

REEXAMINING THE RELATIONSHIP BETWEEN BODY SIZE AND TONAL SIGNALS FREQUENCY IN WHALES: A COMPARATIVE APPROACH USING A NOVEL PHYLOGENY

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ABSTRACT

A negative relationship between cetacean body size and tonal sound minimum and maximum frequencies has been demonstrated in several studies using standard statistical approaches where species are considered independent data points. Such studies, however, fail to account for known dependencies among related species—shared similarity due to common ancestry. Here we test these hypotheses by generating the most complete species level cetacean phylogeny to date, which we then use to reconstruct the evolutionary history of body size and standard tonal sounds parameters (minimum, maximum, and center frequency). Our results show that when phylogenetic relationships are considered the correlation between body size (length or mass) and minimum frequency is corroborated with approximately 27% of the variation in tonal sound frequency being explained by body size compared to

86% to 93% explained when phylogenetic relationships are not considered. Central frequency also correlates with body size in toothed whales, but for other tonal sound frequency parameters, including maximum frequency, this hypothesized correlation disappears. Therefore, constraints imposed by body size seem to have played a role in the evolution of minimum frequency but alternative hypotheses are required to explain variation in maximum frequency.

Key words: evolution, adaptation, independent contrast, scaling, communication, phylogeny, tonal signals, toothed whales, delphinids, Mysticeti.

Cetaceans produce an array of sounds that can be broadly categorized as tonal sounds, pulsed sounds, echolocation clicks, and graded sounds (combination of pulsative units and tones) (reviewed by Richardson *et al.* 1995). Apart from echolocation clicks, tonal signals are among the most studied cetacean sounds. Although similar in their acoustic structure, tonal sounds may be produced by two different mechanisms, possibly laryngeal in baleen whales (Frankel 2002) and in toothed whales sounds are thought to be produced by a complex nasal system (*e.g.*, Cranford *et al.* 1999, Cranford 2000).

In baleen whales, tonal signals are narrowband, low in frequency (<5 kHz), and often produced in a stereotypic fashion (Clark 1990, Richardson *et al.* 1995). These signals are associated with a variety of behavioral contexts such as feeding (in *Eubalaena australis*, D'Vincent *et al.* 1985), courtship and group competition on breeding grounds (*e.g.*, in *Megaptera novaeangliae*, Tyack and Whitehead 1983, Helweg *et al.* 1992), and other social behaviors (*e.g.*, *Eubalaena glacialis*, Parks and Tyack 2005). In toothed whales, tonal sounds (commonly referred to as "whistles") have been documented in monodontids (*e.g.*, Watkins *et al.* 1970, Sjare and Smith 1986, Karlsen *et al.* 2002, Shapiro 2006), most delphinids (*e.g.*, Steiner 1981, Wang *et al.* 1995a, Rendell *et al.* 1999, Oswald *et al.* 2003), some ziphiids (*e.g.*, Dawson and Barlow 1998, Manghi *et al.* 1999, Rogers and Brown 1999), and river dolphin species (Jing *et al.* 1981; Wang *et al.* 1995a, 1999, 2001, 2006; May-Collado and Wartzok 2007). Whistles are primarily used in social contexts such as group cohesion, group coordination during feeding, and individual identifiers (*e.g.*, Dreher and Evans 1964; Caldwell and Caldwell 1965; Caldwell *et al.* 1973; Janik *et al.* 1994; Tyack 1999, 2000; Herzing 2000; Janik 2000; Acevedo-Gutiérrez and Stienessen 2004; Watwood *et al.* 2004; Fripp *et al.* 2005; Pivari and Rosso 2005). Delphinid whistles vary across populations and species: Acoustic parameters such as duration and modulation tend to vary intraspecifically (*e.g.*, Wang *et al.* 1995b; Barzúa-Durán and Au 2002, 2004; Morisaka *et al.* 2005a) whereas frequency components vary across species (*e.g.*, Steiner 1981, Wang *et al.* 1995a, Matthews *et al.* 1999, Rendell *et al.* 1999, Oswald *et al.* 2003). Intraspecific variation may result from adaptation to local ecological conditions or geographical isolation and genetic divergence between groups or populations (*e.g.*, Wang *et al.* 1995b, Barzúa-Durán 2004, Barzúa-Durán and Au 2004, Azevedo and Van Sluys 2005, Morisaka *et al.* 2005b, Rossi-Santos and Podos 2006). In addition there may be variation at a finer scale, such as within individual, between sexes, groups, *etc.* Interspecific variation in frequency components may additionally be the product of zoogeographic relationships (Steiner 1981), habitat (Wang *et al.* 1995a), morphological constraints (Wang *et al.* 1995a, Matthews *et al.* 1999, Podos *et al.* 2002), and phylogenetic relationships (*e.g.*, Steiner 1981, Wang *et al.* 1995a, Matthews *et al.* 1999).

Body size is one of the most important morphological factors believed to influence animal signal frequency (Marquet and Taper 1998). Broadly, body size and the size of sound producing organs correlate (Fletcher 1992) and size of vocal tract places physiological constraints on signal production. For example small body sizes (small sound producing organs) limit animals to the production of relatively high-frequency signals, which are more subject to sound attenuation and degradation, limiting the range at which animals can communicate (Gerhardt 1994, Gerhardt and Huber 2002). Some insects and anurans have solved this problem either by using alternative strategies (*e.g.*, using plants as acoustic baffles, calling from elevated positions, emitting signals from burrows) or by having structural modifications that allow them to produce lower frequencies (*e.g.*, some grasshoppers, cicadas) (Gerhardt and Huber 2002, Lardner and bin Lakim 2002).

In cetaceans, body size has been suggested as a major factor influencing both the maximum and minimum frequency of tonal signals (*e.g.*, Wang *et al.* 1995a, Matthews *et al.* 1999, Podos *et al.* 2002). Using standard statistical methods, these studies found a strong negative relationship between body size and maximum frequency (Wang *et al.* 1995a, Matthews *et al.* 1999, Podos *et al.* 2002) and minimum frequency (Matthews *et al.* 1999) with up to 97% of variation in frequency being explained by body size. However, these methods assume species as independent data points. Felsenstein (1985) emphasized that interspecific comparative studies face the problem of non independence. Failing to account for known dependencies among related species and recognizing that similarity in size or whistles may be due to common ancestry artificially inflates the number of observations (and degrees of freedom) and correlations or regressions based on such observations are suspect. Correlations imply that a change in the independent trait will result in a change in dependent trait. A single, uniform, large clade of small species with high-frequency whistles offers little evidence of correlation as no change is observed in either trait. Of course, these data do not directly *contradict* the correlation hypothesis, they are just insufficient to strongly test it. That is, when the phylogeny is consulted it becomes clear that the number of valid independent comparisons of values for the two traits is far less than the number of species in the clade. However, if these small species were scattered in the phylogeny among larger lower-pitched species, they would provide multiple observations of changes in body size accompanied with a change in pitch thus offering stronger support to the hypothesis of correlation. A series of methods has been developed to account for known dependencies among related species using phylogenies (reviewed by Harvey and Page 1991, Martins *et al.* 2002).

The goal of this study is to reevaluate the hypotheses that variation in maximum or minimum tonal sound frequency across whales is correlated with body size, and then test more specifically this correlation in toothed whales with reference to "whistles." We explore the relationship between several cetacean tonal signal frequency characters and body size using a comparative phylogenetic approach. Our results also cast light on the evolution of body size and the evolutionary history of tonal sounds.

METHODS

Data and Definitions

Published data on body size for length (m) and mass (kg), and standard frequency variables of tonal sound (kHz) were obtained from various sources (see Table 1).

Table 1. Review of published data on Cetacean body size and standard tonal sound frequency variables

Species	Maximum body size		Whistle frequency variables (kHz)						References
	m	kg	Max	MMx	Center	Min	MMin		
Suborder Mysticeti									
<i>Balaena glacialis</i>	17.0	80,000	Bannister 2002; Reidenberg & Laitman 2002	11.23	3.14	?	0.02	0.05	Parks & Tyack 2005
<i>B. mysticetus</i>	19.8	100,000	Bannister 2002; Rugh & Shelden 2002	2	0.165		0.09	0.02	Ljungblad <i>et al.</i> 1982
				1	0.3	0.175	0.02	0.05	Clark & Johnson 1984
<i>Balaenoptera bonaerensis</i>	10.7	13,500	Bannister 2002; Reidenberg & Laitman 2002	?	?	?	?	?	Matthews <i>et al.</i> 1999
<i>B. borealis</i>	18.3	25,000	Reidenberg & Laitman 2002	3.5	?	2.5	1.5	?	Knowlton <i>et al.</i> 1991
				1			~0.1		Matthews <i>et al.</i> 1999
<i>B. edeni</i>	15.6	25,000	Reidenberg & Laitman 2002	0.245			0.07		McDonald <i>et al.</i> 2005
				0.180			0.09		Cummings <i>et al.</i> 1986
				0.079			0.0207		Edds 1993
									Heimlich <i>et al.</i> 2005
						0.128			Matthews <i>et al.</i> 1999
<i>B. musculus</i>	31	200,000	Reidenberg & Laitman 2002	0.0185			0.0157		Mellinger & Clark 2003
				0.0202			0.0182		Stafford <i>et al.</i> 2001
				0.122			—		Alling 2003 pers. comm. to Mellinger & Clark 2003
				0.052			0.011		Ljungblad <i>et al.</i> 1997
				0.0277			0.050		Watkins <i>et al.</i> 2004
					0.0189		0.0189		Sirovic <i>et al.</i> 2004
						0.020		0.0172	Stafford <i>et al.</i> 1994
				0.242	0.0883		0.0143	0.0166	Matthews <i>et al.</i> 1999
									Berchok <i>et al.</i> 2006

Continued.

Table 1. Continued.

Species	Maximum body size		References	Whistle frequency variables (kHz)					References
	m	kg		Max	MMx	Center	Min	MMin	
<i>B. physalus</i>	27	90,000	Reidenberg & Laitman 2002	0.118	0.023	0.062	0.010	0.018	Edds 1988 Watkins 1987
<i>Eschrichtius robustus</i>	15.2	35,000	Jones & Swartz 2002	0.2 0.2	0.042	0.3	0.017	0.020	Thompson & Friedl 1982 Matthews <i>et al.</i> 1999 Cummings <i>et al.</i> 1968 Fish <i>et al.</i> 1974 Dahlheim <i>et al.</i> 1984 Matthews <i>et al.</i> 1999
<i>Megaptera novaeangliae</i>	19.0	48,000	Reidenberg & Laitman 2002	4	1.315	0.150	0.25	0.925	Hafner <i>et al.</i> 1979 Matthews <i>et al.</i> 1999
<i>Captera marginata</i>	6.45	3,500	Bannister 2002; Reidenberg & Laitman 2002	0.135	?	1.108	0.06	?	Dawbin & Cato 1992 Matthews <i>et al.</i> 1999
Suborder Odontoceti									
Kogiidae									
<i>Kogia breviceps</i>	3.7	400	Reidenberg & Laitman 2002	?	?	?	?	?	?
<i>K. simus (sima)</i>	2.7	210	Reidenberg & Laitman 2002	?	?	?	?	?	?
Physeteridae									
<i>Physeter macrocephalus</i>	20.5	57,000	Reidenberg & Laitman 2002	n/a	n/a	n/a	n/a	n/a	n/a
Ziphiidae									
<i>Bevardius bairdii (B. anurxii)</i>	12.8	11,000	Reidenberg & Laitman 2002	8.0	?	6.0	4	?	Dawson & Barlow 1998 Matthews <i>et al.</i> 1999
<i>Hypenodon ampullatus</i>	9.8	?	Reidenberg & Laitman 2002	n/a	n/a	n/a	n/a	n/a	n/a

Continued.

Table 1. Continued.

Species	Maximum body size		References	Whistle frequency variables (kHz)					References
	m	kg		Max	MMx	Center	Min	MMin	
<i>H. planifrons</i>	7.45	?	Reidenberg & Laitman 2002	?	?	?	?	?	
<i>Mesoplodon bidens</i>	5.5	?	Pitman 2002a; Reidenberg & Laitman 2002	?	?	?	?	?	
<i>M. densirostris</i>	4.73	1,033	Pitman 2002a; Reidenberg & Laitman 2002	?	?	?	?	?	
<i>Ziphius cavirostris</i>	7.5	3,000	Reidenberg & Laitman 2002	?	?	?	?	?	
<i>Tasmacetus shepherdi</i>	7.0	?	Mead 2002	?	?	?	?	?	
<i>Indopacetus pacificus</i>	8.0	?	Pitman 2002b	?	?	?	?	?	
Platanistidae									
<i>Platanista gangetica</i>	2.5	85	Reidenberg & Laitman 2002	?	?	?	?	?	
Iniidae									
<i>Inia geoffrensis</i>	2.6	160	Da Silva 2002; Reidenberg & Laitman 2002	48.10	24.71	2.75	5.03	15.06	May-Collado & Wartzok 2007 Matthews <i>et al.</i> 1999
				5.16	2.97	0.22	0.22	2.54	Wang <i>et al.</i> 1995a, 2001
				13			3		Diazgranados & Trujillo 2002
Liporidae									
<i>Lipotes vexillifer</i>	2.53	160	Kaiya 2002; Reidenberg & Laitman 2002	4.5	5.84	6.0	3.8	4.975	Matthews <i>et al.</i> 1999 Wang <i>et al.</i> 1999
				4.6	6.1		3.8	4.9	Wang <i>et al.</i> 2006
Pontoporidae									
<i>Pontoporia blainvilliei</i>	1.77	53	Crespo 2002	?	?	?	?	?	

Continued.

Table 1. Continued.

Species	Maximum body size		References	Whistle frequency variables (kHz)						References	
	m	kg		Max	MMx	Center	Min	MMin			
Super Family Delphinoidea											
Phocoenidae											
<i>Australophocaena dioptrica*</i>	2.4	115	Reidenberg & Laitman 2002; Goodall 2002a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
<i>Phocaena phocaena</i>	2.0	90	Björge & Tolley 2002; Reidenberg & Laitman 2002	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
<i>P. sinus</i>	1.4	?	Rojas-Bracho & Jaramillo-Legorreta 2002	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
<i>P. spinipinnis</i>	2.0	?	Reyes 2002	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
<i>Phocoenoides dalli</i>	2.39	200	Jefferson 2002a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
<i>Neophocaena phocaenoides</i>	1.9	100	Reidenberg & Laitman 2002; Amano 2002	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
Monodontidae											
<i>Monodon monoceris</i>	4.7	1600	Heide-Jørgensen 2002; Reidenberg & Laitman 2002	18	10	0.3	5	0.360	0.718	0.3	Ford & Fisher 1978 Watkins <i>et al.</i> 1970 Matthews <i>et al.</i> 1999 Shapiro 2006
<i>Delphinapterus leucas</i>	5.5	1500	O'Corry-Crowe 2002; Reidenberg & Laitman 2002	8.84	7.18	3.89	0.2	0.4	3.8	3.38	Matthews <i>et al.</i> 1999 Karlsen <i>et al.</i> 2002 Sjare & Smith 1986 Belikov & Bel'kovitch 2001

Continued.

Table 1. Continued.

Species	Maximum body size		References	Whistle frequency variables (kHz)						References	
	m	kg		Max	MMx	Center	Min	MMin			
Delphinidae											
<i>Cephalorhynchus commersonii</i>	1.75	86	Dawson 2002; Reidenberg & Laitman 2002	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
<i>C. entropia</i>	1.67	63	Dawson 2002	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
<i>C. bectori</i>	1.8	60	Reidenberg & Laitman 2002	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
<i>C. beavisidii</i>	1.74	75	Dawson 2002	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
<i>Lagenorhynchus australis</i>	2.18	115	Goodall 2002b	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
<i>L. cruciger</i>	1.87	88	Goodall 2002c	?	?	?	?	?	?	?	
<i>L. obliquidens</i>	2.5	181	Van Waerebeek & Würsig 2002; Reidenberg & Laitman 2002	?	?	?	?	?	?	?	
<i>L. obscurus</i>	2.1	80	Van Waerebeek & Würsig 2002; Reidenberg & Laitman 2002	27.3	16.49	12.4	1.04	8.11	1.04	8.11	Wang et al. 1995a Matthews et al. 1999 Yin 1999
<i>L. acutus</i>	2.7	230	Cipriano 2002; Reidenberg & Laitman 2002	?	13.22	12.14	?	8.15	?	8.21	Steiner 1981 Matthews et al. 1999
<i>Lissodelphinus borealis</i>	3.1	116	Reidenberg & Laitman 2002; Lipsky 2002	?	?	10.37	?	?	?	?	
<i>L. peronii</i>	3.0	116	Lipsky 2002	?	?	?	?	?	?	?	Moore & Ridgway 1995
<i>Delphinus delphis</i>	2.35	200	Perrin 2002a	19.8	11.65	8.81	4.8	6.42	4.8	6.42	Matthews et al. 1999
					13.6			7.4		7.4	Oswald et al. 2003

Continued.

Table 1. Continued.

Species	Maximum body size		References	Whistle frequency variables (kHz)						References
	m	kg		Max	MMx	Center	Min	MMin		
<i>D. capensis</i>	2.55	235	Perrin 2002a	?	15.5	?	?	7.7	Oswald <i>et al.</i> 2003	
<i>Stenella attenuata</i>	2.57	119	Perrin 2002b; Reidenberg & Laitman 2002	21.4	15.72	3.13	12.54	8.73	Wang <i>et al.</i> 1995a Matthews <i>et al.</i> 1999	
<i>S. clymene</i>	2.0	80	Jefferson 2002b; Jefferson & Curry 2003	19.2	18.7	?	11.66	8.2 6.33 9.25	Oswald <i>et al.</i> 2003 Watkins & Wartzok 1985 Mullin <i>et al.</i> 1994 Matthews <i>et al.</i> 1999	
<i>S. frontalis</i>	2.3	143	Perrin 2002c; Reidenberg & Laitman 2002	19.8	16.04	5	11.62	7.91	Wang <i>et al.</i> 1995a Matthews <i>et al.</i> 1999	
<i>S. coeruleoalba</i>	2.4	156	Reidenberg & Laitman 2002	22.99	11.53	1.1	9.07	6.84	Matthews <i>et al.</i> 1999	
<i>S. longirostris</i>	2.16	75	Perrin 2002d; Reidenberg & Laitman 2002	22.5	14.8 15.2	3.91	12.22	8.1 9.03	Oswald <i>et al.</i> 2003 Wang <i>et al.</i> 1995a Matthews <i>et al.</i> 1999	
<i>Tursiops truncatus</i>	4.0	650	Reidenberg & Laitman 2002	41	13.7 16.5 17.56 16.8 14.32	0.85	8.09	9.1 9.99 9.66 10.19 8.76	Oswald <i>et al.</i> 2003 Barzua-Duran & Au 2002 Barzua-Duran & Au 2004 Driscoll 1995 Steiner 1981 Boisseau 2005 Matthews <i>et al.</i> 1999	
				21.6	17.2 11.35/11.95 16.24	1.86/0.94		7.4 5.46 7.33	Oswald <i>et al.</i> 2003 Wang <i>et al.</i> 1995a,b Steiner 1981	

Continued.

Table 1. Continued.

Species	Maximum body size		References	Whistle frequency variables (kHz)						References
	m	kg		Max	MMx	Center	Min	MMin		
<i>Lagenodelphis hosei</i>	2.65	200	Dolar 2002; Reidenberg & Laitman 2002	24.0	16.9	12.82	4.3	9.36	Matthews <i>et al.</i> 1999 Watkins <i>et al.</i> 1994	
<i>Sousa chinensis</i>	3	284	Ross 2002; Reidenberg & Laitman 2002	13.4	16.56	?	0.9	11.949 7.64	Oswald <i>et al.</i> , submitted Leatherwood <i>et al.</i> 1993 Van Parijs & Corkeron 2001 Zbinden <i>et al.</i> 1977	
<i>Sotalia fluviatilis</i> **	2.20	40	Flores 2002	20	16.3	12.68	1.2	4.5	Schultz & Corkeron 1994 Matthews <i>et al.</i> 1999	
<i>Steno bredanensis</i>	2.65	155	Jefferson 2002c; Miyasaki & Perrin 1994	18	19.95	?	1.34	7.21	Azevedo & van Sluys 2005 Wang <i>et al.</i> 1995a, 2001 May-Collado & Wartzok, unpublished.	
<i>Feresa attenuata</i>	2.7	225	Reidenberg & Laitman 2002	17.49	13	5.5	0.5	7.6	Azevedo & Simão 2002 Erber & Simão 2004	
<i>Globicephala macrorhynchus</i>	7.2	3950	Reidenberg & Laitman 2002	38.25	13.312 15.65	7.87	1.031	10.521 9.18	Podos <i>et al.</i> 2002 Busnell & Dziedzic 1968 Matthews <i>et al.</i> 1999 Oswald <i>et al.</i> 2003	
				7.0	9.1	?	?	6.03	Matthews <i>et al.</i> 1999	
				?	?	?	?	?	Rendell <i>et al.</i> 1999	
				23.6	10.87	6.1	0.24	6.25	Oswald <i>et al.</i> 2003	

Continued.

Table 1. Continued.

Species	Maximum body size		References	Whistle frequency variables (kHz)					References
	m	kg		Max	MMx	Center	Min	MMin	
<i>G. melas</i>	6.3	1750	Reidenberg & Laitman 2002	21.2	8.86	4.48	0.32	3.48	Matthews <i>et al.</i> 1999 Rendell <i>et al.</i> 1999 Steiner 1981
<i>Grampus griseus</i>	4.3	500	Reidenberg & Laitman 2002	20	13.44	11.3	1.90	3.9	Matthews <i>et al.</i> 1999 Corkeron & Van Parijs 2001 Rendell <i>et al.</i> 1999
<i>Peponocephala electra</i>	2.75	275	Perryman 2002	24.5	12.14	12.75	5.5	8.83	Matthews <i>et al.</i> 1999 Oswald <i>et al.</i> , submitted Watkins <i>et al.</i> 1997
<i>Pseudorca crassidens</i>	6	2200	Baird 2002; Reidenberg & Laitman 2002	18.1	8.29	6.82	1.87	5.43	Matthews <i>et al.</i> 1999 Rendell <i>et al.</i> 1999
<i>Orcaella brevirostris</i> **	2.75	150	Reidenberg & Laitman 2002	6.0	4.2	?	1.1	4.7	Oswald <i>et al.</i> 2003
<i>Orcinus orca</i>	9.75	10,500	Reidenberg & Laitman 2002	18	6.61	5.0	0.05	3.2	Van Parijs <i>et al.</i> 2000 Ford 1989 Dahleim & Awbrey 1982 Matthews <i>et al.</i> 1999
				8.9	9.9	2.4	2.4	5.4	Steiner <i>et al.</i> 1979 Thomsem <i>et al.</i> 2001
				16.7	12.64			3.36	Riesch <i>et al.</i> 2006

* Now recognized as *Phocoena dioptrica* (Lahille 1912).

** In this paper these species are still treated as one single species (with two ecotypes: riverine and marine), however there is recent evidence that each may be a separate species (see details in Cunha *et al.* 2005 and Beasley *et al.* 2005).

Tonal sounds are produced by both baleen whales (Mysticeti) and toothed whales (Odontoceti) and were defined as narrowband sounds that can be relatively constant in frequency (e.g., *Lipotes vexillifer*, Wang *et al.* 2006; *Sotalia fluviatilis*, Azevedo and Van Sluys 2005; *Stenella longirostris*, Barzúa-Dúran and Au 2002, 2004; baleen whales, e.g., Mellinger and Clark 2003, Watkins *et al.* 2004, McDonald *et al.* 2005), but also greatly modulated (e.g., *Tursiops truncatus*, Wang *et al.* 1995; *Delphinapterus leucas*, Karlsen *et al.* 2002; *Lagenorhynchus albirostris*, Rasmussen and Miller 2002), show variable duration (e.g., 0.01–1.3 s in *Sousa chinensis*, Van Parijs and Corkeron 2001), consist of a single or several units (Richardson *et al.* 1995), and may or may not contain harmonics (e.g., Lammers and Au 2003, Rasmussen *et al.* 2006). Throughout, we assume authors reported the fundamental frequency and that is what we discuss, because not all state if measurements included harmonics or not. Toothed whale tonal sounds (whistles) have been characterized as generally with fundamental frequencies below 20 kHz (Richardson *et al.* 1995). However, this upper limit of around 20 kHz in many cases reflects limitations of recording equipment, rather than those of whistle frequency production (e.g., the following studies in dolphins and river dolphins: Wang *et al.* 1995a, b used a system response up to 24 kHz, Corkeron and Van Parijs 2001 up to 22 kHz, Morisaka *et al.* 2005a, b and Van Parijs *et al.* 2000 up to 20 kHz; in ziphiids: Dawson and Barlow 1998 up to 20 kHz, and Rogers and Brown 1999 up to 16.5 kHz; in belugas: Belikov and Bel'kovich 2001, 2003 up to 20 kHz, *etc.*). Therefore, we do not exclude higher-frequency whistles such as those produced by some delphinids, e.g., *Lagenorhynchus albirostris* whistles go up to 35 kHz (Rasmussen and Miller 2001) and up to 41 kHz in *Tursiops truncatus* (Boisseau 2005) or even higher, e.g., *Inia geoffrensis* up to 48 kHz (May-Collado and Wartzok 2007). All tonal sounds considered for baleen whales in this study were those referred to as exclusively tonal. We did not consider sounds that consisted of a combination of pulsative units and tones for either baleen whales (see Heimlich *et al.* 2005, McDonald *et al.* 2005, Parks and Tyack 2005) or toothed whales (see “graded vocalizations” in Murray *et al.* 1998).

Although focus has traditionally been on toothed whales whistles, we also more broadly examine the optimization of body size and frequency parameters of tonal sounds across cetaceans. It is important to note that the two types of sounds may be produced by different mechanisms (e.g., Cranford *et al.* 1999, Frankel 2002, Reidenberg and Laitman 2004) and sound production of tonal sounds may well be convergent in baleen whales and toothed whales. However, to rule out their homology, data external to this study would be required. Regardless of homology, body size could similarly constrain frequency in the two types of sounds. Therefore, in addition to analyzing them separately, exploring them together as potentially homologous, or as potentially subject to similar constraints, seems worthwhile.

Phylogenetic Analysis and Ancestral Character Reconstruction

The history of character evolution on the phylogeny (character optimization) was estimated using Mesquite 1.12 (Maddison and Maddison 2006). For this purpose we here produce the most complete species level phylogeny of Cetacea to date by adding two species—the blue whale (Accession number AY235202) and the fin whale (Accession number U13126)—to the phylogeny of May-Collado and Agnarsson (2006). Cytochrome b sequences from Genbank were analyzed in a Bayesian framework using MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003) with model parameters and

search strategies as described in May-Collado and Agnarsson (2006). On this phylogeny we optimize body size and whistle frequency using weighted squared-change parsimony (Maddison 1991). Weighted squared-change parsimony minimizes the sum of squared change along all branches of the tree, weighting branches by their length (Maddison and Maddison 2006). Because polytomies (unresolved relationships among lineages) can compromise character optimization and tests of character correlations, characters were optimized on a fully resolved tree, which is the majority rule tree resulting from the MrBayes analysis without collapsing nodes with less than 50% frequency (using the `contype = allcompat` option). We mapped the distribution of body length and mass and each of the following standard whistle parameters: maximum, mean maximum, minimum, and mean minimum frequency. We also mapped the distribution of center frequency, although it is important to note that this parameter is not a direct measurement from the signal itself but an estimation of central tendency calculated and defined by Matthews *et al.* (1999) as the mean of f frequency measurements per call. To normalize the data all parameters, were natural log transformed (Sokal and Rohlf 1981).

Ancestral character reconstruction for each frequency parameter and body size was run separately. This was performed for all species with available tonal frequency parameters, and we also ran a separate optimization including all taxa. In species for which we have more than one frequency value in Table 1, we selected the highest for maximum and mean maximum frequency and the lowest for minimum and mean minimum frequency (selected values shown in bold). The maximum reported value for both body length and mass was used for all optimizations. Assuming a normal distribution a mid point value for all variables optimized in this study would be preferable, but sufficiently detailed data are available only for very few species.

Phylogenetic Comparative Approach: Independent Contrast Method

To account for dependencies among of species, independent contrasts were calculated for each character. The method makes use of the phylogeny, and a model of evolution (Brownian motion), to estimate the number of independent comparisons between species, or groups of species, that can be used in a regression analysis. For example, a clade of ten species that are invariable for the characters under study does not constitute ten independent observations of these characters, instead phylogenetic relationships may explain the character covariation. Independent contrasts were calculated using the PDAP: PDTREE module (Midford *et al.* 2005) in Mesquite 1.06 (build h47). This module analyzes data using the method of phylogenetically independent contrasts developed by Felsenstein (1985). To estimate Felsenstein's independent contrast, branch lengths were used as estimated by MrBayes; branch length transformations were not necessary (lack of fit test $P > 0.05$ for all parameters). The current version of PDAP is known to have some error (see Midford *et al.* 2005) when calculating regressions if some taxa have missing values (unknowns, "?"), although it is unclear how seriously it impacts the analyses. Therefore, in addition to using the full data set (where some of the taxa lack acoustic data), we also ran analyses on pruned data sets where all species lacking the acoustic character under study were removed prior to the regression analysis. These calculations are known to be correct, however, pruning species from the cladogram affects both estimates of branch lengths and optimization of body size (as available information has been thrown out). Although we prefer the pruned analyses, it seems appropriate to report

the values based on both types of analyses; the best estimates may lie somewhere in between.

RESULTS

In the novel phylogeny (Fig. 1) the newly added blue (*Balaenoptera musculus*) and fin (*B. physalus*) whales as expected, are placed within a clade containing other *Balaenoptera*, as well as *Megaptera* (humpback whale) and *Eschrichtius* (gray whale). The fin whale is sister to the humpback whale as also found by Hatch *et al.* (2006) and Sasaki *et al.* (2006) but the placement of the blue whale is less well resolved (Fig. 1). As the two are not each other sister taxon, these largest of whales provide independent evidence of change in body size. In other respects this phylogeny is identical, or nearly so, to the phylogeny of May-Collado and Agnarsson (2006).

Of the many changes in body size implied by the phylogeny the most conspicuous are the differences between baleen and toothed whales (Table 1, Fig. 2). Correlated with these changes in body size is change in tonal sound minimum frequency, whether measured as mean minimum or absolute minimum. Body length explains up to 26% of the variation in minimum frequency across Cetacea and 28% within toothed whales and up to 66% of the mean minimum frequency in baleen whales, although this should be interpreted with care as only four independent contrasts were regressed (Table 2, Fig. 3). When considering body mass, the more commonly used allometric scaling parameter but one more difficult to estimate in cetaceans, minimum frequency (both mean and absolute) across all Cetacea is significantly correlated with biomass ($r^2 = 0.135$ for absolute, $r^2 = 0.101$ for mean). The correlation with mean minimum frequency was also significant within baleen whales, but insignificant within toothed whales, but absolute minimum was not significantly correlated with body

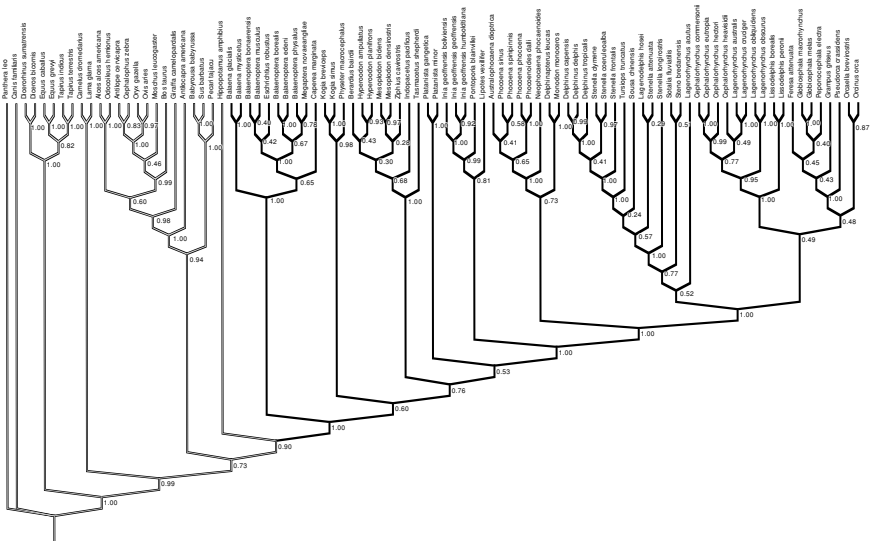


Figure 1. The preferred phylogenetic hypothesis based on the Bayesian analysis of 64 cetaceans and 24 outgroups (gray branches). Numbers at nodes represent the posterior probabilities values.

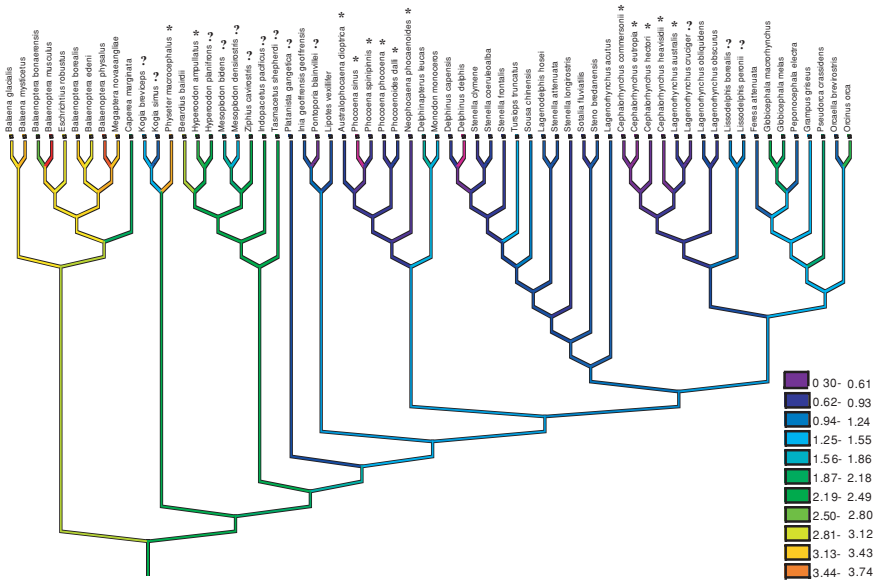


Figure 2. Optimization of overall body length (m) on natural log scale. Species that are known not to produce tonal sounds are denoted with "*" and "?" indicates poorly known species.

mass within each group (marginally insignificant in toothed whales $P = 0.052$). In contrast, body size explains virtually none (1% or less) of the variation in maximum frequency across Cetacea and there is no correlation between body size and maximum frequency in any comparisons (Table 2, results are the same using the raw data without log transformations). The calculated center frequency is significant only within the toothed whales ($r^2 = 0.182$ with length, $r^2 = 0.161$ with mass).

The distribution of tonal sounds and optimization of body size across Odontoceti is summarized in Figure 2. The phylogeny broadly implies that cetaceans were primitively large and that there has been a gradual reduction in size in the lineage leading to dolphins and relatives. However, this optimization should be interpreted with care, including fossil data and information from outgroups will be necessary for a detailed account of body size evolution in Cetacea. In addition, this broad pattern addresses only a portion of the variation; there is much variation in body size at the level of families and genera (Fig. 2). Finally there is considerable intraspecific variation in body size, the exploration of which is beyond the scope of this paper. In general the greatest variation in body size is among baleen whales, nevertheless, size variation among the toothed whales is in the range of an order of magnitude in length, and over two orders of magnitude in body mass (Table 1). Size variation in toothed whales significantly correlates with absolute minimum frequency, and central frequency, of their tonal sounds (Table 2). Hence, even if toothed whales whistles are fundamentally different (produced by different mechanisms) from tonal sounds in baleen whales, size nevertheless constrains minimum frequency in both sound systems. Independently of body size, high-frequency whistles (both in terms of maximum and minimum frequencies) appear to be derived (Fig. 4).

Table 2. Previous and present regression analyses between body size and standard tonal sound frequency variables. This study uses independent contrast both on the entire (values in parenthesis) and pruned (values in bold) data sets (see Methods)

Source	Maximum	Mean maximum	Minimum	Mean minimum	Center
Wang <i>et al.</i> 1995					
<i>Delphinids + Inia</i>					
r^2	79%, 97% (excluding <i>Inia</i>)				
df	9				
P-value	<0.05 ^a				
Matthews <i>et al.</i> 1999					
<i>Toothed whales</i>					
r^2	68% (uwtd.), 76% (wrd.)		86% (uwtd.), 93% (wrd.)		69% (uwtd.), 84% (wrd.)
df	18, 16		18, 16		25, 14
P-value	<0.001, <0.001 ^a		<0.001, <0.001 ^a		<0.001, <0.001 ^a
Matthews <i>et al.</i> 1999					
<i>Baleen whales</i>					
r^2					64% (uwtd.)
df					9
P-value					0.003 ^a
Podos <i>et al.</i> 2002					
<i>Delphinids + Inia</i>					
r^2	85.1%				
df	16				
P-value	<0.05 ^a				
This study body length					
<i>Cetacean tonal sounds</i>					
r^2	0.0963% (0.0406%)	0.18% (0.0732%)	26.3% (22.8%)	12.8% (10.2%)	4.2% (3.5%)
df	32	28	32	29	28
P-value	0.413 (0.455)	0.410 (0.443)	0.001 (0.002) ^a	0.024 (0.040) ^a	0.136 (0.160)

Continued.

Table 2. Continued.

Source	Maximum	Mean maximum	Minimum	Mean minimum	Center
<i>Toothed whales ubistile</i>					
r^2	2.2% (1.45%)	3.9% (4.5%)	27.7% (23%)	6.2% (5.7%)	18.2% (14.1%)
df	23	22	23	23	20
P-value	0.241 (0.283)	0.174 (0.160)	0.003 (0.008) ^a	0.116 (0.125)	0.023 (0.042) ^a
<i>Baleen whales</i>					
r^2	0.052% (0.37%)	33.3% (14.2%) ^b	10.2% (7.8%)	66.2% (80.3%) ^b	0.0028% (0.496%)
df	7	4	7	4	6
P-value	0.476 (0.437)	0.11 (0.230)	0.201 (0.233)	0.024 (0.007) ^a	0.495 (0.434)
This study body mass					
<i>Cetacean tonal sounds</i>					
r^2	0.00427% (0.00463%)	0.520% (0.144%)	13.5% (12.06%)	10.1% (8.2%)	7.4% (6.04%)
df	32	28	32	29	28
P-value	0.485 (0.485)	0.452 (0.421)	0.016 (0.022) ^a	0.040 ^a (0.058)	0.074 (0.095)
<i>Toothed whales ubistile</i>					
r^2	1.04% (0.52%)	3.60% (4.10%)	11.1% (9.3%)	5.2% (4.9%)	16.1% (12.2%)
df	23	22	23	23	20
P-value	0.313 (0.365)	0.186 (0.170)	0.052 (0.068)	0.137 (0.142)	0.033 ^a (0.055)
<i>Baleen whales</i>					
r^2	0.0107 (0.21%)	24.7% (3.2%) ^b	17.4% (16.0%)	65.5% (49.0%) ^b	3.5% (2.10%)
df	7	4	7	4	6
P-value	0.489 (0.452)	0.158 (0.367)	0.130 (0.142)	0.025 ^a (0.059)	0.326 (0.366)

^aSignificant results (based on the level of significance of $P \leq 0.05$).

^bVery small number of contrasts.

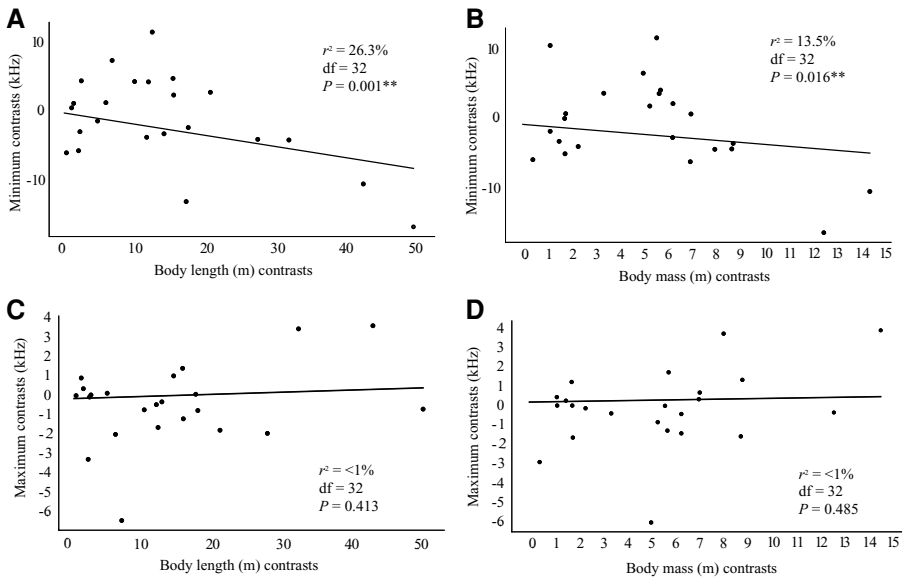


Figure 3. Regression analysis between Cetacean body size and tonal sound absolute minimum (A–B) and maximum (C–D) frequencies after correcting for phylogenetic relationships.

DISCUSSION

The new phylogeny is the most detailed phylogenetic hypothesis of whales currently available. It agrees well with most recent studies in cetacean phylogenetics (e.g., Hatch *et al.* 2006, May-Collado and Agnarsson 2006, Sasaki *et al.* 2006, Nikaido *et al.*, 2007) and, therefore, provides an appropriate phylogeny with which to test the correlation of body size and tonal sound frequency in whales.

Even after accounting for phylogenetic relationships, the hypothesis that the minimum frequency of whistle, or tonal sounds in general, is negatively correlated with body length (Matthews *et al.* 1999) is corroborated. Body mass is more typically used in these regressions because it is thought to be a more accurate proxy for physiological constraints. However, body mass is more difficult to estimate than body length in cetaceans. When body mass is considered instead of length, only the correlation with absolute minimum frequency is still significant within toothed whales albeit with reduced explanatory power. Our results are congruent with Matthews *et al.*'s (1999) hypothesis of a significant relationship between central frequency and body length (but not mass) in toothed whales. However, a much smaller percent of frequency variation is explained by body size after accounting for phylogenetic relationships (for minimum frequency about 28% for toothed whales in our study *vs.* 86%–93% in the study of Matthews *et al.* 1999).

In contrast, the hypothesis that tonal sound (or whistle) maximum frequency is negatively correlated with body size (Wang *et al.* 1995a, Matthews *et al.* 1999, Podos *et al.* 2002) must be rejected. Even though the phylogeny implies broadly that a major decrease in body size and increase in maximum whistle frequency occurred in the common ancestor of pandelphinids (Delphinida *sensu* Muizon 1998 + *Platanista*; May-Collado *et al.*, unpublished data), that single observation does not imply

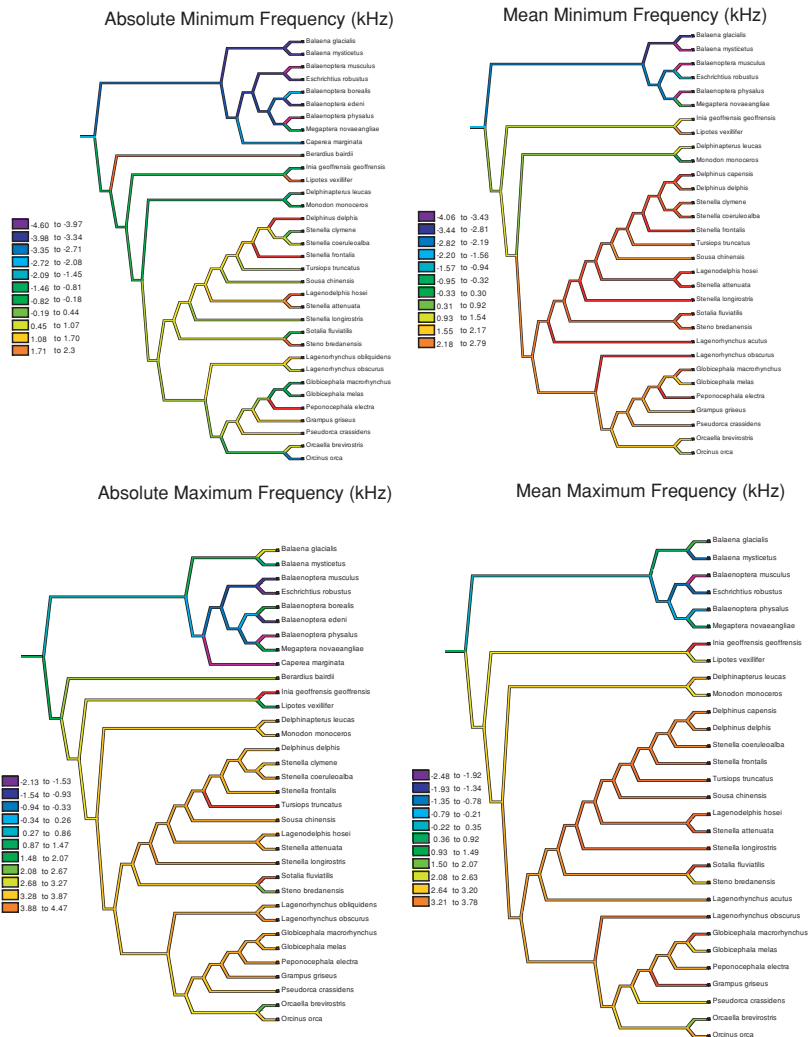


Figure 4. Optimization of Cetacean tonal sounds standard frequency parameters (in natural log scale).

correlation. In general, throughout the phylogeny, body size and maximum whistle frequency vary independently with only a tiny portion of the variation in maximum frequency being potentially explained by body size (Fig. 2, 3; Table 1, 2). We should note here that due to limitations of recording systems in some studies (see Methods), the maximum frequency of some species may be underestimated. Hence, we cannot rule out that when better information is available results of regression analyses will change. However, we do not expect the effect to be dramatic as we see no correlation of body size and maximum frequency in baleen whales where limitation of equipment is not an issue.

Body size is known to be related to a variety of physiological, ecological, and behavioral processes (Marquet and Taper 1998). In acoustic communication, body size has been acknowledged as a major factor determining signal frequency components. In insects, anurans, birds, and mammals negative relationships between signal frequency and body size (particularly body mass) has been largely supported (*e.g.*, Wiley 1991, Hauser 1993, Gerhardt 1994, Wang *et al.* 1995a, Bennet-Clark 1998, Tubaro and Mahler 1998, Matthews *et al.* 1999, Palacios and Tubaro 2000, Seddon 2005). However, as more comparative studies consider phylogenetic hypotheses, this relationship in some cases no longer holds (*e.g.*, Laiolo and Rolando 2003, Farnsworth and Lovette 2005). We do find evidence in cetaceans that body size has constrained the evolution of tonal sounds minimum frequency, although size can only explain a portion of the variation. This suggests (1) that in the evolutionary history of whales there has been a selection for low-frequency sounds, which, *e.g.*, enable communication over long distances and (2) that the degree to which whales have been able to respond to this selection through evolutionary history has been, at least in some cases, constrained by body size. There is no evidence, however, that body size has constrained the evolution of maximum frequency. This certainly does not imply such constraints do not exist—no doubt body size constrains the maximum *possible* frequencies. What it does imply is that, for maximum frequency, the range of tonal sound frequencies *used* by cetaceans seems to lie outside the area where physiological constraints would have an impact.

It is right to point out here that, ideally, recordings and body size measurements should come from the same animal, to account for intraspecific size and frequency variation. However, such data are simply not available. Given that body size and minimum frequency correlate even when such detailed evidence are missing, the likely effect of their inclusion would be to increase the amount of variation in minimum frequency explained by body size. We point out that intraspecific variation could, at least in theory, be used as an independent test of these correlations—a study might record and measure multiple individuals within species and explore the intraspecific correlations of body size and frequency. For such a study, phylogenetic corrections would not be necessary.

Environmental factors seem to be most important in driving the evolution of acoustic signals in birds, insects, and anurans (*e.g.*, Gerhardt 1994, Wiley and Richards 1978, Bertelli and Tubaro 2002, Laiolo and Rolando 2003, Couldridge and van Staaden 2004, Farnsworth and Lovette 2005, Seddon 2005). This may also be the case in the evolution of cetacean tonal signal frequency as has been suggested by some authors (*e.g.*, Wang *et al.* 1995a, Morisaka *et al.* 2005b). Finally, social fluidity is another factor suggested to influence tonal frequency within and across species (Bazúa-Durán 2004). Studies are underway to examine tonal sound evolutionary history taking into considerations some of these factors (May-Collado *et al.*, unpublished data).

Conclusion

Our results support the negative relationship in cetaceans between body size and minimum tonal sound frequency (whether general tonal sounds, or whistles) as proposed by Matthews *et al.* (1999). This suggests that there has been a selection for low-frequency sounds (enabling, *e.g.*, communication over long distances) and that the response to this selection through evolutionary history has been constrained by

body size. In contrast, our results do not support the negative relationship between maximum frequency and body size that has been proposed based on a phylogeny-free analysis of the same data (Wang *et al.* 1995a, Matthews *et al.* 1999, Podos *et al.* 2002). This suggests that if there has been selection for high-frequency sounds, body size has not constrained response to it. In this study we focused on tonal signals because these are the best-documented sounds in cetaceans. We do not suggest generalizing our findings to other organisms, or even to other cetacean sounds such as echolocation clicks. It is not in dispute that body size imposes absolute constraints on sound production in organisms in general. The question is whether such constraints have come into play in the evolution of sound production in any given lineage. To answer such questions it is invalid to use species as independent data points and uninformative to allude to constraints observed in other lineages; rather, the lineage of interest should be looked at in isolation using a comparative phylogenetic approach.

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