancouver	Thomsen *et al.* (2001)
	Pseudorca crassidens	False killer whale	y	1.87	18.1	5.43	8.29	6.82	2186	Grenada & Costa Rica	Rendell *et al.* (1999)
						4.7	6.1		69	Eastern tropical Pacific Ocean	Oswald *et al.* (2003a)
	Feresa attenuata	Pygmy killer whale	y								Martin (1990); but no whistle in Pryor *et al.* (1965)
	Peponocephala electra	Melon-headed whale	y	5.5	24.5	11.73	16.33	12.75	26	Dominica, south eastern Caribbean	Watkins *et al.* (1997)
	Globicephala melas	Long-finned pilot whale	y	0.32	21.2	3.48	5.78	4.48	994	Meditterranean, Newfoundland, Schilly Island	Rendell *et al.* (1999)
						2.82	4.72	3.69	1529	Nova Scotia-Caribbean	Steiner (1981)
	Globicephala macrorhynchus	Short-finned pilot whale	y	0.24	23.6	5.43	9.6	7.87	994	Caribbean & Tenerife	Rendell *et al.* (1999)
					3.6	6.1		153	Eastern tropical Pacific Ocean		Oswald *et al.* (2003a)

Table 2 (*Continued*).

Family	Latin name	Common name	Whistle (kHz) y/n	Mini	Max	Min av	Max av	Centre	Number of analysis	Recording site	Reference
	Grampus griseus	Risso's dolphin	y	1.9	23.8	8.83	13.44	11.3	1264	Azores & Stornoway	Rendell *et al.* (1999)
				4	22	5.58	17.35		60	Newcastle, Australia	Corkeron & Van Parijs (2001)
Delphinidae	*Steno bredanensis*	Rough-toothed dolphin	y			6.3	9.1		68	Eastern tropical Pacific Ocean	Oswald *et al.* (2003a)
	Sotalia fluviatilis fluviatilis	Riverine Tucuxi	y	3.65	23.86	10.21	15.41	12.68	155	Maranon and Tigre rivers, Peru	Wang *et al.* (1995b, 2001)
						9.18	15.65		50	Mamiraua researve, Amazon river	Podos *et al.* (2002)
	Sotalia fluviatilis guianensis	Coastal Tucuxi	y	0.5	18	7.6	13		5086	Guanabara Bay, Brazil	Azevedo & Simão (2002)
				1.031	17.49	10.52	13.31		3350	Sepetiba Bay, Brazil	Erber & Simão (2004)
	Sousa chinensis	Indo-Pacific humpback dolphin	y	0.9	22	7.5	16		329	Stradbroke Island, Australia	Van Parijs & Corkeron (2001
	Lagenodelphis hosei	Fraser's dolphin	y	7.60	13.4	10.15	11.69		8	Dominica, Caribbean	Leatherwood *et al.* (1993)
	Stenella attenuata	Pantropical spotted dolphin	y	3.13	21.4	8.73	15.72	12.54	144	Costa Rica	Wang *et al.* (1995b)
						8.2	18.7		97	Eastern tropical Pacific Ocean	Oswald *et al.* (2003a)
	Stenella longirostris	Spinner dolphin	y	3.91	22.46	9.03	15.2		271	Hawaii	Wang *et al.* (1995b)
						9.1	13.7		112	Eastern tropical Pacific Ocean	Oswald *et al.* (2003a)
						8.76	14.32	11.5	2088	Nova Scotia-Caribbean	Steiner (1981)
				0.85	25.25	10.18	16.13		6462	Main Hawai'ian islands	Bazúa-Durán & Au (2004)
	Tursiops truncatus	Bottlenose dolphin	y	0.94	21.61	5.45	11.32		3449	All over the world	Wang *et al.* (1995a)
						7.4	17.2		157	Eastern tropical Pacific Ocean	Oswald *et al.* (2003a)
						7.33	16.24		858	Nova Scotia-Caribbean	Steiner (1981)
	Tursiops aduncus	Indo-Pacific bottlenose dolphin	y			5.94	11.2		1613	Japan	Morisaka *et al.* (2005)
	Stenella frontalis	Atlantic spotted dolphin	y	5	19.79	7.91	16.04	11.62	80	Bahama	Wang *et al.* (1995b)
						6.53	13.3		567	Nova Scotia-Caribbean	Steiner (1981)
	Stenella coeruleoalba	Striped dolphin	y			8.1	14.8		91	Eastern tropical Pacific Ocean	Oswald *et al.* (2003a)
				1.1	22.99	6.84	11.53	9.07	138	Meditterranean	Smythe (unpublished) in Matthews *et al.* (1999)
	Stenella clymene	Clymene dolphin	y	6.33	19.22				20	Gulf of Mexico	Mullin *et al.* (1994)
	Delphinus delphis	Short-beaked common dolphin	y	4.8	8.81	6.42	11.65		5291	captive	Moore & Ridgway (1995)
						7.4	13.6		88	Eastern tropical Pacific Ocean	Oswald *et al.* (2003a)
	Delphinus capensis	Lond-beaked common dolphin	y			7.7	15.5		73	Eastern tropical Pacific Ocean	Oswald *et al.* (2003a)
	Lissodelphis borealis	Northern right whale dolphin	y	1	16				?	Eastern north Pacific	Leatherwood & Walker (1979)
	Lagenorhynchus obliquidens	Pacific white-sided dolphin	y	2	20	4	12		?	captive	Caldwell & Caldwell (1971b in Richardson *et al.* (1995)
	Lagenorhynchus obscurus	Dusky dolphin	y	1.04	27.3	8.11	16.49	12.4	492	New Zealand	Wang *et al.* (1995b)
	Cephalorhynchus hectori	Hector's dolphin	n								Dawson (1988)
	Cephalorhynchus commersonii	Commerson's dolphin	n								Dziedzic & De Buffrenil (1989)
	Cephalorhynchus heavisidii	Heaviside's dolphin	n								Watkins *et al.* (1977)
	Lagenorhynchus australis	Peale's dolphin	n?								Schevill & Watkins (1971)
	Lagenorhynchus acutus	Atlantic white-sided dolphin	y	6	15	8.21	12.14	10.37	1691	Nova Scotia-Caribbean	Steiner (1981)
	Lagenorhynchus albirostris	White-beaked dolphin	y	3.49	16.5	9.14	13.05	11.16	79	Stornoway	Rendell *et al.* (1999, Matthews *et al.* (1999)

Min, minimum frequency; max, maximum frequency; min av, average of minimum frequencies; max av, average of maximum frequencies; centre, centre frequency of whistles.
'y' and 'n' indicate whistle presence and absence, respectively.

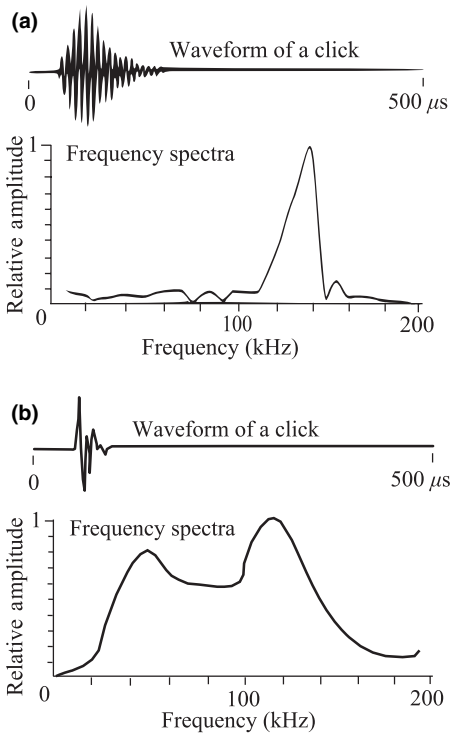

Fig. 2 Examples of representative echolocation click waveforms and frequency spectra; (a) by *Phocoena phocoena*, an NBHF click species (modified from Au, 1993); (b) by *Stenella frontalis*, a whistling species (modified from Au & Herzing, 2003).

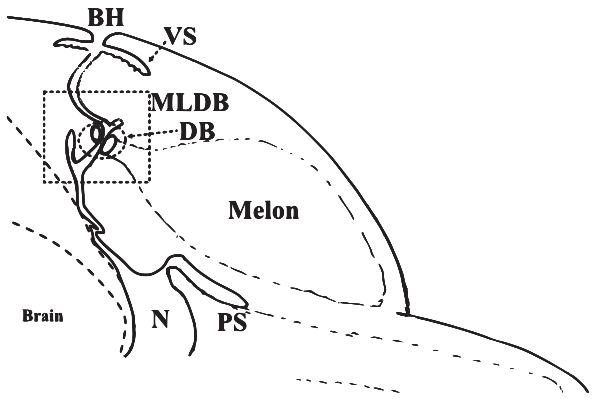

Fig. 3 Schematic diagram of the forehead of the bottlenose dolphin. BH, blowhole; DB, dorsal bursae; MLDB, monkey-lips dorsal-bursae complex; N, bony nares; PS, premaxillary sac; VS, vestibular sac (redrawn from Cranford *et al.* 1996).

odontocetes (see Berta & Sumich, 1999). Subsequent modifications of the MLDB complex associated with click structure differences are less well understood, but Cranford (1992) found striking similarities in the MLDB complex of *P. phocoena* and *Cephalorhynchus commersonii*. The right and left dorsal bursae are almost equal in size in

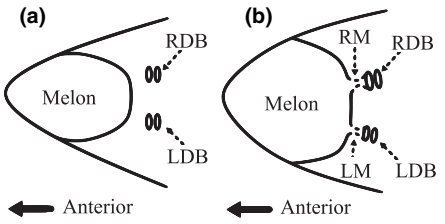

Fig. 4 Examples of horizontal schematic diagram (frontal section) of the forehead of (a) NBHF species, such as *Phocoena phocoena*; and (b) species that produce broadband, short clicks, such as *Tursiops truncatus*. LDB, left dorsal bursae; LM, left branch of melon; RDB, right dorsal bursae; RM, right branch of melon (redrawn from Cranford *et al.* 1996).

these species, or species that produce NBHF clicks, whereas in species that produce broadband, short clicks, the right dorsal bursae is twice as long as the left (Fig. 4). *Pontoporia* shares with other NBHF species symmetrical dorsal bursae, but also has extreme air sac asymmetry and a configuration of the fatty structures (e.g. presence of two branches from melon to dorsal bursae; Fig. 4b) closer to that of delphinids than to that of the porpoises (Cranford *et al.*, 1996). *Kogia*, which is phylogenetically very distant from the other small odontocetes under discussion, exhibits extreme skull asymmetry.

Cranford *et al.* (1996) suggested that dorsal bursae length may be related to click peak frequency. As mentioned above, some odontocete species produce broadband clicks with two frequency peaks (Table 1; Fig. 2; in detail, see Au, 2000). These species have asymmetrical dorsal bursae, where one MLDB complex is approximately twice the size of the other. The longer of the pair may be responsible for the lower frequency peak, whereas the shorter bursae may account for the high frequency peak. In contrast, *Phocoena*, *Cephalorhynchus* and *Pontoporia* have symmetrical dorsal bursae, i.e. two sound sources that are similar in size and shape, and produce NBHF clicks with one peak above 100 kHz. The evolution of extreme asymmetry in *Kogia* has resulted in only one set of phonic lips (the right side), which suggests that *Kogia* has a single sound source (Cranford *et al.*, 1996). Sperm whales, the closest extant relative of *Kogia*, also carry a single sound source, but they produce clicks with short durations and broad bandwidths (Møhl *et al.*, 2003). The extreme asymmetry and single sound source in *Kogia* and the sperm whale are thus thought to reflect their common ancestry.

Whistles

Our understanding of the mechanism of whistle production in odontocetes is less advanced, but some reports suggested that whistles are produced by 1) pressurizing the paired nasal cavities with muscle action (Ridgway & Carder, 1988); and 2) squeezing air past the phonic (monkey) lips, where 3) air-flow instability is caused by

several edges and areas of corrugation along the lips (see review by Ridgway *et al.*, 2001). However, until the mechanism of whistle production is firmly established for species that produce a range of tonal 'whistle' sounds, we cannot say that all whistle-like sounds are produced by the same or different mechanisms. We are, again, left with sound structure and cannot be certain whether differences in 'whistle' like sounds are modifications of a primitive sound production mechanism or are similar because they represent convergent sound production by different mechanisms. Podos *et al.* (2002) argued that delphinid whistles share characteristics that imply a common sound-production mechanism that is derived for the group. These features include not only the narrow band and often frequency modulated structure of whistles but also the predictable manner in which the fundamental frequency declines with increasing body size across species (Wang *et al.*, 1995b; Matthews *et al.*, 1999). However, without a better understanding of how whistle-like sounds are produced, it is difficult to say whether the features that might unite delphinid whistles owe to a common modification of a universal mechanism, or the evolution of a distinct mechanism (see also Podos *et al.*, 2002). For our purpose, it matters not whether the whistle-like sounds of delphinids exhibit derived characteristics unique to that family or not. What matters is the origin of whistle-like sounds with narrow band components. It is quite possible that a more primitive whistle production mechanism has been modified in different ways in different odontocetes. For the rest of this paper, we will use the word whistle to describe all tonal 'whistle-like' sounds (contra Podos *et al.*, 2002).

Phylogeny and the evolution of NBHF clicks and whistles

To evaluate the origin of whistles and NBHF clicks, we examined the distribution of these features against established phylogenies. Recent phylogenies are congruent in showing Physeteridae and Kogiidae as an ancient sister group to other odontocetes (Cassens *et al.*, 2000; Hamilton *et al.*, 2001; Nikaido *et al.*, 2001; Arnason *et al.*, 2004; May-Collado & Agnarsson, 2006; Fig. 5). The studies using a combination analysis of Short Interspersed Element (SINE) and flanking region sequences (Nikaido *et al.*, 2001) or three mitochondrial DNA regions (Hamilton *et al.*, 2001), concluded that the Platanistidae diverged after the Physeteridae and Kogiidae, and that the Ziphiidae and the other (Delphinida) diverged after the Platanistidae. After the Ziphiidae, the Lipotidae diverged, then the Delphinoidea and the other 'river' dolphins (Cassens *et al.*, 2000; Hamilton *et al.*, 2001; Nikaido *et al.*, 2001) (Fig. 5). Cassens *et al.* (2000) failed to resolve the exact phylogenetic position of the Platanistidae by phylogenetic analysis of three mitochondrial and two nuclear genes. Furthermore, relationships among the Ziphiidae, Platanistidae and the other families were unstable in the mitogenomic analysis of Arnason *et al.* (2004). May-Collado & Agnarsson (2006) reported the Ziphiidae, not Platanistidae, diverged just after the Physeteridae and Kogiidae, but Harlin-Cognato & Honeycutt (2006) cautioned that phylogenetic analyses based on mitochondrial data alone, such as May-Collado & Agnarsson (2006), can be misleading. In these cases, we defer to Nikaido *et al.* (2001) and Hamilton *et al.* (2001) (Fig. 5).

Six genetic phylogenies of the Delphinoidea concur that Monodontidae and Phocoenidae are sister groups to the exclusion of the Delphinidae (Rosel *et al.*, 1995; Cassens *et al.*, 2000; Waddell *et al.*, 2000; Nishida *et al.*, 2003; Arnason *et al.*, 2004; May-Collado & Agnarsson, 2006).

Since the family Delphinidae represents a recent radiation, establishing phylogenetic relationships within the group is difficult. Most recent phylogenies (LeDuc *et al.*, 1999; Pichler *et al.*, 2001; Cassens *et al.*, 2003;

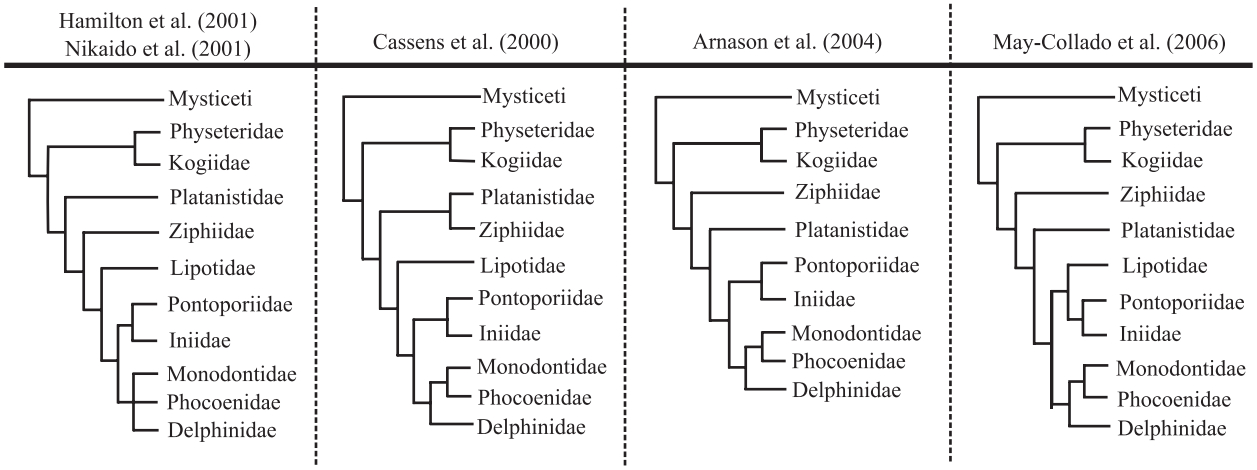

Fig. 5 Previous (but recent) hypotheses of cetacean relationships, especially odontocetes.

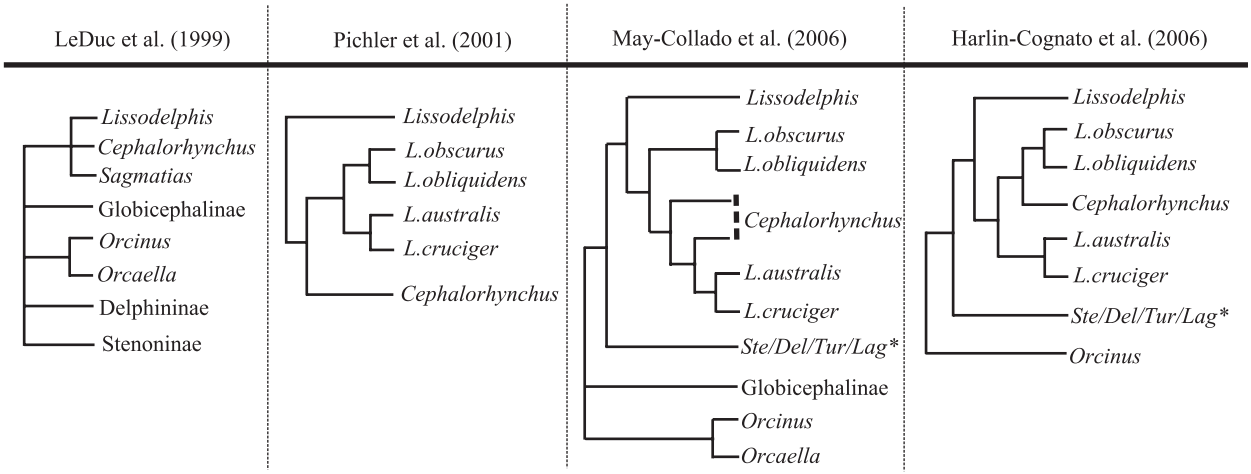

Fig. 6 Recent hypotheses of delphinid relationships, especially among *Lagenorhynchus* and *Cephalorhynchus* species.

Harlin-Cognato & Honeycutt, 2006; Fig. 6) are in agreement that *Cephalorhynchus* is monophyletic and embedded within the delphinidae with *Lagenorhynchus* being the sister group (Sagmatius, LeDuc *et al.*, 1999). In contrast, May-Collado & Agnarsson (2006) found that two *Lagenorhynchus* species, *L. australis* and *L. cruciger*, fall within the genus *Cephalorhynchus* (but see Harlin-Cognato & Honeycutt, 2006) (Fig. 6).

Whistle evolution in odontocetes

It is clear from Table 1 that whistles are widespread in odontocetes. Whistles are present in some Ziphiidae, Lipotidae, Iniidae, Monodontidae and Delphinidae except the genus *Cephalorhynchus*. We consider the Physeteridae, Kogiidae, Platanistidae, Pontoporiidae, Phocoenidae and genus *Cephalorhynchus* to be non-whistling groups. The significance of Schevill & Watkins' (1971) report that *Lagenorhynchus australis* does not whistle depends on resolution of its phylogenetic position (see below). Even though no data were available for *K. simus*, the similarities of sound-production organs between *K. simus* and its non-whistling congener, *K. breviceps*, as well as *Physeter* (Clarke, 2003), leads us to include *Kogia* in the non-whistling category. We follow Wang *et al.* (2001) in considering *Inia* a whistling species. Mizue *et al.* (1971) reported that *Platanista gangetica* produced a few whistles (1% per all sounds) in captivity. However, one of the authors (A. Takemura, personal communication) informed us that the sounds could have come from two *Inia geoffrensis* housed in an adjacent pool. Given that the other three studies failed to record whistles from *Platanista*, we regarded the Platanistidae as a non-whistling group.

Some Ziphiidae, Lipotidae, Iniidae and many Delphinoidea species produce whistles, whereas the Platanistidae and Physeteridae do not. Thus, whistles

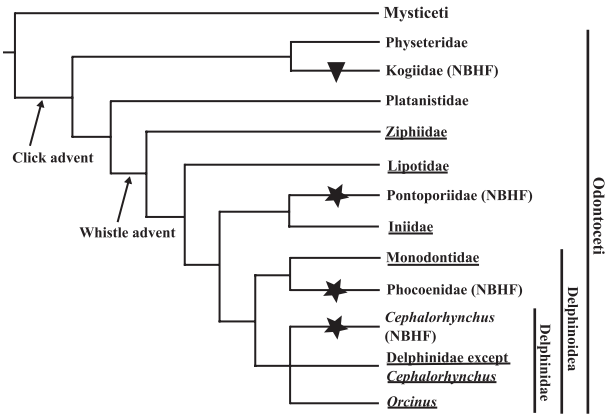

Fig. 7 Phylogenetic relationships among cetaceans. A triangle-mark indicates where NBHF clicks emerged. A star-mark indicates both whistle-loss and NBHF click emergence. The names of groups containing whistling species are underlined. The phylogenetic relationships among Delphinidae are not revealed well. Reconstructed from Cassens *et al.* (2000); Hamilton *et al.* (2001); Nikaido *et al.* (2001); and Arnason *et al.* (2004).

most likely have an early origin in the group, perhaps in the split between Ziphiids and Platanistidae (Fig. 7). It is most parsimonious to conclude therefore, that such sounds have been secondarily lost in *Cephalorhynchus*, Phocoenids and probably *Pontoporia*. Since some Ziphiidae species are reported not to produce whistles (e.g. Madsen *et al.*, 2005b), further research is needed to evaluate whistle evolution within this family.

Odontocete phylogeny (Fig. 7) indicates that the Phocoenids lost their whistles after splitting from the Monodontids. Rosel *et al.* (1995) and Fajardo-Mellor *et al.* (2006) examined the phylogenetic relationships among the Phocoenidae. They concluded that *Neophocaena phocaenoides*, a non-whistling species, is the most basal

member of Phocoenidae. We found no data on *Australophocaena dioptrica* and *P. spinipinnis*, but *P. sinus*, which is most closely related to those two species, does not whistle. There is a strong possibility that no Phocoenid species whistle, implying that whistle loss is a synapomorphy of this family.

Podos *et al.*'s (2002) conclusion that whistles are a delphinid synapomorphy depends on whistles being absent in other taxa, or if they are present, to have evolved independently. Their conclusion that the Monodontidae, a family closely related to Delphinids, do not whistle, is at odds with previous discussions (e.g. Ford & Fisher, 1978; Sjare & Smith, 1986).

Outside of the cephalorhynchids, all delphinids for which we have data are known to whistle, with one exception. Schevill & Watkins (1971) reported that *L. australis* do not whistle, a fact noted by May-Collado & Agnarsson (2006), whose phylogeny nested *L. australis* within *Cephaloryhnchus*. In summary, the evolutionary loss of whistles has occurred at least twice, and likely three times, in odontocete evolution (genus *Cephalorhynchus*, Phocoenidae and Pontoporiidae; Fig. 7). Since whistles likely evolved after the physeteroid clade split from the other odontocetes, whistle loss is not implied for the NBHF species *Kogia*.

Click evolution in odontocetes

The distribution of NBHF clicks on the odontocete tree is identical to that of non-whistling species after the divergence of the Physeteroidea (Physeteridae & Kogiidae) from other odontocetes (Fig. 7). The lack of congruence before this split is explained easily; *Kogia* evolved NBHF clicks independently, but not whistle loss because they never whistled in the first place.

Several authors have suggested that the peak frequency of echolocation clicks is negatively correlated with body length in odontocetes (Watkins, 1980; Thomas *et al.*, 1988; see review Tyack & Clark, 2000). We reanalysed the data, adding recently published data from various sources based on reliable recordings (Table 1, Fig. 8). Some of the scatter in the figure is likely due to the uncertainty of this measurement (Madsen *et al.*, 2004b). In spite of this, the higher peak frequency, lower peak frequency and centroid frequency of echolocation clicks show negative correlations with body length in odontocete species except NBHF species (ANOVA; $F_{1,13} = 6.05$, $P < 0.05$; $F_{1,13} = 4.99$, $P < 0.05$; $F_{1,13} = 22.9$, $P < 0.0001$, respectively). If we averaged the data from species within the same family to minimize effects of phylogeny, the higher peak frequency and centroid frequency of clicks still show negative correlations with body length (ANOVA; $F_{1,3} = 60.3$, $P < 0.05$; $F_{1,2} = 15.4$, $P < 0.05$, respectively), but the lower peak frequency shows only weak negative correlations with body length (ANOVA; $F_{1,2} = 14.3$, $P = 0.06$). However, in NBHF species, the peak frequency of clicks exhibits no correlation with body length (ANOVA; $F_{1,6} = 0.32$, $P = 0.59$ all species included; $F_{1,2} = 0.47$, $P = 0.56$ for family averages). The surprisingly high frequency clicks reported for *L. albirostris* (Rasmussen & Miller, 2004) are interesting but other delphinids may render equally high bandwidths when recorded with the same wide band gear used by Rasmussen & Miller (2004). For the species with a body length < 3 m (except *L. albirostris*), higher peak frequency, lower peak frequency and centroid frequency of clicks do not show any correlations with body length (ANOVA; $F_{1,8} = 1.51$, $P = 0.25$; $F_{1,8} = 0.03$, $P = 0.86$; $F_{1,8} = 0.01$, $P = 0.92$, respectively). The peak frequency of the clicks by NBHF species differed significantly from the lower peak frequency and centroid frequency of the clicks by non-NBHF species, but did not differ from the higher peak frequency of the clicks by non-NBHF species (ANOVA; $F_{3,34} = 51.2$, $P < 0.001$; Tukey–Kramer's HSD *post hoc* test, $\alpha = 0.05$). This implies strongly that selection acted against the lower peak frequency in NBHF species.

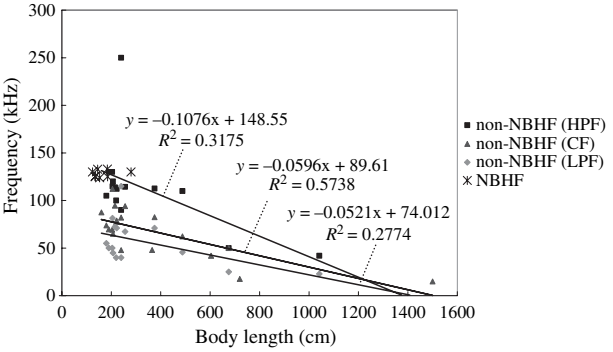

Fig. 8 Relationship between body length and click frequency. Data from Table 1. HPF, CF and LPF indicate high peak frequency, centroid frequency and low peak frequency, respectively.

Killer whales predation risk and the evolution of whistle loss and NBHF clicks

A number of authors, exploring the similar characteristics of Phocoenidae and the genus *Cephalorhynchus*, have pointed out that such convergence must be related somehow to the particular ecological niche occupied by the groups (Watkins *et al.*, 1977; Herman & Tavolga, 1980). A few have attempted explanations linking particular traits to niche components. The killer whale predation hypothesis focuses on one set of traits (acoustic) and one niche component (predation) to explain the evolution of whistle loss and NBHF clicks. Andersen & Amundin (1976) first suggested that the high frequency clicks of harbour porpoises (*P. phocoena*) might be an adaptation to evade acoustic detection by killer whales. They did not mention the lack of whistles.

More recently, Morisaka (2005) and Madsen *et al.* (2005a) linked the convergent evolution of whistle loss and NBHF click production to predation risk from killer whales, which apparently cannot hear NBHF clicks. Specifically, the killer whale predation hypothesis posits that members of these groups have modified the frequency of their sound output to minimize the overlap with the hearing range of killer whales. To explain the evolution of NBHF clicks and whistle loss, the killer whale predation hypothesis must identify specific ecological factors peculiar to non-whistling NBHF species that render them more vulnerable to killer whale predation than other odontocetes. Furthermore, the hypothesis assumes that killer whales use passive listening to locate potential prey. We address these items in turn.

Killer whale predation risk: body size, distribution, costs of grouping and speed

Killer whales are cosmopolitan and capable of successful predatory attacks on any other cetacean species in their range. Thus, we seek factors which render NBHF click, non-whistling species exceptionally vulnerable to killer whale predation, to the extent that the risk of predation exceeds the benefits of sound production in the hearing range of killer whales. We identify a combination of four factors: body size, distribution, cost of grouping and speed.

Body size

The Phocoenids, Cephalorhynchids and *Pontoporia* are all small (< 2 m) species that should be especially vulnerable to killer whale predation. However, *Kogia* is not especially small, reaching lengths of up to 3.8 m, which is larger than many whistling species that produce normal echolocation clicks.

Distribution

The phocoenids and Cephalorhynchids are the only inshore odontocetes to occupy nearshore waters in the cool temperate regions of both hemispheres. These regions are characterized by a high abundance of killer whales and their typical pinniped prey (see Corkeron & Connor, 1999). Two phocoenids, *P. dalli* and *A. dioptrica*, exceed 2 m in length and have a substantial offshore distribution, while *Neophocaena* is a riverine/coastal warm water species. *Pontoporia* is also a nearshore species but it lives in lower latitudes and in warmer water than the other two groups (generally between 20° and 40°; a transition area between the warm current of Brazil and the cold current of the Falklands/Malvinas). Nonetheless, there are recent records of killer whale predation on *Pontoporia* (e.g. Santos & Netto, 2005). The southern part of their distribution is south Argentina, where killer whales are common, especially in March and October when they hunt southern elephant seals (*Mirounga leonine*) and southern sea lions (*Otaria byronia*) (Lopez & Lopez, 1985). There seems to be ample opportunity for killer whales to prey on *Pontoporia*, but we need more data on the abundance of killer whales in the range of *Pontoporia* as well as when Pontoporid whistle loss occurred and their clicks shifted to higher frequency. In fact, the location where the *Orcinus* and Pontoporid fossils were recorded differs from their present distribution (see Discussion).

Cost of grouping

The consistent formation of large groups as a predator defence mechanism does not characterize the NBHF click species. This could be because, given their body size, distribution and swimming ability, grouping would not be effective against predators such as killer whales, or because their foraging strategies render grouping too costly a strategy. Gygax (2002a,b) has suggested that the harbour porpoise, *P. phocoena*, found in small groups in spite of a high predation risk, may employ a cryptic anti-predator strategy. *Kogia* is also described as adhering to a cryptic strategy, given their small group size, surfacing and blows that are difficult to see, a shark-like appearance with a distinctive underslung lower jaw and 'false gills' between their eyes and flippers (McAlpine, 2002), and the 'ink' clouds they produce when disturbed, ostensibly to hide in (Yamada, 1954; Scott & Cordaro, 1987). Given that *Kogia* and other whales have no aerial predators and humans have not hunted *Kogia* extensively, it seem possible that the crypic surfacing of *Kogia* might also retard their detection by killer whales, who are known to use aerial vision to locate pinniped prey on ice. More likely, such gentle movement and respiration at the surface renders *Kogia* less visible acoustically. With hydrophones, Barrett-Lennard *et al.* (1996) detected the sounds of Dall's porpoises (non-whistling NBHF click species) surfacing and breathing up to 25 m away, and suggested that killer whales might use such sounds at greater distances.

Swimming speed

We cautiously suggest that swimming speed might also be an important consideration for why some species appears to have adopted an acoustic crypsis strategy in response to the threat of killer whale predation. Killer whales are the fastest swimming odontocetes (see Williams & Worthy, 2002, p. 77). If *Kogia* is an unusually slow swimmer for its body size (it is sometimes described as slow moving), it might suffer a higher risk of capture if detected by killer whales than a faster species. However, we do not know of any reliable information comparing the burst speed capabilities of *Kogia* with similar sized odontocetes. Furthermore, deep diving species such as *Kogia* likely can seek refuge at depths where killer whales cannot follow.

Costs of whistle loss and NBHF click production

We have identified small body size, small group size, distribution and speed as factors that increase killer whale predation risk and therefore selection for whistle loss and NBHF click production. However, given that killer whales are cosmopolitan they pose some predation risk to the vast majority of small odontocetes that might be able to produce NBHF clicks. If there were no cost to the high and very low frequency restriction, and/or to the low peak-to-peak source level restriction we would expect this adaptation to be much more widespread among cetaceans.

An evaluation of such costs, which would weigh impacts such as detection distance and directionality, awaits functional studies on the communication and echolocation abilities of non-whistling NBHF clicks species. If the clicks are emitted with the same peak-to-peak source level, then clicks with a narrower band-width have better detection capabilities because the narrow bandwidth contains less ambient noise, but they cannot convey as much information from an object. And also the higher frequency of the clicks limits object detection range more, suggesting that NBHF species suffer resolution and object detection costs. NBHF click species may have to compensate for these limitations by emitting longer signals (c.f. Au, 1993). The sonar equations for evaluating the performance of sonar systems [detection threshold or FOM (Figure of Merit): Au, 1993; The Marine Acoustics Society of Japan, 2004] clearly shows that high source levels are important for detection and classification of targets. Thus, producing weak clicks also carries a cost.

An important function of whistles is to maintain group cohesion over large distances (Janik, 2000). It is not clear how NBHF species might compensate for this loss (e.g. Dawson, 1991), although grouping appears to be less important in these species. Producing a very high frequency whistle, even if possible, would be problematic as transmission distance would be sacrificed thereby precluding the main 'distance contact' function of the whistle. Costs are also implied by the large anatomical differences between NBHF species and whistling delphinids as suggested in the Introduction, including symmetrical vs. asymmetrical sound-production organs; the configuration of the fatty structures (melon and dorsal bursae) farther vs. closer (Cranford *et al.*, 1996); and so on.

Alternative to whistle loss and NBHF clicks: behavioural silence

Herman & Tavolga (1980) noted that an effective prey counter strategy is to remain still and silent, unless detected. Beluga whales quickly fell silent when killer whales swam nearby (Schevill, 1964). Oswald *et al.* (2003b) reported hearing more whistles while listening with a towed hydrophone array in the eastern tropical Pacific Ocean compared with the US west coast, a difference they suggest might owe to the greater number of killer whales off the US coast. Tyack *et al.* (2006) also noted that the lack of clicks from acoustical-tagged beaked whales [Cuvier's beaked whales (*Ziphius cavirostris*) and Blainville's beaked whales (*Mesoplodon densirostris*)] in shallow water (< 200 m) may be an adaptation to avoid acoustic detection by a predator, such as killer whales, which spend > 70% of the time in water shallower than 20 m. Silence is effective only if the prey detects the predator first but this may be an option for those species for which the costs of frequency restriction are too great.

Passive listening for prey by killer whales

Odontocetes have three ways to detect the presence of potential prey: vision, echolocation and passive listening, or 'eavesdropping', where they listen for the sounds made by their prey. They lack a sense of smell and taste has not been suggested to play a role in prey detection. The possible importance of passive listening has been explored only recently in spite of earlier observations of captive blindfolded dolphins swimming alongside a swimming fish without emitting detectible echolocation clicks (Wood & Evans, 1980). Passive listening in wild bottlenose dolphins is suggested strongly by the abundance of soniferous prey, including sciaenid and haemulid fish, in the stomachs of dolphins (Barros & Odell, 1990; Mead & Potter, 1990; Barros, 1993; Barros & Wells, 1998; Gannon, 2003; Gannon & Waples, 2004). The first direct evidence was provided by playback experiments in which dolphins responded to fish calls from large distances (Gannon, 2003; Gannon *et al.*, 2005). Gannon *et al.* (2005) found that after prey was detected using passive listening, the rate of echolocation increased during the pursuit and capture phases.

The acoustic crypsis hypothesis demands that killer whales use passive listening to locate odontocete prey (Madsen *et al.*, 2005a; Morisaka, 2005). Barrett-Lennard *et al.* (1996) argued that passive listening by transient (mammal-eating) killer whales is supported by several lines of evidence. They produce fewer clicks than fish-eating killer whales, and more often produce isolated single or paired clicks, that are inconspicuous against background noise, and thus harder for harbour seals to detect. Barrett-Lennard *et al.* (1996) also noted that transient killer whale attacks on Dall's porpoises were not preceded by echolocation. Transients vocalized only after a marine mammal kill or when they were displaying surface-active behaviour when not hunting (Deecke *et al.*, 2005). Records of other marine mammals becoming silent and motionless in response to the presence or sounds of killer whales, supports the use of passive listening in prey detection by killer whales (Jefferson *et al.*, 1991).

Hearing and sound production in killer whales

Killer whales communicate with various signals including whistles and calls. The frequency range of their whistles is 6–12 kHz (Ford, 1989). Killer whales can also easily hear whistles of dolphin prey, which fall within a relatively sensitive range of hearing in killer whales. Szymanski *et al.* (1999) found that two captive killer whales responded to tones between 1 and 100 kHz (and one between 1–120 kHz), with a typical U-shaped response curve. The peak sensitivity of killer whales was 20 kHz, the most sensitive range was 18–42 kHz, and their least sensitive hearing ranged from 60 to 100 kHz (Fig. 9).

Hearing by non-whistling NBHF species

Non-whistling species can hear broader frequency signals than whistling species in spite of the frequency range of their own echolocation clicks (16–160 kHz, Fig. 9). Their hearing may be tuned to killer whales as well as their prey and each other. Andersen & Amundin (1976) suggested that the hearing and sound production of the Harbour porpoise (*P. phocoena*) is adapted to killer whales. The audiograms of *P. phocoena* made by Kastelein *et al.* (2002) indicate that their second peak sensitivity is around 50 kHz, which is the peak frequency of echolocation clicks produced by killer whales (Fig. 9). The audiogram of *N. phocaenoides* by Popov *et al.* (2005) shows that their greatest peak sensitivity is 54 kHz.

Alternative hypotheses

In addition to the killer whale avoidance hypothesis, we have identified four additional hypotheses in the literature that may explain the evolution of a high frequency restriction in odontocetes. High frequency sounds may be a product of or related to prey size, habitat complexity, a naturally occurring low noise window, or group size/cohesion/social relationships. We also consider whether selection for a high frequency restriction in clicks might have produced a correlated loss of whistles.

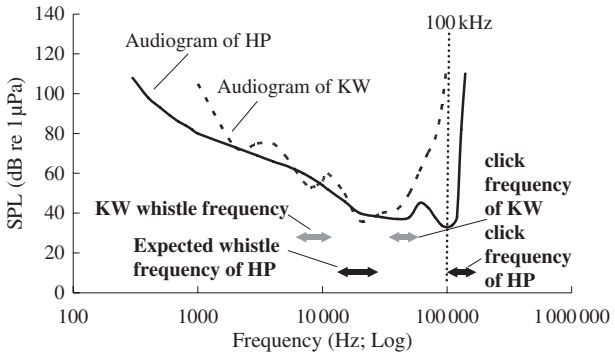

Fig. 9 Audiogram of the killer whale (KW; *O. orca*) and Harbour porpoise (HP; *P. phocoena*) (modified from Szymanski *et al.*, 1999; Kastelein *et al.*, 2002). 'Expected whistle frequency of HP' is based on the whistle frequency of *Sotalia fluviatilis*, which has the same body size as *Phocoena*.

Click frequency and prey size

Evans (1973) and Evans & Awbrey (1988) suggested that the frequency of echolocation clicks may correlate with prey size. Tyack & Clark (2000) noted that echolocation clicks are used primarily to detect prey, that the size of the prey correlates with the size of the predator, and that the acoustic properties of prey vary simply as a function of size. The peak frequency of echolocation clicks (Fig. 8) shows a negative correlation with body length in whistling species, which confirms Tyack & Clark's (2000) point.

High frequencies may allow for discrimination of features in smaller prey (e.g. if the size or shape of the swim-bladder is significant in prey detection) but it remains to be shown that NBHF species feed on prey with smaller swim-bladders than similar sized whistling dolphins. More generally, this hypothesis fails to explain why the lower frequency peak is absent in *Cephalorhynchus*, Phocoenids and Pontoporiidae and it fails to explain why these same species do not whistle. There is no correlation between body length and echolocation click frequency in whistling and non-whistling species under 3 m, and the peak frequency of NBHF clicks do not differ from the higher peak frequencies of small whistling species. Thus, body length and prey size cannot account for NBHF clicks.

Grouping pattern and social relationships

Herman & Tavolga (1980) cautiously suggested a relationship between whistling and gregariousness. They suggested that whistles have adaptive value during communal foraging. There is good evidence that 'signature' whistles are a contact call in bottlenose dolphins (Janik & Slater, 1998) and Lammers & Au (2003) suggest that the relatively high frequency of spinner dolphin whistles may provide useful information to school members on whistler orientation. Unfortunately we do not, 25 years after Herman & Tavolga (1980)'s suggestion, have good information on social relationships or social structure of phocoenids or *Cephalorhynchus*. One line of argument might go as follows: *Cephalorhynchus* have converged with Phocoenids ecologically and socially to the extent that they do not form large groups or even maintain the kind of social relationships typical of other inshore delphinids that favour the use of whistles as a contact call. Selection has thus eliminated whistles because they are not useful. As unlikely as this scenario might be, it is plausible. However, further difficulty is encountered when we find other species that do not form large or especially cohesive groups, such as *Lipotes* and

Inia, but nonetheless produce whistles or other low frequency tonal whistle-like sounds. Perhaps fatally, this hypothesis fails to explain the restriction of echolocation clicks to high frequencies in whistle-loss species.

Noise reduction

Several authors have suggested that background noise might have selected for NBHF clicks. There are two versions of this general hypothesis, one states that animals living in an unusually complex habitat have experienced selection favouring NBHF signals to make fine discriminations among the clutter where they live. Another version, states that selection has acted on some species to take advantage of a naturally existing 'low noise' window between 100 and 150 kHz.

Habitat complexity

Ketten (2000) incorporates habitat complexity into an explanation for the advantage of a high frequency echolocation click. She suggests that odontocetes with peak spectra above 100 kHz live in acoustically complex inshore and riverine waters, pointing out, for example, that *Inia* hunts small fish among roots and stems. Thus, high frequency clicks are functionally advantageous not simply for prey discrimination, but for discriminating prey in a tangle of other small objects. This hypothesis fails to explain why such species do not whistle and again, why the lower frequency component has been lost. Moreover, it fails to explain why the lower frequency component of *Kogia* clicks has also been lost in spite of the very different pelagic habitat of *Kogia*. Furthermore, many species that whistle and produce broadband clicks live in highly cluttered habitats, including many populations of the best studied odontocete, *Tursiops*.

Low noise window

Møhl & Andersen (1973) suggested that the high frequency click of the harbour porpoise might be an adaptation to a low noise window (between 100 and 150 kHz; see Madsen *et al*., 2005a) that is independent of sea state. Madsen *et al.* (2005a) consider whether such an adaptation might account for the convergence between *Cephalorhynchus*, phocoenids and *Kogia*. Madsen *et al.* (2005a) conclude that 'this idea, may, in part, speak to the functional convergence of NBHF biosonar signals in three distant odontocete families living in very different habitats'. However, the niche of *Kogia* is vastly different from the other small, inshore NBHF species and it is not clear why these species but not others would have responded to the low noise window. In our view, unusual vulnerability to killer whale predation is the only factor that that has been offered to date that has the potential to distinguish the NBHF species from others. Given selection from killer whale predation to produce a high frequency signal, the low noise window hypothesis might explain the particular centroid frequency and bandwidth of NBHF species (Madsen *et al*., 2005a). Alternatively, the particular centroid bandwidth above 100 kHz might be related, not to a corresponding low noise window, but simply to the need to avoid significant energy below 100 kHz given that there may be other costs that escalate with both increasing centroid frequency and decreasing bandwidth.

Whistle loss as a correlated response to selection on clicks

We have challenged several of the alternative hypotheses on the basis of their inability to explain both the absence of whistles and the high frequency restriction in clicks. We must, however, consider the possibility that where these character states are strongly associated, as they appear to be in phocoenids, cephalorhynchids and *Pontoporia*, they may be correlated. If there is anatomical overlap in the mechanism of click and whistle production, then selection on one sound type that alters the sound-production anatomy might, as a consequence, alter the production characteristics of the other. Such a constraint can work only in one direction. It does not make sense to suggest that selection against whistle production may constrain clicks to high frequencies. An animal could simply be silent without affecting the structure of clicks (e.g. Madsen *et al*., 2005a). However, one might imagine that selection to restrict clicks to high frequencies might alter the anatomy in ways that renders impossible or impractical whistle production. Thus, if selection has favoured high frequency clicks for prey or prey and habitat discrimination, whistles might have been eliminated as a by-product. Selection that favoured two phonic lips capable of producing high frequency peaks (perhaps to increase detection distance given the rate of transmission loss for higher frequency signals) could have eliminated the ability to produce whistles. Given the importance of whistles for communication in odontocetes, a very strong selection pressure would be required and only the killer whale predation hypothsis can provide such a selection pressure that distinguishes NBHF non-whistling species from others. Unfortunately, we do not know how exactly whistles are produced so solving that mystery should be a priority (effort and funding has overwhelmingly favoured studies on clicks because of interest by the navy in dolphin sonar abilities).

Discussion

We have argued that current evidence supports the hypothesis that the high-frequency restriction of the Phocoenidae, Pontoporiidae, genus *Cephalorhynchus* and Kogiidae is an anti-predator strategy against killer whale predation risk. Selection for acoustic crypsis in these groups must have been strong in the face of the likely

costs of frequency restriction. In the following discussion, we review some additional information which strengthens the 'acoustic crypsis' hypothesis for the evolution of whistle loss and NBHF clicks.

Fossil records of NBHF species

Although comparative analysis of extant species supports the conclusion that the NBHF clicks and whistle-loss evolved independently several times, we can ask if the fossil record further illuminates the issue. NBHF species emerged at the same time or after the killer whale diverged, which indirectly strengthens the idea that NBHF clicks evolved in response to killer whale predation pressure. The oldest fossil record of the genus *Orcinus* is Middle Miocene in age from Italy (Pilleri, 1988 in Ichishima, 2005 and we note that there were other large predatory odontocetes during the middle-late Miocene, Bianucci & Landini, 2006). A fossil phocoenid was found at Baja California Sur, Mexico, which extends back to the Middle Miocene (Barnes, 2002). The oldest Pontoporid is also from the middle Miocene of Peru (*Brachydelphis*, de Muizon, 2002). We have no fossil record of *Cephalorhynchus*, but this genus may have emerged recently considering their position within the Dephinidae (e.g. Harlin-Cognato & Honeycutt, 2006; May-Collado & Agnarsson, 2006). The oldest kogiids are from the late Miocene (8.8–5.2 Ma) of South America and the early Pliocene (6.7–5 Ma) of Baja California (Berta & Sumich, 1999).

Ancestors of non-whistling NBHF species in some cases had a larger body size than extant NBHF species. The most primitive phocoenid, *Piscolithax*, had a large body size, approximately the size of extant *Tursiops truncatus*. Late Miocene phocoenids have longer snouts and some characters which the early phocoenids share with delphinids (Barnes, 2002). Moreover, like *Piscolithax*, *Haborophocoena* has a large and conspicuously skewed skull in contrast to the slight cranial asymmetry found in all other fossil and living phocoenids (Ichishima & Kimura, 2005). Cranford *et al.* (1996) pointed out that the asymmetry/symmetry of the soft tissue in MLDB complex can reflect skull asymmetry/symmetry, which suggests that *Piscolithax* and *Haborophocoena* may have produced broadband clicks. *Brachydelphis* and *Plipontos*, which are known as two fossil genera of Pontoporiidae, were 50% larger than extant *Pontoporia* (de Muizon, 2002). We have no data on the body size of ancestral Kogiidae and *Cephalorhynchus*, but it is interesting to note that the extant species are smaller than their sister taxa, Physeteridae and *Lagenorhynchus*, respectively.

Killer whale's strategy

Transient, mammal-eating killer whales do not produce many clicks and other sounds, but instead make isolated single or paired clicks in order not to be detected by their prey (Barrett-Lennard *et al.*, 1996; Deecke *et al.*, 2005). They use passive listening in prey detection (Jefferson *et al.*, 1991). Killer whales have one of the lowest high-frequency limits among odontocetes as auditory threshold and range of mammals, in general, are constrained by body size. We might expect, however, that an arms race (Dawkins & Krebs, 1979) has occurred between killer whales and NBHF species. Evidence of an arms race could be detected in two ways. First, we predict that killer whales have better high-frequency hearing than expected from the regression line between auditory threshold and body size in odontocetes, and especially dephinids; and second, we suggest that evidence could be sought in the fossil record by matching the evolution of *Orcinus* cochlear structure with skull symmetry in the ancestors of extant NBHF species.

Whistling species' strategy

The Phocoenidae, genus *Cephalorhynchus* and may be Pontoporiidae and Kogiidae appears to have adopted an anti-predator strategy that includes whistle-loss and NBHF clicks to avoid detection by killer whales. However, most odontocetes produce whistles and broadband clicks in spite of the threat from killer whales. How can individuals of these other species afford to be heard by killer whales?

Most odontocetes are highly social animals with a large variation in group size among or within species (Acevedo-Gutiérrez, 2002). Group living appears to be related to food availability and predation pressure in terrestrial and marine mammals (Gygax, 2002b). Acevedo-Gutiérrez (2002) examined the relationship among predation pressure, prey habitat and average group size in 16 delphinid genera. He found that the average group size was larger where predation pressure is high and where prey is found in open waters. Gygax (2002a,b) reported that delphinids may form groups as an antipredator strategy but not the Phocoenids (*P. phocoena* and *P. dalli*). He speculated that *P. phocoena* follows a cryptic antipredator strategy.

Acoustic crypsis in other taxa

For successful predator avoidance, prey species often need to reduce the conspicuousness of their signals (Luczkovich *et al.*, 2000). Many animals, including insects and frogs show 'acoustical avoidance' of predators, or adaptive silence (Curio, 1976). A variety of European passerines produced the 'seeep' alarm call in almost identical form, with an almost pure tone at around 8 kHz, that is difficult for predators to localize (Marler, 1955), or to hear at all (Klump *et al.*, 1986). The hearing threshold of the great tit (*Parus major*) was much better than that of their predator, the European sparrowhawk (*Accipiter nisus*), at such high frequencies (Klump *et al.*, 1986). Ground-nestling wood warblers, which

experience high predation pressure, shifted their begging calls to the limit of their predator's hearing ability (Haskell, 1999).

Acoustic crypsis has been documented in fish prey of odontocetes. Male silver perch (*Bairdiella chrysoura*) reduced the sound level of their mating choruses in response to the whistles of bottlenose dolphins (Luczkovich *et al.*, 2000). American shad (*Alosa sapidissima*) can detect dolphin echolocation at ranges up to 187 m (Mann *et al.*, 1997, 1998).

Prediction to the occurrence of NBHF clicks and whistle-loss in other species

We have identified body size, grouping pattern, distribution and possibly speed as key predation risk factors favouring restriction to frequencies not heard well by killer whales. Can we, therefore, predict the occurrence of NBHF clicks and whistle loss in species whose sounds have yet to be documented? The Ziphiids represent the second largest radiation of odontocetes. To date, sounds have been documented from only a few species (Cuvier's beaked whale, *Z. cavirostris*, the northern bottlenose whale, *Hyperoodon ampullatus*, both *Berardius* species and two species of *Mesoplodon*, *M. densirostris* and *M. carlhubbsi*). The smallest of these is *M. densitrostris*, which grows to at least 4.5 m. All except *Z. cavirostris* produce whistles. The most likely candidate for an NBHF click/non-whistling species that we can identify is the recently discovered pygmy beaked whale, *M. peruvianus*, which is small (< 4 m) and was observed in a small group. It is not clear how often this species might encounter killer whales given that it is not currently known to range in latitudes above 30°. We caution that this is not a strong prediction; finding that *M. peruvianus* is not a NBHF species will not falsify the killer whale predation hypothesis.

Conclusion: testing the acoustic crypsis hypothesis

Several hypotheses have been offered to explain why such a disparate assemblage of odontocetes converged on NBHF clicks and whistle-loss. Our review suggests that only the killer whale crypsis hypothesis fulfils the two requirements required to explain these convergent features 1) it explains why both the low frequency peak (< 100 kHz) *and* whistles have been lost; and 2) it identifies an ecological variable that links these species to the exclusion of others. We have identified distribution, body size, grouping pattern and possibly swimming speed as factors correlated with killer whale predation risk sufficient to outweigh the costs of giving up sound production below 100 kHz.

Work is still needed on the hearing thresholds of *Cephalorhynchus* and *Pontoporia*. If they can easily detect killer whale clicks and whistles, our hypothesis will be strengthened. We will conclude our review with the outline of an experiment that can directly test the killer whale crypsis hypothesis. Playback experiments could be conducted on NBHF species and non-NBHF species in populations that are known to suffer at least occasional predation by killer whales. Subjects should have attached tags capable of recording acceleration and sound. We predict that NBHF species should show a weaker behavioural acoustic response to killer whale sounds than non-NBHF species. However, even NBHF species should reduce physical activity that would reveal their location. This potentially confounding variable can be monitored with an accelerometer.

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Appendix Body length information for all data used in this article.

	Length	Status	Source
Physeter catodon	1500	Mature male average	Martin (1990)
Kogia breviceps	280	Mature	Ross (1984)
Platanista minor	230	Mature	Martin (1990)
Hyperoodon ampullatus	720	Mature	Martin (1990)
Mesoplodon densirostris	439	Average	Ross (1984)
Mesoplodon carlhubbsi	530	Individual	Lynn & Reiss (1992)
Berardius bairdii	1042	Average	Ross (1984)
Berardius arnuxii	861	Average	Ross (1984)
Ziphius cavirostris	604	Average	Ross (1984)
Lipotes vexillifer	222	Individual	Wang *et al.* (1999)
Pontoporia blainvillei	124	Average	Ramos *et al.* (2002)
Inia geoffrensis	230	Mature	Martin (1990)
Delphinapterus leucas	375	Mature	Martin (1990)
Monodon monoceros	365	Mature	Martin (1990)
Phocoena phocoena	153	Mature	Martin (1990)
Phocoena spinipinnis	185	Longest	Martin (1990)
Phocoena sinus	145	Mature	Martin (1990)
Australophocaena dioptrica	210	Longest	Martin (1990)
Neophocaena phocaenoides	185	Mature	Martin (1990)
Phocoenoides dalli	184	Mature	Martin (1990)
Orcaella brevirostris	245	Mature	Martin (1990)
Orcinus orca	675	Mature	Martin (1990)
Pseudorca crassidens	488	Mature	Martin (1990)
Feresa attenuata	220	Mature	Martin (1990)
Peponocephala electra	235	Mature	Martin (1990)
Globicephala melas	440	Mature	Martin (1990)
Globicephala macrorhynchus	368	Mature	Martin (1990)
Grampus griseus	240	Mature	Martin (1990)
Steno bredanensis	240	Mature	Martin (1990)
Sotalia fluviatilis fluviatilis	160	Longest	Martin (1990)
Sotalia fluviatilis guianensis	185	Longest	Martin (1990)
Sousa chinensis	250	Mature	Martin (1990)
Lagenodelphis hosei	240	Mature	Martin (1990)
Stenella attenuata	204	Mature	Martin (1990)
Stenella longirostris	190	Mature	Martin (1990)
Tursiops truncatus	256	Average	Wang *et al.* (2000)
Tursiops aduncus	232	Average	Ross (1984), Wang *et al.* (2000)
Stenella frontalis	207	Average	Schnell *et al.* (1985)
Stenella coeruleoalba	233	Mature	Martin (1990)
Stenella clymene	200	Mature	Martin (1990)
Delphinus delphis	205	Mature	Martin (1990)
Delphinus capensis	235	Average	Ross (1984)
Lissodelphis borealis	211	Mature	Martin (1990)
Lagenorhynchus obliquidens	215	Mature	Martin (1990)
Lagenorhynchus obscurus	180	Mature	Martin (1990)
Cephalorhynchus hectori	135	Mature	Martin (1990)
Cephalorhynchus commersonii	135	Mature	Martin (1990)
Cephalorhynchus heavisidii	170	Mature	Martin (1990)
Cephalorhynchus eutropia	170	Mature	Martin (1990)
Lagenorhynchus australis	216	Longest	Martin (1990)
Lagenorhynchus cruciger	173	Mature	Martin (1990)
Lagenorhynchus acutus	239	Average	Miyazaki & Shikano (1997)
Lagenorhynchus albirostris	240	Average	Miyazaki & Shikano (1997)

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