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Phylogenetic and Ecological Significance in the Evolution of Cetacean Tonal Sounds

Laura Johanna May-Collado
Florida International University, lmayc002@fiu.edu

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FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

PHYLOGENETIC AND ECOLOGICAL SIGNIFICANCE IN THE EVOLUTION OF CETACEAN TONAL SOUNDS

A dissertation submitted in partial fulfillment of the

requirements for the degree of

DOCTOR OF PHILOSOPHY

in

BIOLOGY

by

Laura Johanna May-Collado

2007

To: Interim Dean Mark Szuchman
College of Arts and Sciences

This dissertation, written by Laura Johanna May-Collado, and entitled Phylogenetic and Ecological Significance in the Evolution of Cetacean Tonal Sounds, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this dissertation and recommend that it be approved.

Maureen A. Donnelly

Michael Heithaus

Tim Collins

Zhenim Chen

Douglas Wartzok, Major Professor

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The dissertation of Laura Johanna May-Collado is approved

Interim Dean Mark Szuchman
College of Arts and Science

Dean George Walker
University Graduate School

Florida International University, 2007

DEDICATION

To my husband thank for your endless support, guidance and love. To Douglas Wartzok and Maureen Donnelly for believing in me, thanks for giving me the opportunity to do what I like. A mi papá y mamá, los amo

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ABSTRACT OF THE DISSERTATION

PHYLOGENETIC AND ECOLOGICAL SIGNIFICANCE IN THE EVOLUTION OF CETACEAN TONAL SOUNDS

by

Laura Johanna May-Collado

Florida International University, 2007

Miami, Florida

Professor Douglas Wartzok, Major Professor

Cetaceans are aquatic mammals that rely primarily on sound for most daily tasks. A compendium of sounds is emitted for orientation, prey detection, and predator avoidance, and to communicate. Communicative sounds are among the most studied Cetacean signals, particularly those referred to as tonal sounds. Because tonal sounds have been studied especially well in social dolphins, it has been assumed these sounds evolved as a social adaptation. However, whistles have been reported in 'solitary' species and have been secondarily lost three times in social lineages. Clearly, therefore, it is necessary to examine closely the association, if any, between whistles and sociality instead of merely assuming it. Several hypotheses have been proposed to explain the evolutionary history of Cetacean tonal sounds. The main goal of this dissertation is to cast light on the evolutionary history of tonal sounds by testing these hypotheses by combining comparative phylogenetic and field methods. This dissertation provides the first species-level phylogeny of Cetacea and phylogenetic tests of evolutionary hypotheses of cetacean communicative signals. Tonal sounds evolution is complex in that has likely been shaped by a combination of factors that may influence different aspects of their acoustical structure. At the inter-specific level, these results suggest that only tonal sound *minimum* frequency is constrained by body size. Group size also influences tonal sound minimum frequency. Species that live in large groups tend to produce higher frequency tonal sounds. The evolutionary history of tonal sounds and sociality may be intertwined, but in a complex manner rejecting simplistic views such as the hypothesis that tonal sounds evolved 'for' social communication in dolphins. Levels of social and tonal sound complexity nevertheless correlate indicating the importance of tonal sounds in social communication. At the intraspecific level, tonal sound variation in frequency and temporal parameters may be product of genetic isolation and local levels of underwater noise. This dissertation provides one of the first insights into the evolution of Cetacean tonal sounds in a phylogenetic context, and points out key species where future studies would be valuable to enrich our understanding of other factors also playing a role in tonal sound evolution.

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CHAPTER I

INTRODUCTION

Mammals are among the most morphologically and ecologically diverse vertebrate groups (Perrin 1991). They have colonized greatly contrasting habitats and therefore evolved various ways to communicate and monitor these environments by using visual, olfactory, tactile, and acoustic senses. Most mammals to some extent use all these senses, but aquatic mammals like cetaceans rely predominantly on sound. This dependence on sound stems from light limitations in aquatic environments (Richardson *et al.*1995). Light attenuates rapidly with depth, limiting visual interactions between sender and receiver. Olfactory senses are also less developed in cetaceans than in land mammals, limiting their use for communication purposes (Wartzok and Ketten 1999). Sound, however, has the advantage of having low attenuation, allowing for effective communication and monitoring of aquatic environments over relatively long distances. For instance, baleen whales produce low frequency sounds (<100 Hz), with very small absorption losses; some whales are able to communicate over hundreds of kilometers (Richardson *et al.*1995).

The sophistication of acoustic communication reaches its pinnacle in cetaceans. These animals emit a compendium of communicative sounds that include broadband frequency modulated tonal sounds and narrowband frequency pulsed sounds (i.e., bursts, razors, barks, etc.). Tonal sounds are perhaps the most studied of these sounds, and are produced by both baleen whales (Mysticeti) and toothed whales (Odontoceti)—sister clades containing all extant whales. Baleen whales produce tonal sounds called 'moans' and 'tones' that have fundamental frequencies generally below 5 kHz (Richardson *et* *al.*1995, Clark 1990). In contrast, in toothed whales these tonal sounds are called whistles and have frequencies that typically range from 5-20 kHz (Richardson *et al.*1995). In some species fundamental frequencies can go up to 48 kHz (May-Collado and Wartzok 2007). Although similar in acoustic structure across all whales, tonal sounds are possibly produced by two different mechanisms; the larynx in baleen whales and a complex air sac system in toothed whales (Cranford 2000, Cranford *et al.*1999).

Tonal sounds are produced in a variety of contexts. Baleen whales are believed to use these sounds for long distance communication (e.g., blue whales Sirovic *et al.*2004) and in sexual contexts (e.g., right whales Clark and Johnson 1984, humpback whales Tyack 1983, Tyack and Whitehead 1983). In toothed whales they are used for group cohesion, recruitment during feeding activities, and overall communication (e.g., Dreher and Evans 1964, Caldwell and Caldwell 1965, Herman and Tavolga 1980, Janik 2000, Herzing 2000, Acevedo-Gutierrez and Stienessen 2004). In 'true' dolphins (Delphinidae), signature tonal sounds (referred to as ‘signature whistles’ by Caldwell and Caldwell 1965) allow for mother-calf recognition and formation of male-alliances (e.g., Caldwell and Caldwell 1965; Caldwell *et al.*1990, Fripp *et al.*2005, Herzing 2000, Janik 2000, Tyack 1997, 2000, Watwood *et al.*2004).

Comparative studies have shown that some acoustic parameters of tonal sounds such as duration and modulation tend to vary within species (e.g., Barzúa-Durán and Au 2002, 2004, Morisaka *et al.*2005a, Wang *et al.*1995a) whereas frequency components typically vary across species (e.g., Matthews *et al.*1999, Oswald *et al.*2003, Rendell *et al.*1999, Steiner 1981, Wang *et al.*1995b). Several hypotheses have been proposed to explain this variability. Intraspecific variation has been proposed to be the result of local adaptation to ecological conditions or geographical isolation and genetic divergence between groups or populations (e.g., Azevedo and Van Sluys 2005, Barzúa-Durán 2004, Barzúa-Durán and Au 2004, Morisaka *et al.*2005b, Rossi-Santos and Podos 2006, Wang *et al.*1995b, Camargo *et al.*2007, Ansmann *et al.*2007). Interspecific variation in frequency components may be product of zoogeographic relationships (Steiner 1981), habitat (Wang *et al.*1995a), morphological constraints (Matthews *et al.*1999, Podos *et al.*2002, Wang *et al.*1995a,), phylogenetic relationships (e.g., Steiner 1981, Matthews *et al.*1999, Wang *et al.*1995a), and sociality (Podos *et al.*2002, Herman and Tavolga 1985).

Despite recent technological advances in cetacean bioacoustics, fundamental evolutionary questions remain unanswered. For example, in what context did tonal sounds evolve? What are the selective forces driving intra- and interspecies acoustic signal differentiation? Previous studies addressing such questions have been made with little or no reference to phylogenetic relationships and correlation analyses have relied upon standard statistics, which assume species as independent data points. Interspecific comparative studies, however face problems of non-independence. Failing to account for known phylogenetic dependencies among related species and failing to recognize that similarity in size or tonal sounds 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. Therefore, the goal of my dissertation is to cast light on the evolutionary history of tonal sound signals by (1) establishing a species level phylogeny to test some of the hypotheses of tonal sound evolution at the inter-specific level using phylogenetic comparative methods, (2) confirming the emission of tonal sounds on the river dolphin *Inia geoffrensis* which due to its phylogenetic position is particularly important in this study, and (3) evaluating the role of the environment, sympatry between species, and other species-intrinsic factors on the whistle structure at the intra-specific level.

The dissertation consists of five chapters. Chapters II-V are formatted according to the journals in which they have been published and chapter VI to the format of the journal to which it will be submitted.

In order to test the above hypotheses it was necessary to have a well resolved Cetacean species phylogeny, which was not available at the time. Chapter II thus presents the first species-level cetacean phylogeny, which is based on the mitochondrial gene, Cytochrome-b (cyt-b) and utilizes Bayesian phylogenetic methods. This chapter discusses the utility of cyt-b and the importance of exhaustive taxon sampling (including outgroups) and Bayesian methods in Cetacean phylogenetics. Although based on only a single gene, the phylogeny is deemed reliable—and thus appropriate for hypothesis testing—based on its concordance with well established benchmark clades previously supported by morphological and mitochondrial and nuclear DNA (May-Collado and Agnarsson 2006).

Another important issue to be addressed before testing the above hypotheses was the long controversy of tonal sound ('whistle') production by river dolphins. The controversy stems from the assumption that whistles coevolved as a social adaptation within delphinids, and therefore sounds produced by river dolphins, regardless of the similarities in acoustic structure with whistles, were not considered as such, because river dolphins are largely solitary. Because of the phylogenetic position of *Inia geoffrensis* it was key to ‘solve’ the controversy in order to understand the evolutionary history of Cetacean tonal sounds. Chapter III describes high frequency tonal sounds (i.e. whistles) produced by *Inia geoffrensis* in Ecuadorian waters, and proposes the hypothesis that whistles in this river dolphin may be emitted under a social context different from that of dolphins (May-Collado and Wartzok 2007).

Having produced a species level phylogeny and addressed the issue of whistle production in river dolphins the stage is set to test hypotheses explaining tonal sound acoustic structure variation across species. One hypothesis is that body size constrains frequency in Cetacean tonal sounds. Body size is one of the most important morphological factors believed to influence animal signal frequency (Marquet and Taper 1998). The general idea is that body size and the size of sound producing organs correlate (Fletcher 1992) and the size of vocal tract places physiological constraints on signal production. In cetaceans body size has been suggested as a major factor influencing both the maximum and minimum frequency of tonal signals (e.g., Matthews *et al.*1999, Podos *et al.*2002, Wang *et al.*1995a). Chapter IV reexamines this hypothesis in a phylogenetic context. The findings corroborate the relationship between body size and minimum frequency but suggest that to explain the variation observed in other tonal sound frequency parameters, alternative hypotheses are required. This chapter emphasizes the importance of taking into account phylogenetic relations in comparative studies and considers the other potential factors playing a role in tonal sound variation i.e., sociality and the environment (May-Collado *et al.*2007a).

Chapter V considers the role of sociality as a potential factor affecting tonal sound acoustic variation across species by using several new comparative phylogenetic methods. It addresses problems with evolutionary analyses of broad concepts like ‘whistles’ or ‘tonal sounds’ rather than their component characters. This chapter finds new correlations between social structure and some tonal sound parameters. It proposes novel hypotheses about the role of social structure in tonal sounds and criticizes the over-simplistic hypothesis that whistles evolved ‘for’ communication in Delphinidae (May-Collado *et al.*2007b).

Chapter VI discusses several potential sources of whistle acoustic structure variation at the intra-specific level, including habitat acoustics (ambient noise levels and boat-dolphin interactions), sympatry with other dolphin species, isolation, and behavior in two adjacent bottlenose dolphin populations in the Caribbean of Costa Rica and Panama.

Finally, Chapter VII presents the conclusions and questions that emerge from this dissertation suggesting future directions of study that would continue to increase our knowledge on the evolution of Cetacean acoustic signals.

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CHAPTER II

CYTOCHROME B AND BAYESIAN INFERENCE OF WHALE PHYLOGENY

LAURA MAY-COLLADO[1,2], INGI AGNARSSON[3]

[1] Department of Biological Sciences, Florida International University, 11200 SW 8th Street, Miami, FL 33199, USA.

[2] Escuela de Biologia, Univeridad de Costa Rica, Apto. 2060, San Jose, Costa Rica

[3] The University of British Columbia, Departments of Zoology and Botany, 3529-6270 University Blvd., Vancouver, B.C. V6T 1Z4, Canada.

May-Collado, L. J. and I. Agnarsson. 2006. Cytochrome b and Bayesian inference of whale phylogeny. Molecular Phylogenetics and Evolution. 38: 344–354.

ABSTRACT

In the mid 1990's cytochrome b and other mitochondrial DNA data reinvigorated cetacean phylogenetics by proposing many novel and provocative hypotheses of cetacean relationships. These results sparked a revision and reanalysis of morphological datasets, and the collection of new nuclear DNA data from numerous loci. Some of the most controversial mitochondrial hypotheses have now become benchmark clades, corroborated with nuclear DNA and morphological data; others have been resolved in favor of more traditional views. That major conflicts in cetacean phylogeny are disappearing is encouraging. However, most recent papers aim specifically to resolve higher-level conflicts by adding characters, at the cost of densely sampling taxa to resolve lower-level relationships. No molecular study to date has included more than 33 cetaceans. More detailed molecular phylogenies will provide better tools for evolutionary studies. Until more genes are available for a high number of taxa, can we rely on readily available single gene mitochondrial data? Here we estimate the phylogeny of 66 cetacean taxa and 24 outgroups based on Cytb sequences. We judge the reliability of our phylogeny based on the recovery of several deep-level benchmark clades. A Bayesian phylogenetic analysis recovered all benchmark clades and for the first time supported Odontoceti monophyly based exclusively on analysis of a single mitochondrial gene. The results recover the monophyly of all but one family level taxa within Cetacea, and most recently proposed super- and subfamilies. In contrast, parsimony never recovered all benchmark clades and was sensitive to a priori weighting decisions. These results provide the most detailed phylogeny of Cetacea to date and highlight the utility of both Bayesian methodology in general, and of Cytb in cetacean phylogenetics. They furthermore suggest that dense taxon sampling, like dense character sampling, can overcome problems in phylogenetic reconstruction.

Keywords: Balaneidae; Cetancodonta; Cetartiodactyla; Delphinidae; Delphinoidea; Euungulata, Iniidae; missing data; mitochondrial DNA; Monodentidae; Mysticeti; Odontoceti; monophyly; Perissodactyla; Phocenidae; Platanistidae; phylogeny; taxon sampling; Ziphiidae.

INTRODUCTION

Several issues of Cetacean phylogenetics have been intensely debated, as a result of independent datasets (morphology, nuclear DNA, and mitochondrial DNA) suggesting conflicting hypotheses. These debates include the phylogenetic placement of Cetacea as sister to Artiodactyla (e.g., O'Leary and Geisler, 1999; Luckett and Hong, 1998; see also Gingerich et al., 1990) or embedded within Artiodactyla, a clade called Cetartiodactyla (e.g., Graur and Higgins, 1994; Gatesy et al., 1996, 1999; Gatesy 1997; Hasegawa and Adachi, 1996; Montgelard et al., 1997; Thewissen and Madar, 1999; Thewissen et al., 2001; Shimamura et al., 1999; Nikaido et al., 1999; Lum et al., 2000; Matthee et al., 2001; Arnason et al., 2004; Murphy et al., 2001; Reyes et al., 2004), the relationship between toothed whales and baleen whales (e.g., Luckett and Hong, 1998; Cerchio and Tucker, 1998; Douzery 1993, Messenger and McGuire, 1998; Nikaido et al., 2001; Nishida et al., 2003; Geisler and Sanders, 2003; Milinkovitch et al., 1993, 1994, 1995,1996; Milinkovitch, 1995, 1997), the relationships among delphinoids (e.g., Milinkovitch et al., 1993; Waddel et al., 2000; Nishida et al., 2003), dolphins (e.g., Mead, 1975; Kasuya, 1973; Barnes et al., 1985; deMuizon 1988; Perrin, 1989; Fordyce et al., 1994; LeDuc et al., 1999; Pichler et al., 2001), river dolphins (e.g., Flower, 1867; Winge, 1921; Slijper, 1936; Simpson, 1945; Cozzuol, 1985; Hamilton et al., 2001; Cassens et al., 2000; Nikaido et al., 2001: Yan et al., 2005), and porpoises (Rosel et al., 1995).

Since the mid 1990's mitochondrial DNA data have been at the forefront of advancing understanding of cetacean phylogenetics (e.g., Arnason et al., 1992, 1993, 2004; Arnason and Gullberg, 1993, 1994, 1996; Milinkovitch et al., 1993, 1994; Irwin and Arnason 1994; Milinkovitch, 1995, 1997; Graur and Higgins, 1994; Gatesy et al., 1996, Montgelard et al., 1997; Sasaki et al., 2005), for several reasons. Mitochondrial DNA is relatively easy to amplify and sequence, it is mostly free of problems with paralogy, and it has a relatively high substitution rate and thus offers information at various phylogenetic levels (Irwin et al., 1991; Milinkovitch, 1997). Results based on mitochondrial DNA offered novel, often controversial hypotheses (e.g., Milinkovitch et al., 1993, 1994; Milinkovitch, 1995; Irwin and Arnason, 1994; Arnason and Gullberg, 1994) and sparked renewed interest in the reconstruction of the evolutionary history of whales. Some of these hypothesis such as the placement of Cetacea within Artiodactyla (Cetartiodactyla sensu Montgelard et al., 1997) (e.g., Graur and Higgins, 1994; Irwin and Arnason, 1994), and the unexpected hypothesis of the sister relationship of Cetacea and Hippopotamidae (Cetancodonta sensu Arnason et al., 2000) (see Irwin and Arnason, 1994; Gatesy 1997; Montgelard et al., 1997) have now received support from studies based on new independent datasets. Another unexpected mitochondrial hypothesis (based on Cytb, 12S, and 16S), the placement of baleen whales within toothed whales, however, was recently resolved in a different direction. Using the entire mitochondrial genome reversed the earlier mitochondrial hypothesis and recovered the monophyly of Odontoceti (Arnason et al., 2004). These previously controversial clades can now be labeled as ‘benchmark’ clades, i.e. to be likely true:

Odontoceti: Arnason et al. (2004) (mitogenomic data); Messenger and McGuire (1998) (morphology); Nishida et al. (2003) (nuclear DNA); Nikaido et al. (2001) (retroposon SINE data); O'Leary et al. (2004) (combined morphology, nuclear DNA, mitochondrial DNA, and amino acids).

Cetartiodactyla: Thewissen et al. (2001), and Boisserie et al. (2005) (morphology including fossil taxa); Arnason et al. (2004) (mitogenomic data); Matthee et al. (2001) and Murphy et al. (2001) (nuclear and mitochondrial data); Shimamura et al. (1997, 1999) (retroposon SINE data); O'Leary et al. (2004) (combined morphology, nuclear DNA, mitochondrial DNA, and amino acids).

Cetancodonta (Cetacea + Hippopotamidae): Geisler and Sanders (2003) and Boisserie et al. (2005) (morphology including fossils); Gatesy et al. (1999) (nuclear and mitochondrial data); Lum et al. (2000) (retroposon SINE data); Arnason et al. (2000, 2004) (mitogenomic data); O'Leary et al. (2004) (combined morphology, nuclear DNA, mitochondrial DNA, and amino acids).

Some long standing debates are thus all but resolved: our understanding of deeper level cetacean phylogeny has grown strong. However, the strong focus of most recent studies, aiming specifically to resolve these higher level conflicts by adding mostly characters rather than taxa, has left our understanding of lower level relationships among whale species lagging behind. Mitogenomic data, for example, is available only for 16 cetacean species, and no molecular study to date has included more than 33 cetaceans. It seems timely to focus on more detailed (genus, and species level) molecular phylogenies.

These will provide better tools for detailed evolutionary studies, and are necessary to test existing morphological phylogenetic hypotheses, and current cetacean classification. Furthermore, adding taxa, as adding characters, can be an efficient way of overcoming phylogenetic uncertainty (Hillis, 1996, 1998; Graybeal, 1998; Pollock et al., 2002; Zwickl and Hillis, 2002; Hillis et al., 2003; but see Rosenberg and Kumar, 2001, 2003; Miller and Hormiga, 2004; Rokas and Caroll 2005). Obviously, combining multiple lines of evidence is beneficial to any phylogenetic problem. The study of O'Leary et al. (2004) is an excellent example of how seemingly incongruent data subsets can, when combined, yield a globally robust (and credible) result. However, until more genes are available for a high number of cetacean taxa, can we rely on readily available single gene mitochondrial data? Here we estimate the phylogeny of 66 cetaceans taxa representing 63 species, and 24 outgroups based on Cytb sequences from GenBank. This data matrix approximately doubles the taxon sampling of the most complete previous molecular study on cetacean phylogenetic relationships. We chose Cytb as it is available for more species than any other gene, and as it is a protein coding gene where alignment is trivial; in contrast many portions of the mitochondrial genome are notoriously difficult to align (e.g., Cerchio and Tucker, 1998; Messenger and MacGuire, 1998).

We judge the reliability of our phylogeny based on the recovery of the previously mentioned benchmark clades, in addition to the less controversial clades Perissodactyla, Euungulata (*sensu* Waddell et al. 2001, Perissodactyla + Cetartiodactyla), Cetacea, and Mysticeti. Because Cytb is thought to be most reliable at lower taxonomic levels (due to high substitution rates), recovering ‘known’ deeper clades gives credibility to these new findings which have not been addressed by studies using few taxa. We compare the performance of Bayesian analyses versus parsimony under four different models, and briefly examine the sensitivity of the results to taxon sampling. We use our results to discuss agreement and remaining conflict in cetacean phylogenetics, and provide comments on current classification.

MATERIALS AND METHODS

Cytochrome data was compiled from GenBank for 66 cetaceans representing 63 species (see table 1 for accession numbers). Most previous mitochondrial DNA studies have included relatively few outgroups. For a stronger test of Cetartiodactyla monophyly and deeper level relationships we sampled 24 outgroup taxa using the recent mammalian phylogeny of Murphy et al. (2001) as a guide to outgroup choice. Murphy's et al. (2001) phylogeny, based on 18 gene segments, suggested the following relationships: (Carnivora (Perissodactyla + Cetartiodactyla)). Outgroups therefore include non-cetacean cetartiodactylans (16 species), Perissodactyla (six species), and two carnivores chosen as primary outgroups on which the preferred tree is rooted (Table 1). To minimize potential missing data problems in an already difficult phylogenetic problem, we chose to exclude cetacean taxa when the following two conditions applied: 1) only small partial Cytb sequences were available (less than 50% of the entire sequence), and 2) congeners with longer sequences were already present in the matrix.

The molecular matrices were matched and aligned using the Needleman-Wunsch algorithm (gap cost=10, mismatch=1) in MacClade 4.07 (Maddison and Maddison, 2003). As Cytb is a protein coding gene, the alignment of the Cytb sequences was unambiguous without any gaps.

The data were analyzed using Bayesian, and parsimony methods. The appropriate model for the Bayesian analyses was selected with Modeltest (Posada and Crandall, 1998), using the AIC criterion (Posada and Buckley, 2004) with a parsimony tree chosen as the basis for Modeltest. The best model was GTR + ß§ +I (Rodríguez et al., 1990; Yang et al., 1994). Estimates for the model parameters (-LnL= 23900.7090, K=10, base frequency A=0.368, C=0.400, G=0.0518, T=0.1802).

Bayesian analysis was performed using MrBayes V3.0 (Huelsenbeck and Ronquist, 2001) with the following settings. The maximum likelihood model employed 6 substitution types ("nst=6"), with base frequencies estimated from the data. As substitution frequencies differ starkly between first, second and third positions in Cytb (Irwin et al., 1991), each codon position was treated separately (substitution rate partitioning) (charset 1st_pos = 1-1140\3; charset 2nd_pos = 2-1140\3; charset 3rd_pos =3-1140\3; partition bycodon = 3: 1st_pos; 2nd_pos; 3rd_pos; set partition = bycodon). Rate variation across sites was modeled using a gamma distribution (rates="invgamma"). The Markov chain Monte Carlo search was run with 4 chains for 5,000,000 generations(repeated three times), sampling the Markov chain every 1000 generations, and the sample points of the first 70,000 generations were discarded as "burn-in", after which the chain reached stationarity.

Parsimony analyses were done in PAUP* (Swofford, 1999) and NONA (Goloboff, 1993) through the WINCLADA shell (Nixon, 2002). In each of the analyses, heuristic searches were done with 1000 random stepwise additions, and subtree-pruning and regrafting branch swapping algorithm (chosen arbitrarily). As transitions (Ti) are much more common than transversions (Tv) and different codon positions show different levels of Ti saturations (third position showing the highest), we used some of the many weightings schemes suggested by previous authors. In addition to equal weights (Tv = Ti = all positions = 1), down weighting transitions (Ti = 0, Tv = 1, as suggested by Milinkovitch et al., 1996), (Ti = 1, Tv = 3 as suggested by Milinkovitch, 1994, see Messenger and McGuire, 1998), unequal codon weighting (4:17:1 as suggested by Arnason and Gullberg, 1994).

Node support for the parsimony analyses was estimated using Bootstrapping (Felsenstein, 1985). Each analysis was run for 200 Bootstrap replicates, with 10 random addition sequences, and holding a maximum of 100 trees, per replicate.

To examine the effect of sparse taxon sampling on the Bayesian analysis (numerous previous studies have analyzed smaller Cytb datasets using parsimony) we analyzed two, rather arbitrarily chosen subset of the data. First, we pruned the dataset to contain a comparable taxon sampling to that of Messenger and McGuire (1998) – subsample in Table 1; second, we used the pruned ingroup dataset, but added all the outgroups from the main data matrix (subsample, plus outgroups in Table).

RESULTS

Bayesian analysis

The Bayesian analysis recovered all seven benchmark clades (Table 2). Support for five of the benchmark clades is high (100 posterior probabilities) but rather low for Cetancodonta (79) and marginal for the monophyly of Odontoceti (67) (Figure 1, Table 2). The analysis also recovered all but one family level, and most sub- and super-family level cetacean taxa (Figure 1, for posterior probability values for each clade, see Figure 2). The results thus broadly corroborate current cetacean classification, while also pointing to some lower-level groups that may need redefinition.

Pruned Bayesian analyses

The Bayesian analysis of pruned matrix I (see Table 1) was broadly congruent with the parsimony analysis of Messenger and McGuire (1998) based on a similar taxon sampling, rejecting Odontoceti monophyly. When all outgroups of the main matrix were added (subsample matrix II, see Table 1), however all the benchmark clades were again recovered (Table 2).

Parsimony analyses

The parsimony analyses all recovered Perissodactyla, Cetancodonta, Cetacea, and Mysticeti, with variable support (Table 2). Euungulata was recovered with high support by three out of the four analyses, but not under the 4:17:1 weighting scheme. None of the parsimony analyses unambiguously recovered Cetartiodactyla or Odontoceti. Under equal weights, the majority of the most parsimonous trees supported Odontoceti monophyly while the strict consensus collapses Mysticeti, *Kogia*, *Physeter*, and Ziphidae+*Platanista*, into a pentachotomy with the remaining cetaceans. Cetartiodactyla is not recovered under equal weights, due to the placement of *Camelus*+*Lama* basal to Perissodactyla. Ignoring transitions altogether (see Milinkovitch et al., 1996) was similar to the equal weights analysis, although the strict consensus is less resolved, with the same pentachotomy formed at the base of Cetacea. Weighting transversions three times transitions (see Milinkovitch et al., 1994; McGuire and Messenger, 1998) placed Mysticeti sister to Ziphidae, in turn sister to sperm whales (Table 2).

Apart from benchmark clades, most analyses broadly agreed on the monophyly of superfamily, family, and subfamily level taxa within Cetacea. All cetacean families are supported with the exception of Balaenopteridae which consistently contained Eschrichtiidae. Subfamilies within Phocoenidae and Ziphidae were furthermore contradicted by all analyses. Our results support the transfer of *Lagenorynchus acutus* to *Leucopleurus* (as suggested by LeDuc et al., 1999, 2002), and in our preferred phylogeny (Figures 1-2) this taxon is place sister to Delphinae plus Stenoninae. The following genera are not monophyletic according to our results: *Lagenorynchus* (even after excluding *L. acutus*), *Stenella*, *Phocoena*, and *Balaenoptera*.

DISCUSSION

Recovery of benchmark clades

Many recent cetacean phylogenetic studies include relatively few taxa (exceptions include Arnason and Gullberg, 1996; Messenger and McGuire, 1998; LeDuc, 1999, 2002; Hamilton et al., 2001), in part due to a focus on generating more characters to resolve higher level phylogenetics (see e.g., Lum et al., 2000; Nikaido et al., 2001; Nishida et al., 2003; Arnason et al., 2004). While addressing crucial questions and providing the backbone for lower level phylogenies, such studies have limited utility for classification, and for comparative evolutionary studies. In some cases sparse taxon sampling may also confound the results (Hillis et al., 2003). Of course, taxon sampling is usually simply constrained by the availability of character data, but for some reason many studies have opted to include only one, or a few outgroup taxa, even if many are available. Outgroup choice may have marked impact on any phylogenetic analysis (see e.g., Adachi and Hasegawa, 1995; Milinkovitch and Lyons-Weiler, 1997).

Here we have extensively sampled cetacean taxa, and outgroups, to provide a more detailed phylogenetic hypothesis than previous studies. We analyzed the data using Bayesian methods, increasingly popular in molecular phylogenetics, but hitherto little used in cetacean studies (but see e.g. Yan et al., 2005), in addition to parsimony under various previously proposed weighting schemes.

Given the relatively few characters we certainly acknowledge the limitations of our study, and we did not expect robust clade support, especially for deeper level clades that have been consistently contradicted by previous Cytb analyses. However, we set up to test the reliability and sensitivity of our extended Cytb phylogeny based on the recovery of deep level benchmark clades (Euungulata, Perissodactyla, Cetartiodactyla, Cetancodonta, Cetacea, Mysticeti, and Odontoceti). Our study finds: 1) Bayesian phylogenetic methods outperformed parsimony under various models; 2) increased taxon sampling, in particular outgroup sampling (Table 2) increased congruence with other datasets, e.g. for the first time some of our analyses support Odontoceti monophyly based on Cytb data alone.

We find that as long as outgroup taxon sampling was extensive, Bayesian analyses of Cytb recovered all the a priori identified benchmark clades. When only a few outgroups were chosen, however, the Bayesian analysis negated Odontoceti monophyly (Table 2), as have many previous parsimony analyses of mitochondrial DNA. Furthermore, in almost every detailed comparison possible our results mirror the findings O'Leary et al. (2004), the most 'character-complete' (but including relatively few cetacean taxa) analysis to date (37,000 characters from morphology, SINE, and 51 gene fragments). This result gives credibility to our findings, including previously untested lower level clades.

The low support for Odontoceti is unsurprising given previous analysis of Cytb, and the finding of Arnason et al. (2004) that explosive radiation took place early in the evolutionary history of whales, with little time to accumulate synapomorphies for major lineages such as Odontoceti. The parsimony analyses likewise recover the benchmark clades Perissodactyla, Cetancodonta, Cetacea, and Mysticeti, but support for Cetartiodactyla and Odontoceti was highly sensitive to a priori character weighting schemes. Using the Arnason and Gullberg (1994) codon weighting scheme (4:17:1), a relatively strong support is found for Odontoceti monophyly. This is an interesting example of how dense taxon sampling can impact the phylogenetic signal. Arnason and Gullberg, (1994) used this weighting scheme in an Cytb analysis of 14 cetacean species and one outgroup (cow) suggested the placement of Mysticeti within Odontoceti. Because Bayesian analyses allows for an objective way of weighting characters (Felsenstein, 1981) and because it recovers all the benchmark clades supported by other independent data (e.g., Messenger and McGuire, 1998; Nikaido et al., 2001; Arnason et al., 2000, 2004; O'Leary et al., 2004) we favor the Bayesian hypothesis. As for other clades, most of the analyses showed remarkable congruence with previous phylogenies based on nuDNA, morphology, and mtDNA data (e.g., Rosel et al., 1995; Messenger and McGuire, 1998; LeDuc et al., 1999;Waddel et al., 2000; Cassens et al., 2001; Hamilton et al., 2001; Rychel et al., 2004; Sasaki et al., 2005). Below we briefly review the implications of our results to lower level cetacean phylogenetics and classification.

Monophyly and placement of Mysticeti (baleen whales)

The monophyly of baleen whales is virtually uncontroversial (see e.g. Sasaki et al., 2005). However, their placement has been debated. Based on mitochondrial data Milinkovitch et al. (1993, 1995,1994, 1996) suggested that baleen whales were sister to sperm whales (Physeteroidea), Verma et al. (2004) placed them sister to Platanistidae, while Arnason and Gullberg, (1994) based on Cytb placed baleen whales sister to dolphins (however, with very few taxa presented). These hypotheses have remained contradicted by both morphological and nuclear data, which agree on the sister relationship of monophyletic Odontoceti and Mysticeti. Our phylogenetic results agree with morphological and nuclear DNA data (e.g. O'Leary et al., 2004), echoing a new mitogenomic study by Arnason et al. (2004).

Within Mysticeti, we found support for the monophyly of Balaenidae, and the placement of Neobalaenidae sister to (extended) Balaenopteridae. However, *Eschrichtius robustus* consistently nested within Balaenopteridae, rendering the latter paraphyletic as found by Rychel et al. (2004), O'Leary et al. (2004), and Sasaki et al. (2005).

Monophyly of Odontoceti (toothed whales)

Odontoceti is one of our benchmark clades, and was supported by the Bayesian analysis and one of the parsimony analyses. The recovery of this clade shows that with sufficient taxa mitochondrial phylogenies can be reliable. Within Odontoceti the superfamilies Delphinoidea, Physeteroidea, and Inoidea were monophyletic, and also all family level taxa (Fig. 1).

Delphinoids

All analyses agree on the monophyly of Delphinoidea and monophyly of each of the delphinoid families Monodontidae, Phocoenidae, and Delphinidae, and all subfamilies within Delphinidae. Our results strongly support the relationship Delphinidae (Monodonotidae + Phocoenidae). Waddel et al. (2000) found the same relationships with nuclear genes and Nishida et al. (2003) with SRY (sex determining region of the Y chromosome) gene. Our findings contradict the division of Phocoenidae into two subfamilies Phocoeninae and Phocoenoidinae. The porpoises *Australophoceona dioptrica* and *Phoecoenoides dalli*, rather nested within Phocoeninae, and *Neophocaena phocaenoides* is basal to all the porpoises. As Rosel et al. (1995) suggested, *Australophocoena* should be returned to *Phocoena* where it was originally placed by Lahille (1912), and *Phocoenoies dalli* classification needs further analysis.

LeDuc et al. (1999) and LeDuc (2002) proposed a new classification for Delphinidae based on Cytb data. Unsurprisingly, our results largely agree. *Stenella* and *Lagenorhynchus* are paraphyletic and both need revision. *Grampus griseus* nested within the subfamily Globicephalinae in all our analyses (see also Kasuya, 1973), rather than within Delphininae as previously suggested (Mead, 1975; Barnes et al., 1985; De Muizon, 1988; Perrin, 1989). Orcininae (*Orcinus orca* + *Orcaella brevirostris*), separate from Globicephalinae is supported. *Sousa chinensis* groups within the subfamily Delphininae and not with Stenoninae. Furthermore, our results show a monophyletic Lissodelphininae including *Cephalorhynchus* spp., *Lissodelphis* spp., and

Lagenorhynchus australis, *L. cruciger*, *L. obliquidens* and *L. obscurus*. As suggested by previous studies *Lagenorhynchus* is not monophyletic. Our results support LeDuc et al. (1999) in transferring *Lagenorhynchus acutus* to *Leucopleurus*, but its phylogenetic position also requires the creation of a new subfamily, likely also including *L. albirostris*. LeDuc et al. (1999) and LeDuc (2002) suggested returning these four species to the genus *Sagmatias* (type species *L. cruciger*), however, in our analyses *L. cruciger* and *L. australis* are nested within *Cephalorhynchus*. Thus it may be simplest to transfer the *L. cruciger* and *L. australis* to *Cephalorhynchus*, while retaining *L. obliquidens* and *L. obscurus* in *Lagenorynchus*. Interestingly, the placement of *L. australis* within *Cephalorhynchus* is supported by acoustic data. Uniquely among dolphins, *L. australis*, and the four *Cephalorhynchus* species do not whistle (Schevill and Watkins, 1971). There is not published data on the acoustic behavior of *L. cruciger*.

River Dolphins

Our results agree with most molecular and recent morphological studies that river dolphins are polyphyletic, and do not offer unambiguous support for the infraorder Delphinida (containing Delphinoidea, Lipotidae, Iniidae, Pontoporidae, Platanistidae). As suggested by most studies Platanistidae does not group with other river dolphins, but is here the most basal family of Delphinida (e.g., Messenger and McGuire, 1998; Cassen et al., 2000; Hamilton et al., 2001; Yan et al., 2005). Note that a recent study based on nuDNA and Cytb placed Platanistidae sister to Mysticeti, although with little support

(Verma et al., 2004). *Platanista* is the only surviving genus of the superfamily Platanistoidea which contains the extinct marine families Prosqualodontidae, Dalpiazinidae, Waipatiidae, Squalondontidae, Squalodelphinidae, in addition to Platanistidae (deMuizon, 2002). Although, paleontologists agree that *Platanista* is a close relative of the family Squalodelphinidae (Heyning, 2002) new paleontological data points to *Lipotes vexillifer* and *Inia geoffrensis* as its closest relatives (Geisler and Sanders, 2003).

Geisler and Sanders, (2003) suggest a single ecological shift to riverine habitats in the 'river dolphins', instead of two as argued by other authors (e.g., Cassens et al., 2000; Nikaido et al., 2001; Hamilton et al., 2001). Our results indicate two to three shifts in the 'river dolphins'. An unambiguous one in *Platanista*, and either one in *Inia* and another in *Lipotes*, or a single origin in the node leading to Inoidea plus Lipotoidea with a reversal in *Pontoporia*. In addition, populations of *Sotalia fluviatilis*, *Orcaella brevirostris* (LeDuc, 1999), and the porpoise *Neophocaena phocaenoides*, independently shifted to a riverine habitat.

Previously the three 'river dolphin' genera were placed in a single family Iniidae (Heyning, 1989) or two families Pontoporidae (*Pontoporia* and *Lipotes*) and Innidae (*Inia*) (Fordyce et al., 1994). Our phylogenetic results agree with the classification of the three genera into three families as suggested by Fordyce and deMuizon (2001) with the following relationship ((Pontoporidae + Iniidae) + Lipotidae)). This arrangement is supported by both morphology and molecular data (e.g., Messenger and McGuire, 1998;

Yang and Zhou 1999; Cassen et al., 2000; Hamilton et al., 2001; Nikaido et al., 2001; Yan et al., 2005). Furthermore, the relationship of *Inia* subspecies is unsurprisingly identical to that found by Hamilton et al., (2001) (*I. g. humboldtiana* + *I. g. geoffrensis*) + *I. g. boliviensis*)).

Beaked and sperm whales

Our results support the superfamily Physeteroidea which includes the families Kogiidae and Physeteridae, whereas ziphiids interrelationships were largely unresolved. The molecular work of Dalebout et al. (2004) calls for a revision of Ziphiidae and Mead (2002) proposed the subfamilies Ziphininae (*Berardius* spp., *Tasmacetus shepherdi*, and *Ziphius cavirostris*) and Hyperoodontinae (*Mesoplodon* spp. and *Hyperoodon* spp). Our analyses all indicate *Tasmacetus shepherdi* sister to all other ziphiids. To date, most cetacean phylogenies have not aimed at solving ziphiid species relationships, and thus their relationships are largely unknown. Since low level taxonomic relationships were fairly well supported in other groups of toothed whale, Cytb seems promising in providing future insights in the evolutionary relationships of ziphiids. Physeteroids and ziphiids are the most basal toothed whales. Both groups show a clear reduction in dentition, in physeteroids teeth are only present in the lower jaw, and in most ziphiid species, teeth are reduced or absent in both jaws, with the exception of males that have two prominent teeth in the lower jaw (Mead 2002).

It is interesting to notice that *T. sheperdi* is basal in our ziphiid phylogeny and it is the only beaked whale with full dentition in both jaws. Although this particular relationship is weakly supported, it hints that the loss of teeth may be convergent in Physeteroidea, and within Ziphiidae.

CONCLUDING REMARKS

Substitution saturation imposes limitation on Cytb (and other mitochondrial data) for deeper level phylogenetics, and may lead to misleading results (Irwin et al. 1991; Springer et al. 2001). Furthermore, many studies have shown that single gene analyses rarely agree with global optima (e.g., O'Leary et al., 2004). However, our results show that by densely sampling taxa, especially outgroup taxa, and using appropriate methods of analysis with realistic models of evolution, this problem may be reduced, and in this particular example, mostly overcome. Low-level phylogenies are essential for classification and as a tool for comparative evolutionary (and ecological) studies. In this context 'single gene' phylogenies may be of great value (as long as they are 'reality checked') as relatively many species can be included, offering more detailed phylogenies than currently possible with phylogenies based on multiple genes and morphology. Ultimately, of course, a major goal of phylogenetics is a phylogeny of life (i.e. many taxa), based on multiple lines of evidence (many characters of many types). However, when phylogenies based on relatively few characters can be judged reliable based on external evidence (taxonomic congruence with other phylogenies using many characters, but few taxa), they seem like very promising and useful 'first guess' hypotheses. The evolution of sexual dimorphism, echolocation, social behavior, and whistles and other communicative signals, and major ecological shifts (e.g. transition to fresh water) are among the numerous interesting questions in cetacean biology that this phylogeny can help answer.

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Table 1. Species used in the analyses with respective GenBank accession numbers of cytochrome b sequences.

All species (Bayesian + Parsimony)		**Subsample^1**	**Subsample^2**
Species	**Accession #**		
Carnivora			
Canis familiaris	AY729880		X
Panthera leo	AF053052		X
EUUNGULATA			
Perissodactyla			
Dicerorhinus sumatrensis	AJ245723		X
D. bicornis	X56283		X
Equus caballus	AY515162		X
Equus grevyi	X56282		X
Tapirus indicus	AF145734		X
T. terrestris	AF056030		X
Cetartiodactyla			
Alces alces	M98484		X
Antilocapra americana	AF091629	X	X
Antilope cervicapra	AF022058		X
Babyrousa babyrussa	Z50106		X
Bos Taurus	AB090987	X	X
Camelus dromedarius	X56281	X	X
Cephalophus zebra	AF153903		X
Giraffa camelopardalis	X56287		X
Lama lama	U06429		X
Moschus leucogaster	AF026889		X
Odocoileus hemionus	X56291		X
Oryx gazelle	AF249973		X
Ovis aries	AB006800		X
Pecari tajacu	X56296	X	X
Sus barbatus	Z50107		X
CETANCODONTA			
Hippopotamus amphibius	Y08813		
Cetacea			
Mysticeti			
Balaena glacialis	X75587		
Balaena mysticetus	U13125	X	X
Balaenoptera bonaerensis	X75581	X	

B. borealis	X75582		
B. edeni	X75583		
Capera marginata	X75586		
Eschrichtius robustus	X75585	X	X
Megaptera novaeangliae	X75584	X	X
Odontoceti			
Physeteroidea			
Physeteridae			
Physeter macrocephalus (catodon)	X75589	X	X
Kogidae			
Kogia breviceps	U72040	X	X
Kogia simus	AF304072-U13135	X	X
Ziphoidea			
Ziphiidae			
Berardius bairdii	X92541		
Hyperoodon planifrons	AY579560		
H. ampullatus	AY579558		
Indopacetus pacificus	AY162441		
Mesoplodon densirostris	X92536	X	
M. bidens	X92538	X	
Tasmacetus shepherdi	AF334484		
Ziphius cavirostris	AF304075-U13146	X	X
Platanistoidea			
Platanistidae			
Platanista gangetica	AF304070		
Platanista minor	X92543		
Inoidea			
Pontoporidae			
Pontoporia blainvelli	AF334488		
Iniidae	AF334487		
Inia geoffrensis boliviensis	AF334485	X	X
Inia geoffrensis geoffrensis	AF521110		
Inia geoffrensis humboldtiana			
Lipotoidea			

Lipotidae			
Lipotes vexillifer	AF304071		
Delphinoidea			
Monodontidae			
Delphinapterus leucas	U72037	X	X
Monodon monocerus	U72038		
Phocoenidae			
Australophocoena dioptrica	U09681		
Neophocaena phocaenoides	AF334489		
Phocoena phocoena	U72039	X	X
P. sinus	AF084051		
P. spinipinnis	U09676	X	X
Phocoenoides dalli	U09679		
Delphinidae			
Cephalorhynchus commersonii	AF084073		
C. eutropia	AF084072	X	X
C. hectori	AF084071		
C. heavisidii	AF084070		
Delphinus delphis	AF084085	X	X
D. capensis	AF084087		
D. tropicalis	AF084088		
Feresa attenuata	AF084052		
Globicephala macrorhynchus	AF084055		
G. melas	AF084056	X	X
Grampus griseus	AF084059		
Lagenorhynchus acutus	AF084075		
L. australis	AF084069		
L. cruciger	AF084068		
L. obliquidens	AF084067	X	
L. obscurus	AY257161	X	X
Lagenodelphis hosei	AF084099		
Lissodelphis borealis	AF084064		
L. peronii	AF084065	X	X
Orcinus orca	AF084061		
Orcaella brevirostris	AF084063		
Pseudorca crassidens	AF084057		
Stenella attenuata	AF084096		
S. clymene	AF084083		
S. coeruleoalba	AF084082		
S. frontalis	AF084090		

S. longirostris	AF084103		
Sousa chinensis	AF084080		
Sotalia fluviatilis	AF304067		
Steno bredanensis	AF084077		
Tursiops truncatus	AF084095	X	X

Note: In subsample 1 species were included to mirror taxon selection in Messenger and McGuire (1998) molecular analyses except for the outgroup species *Tragulus napu.* Furthermore, the following cetacean species were replaced by close relatives: *Mesoplodon europaeus* and *M. peruvianus* by *M. bidens* and *M. densirostris*, *Lagenorhynchus albirostris* by *L. obliquidens*, and *Balaenoptera physalus* by *B. bonaerensis*. In subsample 2 the same species were included as in subsample 1 plus all outgroups from this study.

Table 2. Posterior probabilities and bootstrap values for all benchmark clades

	Benchmark clades						
Model	**Euungulata**	**Perissodactyla**	**Cetartiodactyla**	**Cecantodonta**	**Cetacea**	**Mysticeti**	**Odontoceti**
Bayesian GTR+Γ+I	100	100	100	79	100	100	67
Subsample Bayesian	n/a	n/a	n/a	n/a	100	98	NO
Subsample w/outgr.	100	100	100	71	100	99	78
Equally Weigthed MP	100	100	NO	<50	100	100	NO
MP (3:1)	100	100	NO	100	100	100	NO
MP (17:4:1)	NO	100	NO	<50	100	100	<50
MP (1:0)	88	91	NO	<50	97	100	NO

FIG.1

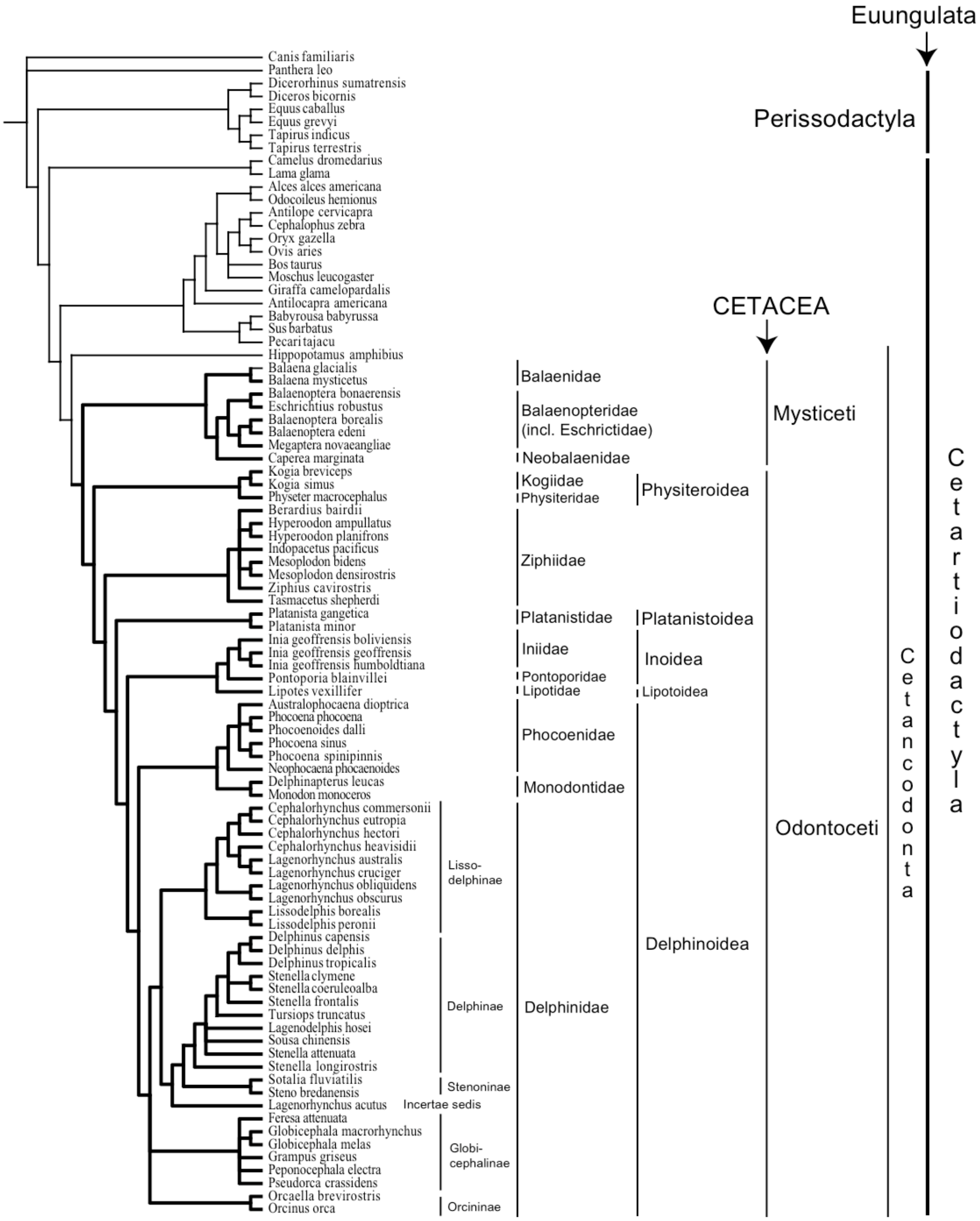
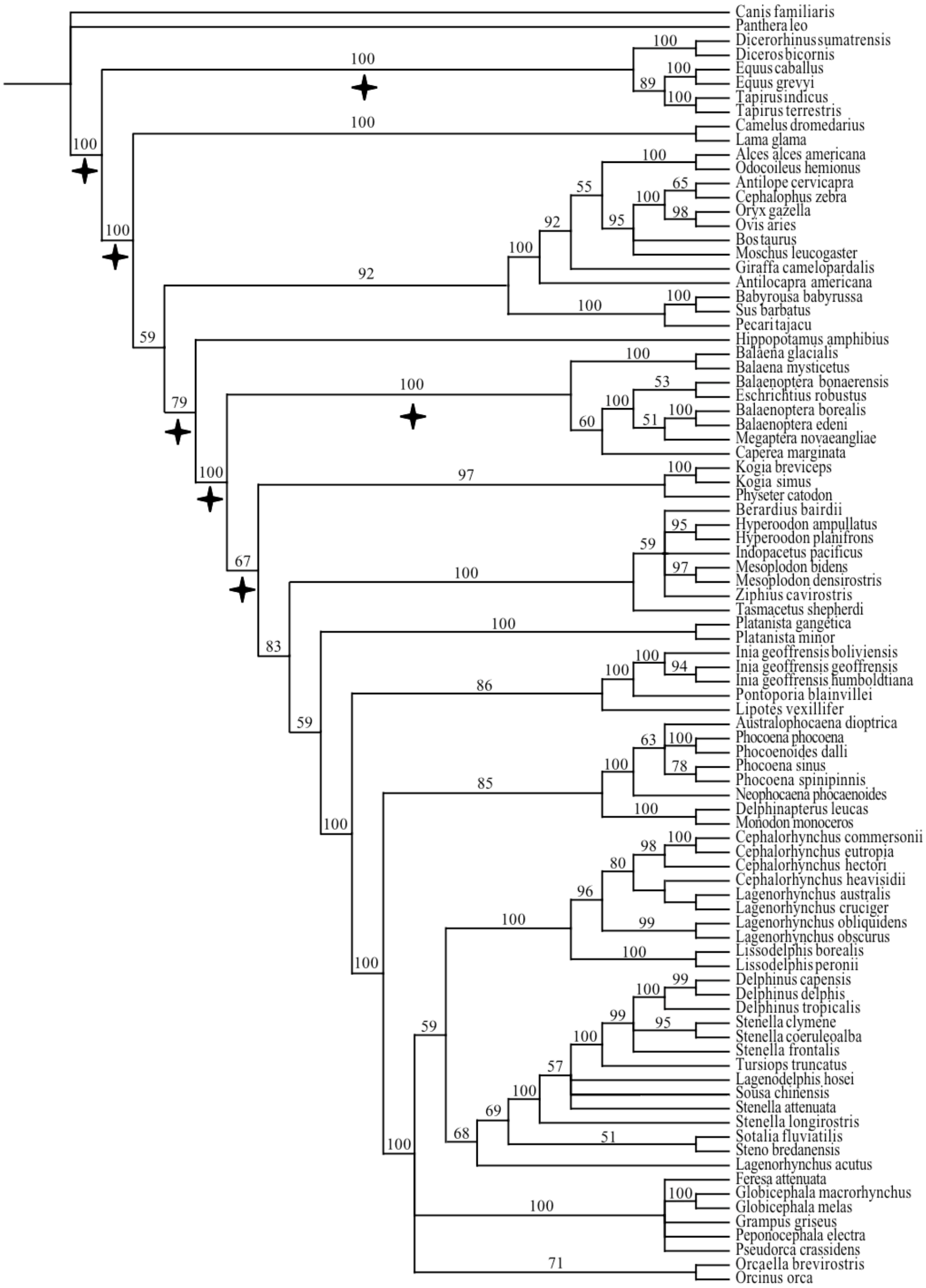

Euungulata
Canis familiaris
Panthera leo
Dicerorhinus sumatrensis
Diceros bicornis
Equus caballus
Equus grevyi
Tapirus indicus
Tapirus terrestris
Perissodactyla
Camelus dromedarius
Lama glama
Alces alces americana
Odocoileus hemionus
Antilope cervicapra
Cephalophus zebra
Oryx gazella
Ovis aries
Bos taurus
Moschus leucogaster
Giraffa camelopardalis
Antilocapra americana
Babyrousa babyrussa
Sus barbatus
Pecari tajacu
CETACEA
Hippopotamus amphibius
Balaena glacialis
Balaena mysticetus
Balaenidae
Balaenoptera bonaerensis
Eschrichtius robustus
Balaenoptera borealis
Balaenoptera edeni
Megaptera novaeangliae
Balaenopteridae
(incl. Eschrictidae)
Caperea marginata
Neobalaenidae
Mysticeti
Kogia breviceps
Kogia simus
Physeter macrocephalus
Kogiidae
Physiteridae
Physiteroidea
Berardius bairdii
Hyperoodon ampullatus
Hyperoodon planifrons
Indopacetus pacificus
Mesoplodon bidens
Mesoplodon densirostris
Ziphius cavirostris
Tasmacetus shepherdi
Ziphiidae
Platanista gangetica
Platanista minor
Platanistidae
Platanistoidea
Inia geoffrensis boliviensis
Inia geoffrensis geoffrensis
Inia geoffrensis humboldtiana
Iniidae
Inoidea
Pontoporia blainvillei
Pontoporidae
Lipotes vexillifer
Lipotidae
Lipotoidea
Australophocaena dioptrica
Phocoena phocoena
Phocoenoides dalli
Phocoena sinus
Phocoena spinipinnis
Neophocaena phocaenoides
Phocoenidae
Delphinapterus leucas
Monodon monoceros
Monodontidae
Cephalorhynchus commersonii
Cephalorhynchus eutropia
Cephalorhynchus hectori
Cephalorhynchus heavisidii
Lagenorhynchus australis
Lagenorhynchus cruciger
Lagenorhynchus obliquidens
Lagenorhynchus obscurus
Lissodelphis borealis
Lissodelphis peronii
Lisso-
delphinae
Delphinus capensis
Delphinus delphis
Delphinus tropicalis
Stenella clymene
Stenella coeruleoalba
Stenella frontalis
Tursiops truncatus
Lagenodelphis hosei
Sousa chinensis
Stenella attenuata
Stenella longirostris
Delphinae
Delphinidae
Delphinoidea
Sotalia fluviatilis
Steno bredanensis
Stenoninae
Lagenorhynchus acutus
Incertae sedis
Feresa attenuata
Globicephala macrorhynchus
Globicephala melas
Grampus griseus
Peponocephala electra
Pseudorca crassidens
Globi-
cephalinae
Orcaella brevirostris
Orcinus orca
Orcininae
Odontoceti
Cetancodonta
Cetartiodactyla

FIG. 2


Canis familiaris
Panthera leo
Dicerorhinus sumatrensis
Diceros bicornis
Equus caballus
Equus grevyi
Tapirus indicus
Tapirus terrestris
Camelus dromedarius
Lama glama
Alces alces americana
Odocoileus hemionus
Antilope cervicapra
Cephalophus zebra
Oryx gazella
Ovis aries
Bos taurus
Moschus leucogaster
Giraffa camelopardalis
Antilocapra americana
Babyrousa babyrussa
Sus barbatus
Pecari tajacu
Hippopotamus amphibius
Balaena glacialis
Balaena mysticetus
Balaenoptera bonaerensis
Eschrichtius robustus
Balaenoptera borealis
Balaenoptera edeni
Megaptera novaeangliae
Caperea marginata
Kogia breviceps
Kogia simus
Physeter catodon
Berardius bairdii
Hyperoodon ampullatus
Hyperoodon planifrons
Indopacetus pacificus
Mesoplodon bidens
Mesoplodon densirostris
Ziphius cavirostris
Tasmacetus shepherdi
Platanista gangetica
Platanista minor
Inia geoffrensis boliviensis
Inia geoffrensis geoffrensis
Inia geoffrensis humboldtiana
Pontoporia blainvillei
Lipotes vexillifer
Australophocaena dioptrica
Phocoena phocoena
Phocoenoides dalli
Phocoena sinus
Phocoena spinipinnis
Neophocaena phocaenoides
Delphinapterus leucas
Monodon monoceros
Cephalorhynchus commersonii
Cephalorhynchus eutropia
Cephalorhynchus hectori
Cephalorhynchus heavisidii
Lagenorhynchus australis
Lagenorhynchus cruciger
Lagenorhynchus obliquidens
Lagenorhynchus obscurus
Lissodelphis borealis
Lissodelphis peronii
Delphinus capensis
Delphinus delphis
Delphinus tropicalis
Stenella clymene
Stenella coeruleoalba
Stenella frontalis
Tursiops truncatus
Lagenodelphis hosei
Sousa chinensis
Stenella attenuata
Stenella longirostris
Sotalia fluviatilis
Steno bredanensis
Lagenorhynchus acutus
Feresa attenuata
Globicephala macrorhynchus
Globicephala melas
Grampus griseus
Peponocephala electra
Pseudorca crassidens
Orcaella brevirostris
Orcinus orca
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CHAPTER III

THE FRESHWATER DOLPHIN *INIA GEOFFRENSIS GEOFFRENSIS* PRODUCES HIGH FREQUENCY WHISTLES

LAURA J. MAY-COLLADO[1,2], DOUGLAS WARTZOK[1]

[1]Florida International University, Department of Biological Sciences, 11200 SW 8th Street, Miami Florida 33199

[2]Universidad de Costa Rica, Escuela de Biología, Apto. 2060 San Pedro, Costa Rica

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ABSTRACT

Because whistles are most commonly associated with social delphinids, they have been largely overlooked, ignored, or presumed absent, in solitary freshwater dolphin species. Whistle production in the freshwater dolphin, the boto (*Inia geoffrensis geoffrensis*), has been controversial. Because of its sympatry with tucuxi dolphins (*Sotalia fluviatilis*), a whistling species, some presume tucuxi whistles might have been erroneously assigned to the boto. Using a broadband recording system we recorded over 100 whistles from boto dolphins in the Yasuní River, Ecuador where the tucuxi dolphins are absent. Our results therefore provide conclusive evidence for whistle production in *Inia geoffrensis geoffrensis*. Furthermore, boto whistles are significantly different from tucuxi whistles recorded in nearby rivers. The Ecuadorian boto whistle with a significantly greater frequency range (5.30 to 48.10 kHz) than previously reported in other populations (Peru and Colombia) that were recorded with more bandwidth limited equipment. In addition the top frequency and the range are greater than in any other toothed whale species recorded to date. Whistles production was higher during resting activities alone or in the presence of other animals. The confirmation of whistles in the boto has important implications for the evolution of whistles in Cetacea and their association with sociality.

INTRODUCTION

The Amazon River dolphin, or boto, is known to produce a variety of sounds e.g., echolocation clicks, single intense clicks, jaw snaps, and burst-pulsed sounds (Caldwell and Caldwell 1967, Caldwell *et al.* 1966). Whistles were first reported by Nakasai and Takemura (1975) in Peru and later documented in more detail by Wang *et al.* (1995a, 2001). Whistles have been also reported in the boto from the Orinoco River (Diazgranados and Trujillo 2002). Despite these reports, whistle production in this riverine dolphin has been questioned on the basis that boto distribution overlaps largely with tucuxi dolphins (*Sotalia fluviatilis*), a well documented whistling species. Hence, tucuxi whistles may have been erroneously assigned to the boto (e.g., Podos *et al.* 2002). In fact, it has been suggested that whistles are unique to social delphinids (Herman and Tavolga 1980, Podos *et al.* 2002). Certainly, whistles are best studied in social delphinids, where they are used for various communication purposes such as individual identifiers, coordination of group behavior, and maintenance of group cohesion (e.g., Caldwell and Caldwell 1965; Caldwell *et al.* 1990, Fripp *et al.* 2005, Herzing 2000, Janik 2000, Tyack 1997, 2000, Watwood *et al.* 2004). However, non-delphinid toothed whale species like the Chinese river dolphin *Lipotes vexillifer* (Jing *et al.* 1981, Xianying *et al.* 1981,Wang *et al.* 1989, Wang *et al.* 2006), the beaked whales of the genus *Berardius* spp (Dawson *et al.* 1998, Rogers and Brown 1999), the narwhal *Monodon monocerus*, and the beluga *Delphinapterus leucas* (e.g., Belikov and Bel'kovich 2001, 2003, Ford and Fisher 1978, Karlsen *et al.* 2002, Shapiro 2006, Sjare and Smith 1986, Watkins *et al.* 1970) are known to produce whistles as well in a variety of contexts.

Here we document whistles and their behavioral context in the boto dolphins of the Yasuní River, Ecuador and discuss the potential of these signals as communicative signals in this solitary freshwater dolphin.

MATERIALS AND METHODS

Study Site

The boto is one of the most widely distributed freshwater dolphins. In parts of its distribution it is sympatric with *Sotalia fluviatilis* (da Silva 2002). The boto inhabits principal tributaries of the Amazon River as well as small rivers and lakes across its distribution (da Silva 2002). Since one of the main criticisms of previous work on boto whistles is the presence of *S. fluviatilis* in the area of recordings, it was important for our study to be conducted in areas where only botos were found. We selected the Yasuní River a tributary of the Napo River, a narrow river that inundates the adjacent forest and lagoons, during the high-water season (Fig.5). During the low-water season the river becomes narrower and the lagoons dry out (Galacatos *et al.* 2004), not the type of habitat in which *S. fluviatilis* is known to occur (da Silva 2002).

Overall *S. fluviatilis* is believed to have low population densities in Ecuador (Dekinger 2001, Zapata-Rios and Utreras 2004). While relatively common in the Putumayo and Morona Rivers, local biologists (Zapata-Rios and Utreras 2004, Victor Utreras pers. comn. 2006), park rangers, and inhabitants of the area confirm that *S. fluviatilis* is rare in the Yasuní, Napo, and Aguarico rivers, and absent in theYasuní during the low-water season. Our study took place in the Yasuní River during the low-water season when boto were confined to deeper areas of this narrow river.

We recorded boto dolphins from 14 to 19 August 2005 between 6 a.m. to 6 p.m. In order to decrease chances of encountering (and accidentally recording) *S. fluviatilis* we recorded botos at least 1.5 km away from the point of intersection with the Napo River where the chances to see *S. fluviatilis* may be higher (Zapata-Rios and Utreras 2004). As expected we observed only botos in the Yasuní River and are thus confident that all the whistles presented in this study correspond exclusively to the boto. To verify this, we compare and contrast boto whistles with 20 whistles recorded from six individuals of *S. fluviatilis* and 13 whistles from one group that contained both species at the intersection between the Napo and the Aguarico rivers, about 14 km downstream from the intersection between Yasuní and the Napo rivers. The 20 whistles recorded from single animals, were very similar in contour, time, and frequency parameters to other *S. fluviatilis* populations (e.g., Podos *et al.* 2002, Azevedo and Van Sluys 2005, Wang *et al.* 1995a, 2001). These single animals were recorded near the boat and botos were not present in the area. The other 13 whistles were identical to these in all acoustic parameters therefore they were assigned to *S. fluviatilis*.

Whistle Definition

To understand the evolutionary history of whistles and the factors that may have influenced their evolution we must first understand their distribution among cetaceans. To do so it is important not to *a priori* bias whistle definition e.g. by defining them in the context of a behavior that may have much more limited distribution than the sounds themselves. Rather, it seems less presumptuous to define sounds in terms of acoustic parameters. Whistles are tonal sounds produced by toothed whales. These sounds have a specific acoustic structure that consists of narrowband and frequency modulated sounds (Richardson *et al.* 1995). Whistles may be complex in contour (e.g., sine, convex, concave, upsweep, downsweep) or simply constant in frequency e.g., *Lagenorhynchus albirostris* (Rasmussen and Miller 2002), *Sotalia guianensis* (Azevedo and Van Sluys 2005) and *Stenella longirostris* (Barzúa-Durán and Au 2002). Often whistle fundamental frequency is below 20 kHz (Richardson *et al.* 1995), but not limited to this range e.g., Oswald *et al.* (2004) found that *Delphinus delphis, Stenella attenuata, S. coeruleoalba*, and *S. longirostris* produced whistles with frequencies up to 24 kHz, in *Lagenorhynchus albirostris* whistle fundamental frequency can go up to 35 kHz (Rasmussen and Miller 2002) and up to 41 kHz in *Tursiops truncatus* (Boisseau 2005). Whistles may be continuous or consist of series of breaks and segments (Richardson *et al.* 1995) and contain or not harmonics (Au 2000). Some dolphin species like *S. longirostris* (Lammers and Au 2003) and *L. albirostris* (Rasmussen *et al.* 2006) produce whistles with high order-harmonics. Finally whistles vary greatly in duration. For instance, *Sousa chinensis* whistles can range from 0.01 to 1.3 seconds (Van Parijs and Corkeron 2001) and in *Tursiops truncatus* from 0.05 to 3.2 seconds (Wang *et al.* 1995b).

Recordings and Behavioral observations

Dolphin signals were recorded using a broadband system consisting of a RESON hydrophone (-203 dB re 1V/µPa, 1 Hz to 140 kHz) connected to AVISOFT recorder and Ultra Sound Gate 116 (sampling rate 400-500 kHz 16 bit) that sent the signals to a laptop. Recordings were made continuously. For accompanying behavioral observations, recording sessions were segmented into three-minute intervals. Behavioral observations were made in every other three-minute interval and the predominant behavior during that interval was recorded. Because the river was narrow and relatively shallow, animals were in sight for the observers most of the time. When animals were not in sight during a 3-min scanning period, the behavior was noted as unknown. Only 3-min periods with acoustic and behavioral information were used for the analyses. Five behavioral categories were defined: (1) Feeding/Foraging, animals that were actively searching, pursuing, and/or consuming prey were assigned to this category, (2) Social activities, when dolphins interacted among themselves e.g., body contact, tail slapping, and animals following the boat or other animals, (3) Traveling, when dolphins were swimming either slowly or fast while maintaining a defined direction, (4) Resting was defined as in Dekinger (2001) were animals showed non directional swimming and surfaced regularly at a slow speed or when surfacing occurred in the same area without any abrupt or fast movement, (5) Unknown behavior, was assigned when the animals were not in sight and thus the behavior activity could not be determined.

Group size, group composition, photo-ID, and geographical position data were also collected. Recordings were obtained from 14 to 19 August 2005, giving a total of 214 files recorded (~ 9 hours and 45 minutes of recorded time). We analyzed all good quality whistles using the program Raven 1.1 (Cornell Laboratory of Ornithology, New York) with a FFT size of 1024 points, an overlap of 50%, and using a 512-522 sample Hann window.

Eight parameters were measured for each whistle: starting frequency (SF), ending frequency (EF), minimum frequency (MinF), maximum frequency (MaxF), delta frequency (DF=MaxF—MinF), peak frequency (PF, measured in the whistle contour were intensity was the highest), duration (s), number of inflection points and contour type. Contour type was categorized as by Azevedo and Simão (2002).

We used SYSTAT® statistical software for descriptive and non-parametric statistics. After testing for normality using the K-S Lilliefors, Skewness, and Kurtosis Tests, non-parametric tests were selected to analyze the data. The Kruskal-Wallis test was used to determine if whistle acoustic parameters varied across behavioral states and groups [sightings] and Chi-square one sample test for Goodness of Fit to determine if whistle production rate (#whistles/min/individual) varied across behaviors. The Kolmogorov-Smirnov test for two independent samples was used to determine if the medians of the acoustical parameters differed between the two species. A multivariate Discriminant Function Analysis was used to classify whistles within and between species. The Jackknife method was used to calculate the percent of correct classification for each species.

RESULTS

A total of 121 high quality tonal sounds fitted the definition of 'whistles' (see above) until now only described in delphinids and a few other toothed whales. However, these whistles were not produced in bouts as in many delphinids species. They were produced singly and spaced in time. The overall whistle production was 0.015 whistles per minute per individual.

Whistle fundamental frequency ranged from 5.30 up to 48.10 kHz and were short in duration (0.002-0.080 sec) (Table 3, Fig.6). About half (48%; n=58) of the whistles had maximum frequency values above 24 kHz. This demarcation point was chosen because most dolphin whistles reportedly do not go beyond 24 kHz (with the exceptions mentioned earlier) and this is often the upper limit of recording equipment used in many earlier studies. Similarly 42.1% (n=51) of beginning frequency, 13.2% (n=16) of peak frequency, 5.78% (n=7) of end frequency, and 1.65% (n=2) of minimum frequency measurements were above 24 kHz.

In terms of whistles contours 95.8% (n=116) of the whistles were descending in frequency. Examples of whistle contours produced by botos are shown in Figure 2 in conjunction with tucuxi whistles for comparison purposes. Only five of all selected whistles had harmonics. The highest frequency harmonic reached 43.5 kHz.

The whistles were recorded during three behavioral categories: slow traveling, feeding, and resting. Although more whistles were produced during travel activities when accounting for time and number of individuals, whistle production was significantly higher during resting activities with 0.24 whistles per minute per individual ($\chi^2=0.50$, df=1, $p<0.05$) compared to traveling (0.03) and feeding (0.03). There were no significant differences in the acoustic parameters of whistles across behaviors at p-value 0.05 level (Table 4).

Whistles did vary significantly in their acoustic structure across sighted groups (only groups with more than five whistles were compared) for all whistle parameters except delta frequency (Kruskal-Wallis test, df=8, n=121: MinF χ^2=20.31, p=0.026; MaxF χ^2=25.46, p=0.005; SF χ^2=23.31, p=0.010; EF χ^2=23.86, p=0.008; PF χ^2=23.28, p=0.010; Duration χ^2=25.46, p=0.005, DF p>0.05, Table 5). Whistle acoustic parameters did not vary significantly when comparing whistles of groups consisting of adults with groups of adults with calves (p>0.05).

When comparing boto and tucuxi whistles we found significant differences in all whistle parameters medians (MinF Kolmogorov Smirnov (KS)=0.543, p<0.001; MaxF KS=0.537, p<0.001; DF KS=0.190, p<0.001, SF KS=0.683, p<0.001; EF KS=0.298, p<0.001; PF KS=0.336, p<0.001; Duration KS=0.901, p<0.001). The boto whistles were higher in frequency for all frequency parameters and much shorter in duration than the whistles produced by tucuxis recorded from the Napo and Aguarico rivers (Fig. 3). Tucuxis produced two classes of whistles that can be described as (1) whistles with maximum frequencies below 20 kHz and minimum frequencies below 10 kHz, and (2) whistles with maximum frequencies below 25 kHz and minimum frequencies above 10 kHz (see Fig. 4). Both categories of whistles overlap with boto whistles. Despite of this overlap in frequency, the discriminant function analysis correctly classified (based on all acoustical parameters) all boto whistles (100%). Only 15% of the tucuxi whistles were incorrectly classified.

DISCUSSION

Our results confirm previous findings that botos indeed whistle (Wang *et al.* 1995, 2001, Diazgranados and Trujillo 2002) and suggest that boto whistles are frequency modulated with one of the widest frequency ranges ever reported in a toothed-whale species. Interestingly, the acoustic structure of these whistles is not only distinct from those of the sympatric *S. fluviatilis* but also appears quite distinct from other acoustically known boto populations in Colombia (*Inia geoffrensis humboldtiana*) (Diazgranados and Trujillo 2002) and Perú (*Inia geoffrensis geoffrensis*) (Wang *et al.* 1995a, 2001). However, the comparison between these studies is difficult due to differences in recording equipment as discussed below.

Between and within species variation

Boto whistles differ from tucuxi whistles in all their acoustical parameters. As shown in Figure 4, botos produced higher frequency whistles. These whistles are more limited in their contour diversity (95.8% of the whistles were downsweep) than tucuxi whistles (and those of most other dolphins). Several factors have been proposed to explain interspecific whistle variation including: morphological constraints (Wang *et al.* 1995a, Matthews *et al.* 1999), environment (Wang *et al.* 1995a), sociality (Podos *et al.* 2002), zoogeographical relationships (Steiner 1981), and phylogenetic relationships (Steiner 1981, Wang *et al.* 1995a).

Body size is the most important morphological factor believed to influence signal frequency in animals (Marquet and Taper 1998). Overall, the larger the animal the lower frequency sounds it tends to produce. This is because body size and the size of sound producing organs are often correlated (Fletcher 1992). Some authors (e.g., Wang *et al.* 1995a, Podos *et al.* 2002) have proposed a similar relationship between body size and maximum frequency. However, in the case of cetaceans a recent study showed that when accounting for phylogeny the proposed relationship between body size and maximum frequency disappears (May-Collado *et al.* 2007a). Thus the fact that botos (~2.6 m, 160 kg) can produce much higher frequency whistles than the smaller tucuxis (~1.52 m, 40 kg) is not counter to any general rule.

It is unlikely that whistle variation is explained by differences in habitat acoustic structure since both species live in very similar environmental conditions. Another proposed factor to explain interspecific whistle variation is zoogeographical relations. Steiner (1981) suggested “the degree of differences in the whistle vocalizations among [five dolphin] species closely followed predictions based on classic allopatric/sympatric relations among species”. This idea is congruent with the “species recognition hypothesis” (see Sætre *et al.* 1997) that states that animal vocal acoustic structure has evolved 'to' reduce hybridization. Unfortunately, there is very little quantitative information of the extent to which botos and tucuxis are allopatric and sympatric at both spatial and temporal scales to test this idea.

Botos and tucuxis are not closely related (e.g., Hamilton et al. 2001, May-Collado and Agnarsson 2006) which could largely explain their differences in whistle structure. However, there is recent evidence that social structure (or at least some components of sociality) could also explain part of this variation. For instance, differences in whistle contour and frequency and time parameters of the distantly related spinner and bottlenose dolphins (e.g., Hamilton *et al*. 2001, LeDuc *et al.* 1999, May-Collado and Agnarsson

2006) have been largely explained in terms of “group fluidity” [a component of sociality] (Barzúa-Durán 2004). Botos and tucuxis are not only more distantly related but also differ even more radically in their social structure. While botos appear to be solitary (Best and da Silva 1993) or at least live in small non-structured groups (where the strongest social bond appear to be limited to mother and calf) (e.g., Aliaga-Rossel 2002, McGuire and Winemiller 1998), *Sotalia* spp. lives in structured social groups (Monteiro-Filho 2000). Additionally, May-Collado *et al.* 2007b found that whistle complexity—a concept based on whistle mean number of inflection points—may be influenced by group size and social structure [two components of sociality]. More specifically, they found that simple whistles (mean number of inflection points equal or below one) were particularly concentrated in ‘solitary’ species while the phylogenetic distribution of complex whistles and social species largely overlap.

Although boto dolphins from the Yasuní River produced whistles with frequency parameters that appear to be far above (5.30 to 48.10 kHz) the values reported by Wang *et al.* (1995a, 2001) in botos from the Marañon and Tigre Rivers in Peru (0.22 to 5.16 kHz) and by Diazgranados and Trujillo (2002) in the Orinoco River (3 to 13 kHz) (Table 3) comparisons can not be done at this point. This is due in part to differences in the recording systems maximum frequency limitations (up to 25 kHz), to the lack of information on several standard acoustic parameters (Diazgranados and Trujillo (2002), and the uncertainty regarding the assignment of the low frequency whistles to boto dolphins (Wang *et al.* 1995a, 2001). Therefore, until we have full frequency range recordings from other botos populations, comparisons are difficult and speculative.

We limit this part of the discussion to the observed differences among ‘groups’ groups [note that several of the 'groups' consisted of only one individual] where with the exception for delta frequency, whistle acoustic parameters vary significantly across groups (Table 5). In most delphinids within species variation is primarily in duration and modulation (e.g., Wang *et al.* 1995b, Morisaka *et al.* 2005a-b, Barzúa-Dúran and Au 2002, 2004) rather than in frequency as observed in this boto population (also see Azevedo and Van Sluys 2005, Rossi-Santos and Podos 2006 for *Sotalia guianensis*). In part, this variation has been explained as product of adaptation to local ecological conditions (e.g., ambient noise, see Morisaka *et al.* 2005b). It is unlikely that the among group whistle differences observed in this boto population are explained by contrasting habitat acoustic characteristics alone, since recorded single animals and groups were in the same environment. Furthermore, age composition and behavioral states appear not to influence whistle variation either. However, our sample size is too small and geographically restricted to conclude age and behavior does not have some influence on boto dolphin whistles acoustic structure. In addition to these two factors, others such as genes, gender, and overall inter-individual variation, merit further study.

Behavior and Communication

Diazgranados and Trujillo (2002) reported that boto whistles were produced within groups that engaged in social and feeding activities. Half of the whistles produced by the botos in this study occurred during traveling activities, but when accounting for time of the encounter and number of individuals present, whistles production was higher during resting activities. In addition, whistles were produced by both solitary and grouped animals.

The closest neighbor maximum distance was found at approximately 0.15 to 1.5 km, suggesting these animals might be still in acoustic contact. Because of the behavioral context at which most whistles were emitted and the low whistle production, it is possible that whistles in boto dolphins may be used to keep distance between animals, rather than promote social interactions or cohesion among individuals as it occurs in delphinids (e.g., Jones and Sayigh 2002). Assuming cylindrical spreading loss and freshwater absorption at the mean maximum frequency, the boto whistles could propagate as far as 3.3 km before falling below the ambient noise although the actual range will be less depending on channel depth, bottom type, and vegetation (Quitana-Rizzo *et al.* 2006). Wang *et al.* (2006) assuming spherical spreading losses estimated that *Lipotes vexillifer* low frequency whistles (with dominant frequency 5.7 kHz) could propagate in a very calm environment up to 6.6 km, but possibly only 22-220 m considering the noisy conditions of the Yangtzee River. The Yasuní River is a very calm environment, unlike the Yangtzee River, it is protected and boat traffic is limited to park rangers and scientists.

During the period of this study botos produced whistles randomly and not in bouts as many delphinids species. Based on our data it appears that boto dolphins in Yasuní whistle rarely. Our sample size is too small not only to clearly associate these sounds with the same social contexts as in delphinids but also to determine how frequently botos and other riverine dolphin species generally whistle. Nevertheless, confirming the presence of whistles in botos and other freshwater toothed whales helps illuminate the evolutionary history of whistles, and their relation to sociality—a factor proposed to have shaped the complexity of toothed whale whistles (May-Collado *et al.* 2007b).

CONCLUDING REMARKS

This study confirms whistles in the solitary freshwater dolphin *Inia geoffrensis geoffrensis*. The frequency range of boto whistles we document is among the greatest ever reported in a cetacean species. The acoustic structure of these whistles in Ecuadorian botos differs from that of the sympatric *Sotalia fluviatilis* and apparently from conspecific populations from Perú and Colombia. Differences in the acoustic structure of boto and tucuxi whistles may be in large a product of their distant phylogenetic relationships and their different social structure. Although, our study suggests remarkable whistle variation between populations this may be largely a product of limited recording systems used by previous studies. Finally, although the use of whistles for communication purposes has been largely attributed to social dolphin species, it is possible that botos (even solitary animals) use them to communicate but in the context of keeping distances among animals rather than to promote group cohesion. We propose this based on two observations (1) whistles were produced when the animals were engaged in resting activities, and (2) based on the fact that solitary animals were potentially within acoustic range of each other (estimated maximum of 3.3 km). Finally, better understanding of whistle production in solitary freshwater species will further understanding of the evolutionary history of whistles and their proposed association with sociality.

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Table 3. Descriptive statistics of boto whistles with comparison to previously published data (in bold values for all 121 whistles and in parenthesis values for 70 whistles with frequency values below 25 kHz for comparison purposes).

	Min F (kHz)	*Max F (kHz)*	*Start F (kHz)*	*End F (kHz)*	*Delta F (kHz)*	*Peak F (kHz)*	*Duration (s)*
This Study							
Mean	**14.54** (12.59)	**24.71** (19.26)	**23.30** (18.49)	**15.48** (13.10)	**10.18** (6.71)	**18.62** (15.36)	**0.009** (0.010)
SD	**4.32** (3.96)	**8.37** (4.0)	**8.53** (4.10)	**5.70** (4.35)	**7.02** (2.47)	**6.61** (4.52)	**0.011** (0.014)
Range	**5.30-26.44**	**10.88-48.10**	**9.77-48.10**	**5.30-42.99**	**2.94-34.39**	**3.22-48.83**	**0.002-0.080**
	(5.30-21.37)	(10.88-24.89)	(9.77-24.89)	(5.30-24.62)	(2.99-16.52)	(6.35-22.95)	(0.002-0.080)
CV%	**29.7** (31.5)	**33.9** (20.8)	**36.1** (22.1)	**38.60** (33.3)	**68.9** (36.9)	**35.50** (29.5)	**128.2** (134.2)
Wang *et al.* (1995, 2001)*							
Mean	2.54	2.97	2.61	2.86	------------	------------	1.14
SD	0.76	0.84	0.75	0.77	------------	------------	1.01
Range	0.220-4.22	0.5-5.16	0.220-4.22	0.360-4.86	------------	------------	0.16-4.42
CV%	29.88	28.11	28.55	27.01	------------	------------	91.10
Diazgranados and Trujillo (2002)							
Mean	------------	------------	------------	------------	------------	------------	------------
SD	------------	------------	------------	------------	------------	------------	------------
Range	3	13	------------	------------	------------	------------	------------
CV%	------------	------------	------------	------------	------------	------------	------------

*Recording system with maximum frequency limited to 25 kHz

Table 4. Descriptive statistics for each behavioral class for a total of 121 whistles recorded in relation to their behavioral context (there were not significant differences for any of these parameters across behaviors).

Parameters	**Feeding** ***(n=32)***	**Resting** ***(n=21)***	**Slow Traveling** ***(n=68)***
Min F (kHz) *(mean±SD)* *Range* *CV%*	14.48±4.95 6.56-21.22 28.0	14.59±4.66 6.26-23.10 32.0	14.56±4.39 5.30-26.44 30.2
Max F (kHz) *(mean±SD)* *Range* *CV%*	25.25±9.28 11.83-43.68 36.8	22.84±6.97 12.76-41.72 30.5	25.03±8.36 10.88-48.06 33.4
Delta F (kHz) *(mean±SD)* *Range* *CV%*	10.84±7.84 3.82-28.24 72.3	8.25±6.48 2.99-30.35 78.6	10.47±6.77 2.94-34.40 64.7
Start F (kHz) *(mean±SD)* *Range* *CV%*	22.79±9.06 11.83-43.68 39.7	22.15±7.14 12.76-41.72 32.2	24.43±8.68 9.77-48.06 35.5
End F (kHz) *(mean±SD)* *Range* *CV%*	16.85±7.85 7.06-42.98 46.6	15.62±5..21 6.26-26.85 33.3	14.80±4.50 5.30-27.34 30.4
Peak F (kHz) *(mean±SD)* *Range* *CV%*	17.95±4.95 7.81-27.34 27.6	16.15±5.80 3.22-26.86 35.9	18.49±5.75 6.35-33.69 31.1
Duration (s) *(mean±SD)* *Range* *CV%*	0.006±0.007 0.002-0.039 111.5	0.008±0.008 0.002-0.039 103.4	0.010±0.014 0.002-0.080 129.4

Table 5. Whistle acoustic structure described for each recorded single animal and group.

Groups	Min F (kHz)	Max F (kHz)	Delta F (kHz)	Start F (kHz)	End F (kHz)	Peak F (kHz)	Duration (s)	# whistles	#Individuals present	Group Composition
G1 *Mean±SD*	17.20±2.48	30.23±8.28	13.04±7.62	29.63±9.27	17.80±2.60	23.43±4.56	0.006±0.007	6	1	Adult*
Range	13.90-20.04	19.71-38.60	3.62-23.27	16.10-38.60	13.9-20.04	17.58-27.34	0.002-0.019			
C.V.%	14.4	27.4	58.4	31.3	14.6	20.0	111.8			
G2 *Mean±SD*	14.44±4.18	23.68±8.93	9.24±7.56	23.44±9.13	14.53±4.01	17.32±4.69	0.005±0.003	23	3	Adults
Range	7.18-24.90	11.83-43.68	3.82-28.02	11.83-43.68	7.44-21.22	7.81-24.90	0.002-0.017			
C.V.%	27.1	37.7	81.8	38.9	27.6	27.1	76.0			
G3 *Mean±SD*	16.08±5.03	26.95±7.82	10.87±7.72	26.37±8.22	16.19±5.11	19.03±6.6.30	0.009±0.015	33	4	3 Adults
Range	5.30-26.44	12.58-48.10	2.94-34.39	9.77-48.07	5.30-27.34	3.22-27.83	0.002-0.080			1 calf**
C.V.%	31.1	29	71.0	31.2	31.6	33.1	156.9			
G4 *Mean±SD*	14.60±3.22	24.36±6.40	9.77±4.47	24.36±6.40	14.60±3.22	18.80±4.85	0.004±0.002	8	3	2 Adults
Range	7.43-17.68	12.07-33.14	4.64-18.14	12.07-33.14	7.43-17.68	9.76-24.41	0.002-0.007			1 Juvenile***
C.V.%	22.1	26.3	45.7	26.3	22.1	25.8	43.1			
G5 *Mean±SD*	14.53±3.72	24.39±9.84	9.84±7.89	23.80±10.17	14.66±3.76	17.94±6.35	0.008±0.009	12	3	2 Adults
Range	7.85-18.31	10.88-41.44	2.99-25.02	10.84-41.44	7.85-18.31	8.79-33.69	0.002-0.030			1 Juvenile
C.V.%	25.6	40.4	80.2	42.7	25.7	35.4	116.2			
G6 *Mean±SD*	8.92±3.48	16.20±4.07	7.28±1.07	16.03±4.15	8.92±3.48	11.28±3.52	0.026±0.014	9	1	Adult
Range	6.53-17.80	14.13-27.01	6.02-9.21	13.67-27.01	6.53-17.80	7.81-19.53	0.002-0.046			
C.V.%	39.0	25.1	14.8	25.9	39.0	31.2	54.4			
G7 *Mean±SD*	13.84±4.10	27.89±9.81	14.05±8.09	19.17±6.48	22.56±13.40	18.30±5.35	0.012±0.012	7	2	1Adult
Range	7.06-18.87	13.98-42.99	6.93-28.24	13.98-29.92	7.06-42.99	10.90-21.41	0.002-0.039			1calf
C.V.%	29.6	35.2	57.6	33.8	59.4	29.3	105.3			
G8 *Mean±SD*	13.83±2.11	21.83±2.36	8.0±2.44	20.51±2.87	14.93±2.22	18.42±2.58	0.010±0.011	7	2	Adults
Range	11.71-16.66	17.11-24.39	4.01-10.98	16.11-23.44	12.7-18.55	14.65-22.95	0.003-0.033			
C.V.%	15.3	10.8	30.6	14	14.9	14	111.9			
G9 *Mean±SD*	13.98±3.17	26.63±8.06	9.65±7.76	22.63±8.31	15.25±4.51	17.14±4.39	0.007±0.003	13	2	1 Adult
Range	9.12-19.60	17.11-41.72	3.45-30.35	16.11-41.72	9.12-26.85	11.23-26.86	0.002-0.012			1 calf
C.V.%	22.7	34.1	80.4	36.7	29.6	25.6	45.3			
G10	17.27	34.10	17.98	27.85	23.51	23.9320.51-	0.006	2	2	1Adult
Median±SD	15.53-19.01	28.02-40.18	14.78-21.17	15.53-40.18	19.01-28.02	27.34	0.004-0.008			1calf
Range	14.2	25.2	25.2	62.6	27.1	20.2	47.1			
C.V.%										
G11 *Mean±SD*	12.51	17.66	5.15	16.11	17.66	12.51	0.008	1	1	Adult
Range	--	--	--	--	--	--	--			
C.V.%	--	--	--	--	--	--	--			

*Adult is defined as full sized individuals

**Calf is defined as an individual that is less than half the adult's size

***Juvenile defined as an individual larger than a calf but not as big as an adult

FIG.3

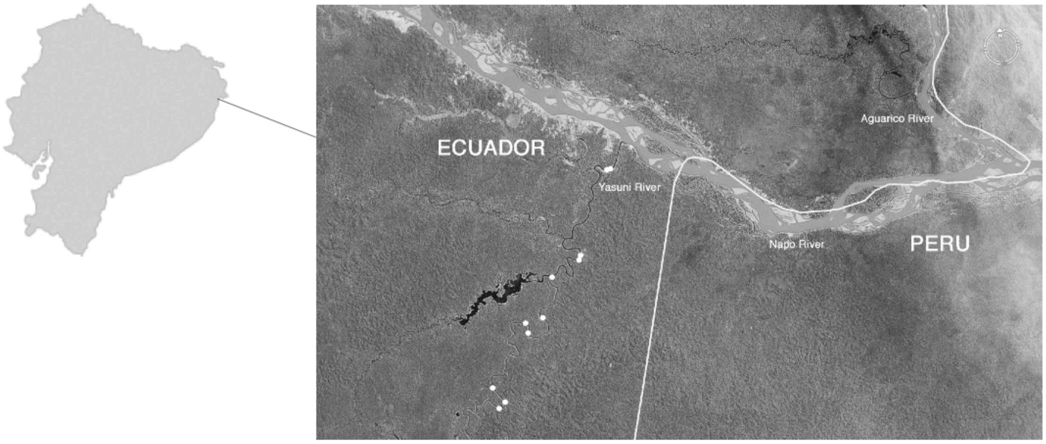
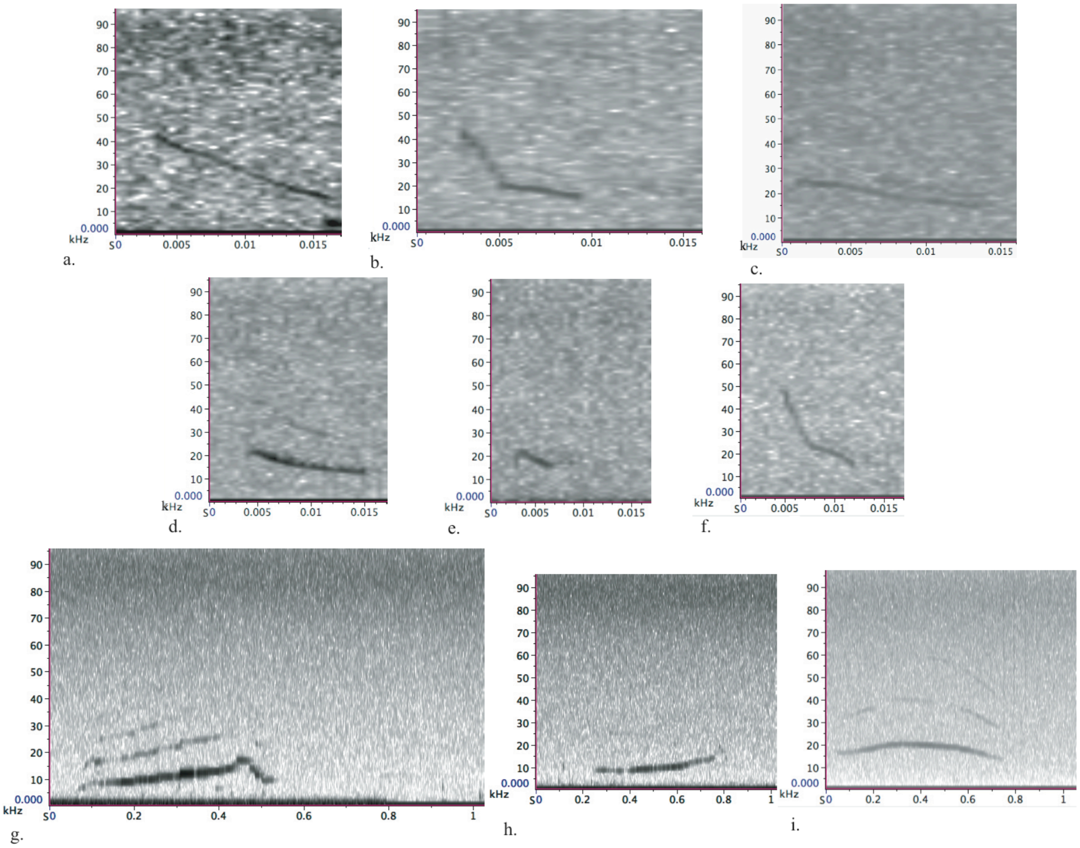


FIG. 4



90
80
70
60
50
40
30
20
10
0.000
kHz
S0
0.005
0.01
0.015
a.
b.
c.
d.
e.
f.
0.2
0.4
0.6
0.8
1
g.
h.
i.

FIG.5

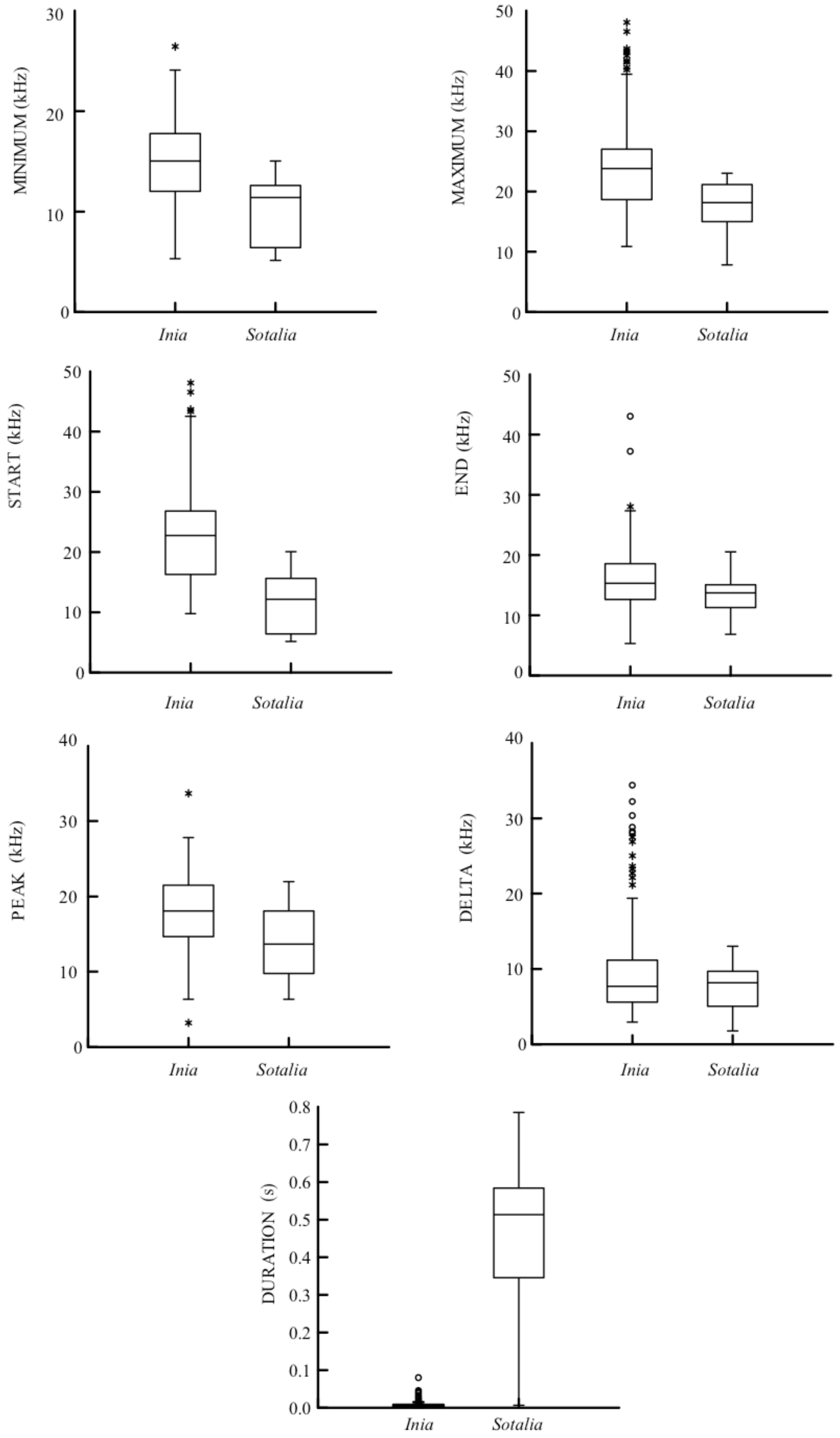
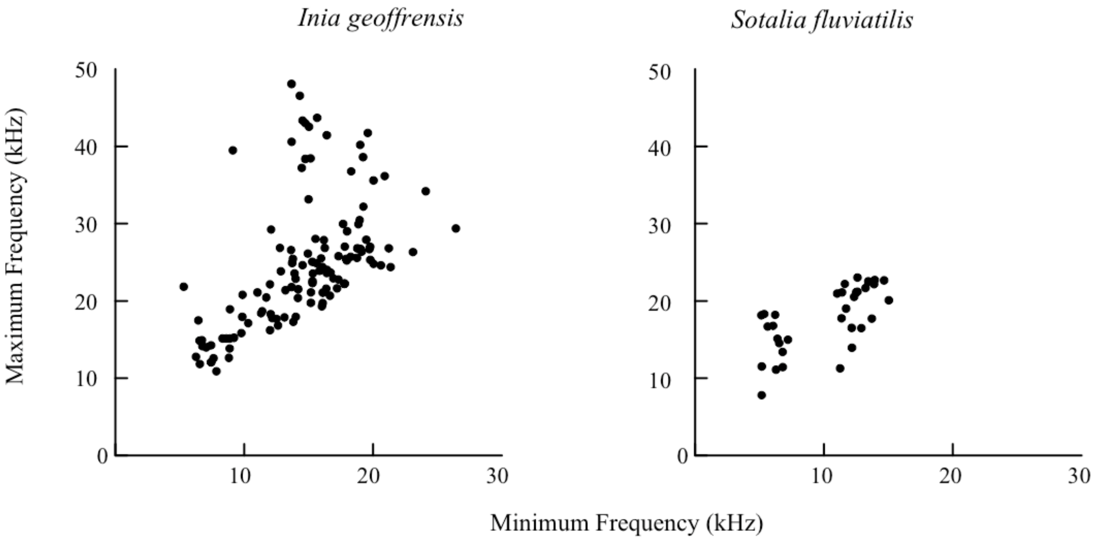

MINIMUM (kHz)
0
10
20
30
MAXIMUM (kHz)
0
10
20
30
40
50
START (kHz)
0
10
20
30
40
50
END (kHz)
0
10
20
30
40
50
PEAK (kHz)
0
10
20
30
40
DELTA (kHz)
0
10
20
30
40
DURATION (s)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
Inia
Sotalia

FIG.6



Inia geoffrensis
Sotalia fluviatilis
Maximum Frequency (kHz)
Minimum Frequency (kHz)
0
10
20
30
40
50
10
20
30

CHAPTER IV

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

LAURA J. MAY-COLLADO[1,2], INGI AGNARSSON[3,4], DOUGLAS WARTZOK[1]

[1]Florida International University, Department of Biological Sciences, 11200 SW 8th Street, Miami Florida 33199

[2]Universidad de Costa Rica, Escuela de Biología, Apto. 2060 San Pedro, Costa Rica

[3]The University of British Columbia, Departments of Zoology and Botany, 3529-6270 University Blvd., Vancouver, BC., Canada V6T 1Z4.

[4]Systematic Biology-Entomology, E-530, Smithsonian Institution, NHB-105, P.O. Box 37012, Washington, DC 20013-7012, USA

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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, while 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 while alternative hypotheses are required to explain variation in maximum frequency.

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

INTRODUCTION

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) while 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*, Helweg *et al.* 1992, Tyack and Whitehead 1983), 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., Karlsen *et al.* 2002, Shapiro 2006, Sjare & Smith 1986, Watkins et al. 1970), most delphinids (e.g., Oswald *et al.* 2003, Rendell *et al.* 1999, Steiner 1981, Wang *et al.* 1995a), some ziphiids (e.g., Dawson and Barlow 1998, Manghi *et al.* 1999, Rogers and Brown 1999), and river dolphin species (Jing *et al.* 1981, May-Collado and Wartzok 2007, Wang *et al.* 1995a, 1999, 2001, 2006). Whistles are primarily used in social contexts such as group cohesion, group coordination during feeding, and individual identifiers (e.g., Acevedo-Gutiérrez and Stienessen 2004, Caldwell and Caldwell 1965, Caldwell *et al.* 1973, Dreher and Evans 1964, Fripp *et al.* 2005, Herzing 2000, Janik

2000, Janik *et al.*1994, Pivari and Rosso 2005, Tyack 1999, 2000, Watwood *et al.* 2004). Delphinid whistles vary across populations and species: acoustic parameters such as duration and modulation tend to vary intraspecifically (e.g., Barzúa-Durán and Au 2002, 2004, Morisaka *et al.* 2005a, Wang *et al.* 1995b) whereas frequency components vary across species (e.g., Matthews *et al.* 1999, Oswald *et al.* 2003, Rendell *et al.* 1999, Steiner 1981, Wang *et al.* 1995a). Intraspecific variation may result from adaptation to local ecological conditions or geographical isolation and genetic divergence between groups or populations (e.g., Azevedo and Van Sluys 2005, Barzúa-Durán 2004, Barzúa-Durán and Au 2004, Morisaka *et al.* 2005b, Rossi-Santos and Podos 2006, Wang *et al.* 1995b). 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 (Matthews *et al.* 1999, Podos *et al.* 2002, Wang *et al.* 1995a,), and phylogenetic relationships (e.g., Steiner 1981, Matthews *et al.* 1999, Wang *et al.* 1995a).

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., Matthews *et al.* 1999, Podos *et al.* 2002, Wang *et al.* 1995a). Using standard statistical methods these studies found a strong negative relationship between body size and maximum frequency (Matthews *et al.* 1999, Podos *et al.* 2002, Wang *et al.* 1995a) 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 offer stronger support to the hypothesis of correlation. A series of methods have been developed to account for known dependencies among related species using phylogenies (reviewed by Harvey and Pagel 1991, Martins *et al.* 2002).

The goal of this study is to reevaluate the hypotheses that variation in maximum and/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.

MATERIALS AND 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 (published literature, personal communications, and L. May-Collado unpublished data) (see Table 1).

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., McDonald *et al.* 2005, Mellinger and Clark 2003, Watkins *et al.* 2004) but also greatly modulated (e.g., *Tursiops truncatus*, Wang *et al*. 1995b, *Delphinapterus leucas*, Karlsen *et al.* 2002; *Lagenorhynchus albirostris*, Rasmussen and Miller 2002), show variable duration (e.g., 0.01 to 1.3 sec 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, since 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 delphinid 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 *et al.* 2005) or toothed whales (see "graded-vocalizations" in Murray *et al.* 1998).

While 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). Since 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 a 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 were 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 10 species that are invariable for the characters under study does not constitute 10 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 (PIC) developed by Felsenstein (1985). To estimate Felseinstein'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 dataset (where some of the taxa lack acoustic data) we also ran analyses on pruned datasets 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). While we prefer the pruned analyses, it seems appropriate to report the values based on both types of analyses; the best estimates may lay 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* (grey whale). The fin whale is sister to the humpback whale as also found by Hatch *et al.* (2006) and Sasaki *et al*. (2006) while 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 4 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 = .135 for absolute, R^2 = .101 for mean). The correlation with mean minimum frequency was also significant within baleen whales, but insignificant within toothed whales, while absolute minimum was not significantly correlated with body mass within each group (marginally insignificant in toothed whales p = .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 ($R^2 = .182$ with length, $R^2 = .161$ 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).

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; Nikaido *et al*. 2007; Sasaki *et al.* 2006) and therefore provides an appropriate phylogenetic hypothesis 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.*'s 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 versus 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 (Matthews *et al.* 1999, Podos *et al.* 2002, Wang *et al.* 1995a) 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*, see May-Collado *et al.* submitted), that single observation does not imply 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 (Figs 2-3, Tables 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 limitations 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., Bennet-Clark 1998, Gerhardt 1994, Hauser 1993, Matthews *et al.*1999, Palacios and Tubaro 2000, Seddon 2005, Tubaro and Mahler 1998, Wang *et al.* 1995a, Wiley 1991). However, as more comparative studies consider phylogenetic hypotheses, this relationship in some cases no longer holds (e.g., Farnsworth and Lovette 2005, Laiolo and Rolando 2003). 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., Bertelli and Tubaro 2002, Couldridge and van Staaden 2004, Farnsworth and Lovette 2005, Gerhardt 1994, Laiolo and Rolando 2003, Seddon 2005, Wiley and Richards 1998). This may also be the case in the evolution of cetacean tonal signal frequency as has been suggested by some authors (e.g., Morisaka *et al.* 2005b, Wang *et al.* 1995a). 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. submitted).

CONCLUDING REMARKS

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 (Matthews *et al.* 1999, and Podos *et al.* 2002, Wang *et al.* 1995a). 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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Table 6. Review of published data on Cetacean body size and standard tonal sound frequency variables.

Species	**Maximum Body Size**		**References**	**Whistle Frequency Variables (kHz)**					**References**
	m	**Kg**		**Max**	**MMx**	**Center**	**Min**	**MMin**	
SubOrder Mysticeti									
Balaena glacialis	17.0	80,000	Bannister 2002; Reidenberg & Laitman 2002	11.23	3.14	?	0.02	0.05	Parks & Tyack 2005
B. mysticetus	19.8	100,000	Bannister 2002; Rugh & Shelden 2002	**2**	0.165		0.09	**0.02**	Ljungblad *et al.* 1982
				1	**0.3**		**0.02**	0.05	Clark & Johnson 1984
						0.175			Matthews *et al.* 1999
Balaenoptera bonaerensis	10.7	13,500	Bannister 2002; Reidenberg & Laitman 2002	?	?	?	?	?	?
B. borealis	18.3	25,000	Reidenberg & Laitman 2002	**3.5**	?		1.5	?	Knowlton *et al.* 1991
						2.5			Matthews *et al.* 1999
				1			~**0.1**		McDonald *et al.* 2005
B. edeni	15.6	25,000	Reidenberg & Laitman 2002	**0.245**			0.07		Cummings *et al.* 1986
				0.180			0.09		Edds 1993
				0.079			**0.0207**		Heimlich *et al.* 2005
						0.128			Matthews *et al.* 1999
B. musculus	31	200,000	Reidenberg & Laitman 2002	0.0185			0.0157		Mellinger & Clark 2003
				0.0202			0.0182		Stafford *et al.* 2001
				0.122			-		Alling 2003 pers. comm. to Mellinger & Clark 2003
							0.011		Ljungblad *et al.* 1997
				0.052			0.050		Watkins *et al.* 2004
				0.0277			0.0189		Sirovic *et al.* 2004
					0.0189			0.0172	Stafford *et al.* 1994
						0.020			Matthews *et al.* 1999
				0.242	**0.0883**		0.0143	**0.0166**	Berchok et al. 2006
B. physalus	27	90,000	Reidenberg & Laitman 2002	**0.118**			**0.010**		Edds 1988
					0.023			**0.018**	Watkins 1987
				0.058	**0.042**		0.017	0.020	Thompson & Friedl 1982
						0.062			Matthews *et al.* 1999
Eschrichtius robustus	15.2	35,000	Jones & Swartz 2002	**0.2**			**0.02**		Cummings *et al.* 1968
				0.2			0.1		Fish *et al.* 1974
					0.3			0.25	Dahlheim *et al.* 1984
						0.150			Matthews *et al.* 1999
Megaptera novaeangliae	19.0	48,000	Reidenberg & Laitman 2002	4	1.315		0.25	0.925	Hafner *et al.* 1979

						1.108			Matthews *et al*. 1999
Capera marginata	6.45	3,500	Bannister 2002; Reidenberg & Laitman 2002	0.135	?	0.07	0.06	?	Dawbin & Cato 1992 Matthews *et al*. 1999
SubOrder Odontoceti									
Kogiidae									
Kogia breviceps	3.7	400	Reidenberg & Laitman 2002	?	?	?	?	?	
K. simus (sima)	2.7	210	Reidenberg & Laitman 2002	?	?	?	?	?	
Physeteridae									
Physeter macrocephalus	20.5	57,000	Reidenberg & Laitman 2002	n/a	n/a	n/a	n/a	n/a	
Ziphiidae									
Berardius bairdii (B. anurxii)	12.8	11,000	Reidenberg & Laitman 2002	8.0	?	6.0	4	?	Dawson & Barlow 1998 Matthews *et al*. 1999,
Hyperoodon ampullatus	9.8	?	Reidenberg & Laitman 2002	n/a	n/a	n/a	n/a	n/a	
H. planifrons	7.45	?	Reidenberg & Laitman 2002	?	?	?	?	?	
Mesoplodon bidens	5.5	?	Pitman 2002a; Reidenberg & Laitman 2002	?	?	?	?	?	
M. densirostris	4.73	1,033	Pitman 2002a; Reidenberg & Laitman 2002	?	?	?	?	?	
Ziphius cavirostris	7.5	3,000	Reidenberg & Laitman 2002	?	?	?	?	?	
Tasmacetus shepherdi	7.0	?	Mead 2002	?	?	?	?	?	
Indopacetus pacificus	8.0	?	Pitman 2002b	?	?	?	?	?	
Platanistidae									
Platanista gangetica	2.5	85	Reidenberg & Laitman 2002	?	?	?	?	?	
Iniidae									
Inia geoffrensis	2.6	160	Da Silva 2002; Reidenberg & Laitman 2002	**48.10** 5.16 13	**24.71** 2.97	2.75	5.03 **0.22** 3	15.06 **2.54**	May-Collado & Wartzok 2007 Matthews *et al*. 1999, Wang *et al*. 1995a, 2001 Diazgranados & Trujillo 2002
Lipotidae									
Lipotes vexillifer	2.53	160	Kaiya 2002; Reidenberg & Laitman 2002	4.5 **4.6**	5.84 **6.1**	6.0	3.8 3.8	4.975 **4.9**	Matthews *et al*. 1999, Wang *et al*. 1999 Wang *et al*. 2006
Pontoporidae									
Pontoporia blainvillei	1.77	53	Crespo 2002	?	?	?	?	?	
Super Family Delphonidea									
Phocoenidae									
*Australophocaena dioptrica**	2.4	115	Reidenberg & Laitman 2002; Goodall 2002a	n/a	n/a	n/a	n/a	n/a	
Phocoena phocoena	2.0	90	Bjøge *et al*. 2002; Reidenberg	n/a	n/a	n/a	n/a	n/a	

			& Laitman 2002						
P. sinus	1.4	?	Rojas-Bracho & Jaramillo-Legorreta 2002	n/a	n/a	n/a	n/a	n/a	
P. spinipinnis	2.0	?	Reyes 2002	n/a	n/a	n/a	n/a	n/a	
Phocoenoides dalli	2.39	200	Jefferson 2002a	n/a	n/a	n/a	n/a	n/a	
Neophocaena phocaenoides	1.9	100	Reidenberg & Laitman 2002; Amano 2002	n/a	n/a	n/a	n/a	n/a	
Monodontidae									
Monodon monocerus	4.7	1600	Heide-Jørgensen 2002; Reidenberg & Laitman 2002	**18**			**0.3**		Ford & Fisher 1978,
				10			5		Watkins *et al.*1970;
						5.2			Matthews *et al.* 1999
				8.84	7.18		0.360	0.718	Shapiro 2006
Delphinapterus leucas	5.5	1500	O'Corry-Crowe 2002; Reidenberg & Laitman 2002			3.89			Matthews *et al.* 1999,
				19.6	6.8		**0.2**	3.8	Karlsen *et al.* 2002;
				15.8	4.33		0.4	3.38	Sjare & Smith 1986
					11.65			**1.99**	Belikov & Bel'kovitch 2001
Delphinidae									
Cephalorhynchus commersonii	1.75	86	Dawson 2002; Reidenberg & Laitman 2002	n/a	n/a	n/a	n/a	n/a	
C. eutropia	1.67	63	Dawson 2002	n/a	n/a	n/a	n/a	n/a	
C. hectori	1.8	60	Reidenberg & Laitman 2002	n/a	n/a	n/a	n/a	n/a	
C. heavisidii	1.74	75	Dawson 2002	n/a	n/a	n/a	n/a	n/a	
Lagenorhynchus australis	2.18	115	Goodall 2002b	n/a	n/a	n/a	n/a	n/a	
L.cruciger	1.87	88	Goodall 2002c	?	?	?	?	?	
L. obliquidens	2.5	181	Van Waerebeek & Würsig 2002; Reidenberg & Laitman 2002	?	?	?	?	?	
L. obscurus	2.1	80	Van Waerebeek & Würsig 2002; Reidenberg & Laitman 2002	27.3	**16.49**		1.04	**8.11**	Wang *et al.* 1995a
						12.4			Matthews *et al.* 1999
					13.22			8.15	Yin 1999
L. acutus	2.7	230	Cipriano 2002; Reidenberg & Laitman 2002	?	12.14		?	8.21	Steiner 1981
						10.37			Matthews *et al.* 1999
Lissodelphins borealis	3.1	116	Reidenberg & Laitman 2002; Lipsky 2002	?	?	?	?	?	
L. peronii	3.0	116	Lipsky 2002	?	?	?	?	?	
Delphinus delphis	2.35	200	Perrin 2002a	19.8	11.65		4.8	**6.42**	Moore & Ridgway 1995
						8.81			Matthews *et al.* 1999,
					13.6			7.4	Oswald *et al.* 2003
D. capensis	2.35	235	Perrin 2002a	?	15.5	?	?	7.7	Oswald *et al.* 2003
Stenella attenuata	2.57	119	Perrin 2002b; Reidenberg &	21.4	15.72		3.13	8.73	Wang *et al.* 1995a

			Laitman 2002			12.54			Matthews *et al.* 1999,
					18.7			**8.2**	Oswald *et al.* 2003
S. clymene	2.0	80	Jefferson 2002b, Jefferson & Curry 2003	**19.2**	?		?	**6.33**	Watkins & Wartzok 1985
				13.62				9.25	Mullin *et al.* 1994
						11.66			Matthews *et al.* 1999
S. frontalis	2.3	143	Perrin 2002c; Reidenberg & Laitman 2002	19.8	16.04		5	7.91	Wang *et al.* 1995a
						11.62			Matthews *et al.* 1999
S. coeruleoalba	2.4	156	Reidenberg & Laitman 2002	22.99	11.53	9.07	1.1	**6.84**	Matthews *et al.* 1999,
					14.8			8.1	Oswald *et al.* 2003
S. longirostris	2.16	75	Perrin 2002d; Reidenberg & Laitman 2002	22.5	15.2		3.91	9.03	Wang *et al.* 1995a
						12.22			Matthews *et al.* 1999;
					13.7			9.1	Oswald *et al.* 2003;
				24	16.5		**0.85**	9.99	Barzua-Duran & Au 2002,
				25.25	**17.56**			9.66	Barzua-Duran & Au 2004
				23.04	16.8		4	10.19	Driscoll 1995
					14.32			8.76	Steiger 1981
Tursiops truncatus	4.0	650	Reidenberg & Laitman 2002;	**41**					Boisseau 2005
						8.09			Matthews *et al.* 1999; Oswald
					17.2			7.4	*et al.* 2003;
				21.6	11.35/11.95		1.86/**0.94**	**5.46**	Wang *et al.* 1995a,b;
					16.24			7.33	Steiner 1981
Lagenodelphis hosei	2.65	200	Dolar 2002; Reidenberg & Laitman 2002			12.82			Matthews *et al.* 1999;
				24.0	**16.9**		4.3	9.36	Watkins *et al.* 1994
					16.56			11.949	Oswald *et al.* submitted
				13.4				**7.64**	Leatherwood *et al.* 1993
Sousa chinensis	3	284	Ross 2002; Reidenberg & Laitman 2002	**22**	16.3	?	**0.9**	4.5	Van Parijs & Corkeron
							3		2001;
				20			1.2		Zbinden *et al.* 1977;
									Schultz & Corkeron 1994
*Sotalia fluviatilis***	2.20	40	Flores 2002			12.68			Matthews *et al.* 1999;
					19.95		1.34	**7.21**	Azevedo & van Sluys 2005;
				23.9	15.41		3.65	10.2	Wang *et al.* 1995a, 2001;
				38.25	**21.32**		2.714	13.14	May-Collado & Wartzok unpublished.
				18	13		**0.5**	7.6	Azevedo & Simao 2002;
				17.49	13.312		1.031	10.521	Erber & Simao 2004
					15.65			9.18	Podos *et al.* 2002
Steno bredanensis	2.65	155	Jefferson 2002c; Miyasaki & Perrin 1994	7.0			4		Busnell & Dziedzic 1968
						5.5			Matthews *et al.* 1999;
					9.1			6.03	Oswald *et al.* 2003;
Feresa attenuata	2.7	225	Reidenberg & Laitman 2002	?	?	?	?	?	

Globicephala macrorhynchus	7.2	3950	Reidenberg & Laitman 2002			7.87			Matthews *et al.* 1999;
				23.6	**10.87**		0.24	6.25	Rendell *et al.* 1999;
					6.1			**3.6**	Oswald *et al.* 2003
G. melas	6.3	1750	Reidenberg & Laitman 2002			4.48			Matthews *et al.* 1999;
				21.2	**8.86**		0.32	3.48	Rendell *et al.* 1999;
					4.716			**2.82**	Steiner 1981
Grampus griseus	4.3	500	Reidenberg & Laitman 2002			11.3			Matthews *et al.* 1999;
					20			**3.9**	Corkeron & Van Parijs 2001;
				23.8	13.44		1.90	8.83	Rendell *et al.* 1999
Peponocephala electra	2.75	275	Perryman 2002			12.75			Matthews *et al.* 1999,
					12.14			8.381	Oswald *et al.* submitted,
				24.5			5.5		Watkins *et al.* 1997
Pseudorca crassidens	6	2200	Baird 2002; Reidenberg & Laitman 2002			6.82			Matthews *et al.* 1999;
				18.1	**8.29**		1.87	5.43	Rendell *et al.* 1999;
					6.1			**4.7**	Oswald *et al.* 2003
*Orcaella brevirostris***	2.75	150	Reidenberg & Laitman 2002	6.0	4.2	?	1.1	3.2	Van Parijs *et al.* 2000
Orcinus orca	9.75	10,500	Reidenberg & Laitman 2002	**18**				**1.5**	Ford 1989;
					6.61			4.27	Dahleim & Awbrey 1982;
						5.0			Matthews *et al.* 1999
				8.9			**0.05**		Steiner *et al.* 1979
				16.7	9.9		2.4	5.4	Thomsem *et al.* 2001
					12.64			3.36	Riesch *et al.* 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)

Table 7. 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 et al. 1995 *Delphinids + Inia* R-square d.f. p-value	79%, 97% (excluding *Inia*) 9 <0.05**	---------	---------	---------	---------
Matthews et al. 1999 *Toothed-whales* R-square d.f. p-value	68% (uwtd.), 76% (wtd.) 18,16 <0.001, <0.001**	---------	86% (uwtd.), 93% (wtd.) 18,16 <0.001, <0.001**	---------	69% (uwtd.), 84% (wtd.) 25,14 <0.001, <0.001**
Matthews et al. 1999 *Baleen-whales* R-square d.f. p-value	---------	---------	---------	---------	64% (uwtd.) 9 0.003**
Podos et al. 2002 *Delphinids+Inia* R-square d.f. p-value	85.1% 16 <0.05**	---------	---------	---------	---------
This study Body Length *Cetacean-Tonal Sounds* R-square d.f. p-value	**0.0963 %** (0.0406%) 32 **0.413** (0.455)	**0.18%** (0.0732%) 28 **0.410** (0.443)	**26.3%** (22.8%) 32 **0.001** (0.002)**	**12.8%** (10.2%) 29 **0.024** (0.040)**	**4.2%** (3.5%) 28 **0.136** (0.160)
Toothed-Whales-Whistle R-square d.f. p-value	**2.2%** (1.45%) 23 **0.241** (0.283)	**3.9%** (4.5%) 22 **0.174** (0.160)	**27.7%** (23%) 23 **0.003** (0.008)**	**6.2%** (5.7%) 23 **0.116** (0.125)	**18.2%** (14.1%) 20 **0.023** (0.042**)
Baleen-whales R-square d.f. p-value	**0.052%** (0.37%) 7 **0.476** (0.437)	**33.3%** (14.2%) **(!)** 4 **0.11** (0.230)	**10.2%** (7.8%) 7 **0.201** (0.233)	**66.2%** (80.3%) **(!)** 4 **0.024** (0.007)**	**0.0028** (0.496%) 6 **0.495** (0.434)
This study Body Mass *Cetacean-Tonal Sounds* R-square d.f. p-value	**0.00427%** (0.00463%) 32 **0.485** (0.485)	**0.520%** (0.144%) 28 **0.452** (0.421)	**13.5%** (12.06%) 32 **0.016** (0.022)**	**10.1%** (8.2%) 29 **0.040** **(0.058)	**7.4%** (6.04%) 28 **0.074** (0.095)
Toothed-Whales-Whistle R-square d.f. p-value	**1.04%** (0.52%) 23 **0.313** (0.365)	**3.60%** (4.10%) 22 **0.186** (0.170)	**11.1%** (9.3%) 23 **0.052** (0.068)	**5.2%** (4.9%) 23 **0.137** (0.142)	**16.1%** (12.2%) 20 **0.033****(0.055)
Baleen-whales R-square d.f. p-value	**0.0107** (0.21%) 7 **0.489** (0.452)	**24.7%** (3.2%) (!) 4 **0.158** (0.367)	**17.4%** (16.0%) 7 **0.130** (0.142)	**65.5%** (49.0%) (!) 4 **0.025** **(0.059)	**3.5%** (2.10%) 6 **0.326** (0.366)

** Significant results (based on the level of significance of p ≤0.05)

(!) very small number of contrasts

FIG. 7

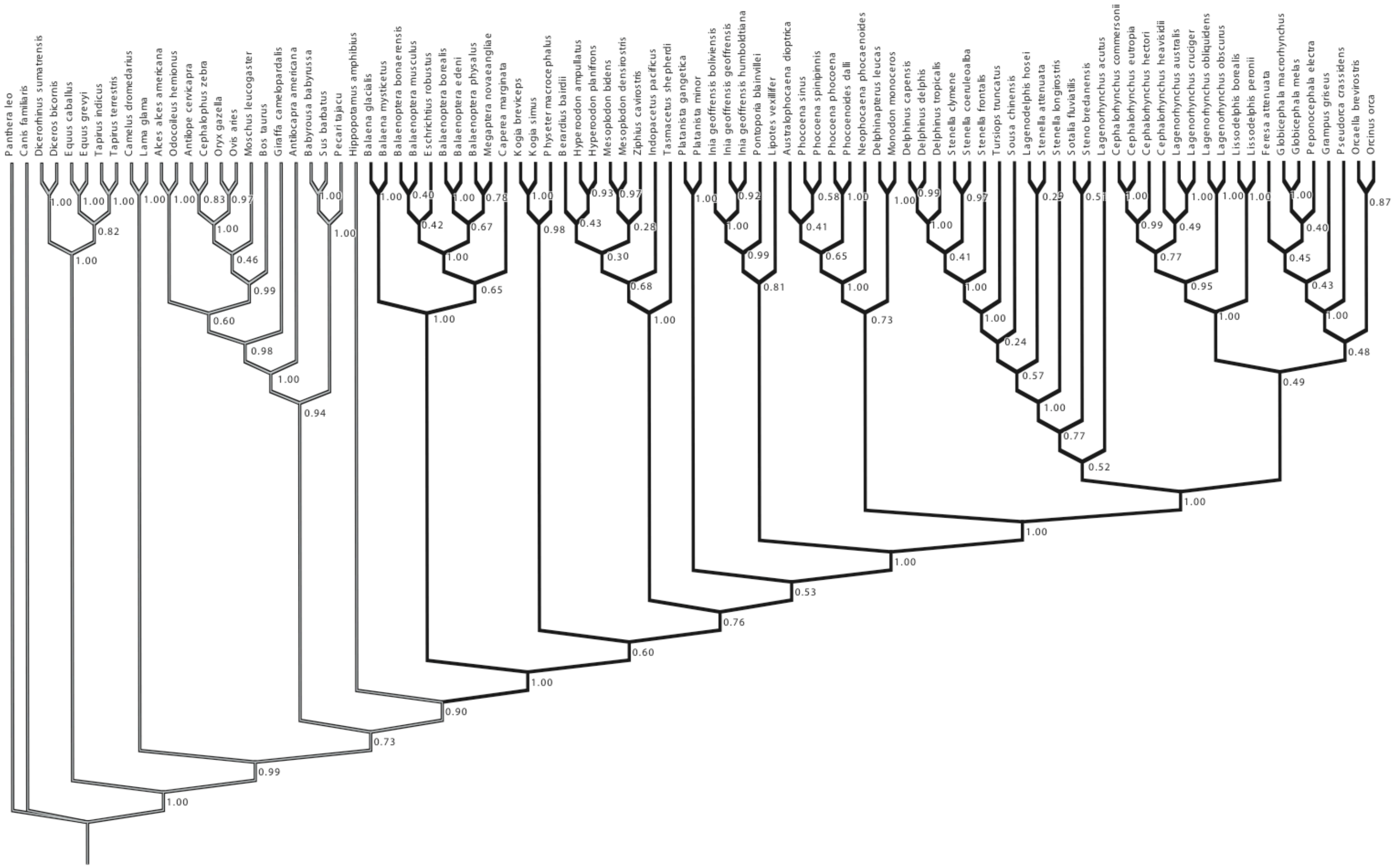

Panthera leo
Canis familiaris
Dicerorhinus sumatrensis
Diceros bicornis
Equus caballus
Equus grevyi
Tapirus indicus
Tapirus terrestris
Camelus dromedarius
Lama glama
Alces alces americana
Odocoileus hemionus
Antilope cervicapra
Cephalophus zebra
Oryx gazella
Ovis aries
Moschus leucogaster
Bos taurus
Giraffa camelopardalis
Antilocapra americana
Babyrousa babyrussa
Sus barbatus
Pecari tajacu
Hippopotamus amphibius
Balaena glacialis
Balaena mysticetus
Balaenoptera bonaerensis
Balaenoptera musculus
Eschrichtius robustus
Balaenoptera borealis
Balaenoptera edeni
Balaenoptera physalus
Megaptera novaeangliae
Caperea marginata
Kogia breviceps
Kogia simus
Physeter macrocephalus
Berardius bairdii
Hyperoodon ampullatus
Hyperoodon planifrons
Mesoplodon bidens
Mesoplodon densirostris
Ziphius cavirostris
Indopacetus pacificus
Tasmacetus shepherdi
Platanista gangetica
Platanista minor
Inia geoffrensis boliviensis
Inia geoffrensis geoffrensis
Inia geoffrensis humboldtiana
Pontoporia blainvillei
Lipotes vexillifer
Australophocaena dioptrica
Phocoena sinus
Phocoena spinipinnis
Phocoena phocoena
Phocoenoides dalli
Neophocaena phocaenoides
Delphinapterus leucas
Monodon monoceros
Delphinus capensis
Delphinus delphis
Delphinus tropicalis
Stenella clymene
Stenella coeruleoalba
Stenella frontalis
Tursiops truncatus
Sousa chinensis
Lagenodelphis hosei
Stenella attenuata
Stenella longirostris
Sotalia fluviatilis
Steno bredanensis
Lagenorhynchus acutus
Cephalorhynchus commersonii
Cephalorhynchus eutropia
Cephalorhynchus hectori
Cephalorhynchus heavisidii
Lagenorhynchus australis
Lagenorhynchus cruciger
Lagenorhynchus obliquidens
Lagenorhynchus obscurus
Lissodelphis borealis
Lissodelphis peronii
Feresa attenuata
Globicephala macrorhynchus
Globicephala melas
Peponocephala electra
Grampus griseus
Pseudorca crassidens
Orcaella brevirostris
Orcinus orca
1.00
1.00
0.82
1.00
1.00
1.00
1.00
0.83
0.97
1.00
0.46
0.99
0.60
0.98
1.00
0.94
1.00
1.00
1.00
0.40
0.42
1.00
1.00
0.78
0.67
0.65
1.00
1.00
0.98
0.93
0.43
0.30
0.97
0.28
0.68
1.00
1.00
1.00
0.92
0.99
0.81
0.41
0.58
0.65
1.00
1.00
0.73
1.00
0.99
1.00
0.41
0.97
1.00
1.00
0.24
0.29
0.57
1.00
0.51
0.77
0.52
1.00
0.99
0.77
0.49
1.00
0.95
1.00
1.00
1.00
1.00
0.45
0.40
0.43
1.00
0.48
0.49
0.87
1.00
1.00
1.00
0.53
0.76
0.60
1.00
0.90
0.73
0.99
1.00

FIG. 8

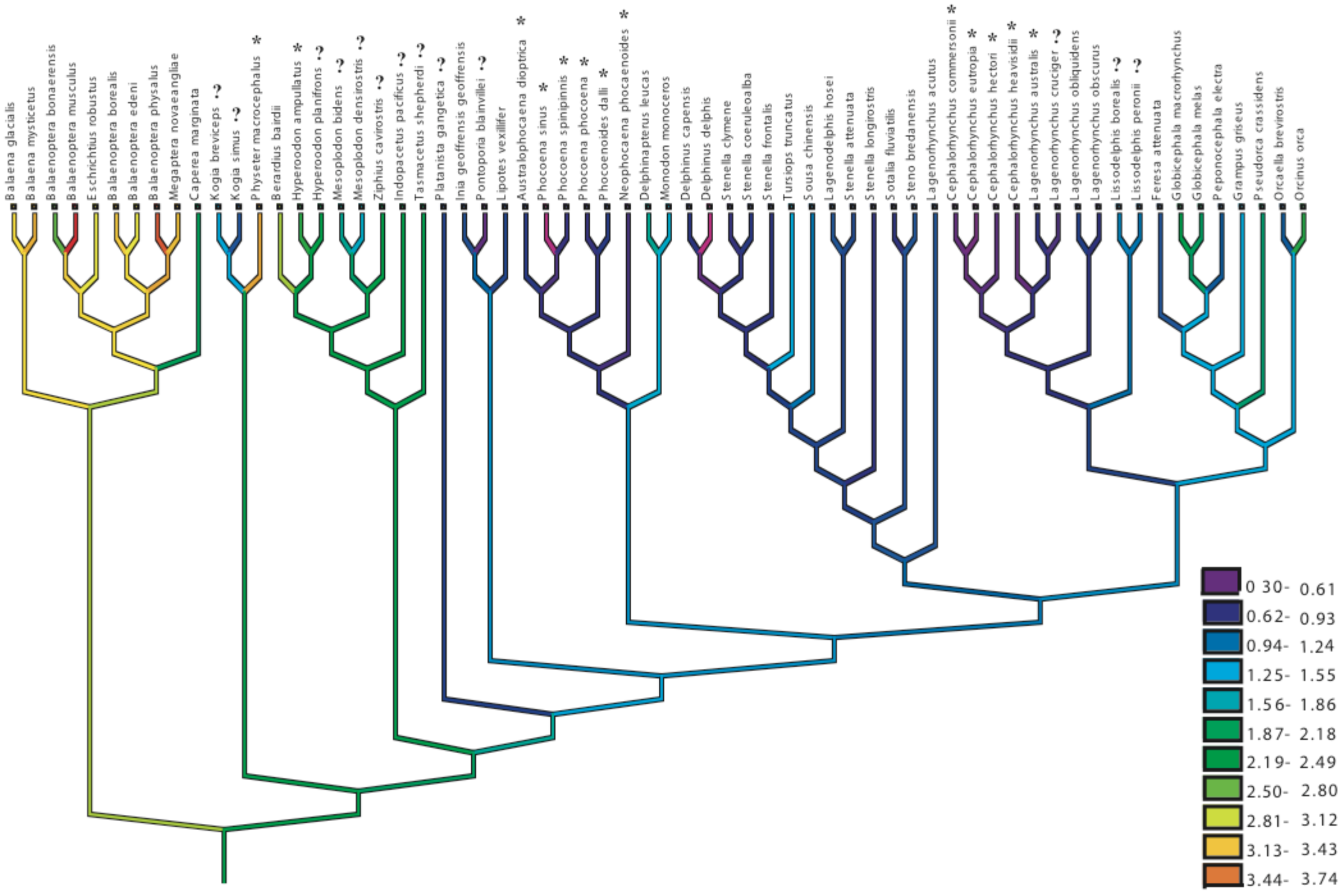
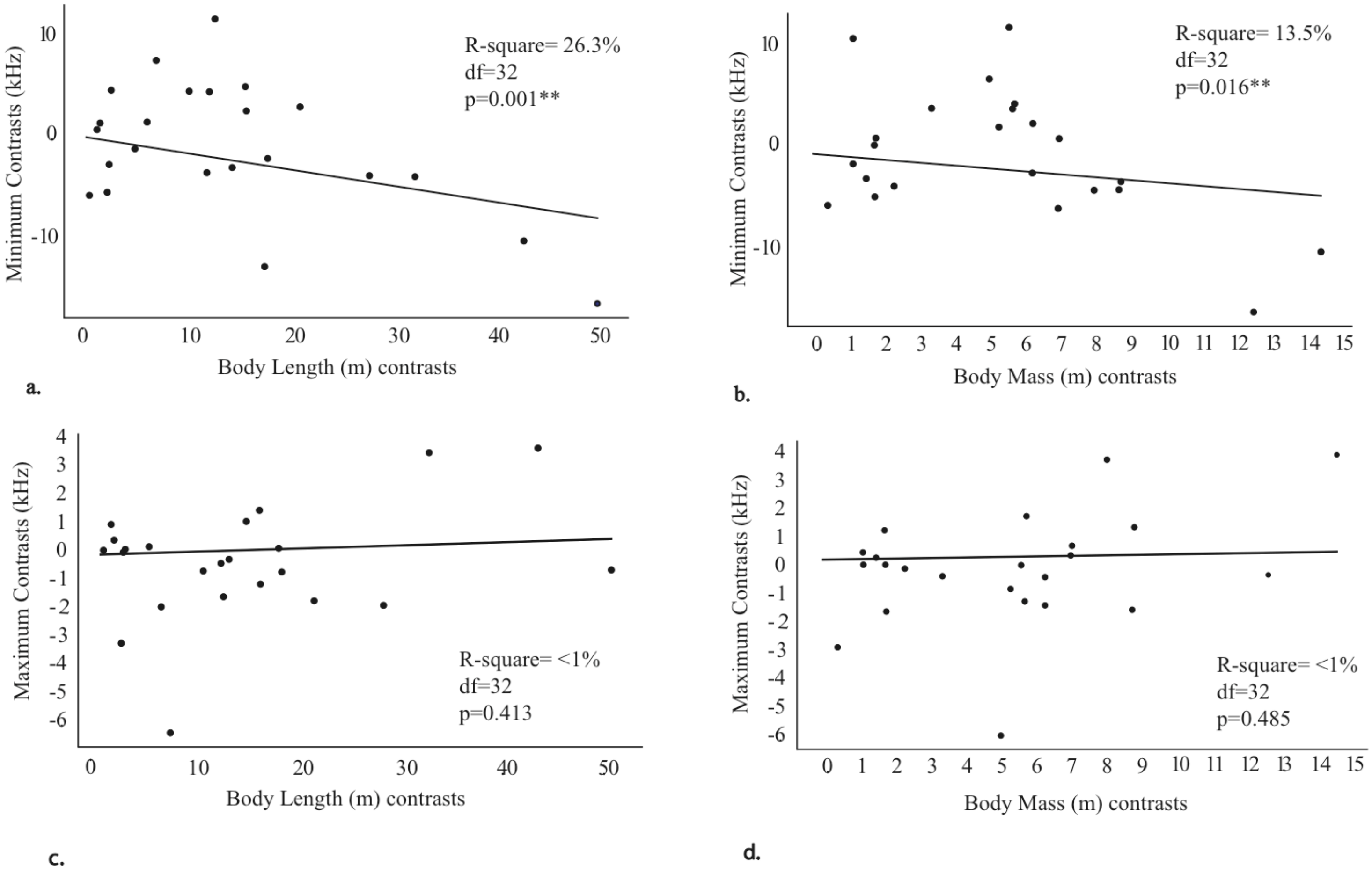
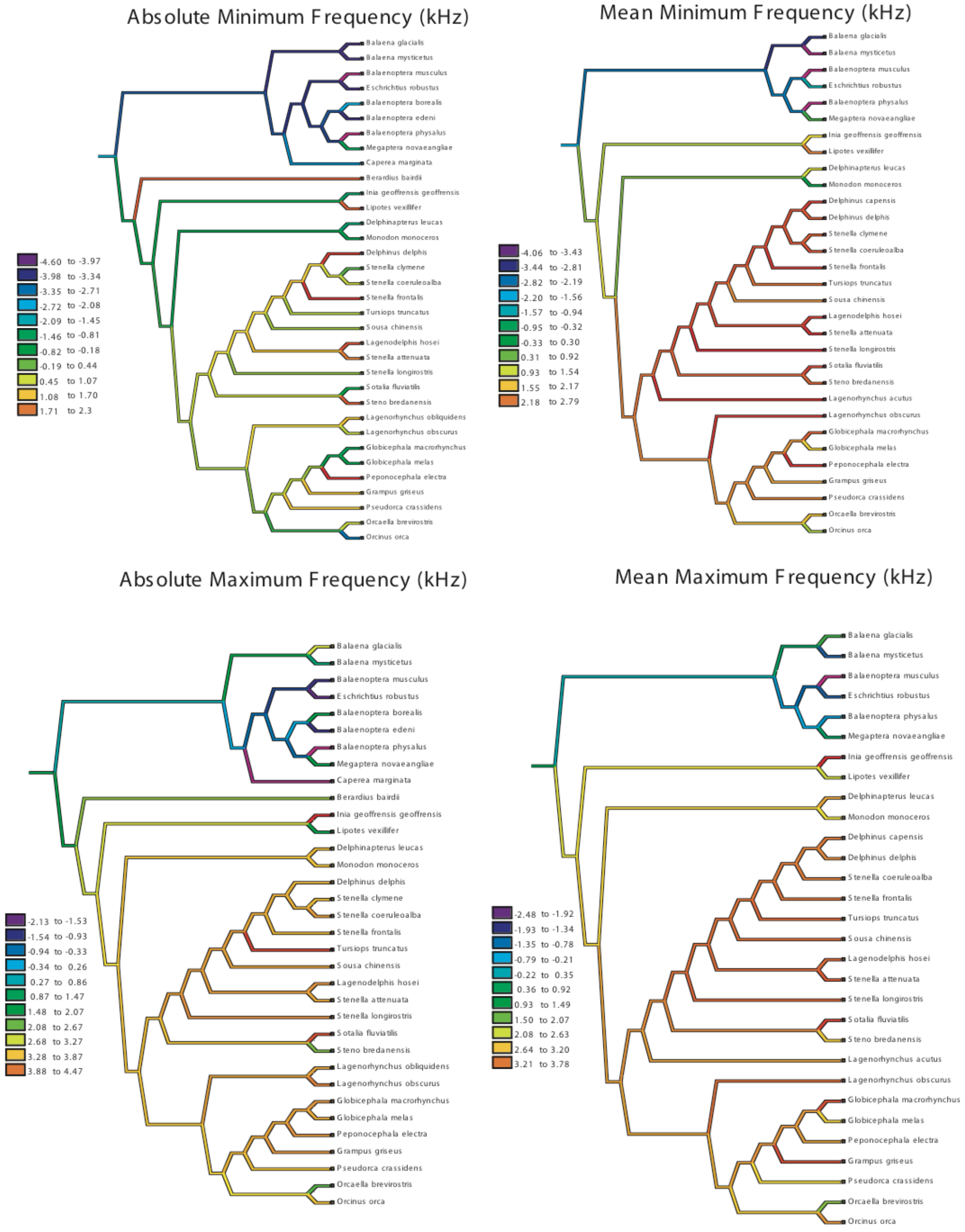

Balaena glacialis
Balaena mysticetus
Balaenoptera bonaerensis
Balaenoptera musculus
Eschrichtius robustus
Balaenoptera borealis
Balaenoptera edeni
Balaenoptera physalus
Megaptera novaeangliae
Caperea marginata
Kogia breviceps ?
Kogia simus ?
Physeter macrocephalus *
Berardius bairdii
Hyperoodon ampullatus *
Hyperoodon planifrons ?
Mesoplodon bidens ?
Mesoplodon densirostris ?
Ziphius cavirostris ?
Indopacetus pacificus ?
Tasmacetus shepherdi ?
Platanista gangetica ?
Inia geoffrensis geoffrensis
Pontoporia blainvillei ?
Lipotes vexillifer
Australophocaena dioptrica *
Phocoena sinus *
Phocoena spinipinnis *
Phocoena phocoena *
Phocoenoides dalli *
Neophocaena phocaenoides *
Delphinapterus leucas
Monodon monoceros
Delphinus capensis
Delphinus delphis
Stenella clymene
Stenella coeruleoalba
Stenella frontalis
Tursiops truncatus
Sousa chinensis
Lagenodelphis hosei
Stenella attenuata
Stenella longirostris
Sotalia fluviatilis
Steno bredanensis
Lagenorhynchus acutus
Cephalorhynchus commersonii *
Cephalorhynchus eutropia *
Cephalorhynchus hectori *
Cephalorhynchus heavisidii *
Lagenorhynchus australis *
Lagenorhynchus cruciger ?
Lagenorhynchus obliquidens
Lagenorhynchus obscurus
Lissodelphis borealis ?
Lissodelphis peronii ?
Feresa attenuata
Globicephala macrorhynchus
Globicephala melas
Peponocephala electra
Grampus griseus
Pseudorca crassidens
Orcaella brevirostris
Orcinus orca
0.30- 0.61
0.62- 0.93
0.94- 1.24
1.25- 1.55
1.56- 1.86
1.87- 2.18
2.19- 2.49
2.50- 2.80
2.81- 3.12
3.13- 3.43
3.44- 3.74

FIG.9



a.
Minimum Contrasts (kHz)
10
0
-10
Body Length (m) contrasts
0
10
20
30
40
50
R-square= 26.3%
df=32
p=0.001**
b.
Minimum Contrasts (kHz)
10
0
-10
Body Mass (m) contrasts
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
R-square= 13.5%
df=32
p=0.016**
c.
Maximum Contrasts (kHz)
4
3
2
1
0
-1
-2
-3
-4
-5
-6
Body Length (m) contrasts
0
10
20
30
40
50
R-square= <1%
df=32
p=0.413
d.
Maximum Contrasts (kHz)
4
3
2
1
0
-1
-2
-3
-4
-5
-6
Body Mass (m) contrasts
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
R-square= <1%
df=32
p=0.485

FIG.10


Absolute Minimum Frequency (kHz)
Balaena glacialis
Balaena mysticetus
Balaenoptera musculus
Eschrichtius robustus
Balaenoptera borealis
Balaenoptera edeni
Balaenoptera physalus
Megaptera novaeangliae
Caperea marginata
Berardius bairdii
Inia geoffrensis geoffrensis
Lipotes vexillifer
Delphinapterus leucas
Monodon monoceros
Delphinus delphis
Stenella clymene
Stenella coeruleoalba
Stenella frontalis
Tursiops truncatus
Sousa chinensis
Lagenodelphis hosei
Stenella attenuata
Stenella longirostris
Sotalia fluviatilis
Steno bredanensis
Lagenorhynchus obliquidens
Lagenorhynchus obscurus
Globicephala macrorhynchus
Globicephala melas
Peponocephala electra
Grampus griseus
Pseudorca crassidens
Orcaella brevirostris
Orcinus orca
-4.60 to -3.97
-3.98 to -3.34
-3.35 to -2.71
-2.72 to -2.08
-2.09 to -1.45
-1.46 to -0.81
-0.82 to -0.18
-0.19 to 0.44
0.45 to 1.07
1.08 to 1.70
1.71 to 2.3
Mean Minimum Frequency (kHz)
Balaena glacialis
Balaena mysticetus
Balaenoptera musculus
Eschrichtius robustus
Balaenoptera physalus
Megaptera novaeangliae
Inia geoffrensis geoffrensis
Lipotes vexillifer
Delphinapterus leucas
Monodon monoceros
Delphinus capensis
Delphinus delphis
Stenella clymene
Stenella coeruleoalba
Stenella frontalis
Tursiops truncatus
Sousa chinensis
Lagenodelphis hosei
Stenella attenuata
Stenella longirostris
Sotalia fluviatilis
Steno bredanensis
Lagenorhynchus acutus
Lagenorhynchus obscurus
Globicephala macrorhynchus
Globicephala melas
Peponocephala electra
Grampus griseus
Pseudorca crassidens
Orcaella brevirostris
Orcinus orca
-4.06 to -3.43
-3.44 to -2.81
-2.82 to -2.19
-2.20 to -1.56
-1.57 to -0.94
-0.95 to -0.32
-0.33 to 0.30
0.31 to 0.92
0.93 to 1.54
1.55 to 2.17
2.18 to 2.79
Absolute Maximum Frequency (kHz)
Balaena glacialis
Balaena mysticetus
Balaenoptera musculus
Eschrichtius robustus
Balaenoptera borealis
Balaenoptera edeni
Balaenoptera physalus
Megaptera novaeangliae
Caperea marginata
Berardius bairdii
Inia geoffrensis geoffrensis
Lipotes vexillifer
Delphinapterus leucas
Monodon monoceros
Delphinus delphis
Stenella clymene
Stenella coeruleoalba
Stenella frontalis
Tursiops truncatus
Sousa chinensis
Lagenodelphis hosei
Stenella attenuata
Stenella longirostris
Sotalia fluviatilis
Steno bredanensis
Lagenorhynchus obliquidens
Lagenorhynchus obscurus
Globicephala macrorhynchus
Globicephala melas
Peponocephala electra
Grampus griseus
Pseudorca crassidens
Orcaella brevirostris
Orcinus orca
-2.13 to -1.53
-1.54 to -0.93
-0.94 to -0.33
-0.34 to 0.26
0.27 to 0.86
0.87 to 1.47
1.48 to 2.07
2.08 to 2.67
2.68 to 3.27
3.28 to 3.87
3.88 to 4.47
Mean Maximum Frequency (kHz)
Balaena glacialis
Balaena mysticetus
Balaenoptera musculus
Eschrichtius robustus
Balaenoptera physalus
Megaptera novaeangliae
Inia geoffrensis geoffrensis
Lipotes vexillifer
Delphinapterus leucas
Monodon monoceros
Delphinus capensis
Delphinus delphis
Stenella coeruleoalba
Stenella frontalis
Tursiops truncatus
Sousa chinensis
Lagenodelphis hosei
Stenella attenuata
Stenella longirostris
Sotalia fluviatilis
Steno bredanensis
Lagenorhynchus acutus
Lagenorhynchus obscurus
Globicephala macrorhynchus
Globicephala melas
Peponocephala electra
Grampus griseus
Pseudorca crassidens
Orcaella brevirostris
Orcinus orca
-2.48 to -1.92
-1.93 to -1.34
-1.35 to -0.78
-0.79 to -0.21
-0.22 to 0.35
0.36 to 0.92
0.93 to 1.49
1.50 to 2.07
2.08 to 2.63
2.64 to 3.20
3.21 to 3.78

CHAPTER V

PHYLOGENETIC REVIEW OF TONAL SOUND PRODUCTION IN WHALES IN RELATION TO SOCIALITY

LAURA J. MAY-COLLADO[1,2], INGI AGNARSSON[3,4], DOUGLAS WARTZOK[1]

[1]Florida International University, Department of Biological Sciences, 11200 SW 8th
Street, Miami, FL 33199, USA
[2]Universidad de Costa Rica, Escuela de Biología, Apto. 2060 San Pedro, Costa Rica
[3]Department of Biology, University of Akron, Akron, OH 44325-3908, USA.
[4]Systematic Biology-Entomology, E-530, Smithsonian Institution, NHB-105, P.O. Box
37012, Washington, DC 20013-7012, USA

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ABSTRACT

Background

It is widely held that in toothed whales, high frequency tonal sounds called 'whistles' evolved in association with 'sociality' because in delphinids they are used in a social context. Recently, whistles were hypothesized to be an evolutionary innovation of social dolphins (the ‘dolphin hypothesis’). However, both 'whistles' and 'sociality' are broad concepts each representing a conglomerate of characters. Many non-delphinids, whether solitary or social, produce tonal sounds that share most of the acoustic characteristics of delphinid whistles. Furthermore, hypotheses of character correlation are best tested in a phylogenetic context, which has hitherto not been done. Here we summarize data from over 300 studies on cetacean tonal sounds and social structure and phylogenetically test existing hypotheses on their co-evolution.

Results

Whistles are 'complex' tonal sounds of toothed whales that demark a more inclusive clade than the social dolphins. Whistles are also used by some riverine species that live in simple societies, and have been lost twice within the social delphinoids, all observations that are inconsistent with the dolphin hypothesis as stated. However, cetacean tonal sounds and sociality are intertwined: (1) increased tonal sound modulation significantly correlates with group size and social structure; (2) changes in tonal sound complexity are significantly concentrated on social branches. Also, duration and minimum frequency correlate as do group size and mean minimum frequency.

Conclusions

Studying the evolutionary correlation of broad concepts, rather than that of their component characters, is fraught with difficulty, while limits of available data restrict the detail in which component character correlations can be analyzed in this case. Our results support the hypothesis that sociality influences the evolution of tonal sound complexity. The level of social and whistle complexity are correlated, suggesting that complex tonal sounds play an important role in social communication. Minimum frequency is higher in species with large groups, and correlates negatively with duration, which may reflect the increased distances over which non-social species communicate. Our findings are generally stable across a range of alternative phylogenies. Our study points to key species where future studies would be particularly valuable for enriching our understanding of the interplay of acoustic communication and sociality.

BACKGROUND

Cetacean tonal signals are broadly defined as narrowband, frequency modulated sounds [1-3]. Such sounds are produced by both baleen whales (Mysticeti) and toothed whales (Odontoceti)—sister clades containing all extant whales. They are also produced by other mammals [e.g., 4] and thus appear primitively present in the order. Baleen whales produce sounds that have fundamental frequencies generally below 5 kHz [2,5], as do members of the sister lineage of Cetacea, the hippos [4]. In toothed whales, in contrast, these sounds most commonly range from 5-20 kHz [2], and in some species, e.g. *Delphinus delphis, Stenella attenuata, S. coeruleoalba*, *S. longirostris* [6] *Lagenorhynchus albirostris* [7]*, Tursiops truncatus* [8], fundamental frequencies can go as high as 48 kHz in *Inia geoffrensis* [9]. In delphinid toothed whales these high frequency tonal sounds, especially when complex, are often referred to as 'whistles', although within the group whistle acoustic characteristics vary enormously. Several species produce both frequency modulated whistles (e.g., sine, convex, concave, upsweep, downsweep) and simple whistles that are relatively constant in frequency (e.g., *Lagenorhynchus albirostris,* [7]; *Sotalia fluviatilis* [10]; *Stenella longirostris* [11], others are limited to simple whistles (*Lipotes vexillifer*) [12] or to few frequency modulated whistles (e.g., mostly downsweep in *Inia geoffrensis*) [9]. In addition, whistle contour may be continuous or consist of a series of breaks and segments [2]. Whistles may or not contain harmonics [2]. In delphinid species like *S. longirostris* [13] and *L. albirostris* [14] whistles can contain high order-harmonics. Finally, whistle duration is very variable. For instance, in *Sousa chinensis* whistles can range from 0.01 to 1.3 seconds [15] and in *Tursiops truncatus* from 0.05 to 3.2 seconds [16]. In delphinids, whistle frequency modulation and duration varies within species in relation to geography [e.g., 10, 11,16,17], and related species differ in many whistle frequency components (e.g., maximum, minimum, end, and start frequency) [e.g., 18-22].

Baleen whales produce a great variety of sounds, among them tonal sounds that like toothed whale 'whistles', are narrowband and frequency modulated, although typically much lower in frequency [1]. These tonal sounds can be produced in isolation or in combination with other sounds (e.g. pulsative sounds). In the Right whale (*Balaena glacialis*) these tonal sounds, again like 'whistles' in toothed whales, are used in a social context [23]. For example, in Blue whales (*Balaenoptera musculus*) tonal sounds are presumably used for long-distance communication [24], and in Right whales tonal sounds are used in combination with pulsative sounds in a sexual context [25]. However, in baleen whales, these tonal sounds are never referred to as whistles, but as 'calls', 'moans' or 'tones' [26, 24, 27-29]. Nomenclature of sounds, both in toothed and baleen whales, is confusing. As stated by Au (2000: 31) [1] in baleen whales "as with dolphins there is a lack of any standard nomenclature for describing emitted sounds", this frustrates comparison of sounds across taxa and obscures homologies. It remains unclear exactly what is a 'whistle', and if narrowband, frequency modulated tonal sounds of baleen whales and toothed whales are homologous at some level. One reason to question tonal sound homology across whales is that the sound production mechanisms of baleen whales and toothed whales are dramatically different. In baleen whales tonal sounds are thought to be laryngeal [30, 31], as they are in other related mammals [e.g. 4, 32], but in toothed whales sounds are produced by a unique and complex nasal system [e.g. 33, 34]. This offers some support for the hypothesis that toothed whales ‘whistles’ are unique and different from (not homologous with) baleen whale tonal sounds. However, this also suggests that high frequency tonal sounds are homologous across toothed whales and such sounds in non-delphinid toothed whales should also be called whistles (contra Podos et al. 2002) [35]. To accommodate both possibilities we do all analyses across all whales (allowing for potential homology of tonal sounds across the order) and separately within toothed whales.

Most of the work on whistles has been done with social delphinids, where they are often referred to as "social signals" and are thought to facilitate individual recognition, group cohesion, recruitment during feeding activities, and overall communication [e.g., 1, 3, 36-44]. Generalizations about the function of whistles have translated into the hypothesis that whistles evolved in concert with sociality, and that the two traits are tightly correlated [e.g., 45, 35]. Herman and Tavolga (1980) [45] suggested that the degree of gregariousness in toothed whales seemed to be related to whistle production [see also 46]. More specifically, they proposed that species that live in small groups or are solitary tend not to whistle, whereas species that live in large groups frequently do. Recently, Podos *et al.* (2002) [35] proposed that whistles are an innovation of social delphinids; in other words that whistles are synapomorphic for a clade within Delphinidae. However, even within delphinids some social species such as *Cephalorhynchus* spp and some species of *Lagenorhynchus* do not whistle [e.g., 46, 47], which seems to contradict the dolphin hypothesis. The hypothesis was furthermore based on an assumption of the absence of whistles in river dolphins (*Inia*, *Lipotes*, *Platanista*, and *Pontoporia*), porpoises (Phocoenidae), beaked whales (ziphids) and belugas and narwhals (Monodontidae). However, we do not believe this assumption is justified. Tonal sounds from *Inia geoffrensis*, for example, have been independently recorded in several studies [9, 21, 22, 48]. These sounds, just like in other toothed whales, have been referred to as whistles, although they are simpler and shorter in duration, and higher in frequency than the whistles of some dolphins [9]. Similar whistles have also been reported in another river dolphin *Lipotes vexillifer* [e.g., 12, 49, 50] and in social non-delphinid toothed whales such as some beaked whales [51, 52], and the Monodontidae, belugas and narwhals [e.g. 53-57). Podos et al. (2002) [35] concluded that the tonal sounds in these species should not be classified as 'whistles', and hence found support for the dolphin hypothesis. While we agree with Podos et al. that whistle structure seems different in delphinids and non-delphinid toothed whales we believe this demonstrates the basic problem of treating broad, arbitrary, concepts as single traits in evolutionary analyses. To define whistles as social sounds produced by delphinids—a priori denying homology with tonal sounds in related taxa—and then concluding that they evolved in association with sociality in Delphinidae risks circularity. In such a framework reconstructing the origin of 'whistles' on a phylogeny will simply depend on the whistle definition chosen by any given author.

To facilitate discussion, and comparability with previous research, we use the word 'whistle' for toothed whales tonal sounds, however, we do not imply that whistles are necessarily non-homologous to baleen whale tonal sounds—their homology requires further study. We use whistles as a category for some of our analyses, mainly to test the dolphin hypothesis as it was proposed. It is not very informative, however, to simply map the distribution of 'whistles' on a phylogeny (Fig. 11, [see Appendix 1]). Authors differ in their interpretation on the presence or absence of whistles across species, e.g. some define them in the context of a behavior that may have much more limited distribution than the sounds themselves. Furthermore, even within dolphins 'whistles' can be highly variable. We thus highlight the need to focus on the various acoustic parameters (such as frequency variables, modulation, etc.) that may vary independently and have non-identical phylogenetic distributions [see Appendix 1 for rationale]. Hence, our major focus is on such analyses which may reveal which, if any, of the characteristics of 'whistles', or tonal sounds in general, seem associated with sociality.

Our understanding of tonal sound acoustic structure, diversity, and use, is growing, but the evolution of tonal sounds and their association with sociality remains highly speculative. We therefore believe we here improve upon previous studies by providing a more detailed analysis, and using novel and more detailed phylogenies than any study hitherto. We also test these hypotheses across a range of alternative phylogenies.

In sum, we here review current knowledge of both tonal sound production and social structure in Cetacea, and explore the evolution of tonal sounds and the association of individual tonal sound components with sociality (overall social structure and social components). Taking advantage of a new species-level cetacean phylogeny [58, 59] we provide the first phylogenetic test of the hypotheses of Herman and Tavolga (1980) [45] and Podos *et al.* (2002) [35]. This study identifies large gaps in knowledge on both traits, and points to key species where future studies would be particularly valuable for enhancing our understanding of the interplay of tonal sounds and sociality.

RESULTS

Testing the Dolphin Hypothesis

The following is presented merely to test the dolphin hypothesis as stated (see Introduction, Methods, and [see Appendix 1] for problems with this coarse approach). Under the definition of 'whistle' we use here, the optimization of whistles on the phylogeny is ambiguous (Fig. 11b). However, all of the equally most parsimonious reconstructions reject the dolphin hypothesis. The phylogeny implies that whistles either evolved independently twice, once in *Berardius* and once in the node leading to Delphinida *sensu* Muizon (1988) [60], delphinoids plus river dolphins + *Platanista* (a clade we here refer to as Pandelphinida), with secondary losses in Phocoenidae and within Delphinidae (*Cephalorhynchus* spp. and *Lissodelphis* spp.). Alternatively whistles evolved once in the common ancestor of ziphiids plus pandelphinids and then were subsequently lost thrice in *Hyperoodon*, phocenids and within delphinids (the optimization of whistles is equally ambiguous on previously published phylogenies, [see Appendixs 2-4], while dual origin of whistles is better supported when optimized across the entire set of filtered post-burnin trees, see Methods). Likewise, there are two possible optimizations of sociality under a broad concept approach. One is that sociality evolved in the common ancestor of Odontoceti and was then lost secondarily twice in the riverine species (Fig. 11b). Alternatively sociality may have evolved independently four times (in *Physeter macrocephalus*, within *Ziphiidae*, *Pontoporia*, and in Delphinoidea). The optimization of sociality is ambiguous on over 99% of the alternative trees examined, however, the multiple loss of sociality within Cetacea seems more likely in general, given that relatives of whales are social. Regardless of choice of optimizations, whistles did not originate in the lineage leading to the social dolphins, contra the dolphin hypothesis.

Character Optimizations

Results of character optimizations led to the same conclusions across all alternative phylogenies examined (previously published hypotheses, [see Appendixs 2-4], and post-burnin trees from our Bayesian analysis of Cytochrome b), unless otherwise noted.

Group sizes in Cetacea [see Appendix 5] appear to have been ancestrally small, but to have gradually increased in the lineage leading to the dolphins, with a number of independent derivations of societies with hundreds of individuals and some secondary reductions in group size (e.g., *Cephalorhynchus* spp, *Orcaella* and *Orcinus* Fig. 12).

Here we present some alternative optimizations of sociality under both a 'broad two and four state concept' framework simply to test the dolphin hypothesis and under a multiple component framework. We note, however, that our study offers limited insights into the evolution of sociality in cetaceans. Future studies will require examining a greater number of component characters of sociality as such data becomes available, and it will require the inclusion of comparative social data also from the outgroups.

We compare three optimizations of sociality represented as a four-state character (social structure) (see Table 8 and [see Appendix 5]). First, we keep polymorphic species (species reported to show more than one type of social organizations) as such and then compare results when the ‘lowest' and 'highest' social state is chosen for each polymorphic species (Fig. 13). All three optimizations have some ambiguity, but optimizations across all trees suggest that family based groups evolved independently at least three times (*Physeter*, *Monodon*, and Globicephalinae Fig. 13,). The optimization of social components (including polymorphism) is shown in additional material [see Appendix 6]. Group composition appears to have ancestrally been simple groups consisting only of mother and calf. Segregated (by sex and/or age) and mixed groups may have evolved independently at least four times [see Appendix 6b]. Finally, member associations appear to have evolved from simple mother and calf interactions to complex family based associations [see Appendix 6c].

Figure 4 shows the optimization of each acoustic character (all transformed using the natural log). Relatively high maximum and minimum frequencies (both absolute and mean) appear derived in toothed whales (Fig. 14a-b,d-e). Particularly high mean maximum and minimum frequencies have evolved within delphinids (note that some of the variation within delphinids and other groups is visually masked by the way Mesquite groups continuous variables in color ranges; [see Appendix 7 for greater detail].

There appears to be a similar trend in the number of tonal sound inflection points (an indicator of tonal sound complexity) going from few ancestrally and increasing in the lineage leading to the dolphins (Fig. 14f). There is an inverse trend in tonal sound duration, where particularly short tonal sounds appear to be derived within the delphinids (Fig. 14c).

Character regressions and correlations

Under the independent contrast method the regression between group size and the mean number of inflection points was marginally significant: species with larger groups tend to produce tonal sounds with greater mean number of inflection points. Group size explained approximately 7.9% of the variation in inflection points across cetaceans (p=0.05, df=33 see Fig. 15 (this and some of the following results are dependent on the choice of phylogeny, see section *Phylogenetic uncertainty*). Group size also significantly explained variation in the mean minimum tonal sound frequency within toothed whales (R^2=12.4%, df=23, $p\text{-}_{1\text{tailed}}$=0.04). We justify using a one-tailed test based on the expectancy that low frequency sounds travel longer distances so that a priori one might expect that low frequency tended to be associated with solitary species, while species that live their entire lives in large groups need only communicate over short distances. However, given that the two tail test is non-significant we consider this hypothesis only weakly supported. Regressions between group size and other acoustic parameters were not significant.

In addition, there is a significant negative relationship between tonal sound duration and absolute and mean minimum frequency both for all cetaceans (Abs-MinF, R-square=17%, p=0.02, df= 31, Mean-MinF, 17.5%, p=0.02, df=29) and for toothed whales (Asb-MinF, R-square=38%, p<0.001, df=22, Mean-MinF, R-square=24%, p=0.01, df=23). There was a significant positive relationship between tonal sound duration and complexity for all cetaceans (R-square=12%, p=0.04, df=32) and for toothed whales (R-square=45%, p<0.001, df=23).

Changes in tonal sound complexity were significantly concentrated within social lineages in four of the five most parsimonious reconstructions when both traits were treated as two state characters [see Appendix 8] f.

Tests of character state associations (SIMMAP) show that complex whistles (state 1 = more than one inflection points) were positively associated with group living species

(Dij=0.13, $p > 0.999$) and negatively with less social species (Dij=-0.024, $p < 0.001$) treating social complexity as a two state character. In general there was an association between tonal sound complexity and social structure ($D_{statistic}$=0.376, $p < 0.001$, Table 9). However, the associations between individual states vary depending on how finely tonal sound and social characters are divided (Table 9). For instance, when treating social complexity as a four state character but tonal complexity as a two state character we find a significant positive association between highly social species (states 2 and 3) and complex tonal sounds and a negative association between complex tonal sounds and 'solitary' (state 0) species (Table 9). When both are treated as four state characters only negative associations are significant (but in the same directions as before, see Table 9).

When three component characters of sociality were analyzed we found similar significant character associations with inflection points (Group size $D_{statistic}$=0.394, $p < 0.001$; Group Composition $D_{statistic}$=0.306, $p < 0.001$; Stability/Associations $D_{statistic}$=0.364, $p < 0.001$, [see Appendix 9 and legend for detail], all indicating association between complex whistles and high levels of sociality.

Phylogenetic uncertainty

In general, most of our findings are not strongly dependent on the phylogeny of choice, as long as all the species are included. In other words, results in most cases are similar whether the data are analyzed across the trees favored by our own analyses (all post burnin trees and post burnin trees filtered using agreement among multiple studies), or restricted to trees filtered to be congruent with the alternative hypotheses of Messenger and McGuire (1998) [61], Nikaido et al. (2001) [62] or Arnason et al. (2004) [63], respectively (see Methods for detail). On the all-species phylogenies results significant in the main analyses were also significant across all sets of trees for all SIMMAP analyses. The only difference between analyses was that social and whistle character states were more strongly associated on the trees constrained by the Messenger and McGuire hypothesis than in the remainder [see Appendix 10]. Similarly, the PDAP analyses results agree irrespective of phylogeny choice [see Appendixs 11 and 12], except the following. Group size and number of inflexion points correlate significantly except on trees constrained by the hypotheses of Arnason et al. (2004) [63] or Nikaido et al. (2001) [62], and group size and mean minimum frequency correlate except on trees constrained by the Messenger and McGuire (1998) [61] hypothesis. For ancestral character reconstruction under parsimony, the optimizations of the continuous characters such as group size, tonal sound frequencies, duration, and inflexion points are nearly identical across the trees considered. The optimization of whistles as a presence/absence character was ambiguous on our, and previous, phylogenetic hypotheses. However, on 70% of the filtered post-burnin trees dual origin of whistles was preferred (see above). The optimization of sociality (as a two state character) was ambiguous (single origin followed by multiple losses, or two origins followed by fewer losses), except on the Nikaido et al. (2001) [62] hypothesis which favors two origins of sociality. Similarly optimizations of whistles and sociality as multistate characters varied little across trees with no impact on conclusions.

When we used the phylogenies resulting from reanalyzes of the data of Messenger and McGuire (1998) [61], however, significance was lost in a higher number (although not the majority) of the hypotheses tests [see Appendixs 10-12] and some character optimizations changed. Although this can in theory imply sensitivity to phylogenetic pattern, a simpler explanation for this finding seems to be that much of the power of the comparative tests is lost as Messenger and McGuire's data [61] includes only a portion of the species of our main dataset. Hence we do not see a reason to discuss these 'disagreements' further.

DISCUSSION AND CONCLUSIONS

Our results show that the interplay of tonal sounds and sociality is complicated and that studying the relationship between conglomerate characters such as 'whistles' and 'sociality' largely conceals these intricacies. Under the very simple 'concept approach' the cladistic test [see 64] rejects the dolphin hypothesis stating that 'whistles' evolved as an adaptation for social communication in dolphins. Whistles, as here defined, appear to be a synapomorphy of pandelphinids, or even a more inclusive group including ziphiids (Fig. 11b). Therefore, the current evidence implies that whistles arose earlier in the evolutionary history of whales than presumed by Podos *et al.* (2002) [35], and whistles are furthermore present in some non-social species, and have been lost more than once within social clades. Apparently then, whistles are not necessary for functional cetacean societies and social communication, and they can play some role in communication in solitary species.

Our findings highlight some of the problems with evolutionary analyses of imprecise, broad concepts. Even though 'whistles' do not correlate with any measure of sociality we find evidence that the evolutionary histories of sociality and tonal sounds are intertwined in the direction suggested by many authors, including Podos *et al.* (2002) [35]. This is evidenced mainly by two findings. (1) The significant association between group size and tonal sound inflection points (complexity) whether tested using independent contrasts, concentrated changes, or character association tests; and (2) the association between group size and minimum tonal sound frequency (and the association of the latter with duration). Simple tonal sounds are mostly confined to species with simple societies (mostly solitary) such as river dolphins and rorquals while tonal sound and social complexity increase in the lineage leading to Delphinoidea (Tables 2). Within that lineage reversal to simpler societies has occurred twice and each time tonal sounds have been secondarily lost (Figs 1a-b, 3), although whistle loss may represent a response to predatory pressure rather than change in social structure (see below).

In addition, especially in toothed whales, species emitting longer tonal sounds tend to show a greater number of inflection points. These observations and tests are congruent with hypotheses stating that complex tonal sounds function as social signals for group cohesion (e.g., most delphinids) during social, traveling, and feeding activities [e.g.,42, 65] or individual recognition (e.g., bottlenose dolphins, Atlantic spotted dolphins) [e.g., 3, 37, 41, 66, 67].

But functionality in a social context can only explain a portion of the variation in tonal sound production and complexity. The secondary loss of tonal sounds in porpoises and the dolphin clade containing *Lagenorhynchus australis, L. cruciger* and *Cephalorhynchus spp*, for example, suggests these signals may sometimes be costly, for example in terms of energy production or predation risk. These odontocetes live in very fluid societies where acoustic communication is accomplished by means of rapid pulsed sounds [47, 68]. One potential costs of tonal sounds is that these signals may be intercepted (eavesdrop) by an unintended receiver [69, 70]. Delphinid tonal sounds are within a frequency range that is readily detected by predators like killer whales which are known to predate on many marine mammal species including these non-whistling species. Furthermore, porpoises and *Cephalorhynchus* seem to have converged upon similar morphology and biosonar systems [71, 72], both have ears tuned for high frequency sounds and produce narrowband clicks [73] that are used for echolocation purposes and communication [74, 75]. As emphasized by Morisaka and Connor (2007) [76] if killer whales poorly detect these signals, then it may be beneficial for these species to use high frequency signals for social communication [73, 74] instead of tonal sounds.

In stable societies like those of *Physeter macrocephalus* and *Orcinus orca*, animals tend to produce group-specific sounds (termed codas and calls respectively) whereas in fission-fusion societies like those of *Tursiops truncatus* and *Stenella frontalis*, animals produce individual-specific whistles, so called "signature whistles" [see 3, 15, 41, 38]. Signature whistles are sounds (single-loop and multiple-loop) [see 75] that to date have only been found in species with fluid societies where mother and calf use them as contact calls and some animals (particularly males) form coalitions (individual recognition may be important when forming these alliances) [e.g., 15, 37, 38, 44, 66, 67, 73, 77-82].

We found evidence for association between group size and the mean minimum frequency, as well as between mean minimum frequency and duration. Given that the former was only marginally significant, we will not place much emphasis on this finding. However, if this finding will be better supported with the addition of further data it may suggest that low minimum frequency (and long duration) is selected for in mostly solitary species which must communicate with other individuals over relatively greater distances than do species that live in permanent societies. It should be noted that May-Collado et al. (2007) [59] found a correlation between minimum frequency and body size across whales. This may explain a part of the observed pattern here, as social species are often small, but it remains to be explored if sociality and body size are correlated.

Despite the possible differences in the context in which tonal sounds are produced by riverine dolphins and other delphinoids, there is no *a priori* reason to assume that whistles produced by these toothed whales are not homologous (contra Podos *et al.* 2002) [35], and phylogenetically their homology is supported (Fig. 11). It has been proposed that marked deviations of *Inia* from delphinids in scaling relationship in body size and frequency [e.g., 21, 83] is evidence that their sounds are produced by mechanisms different from those used by delphinoids. This is primarily based on the assumption that vertebrate scaling of vocal frequency occurs through size-dependent effects on a common vocal apparatus [e.g. 80], thus deviations from scaling relationships might indicate an independent proximate mechanism [35]. However, these scaling patterns, for maximum frequency disappear once phylogenetic relationships are taken into account [59].

While some cetacean societies have been studied for a long time, detailed observations are lacking for many species and it is difficult to define and compare levels of sociality across cetacean species. Likewise there are many gaps in our knowledge of tonal sound production [see Appendixs 5 and 7]. Our study highlights critical gaps in knowledge, and pinpoints key taxa whose future study could quickly enhance our understanding of the evolution of tonal sounds. As can be seen in Figure 1, tonal sound data would be especially valuable from *Kogia*, ziphiids other than *Berardius*, and from *Platanista* and *Pontoporia*. In a similar manner information on social structure of *Kogia*, *Mesoplodon*, and *Ziphius* would help resolve the optimization of sociality.

Many factors in addition to sociality have been proposed to have influenced the evolution of tonal sounds, including body size and maximum frequency scaling [21, 35, 59, 83, 84], habitat [21], predation [76], and zoogeographical [20] and phylogenetic relationships [20, 21]. Given that multiple factors are at work true co-evolutionary histories of any given characters could easily be masked. Hence, finding significant correlations between tonal sounds and social structure is particularly interesting. For example, we find a significant, but rather weak, correlation between group size and inflexion points using the independent contrast method. One of the conspicuous outliers in this analysis is *Orcinus orca*, a social delphinid living in relatively small groups that nevertheless produces extremely modulated whistles. Thomsen et al. (2001) [85] discuss these extreme modulations and suggest that whistles in killer whales serve a different function than in related dolphins. Removing *O. orca* from the analyses increases the strength of the correlation between whistle complexity and group size (R-square=9.7%, p-value=0.03). It should furthermore be noted that comparative biology is fraught with difficulty, getting enough data together for a strong hypothesis testing is typically difficult and missing data results in a loss of power. By accounting for uncertainty in phylogenetic relationships we hope to reduce the rate of type I error. Further, accounting for differences in interpreting and scoring whistle and sociality data attempts to reduce type I error. It is quite possible that in an attempt to avoid type I error we are introducing an unacceptable amount of type II errors. In other words, our ability to detect true character correlations in evolutionary history may be compromised. In this study, however, most of the results were not sensitive to choice of phylogeny or alternative scoring scenarios which adds some confidence to our conclusions.

Our findings point to gaps in knowledge of both tonal sounds and social structure that need to be filled to significantly advance our understanding of their putative co-evolutionary histories. Nevertheless, our results allow us to reject the simple hypothesis that 'whistles' evolved for social communication in dolphins. However, group size explains some of the variation in tonal sound frequency and frequency modulation indicating a special role for complex tonal sounds in a (complex) social context and perhaps for low frequency, long-duration sounds in solitary species. May-Collado and Wartzok (2007) [9] suggested that whistles in *Inia geoffrensis* may be use to keep distance between animals rather than to stimulate social interactions. However, this hypothesis needs to be tested. Future studies should focus on particularly poorly known groups of species such as riverine species, ziphiids, and *Kogia* spp.

METHODS

Definitions

For purposes of this study the association between tonal sounds and sociality will be studied under both a broad concept [tonal sounds and whistles versus sociality, emulating previous studies], and using a ‘component’ approach whereby tonal sounds and sociality are dissected into (some of) their component characters. For tonal sounds, standard acoustic parameters we use here include absolute and mean minimum and maximum frequencies (kHz), duration (s), and number of inflection points (a measure of whistle modulation, and a proxy for whistle complexity) [see Appendix 7].

Current knowledge on cetacean sociality indicates the existence of a wide range of social structures, ranging from ‘solitary’ to highly structured group living species [see 86]. Generally in the study of cetacean sociality, social species are those that show evidence of group living [87] where animals are associated in a nonrandom fashion [88]. Under the broad concept approach, we have classified species into two general social frameworks, one simply organizing species into non-group living species (state 0) and group living species (state 1) and a second one assigning species to four social types (Table 8, [see Appendix 5]. Under the component approach, we also examine some component characters of sociality for which there is sufficient data available (group size, composition, and stability/associations) either from short and/or long term studies as well as anecdotal observations (Table 8, [see Appendix 5]). Table 8 provides detailed descriptions of these character and their states. It is important to note that for any type of qualitative characterization of sociality, some species may fit into more than one category due to intraspecific variation. For instance, some populations of *Stenella longirostris* have unstable (or ‘fluid’) groups whose compositions change throughout the day, while populations in the Hawaiian atolls exhibit long-term group fidelity and social stability [89]. These, and other limitations of this study should be kept in mind when interpreting our findings, nevertheless, we believe our approach improves upon previous attempts to detect the associations between sociality and tonal sound production in whales.

Character Optimizations

Published data on cetacean tonal sound production and sociality were obtained from literature and personal communications [see Appendixs 5 and 7]. For tonal sounds we compiled information on the most used acoustic parameters: absolute and mean minimum frequency, absolute and mean maximum frequency, duration, and mean number of inflection points. We only considered studies conducted in the wild or in captivity where, based on the information provided by the authors, it could be assumed species were not recorded in mixed-species groups. We assumed authors were not including harmonics in the acoustic measurements of the tonal sounds emitted by the studied species, unless specified. Information about the social structure of cetaceans was obtained from short to long-term studies, as well as anecdotal information. We searched for information for each of the following social components group size, composition, stability and associations patterns. In addition, information on these social components was used to define four social categories. A minimum of two components was required to place a species within a social category as defined in Table 8. Species for which insufficient components were available were coded as unknown. For species with populations that varied in their social structure or any of the social components (‘polymorphic’) we selected the highest social state for that particular character. Group size is analyzed as a continuous character using the highest mean group size found in the literature, and also as a discrete character which allows the inclusion of more species [see Appendix 6] since many authors do not provide a mean value but instead offer a description of group sizes.

We relied upon the recent species level phylogenies provide by May-Collado and Agnarsson (2006) [58] and May-Collado et al. (2007) [59]. All the main analyses were made using the preferred tree from May-Collado et al. (2007) [59] [see Appendix 13]. Because polytomies 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 a MrBayes analysis (see May-Collado and Agnarsson 2007 for details) [58] without collapsing nodes with less than 50% frequency (using the contype=allcompat option). However analyses were also run on a range of alternative phylogenies (see below) Character optimization was performed with the program Mesquite 1.12 [90], using weighted squared-change parsimony [91].

Acoustic characters were optimized in two data sets (1) with of all cetacean species and (2) pruning species that are known not to emit tonal sounds, species for which acoustic behavior is poorly known, and species that are known to produce tonal sounds but for which detailed information for the character under study was not available. When several values were reported in a species for a particular trait the largest maximum frequency and duration, and the smallest for minimum frequency were used for the analyses [see values in bold in Appendix 7]. Number of inflection points was analyzed both as continuous, reflecting the continuous nature of the data, but also as a two and four state discrete character to facilitate additional analyses that require ordinal data (Table 8, [see Appendixs 5 and 9]).

Sociality was optimized as discrete two and four state characters, and using the social components: group size, composition, stability and association patterns (Table 8, [see Appendix 5]). Because several species were polymorphic for one or several characters we optimized species in three ways (1) as polymorphic, (2) emphasizing their 'highest' social level reported, and (3) emphasizing their 'lowest' social level reported. Finally, we analyzed group size as a continuous character.

Independent Contrasts

Assuming group size as a coarse proxy for social complexity (as defined above by Connor 2000) [87] we regressed it against tonal sound parameters to examine the association of sociality and tonal sound production. Contrasts were calculated using the method of phylogenetically independent contrasts [92]. The method takes into account known dependencies among observations due to phylogenetic relationship of species, and therefore reduces error [93]. Independent contrasts were calculated using the PDAP: PDTREE module [94, using an unpublished version provided by P. Midford] in Mesquite 1.12 (build h47, 85). To estimate independent contrasts, branch lengths were used as estimated by MrBayes; branch length transformations were necessary for group size (Lack of fit test $p<0.05$) and were exponentially transformed. We also tested the relationship between tonal sound frequency and complexity [mean number of inflection points] and tonal sound duration using the independent contrast method.

Character correlations

We also tested character associations between discrete characters of sociality and tonal sound complexity using two different methods. First we used the software SIMMAP 1.0 [95] which allows for multistate character associations. We did the following tests using all post-burnin trees (n=2000) from our Bayesian analysis (May-Collado et al. 2007) [59] using default settings of the program and employing a rough false discovery rate (FDR) to correct for multiple simultaneous comparisons (critical p values for tests of 8, 12, and 16 comparisons are 0.028 (0.972), 0.027 (0.973), and 0.27 (0.973), respectively). We tested the association of (1) sociality and tonal sound complexity both scored as two state characters, (2) social structure and tonal complexity scored as four state characters, and (3) each of the social components and tonal sound complexity scored as two and four states characters [see Appendix 5]. Second using the concentrated changes test [96] in the software MacClade [97] we tested if changes in tonal sound complexity were concentrated on social branches. For this test we used only two state characters.

It is important to note that testing the role (if any) of sociality in tonal sound evolution is challenging due to the large gaps in our knowledge of cetacean societies, difficulties of objectively defining tonal sound complexity, and levels of sociality, and the limitations of available methods. We note that, as with all of the ordinal data we use here, the divisions between character states are rather arbitrary and open to criticism and alternative coding. Nevertheless we believe that our, be it coarse, phylogenetic approach represents an advance over previous studies that have speculated on social and whistle evolution using less data and lacking a phylogenetic reference. We have tried to test the association of characteristics such as group size and whistle parameters using various different approaches (independent contrast test, concentrated changes test, pairwise comparisons on the phylogeny, and character association test for multistate characters), testing them across various alternative phylogenies, and our results are presented in the form of hypotheses that we hope will subsequently be better tested upon the availability of more data and more sophisticated methods. Also, importantly, our data highlight gaps in knowledge and should guide future studies to where allocating resources might be most beneficial.

Current Knowledge on Cetacean Sociality and Tonal Sounds

Connor *et al.* 1998 [86] and Matthews *et al.* 1999 [83] provided brief reviews of the evolution of sociality in toothed whales and tonal sounds in cetaceans, respectively. Connor *et al.* 1998 [86] review highlighted the lack of knowledge for most toothed whale species and focused on the social structure of a few species including *Tursiops truncatus, Orcinus orca, Globicephala spp., Berardius bairdii, Physeter macrocephalus*. They compared toothed whale social structure with some terrestrial mammals e.g. elephants and chimpanzees, and found both similarities between the two, but also identified some social elements unique to toothed whales. Matthews *et al.* 1999 [83] summarized the frequency and time parameters of 40 cetacean species tonal sounds in relation their body size.

This review summarizes information from 335 sources on sociality and tonal sounds for 64 and 36 Cetacean species, respectively [see Appendixs 5 and 7]. The information was gathered from via searches on Web of Science and Google Scholar, and include scientific papers in peer-reviewed journals, conference abstracts, M.Sc. theses, Ph.D. dissertations, technical reports to international organizations, etc.

Although not the main aim of this paper, a few summary statements can be made about current knowledge of sociality and tonal sound production in whales [see Appendixs 5 and 7]. Baleen whales have a rather uniform social structure, generally live in simple societies where animals spend considerable time solitary. Weak associations are limited to aggregations form during the breeding and feeding time, and long-term associations appear to be limited to the time mother and calf remained together. In contrast, toothed whale social structure varies enormously, ranging from solitary to species living in huge groups. In groups, group members show an array of association patterns, from weak to stable family associations. For porpoises (Phocoenidae) and several of the freshwater cetacean species (e.g., *Platanista*, *Lipotes*, *Inia*) authors have described group member associations as 'undeveloped', 'weak', or 'fluid'. Such description are difficult to interpret and do not necessarily mean that the authors are suggesting these species live in a fission-fusion society as reviewed in Connor et al. 1998 [86] for *Tursiops truncatus*. For most delphinids, association patterns have been described as 'fluid', 'highly fluid fussion-fusion', or 'fluid with short-lasting associations'. In these cases authors appear to imply by 'fluid' that the species do live in fission-fusion societies [as described by 86]. In these species males tend to form coalitions and alliances to 'capture' and maintain consortship with females. Finally, the most stable social structures have been described in the Sperm whale, (Physeteroidea), most members of the subfamily Globicephalinae, and possibly the Narwhal (Monodontidae). Notably, these species are not all closely related so that "stable" societies have evolved convergently, however, species differ in the degree of dispersal particularly male dispersal from the group.

Our review updates Matthews *et al.* (1999) [79] review on Cetacean tonal sounds. We included recently reported information on species like *Delphinus capensis* and *Sotalia guianensis* [see Appendix 7]. We also updated information on several others like the Narwhal and Beluga (Monodontidae) and the river dolphins *Lipotes* and *Inia* where more data has become available. The previous review [83] included tonal sound information from two beaked whale species (*Mesoplodon densirostris, M. carlhubbsi*) that we considered controversial due to the possible pulsative nature of these sounds, thus exclude this information from the table. In addition, *Sousa chinensis* and *Sousa plumbea* were considered here a single species, since no clear evidence yet exists to separate them into two distinct species. Likewise, we consider *Stenella plagiodon* as a synonym of *Stenella frontalis*.

Despite of the increasing knowledge on sociality and tonal sounds the information remains lacking, or scattered, for many species. Here we are highlighting some of these species, particularly key species in the phylogeny that would 'resolve' the ambiguities observed in the evolution of sociality and tonal sounds.

Pygmy and Dwarf sperm whales (*Kogia breviceps* and *K. sima*) [98] are close relatives of the Sperm whale (*Physeter macrocephalus*) a species that shows a matrilineal society and does not produce tonal sounds. There are no indications that these species show a similar society to that of the Sperm whale. In general their social structure and acoustic signals are poorly known [99-104]. Pygmy and Dwarf sperm whales are often seen and strand in small groups that are can be segregated by age and sex or mixed [102], see Table 8]. The few published accounts on their sounds describe click trains [99,101,103] and cry-like sounds [104] but no tonal sounds.

Beaked Whales (Ziphiidae) are largely unknown. The social structure of the Northern Bottlenose Whale (*Hyperoodon ampullatus*) is the best known of all beaked whales [e.g, 105-109]. The Baird's Beak Whale (*Berardius bairdii*) is believed to live in stable groups where males may perform parental care [e.g., 86,110, 111]. However, other sources suggest these species live in fission-fusion societies [51]. However both sources report anecdotal evidence and long-term studies are necessary. The social structure of other beaked whales is largely unknown. In terms of tonal sounds, Winn *et al.* (1970) [112] reported whistles in *H. ampullatus*, but it appears to be the general consensus that this species does not produce tonal sounds [e.g. 109, Whitehead pers. comn. 2005]. Tonal sounds have been reported as well in the Cuvier's beaked whale, *Ziphius cavirostris* by Manghi *et al.* (1999) [113] but other acoustic studies only recorded pulsed sounds [e.g., 114,115]. The only beaked whales for which tonal sounds have been reported are the Baird's Beaked Whale [52] and the Arnoux's Beaked whale (*Berardius arnuxii*) [51]. There is some possibility that the recordings of Dawson *et al.* (1998) [52] were of a sympatric dolphin species (Dawson pers. comm.), however, the recordings of Rogers and Brown (1999) [51] seem conclusive.

Inia, *Platanista*, *Lipotes, Orcaella, Neophocaena* live in freshwater environments. Generally riverine species are considered solitary, however in some areas these species are often seen forming small groups [see Appendix 1 and respective references]. Although, most authors describe group member interactions in riverine species as weak, there is really little knowledge about their societies. In terms of sound production, like the rest of the family (Phocoeenidae) [2], *Neophocaena* does not produce tonal sounds instead the species emits burst pulses under social context [2]. Tonal sounds have been described for two of the subspecies of *Inia geoffrensis, Lipotes vexillifer* [see Appendix 7], but not for *Pontoporia* [116]. Mizue *et al.* (1971) [117] reported whistles from *Platanista gangetica,* recorded in captive conditions. However, it is not clear if the animals were acoustically isolated from another riverine dolphin (*I. geoffrensis*), which produces tonal sounds.

The dolphins *Lagenorhynchus cruciger, L. australis*, *Lissodelphis* spp, *Steno bredanensis*, *Feresa attenuata,* and *Peponocephala electra* social structure is largely unknown. Most available information comes from stranding and anecdotic information. Although Fish and Turl (1976) [118] documented whistles in *Lissodelphis* spp., recent work did not find whistles (Oswald pers. comn). No published accounts on tonal sounds for *Feresa* and *L. cruciger* were found. May-Collado and Agnarsson (2006) [58] predict that *L. cruciger* may not emit whistles as it nests within a clade of species that do not.

Phylogenetic uncertainty

Taking phylogenetic relationships among species into account is crucial for hypotheses testing in comparative biology. However, this is no simple procedure – phylogenies themselves are merely hypotheses and for any given comparative study the number of possible alternative phylogenetic arrangements grows exponentially with the number of species being considered. The key question then becomes, how dependent are our conclusions on the choice of phylogeny? Do the results remain mostly unchanged—implying robustness to phylogenetic uncertainty—or do they change when tests are run on alternative “reasonable” phylogenies. Alternative phylogenies can come from several sources, e.g. from previously published independent phylogenetic studies, or from the set of near-optimal trees from a given analysis, e.g. each unique tree from the post burnin set of a Bayesian analysis. If the results of the comparative analyses are different under some of the alternative phylogenies we have not rejected our conclusions but we have been cautioned that the conclusions are dependent on the chosen phylogeny and may be altered as new phylogenetic data become available. If, however, the results are the same across the set of alternative phylogenies then confidence is gained in the conclusions. Here, we attempt to account for phylogenetic uncertainty using various approaches.

The total number of trees in the post-burnin set from the Bayesian analysis is 2000. Instead of basing sensitivity analyses on the 95% credibility set (which includes a number of trees that contradict all recent studies of whale phylogenetics) we use all the post burnin trees filtered based on various constraints reflecting external phylogenetic evidence. This filtering reduces the number of trees facilitating analyses, without much risk of compromising concerns for phylogenetic uncertainty as the constrained clades are, by any standard, uncontroversial. Rather, considering trees that contradict all available phylogenetic evidence would seem more likely to be misleading than useful. Here, we (1) ran analyzes across the post-burnin set of trees from May-Collado et al. (2007) [59] filtered by constraining major clades all recent phylogenetic studies of Cetacea agree have supported (see below), and (2) using subsets of the post-burnin trees filtered so as to be congruent with other recently published phylogenetic hypotheses of cetaceans chosen as they are based on various types of data: morphological/palaentological (Geisler 2003) [119], mitogenomic (Arnason et al. 2004) [53], a combination of molecular and morphological data (Messenger and McGuire 1998) [61] and SINE's (Nikaido et al. 2001) [62]. We chose to use previously published phylogenies as guides to filter trees from the Bayesian post-burnin tree set, rather than to use them directly for analyses (but see below). This is simply because each of these phylogenies contains only a small subset of cetacean species making them poor for the purposes of comparative analyses. Nevertheless, they represent relatively well supported and conflicting hypotheses on the interrelationships of some of the major cetacean clades, whose resolution may impact the findings of our study. Finally, we ran analyses on trees resulting from re-analyses of the Messenger and McGuire dataset, which is the most taxon-rich previously published phylogeny.

We constructed constraint trees in McClade [see Appendix 2] representing each of the previously published phylogeny (see above) and filtered trees from the post-burnin set based on these constraint trees. The constraint trees merely reflect the interrelationships of major clades (families and more inclusive clades, [see Appendix 2]). Species level relationships are not constrained as most of the studies include very few species so that they represent poor tests of lower level phylogenetic structure. Finally, we produced one constraint tree representing only clades that all the previously published studies agree on. This filtering process produced the following datasets: Arnason constraint set (325 trees), Nikaido constraint set (341 trees), Messenger and McGuire constraint set (4 trees), and the all study agreement constraint set (1069 trees). None of the post-burnin trees were congruent with the hypothesis of Geisler (2003) [119]. In fact all other recent molecular, morphological, and combined analyses refute aspects of that hypothesis, in particular the monophyly of all river dolphins (other studies all agree that

Platanista is not closely related to the remaining river dolphins), and the monophyly of Physeteroidea (other studies refute the sister relationships of Ziphiidae and Physeteridae). Hence we did not further consider that hypothesis, although it played a role in the construction of the ‘all study agreement’ subset.

SIMMAP analyses were run across all trees in each subset, while PDAP analyses were conducted on the majority rule tree (using contype=allcompat) of each of the subsets. Furthermore, parsimony ancestral character reconstructions were examined on each of the majority rule trees and across all trees from the all study agreement tree subset.

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Table 8. Definitions of sociality and tonal sound characters and respective states

Sociality-Broad Concept Approach				
Character/States	**0**	**1**	**2**	**3**
Sociality	Species do not live in groups. Mainly found singly or in pairs. Pairs are primarily mother with their calf. Sometimes groups may form but these are temporal (e.g., breeding, feeding, or migration) and do not show any social structure apart from that of mother and calf	Group living species. In addition to mother and calf associations animals are continuously associating with other conspecific. These associations may be short or long-term. Animals within a group may or not be related. Living singly is extremely rare within this species and it is probably limited to old or outcast animals.		
Social Structure	Solitary species with strong social bonds limited to the time the calf is dependent of the mother. Animals may aggregate for breeding, feeding, or migration but associations are limited to the duration of these periods. Groups are not socially structured	Group living species where all group members show weak or fluid associations. Both sexes disperse from natal group.	Group living species. Group members show fluid associations but may have long-term associations with specific group members that are not close relatives e.g, male alliances and coalitions. Both sexes disperse from natal group.	Group living species. Group members are close relatives. Natal philopatry is sex dependent but in some species there is no dispersion. Long-term associations.
Sociality-Multi Component Approach				
Group Type	Species described as largely solitary, but that are often found in pairs (mother-calf)	Group living species that are generally found in small groups	Group living species that are generally found in medium to large size schools	
Group Stability/Associations	Short when found in non-socially structured groups. Limited to the time the calf is dependent of the mother.	Species where group stability is short. Animals join and leave the group through the day. Described in literature as fluid societies.	Species with fluid societies but were some conspecific group show relatively long lasting associations e.g., male alliances, female nurseries	Species that live in their natal group for life. Animals are related to group members and dispersal is limited showing long-lasting associations
Group Composition	Mother and calf	Segregated by age and sex	Mixed (contain both sexes and several ages)	Both segregated and mixed (state only used for the test of association not for optimizations)
Tonal Sound Complexity Discrete Approach				
Tonal Sound Complexity (2-state)	Mean inflection point is less or equal to 1	Mean inflection point is more than 1		
Tonal Sound Complexity (2-state)	Mean inflection point is between 0-1	Mean inflection point is between 1.1-2	Mean inflection point is between 2.1-3	Mean inflection point is more than 3.1

Table 9. Probabilities of association between sociality (selecting the highest social state for polymorphic species) and tonal sound complexity. Significant positive associations at p-values >0.972 and 0.973** for two and four state complexity characters, respectively and significant negative associations at p-values <0.028 and 0.027* for two and four state complexity characters, respectively

Tonal Sound Complexity [two & four state character]	Social Structure [four state character]			
	0	1	2	3
0 (≤ 1 mean inflection point) *D-statistic* *p-value*	0.0821 0.798	0.0536 0.728	-0.0424 p<0.0001*	-0.0047 0.003*
1 (≤ 1 mean inflection point) *D-statistic* *p-value*	-0.0440 p<0.0001*	0.00045 0.90	0.113 0.99**	0.0360 0.99**
0 (0-1) *D-statistic* *p-value*	0.084 0.93	-0.00029 0.055	-0.0338 0.002*	0.009 0.88
1 (1.1-2) *D-statistic* *p-value*	-0.038 0.002*	0.027 0.91	0.0781 0.92	0.022 0.92
2 (2.1-3) *D-statistic* *p-value*	-0.003 0.018*	0.0121 0.89	0.0198 0.91	-0.0033 0.014*
3 (>3.1) *D-statistic* *p-value*	-0.0046 0.012*	0.0151 0.90	0.0065 0.86	0.0023 0.84

*Significant negative associations **Significant positive associations

D=0.362 p<0.0001, $n_{p\text{-value}}$=1465, n_D=2000 Social Structure and Tonal Sound Complexity (4-state)

D=0.376 p<0.0001 $n_{p\text{-value}}$=343, n_D=2000 Social Structure and Tonal Sound Complexity (2-state)

FIG. 11

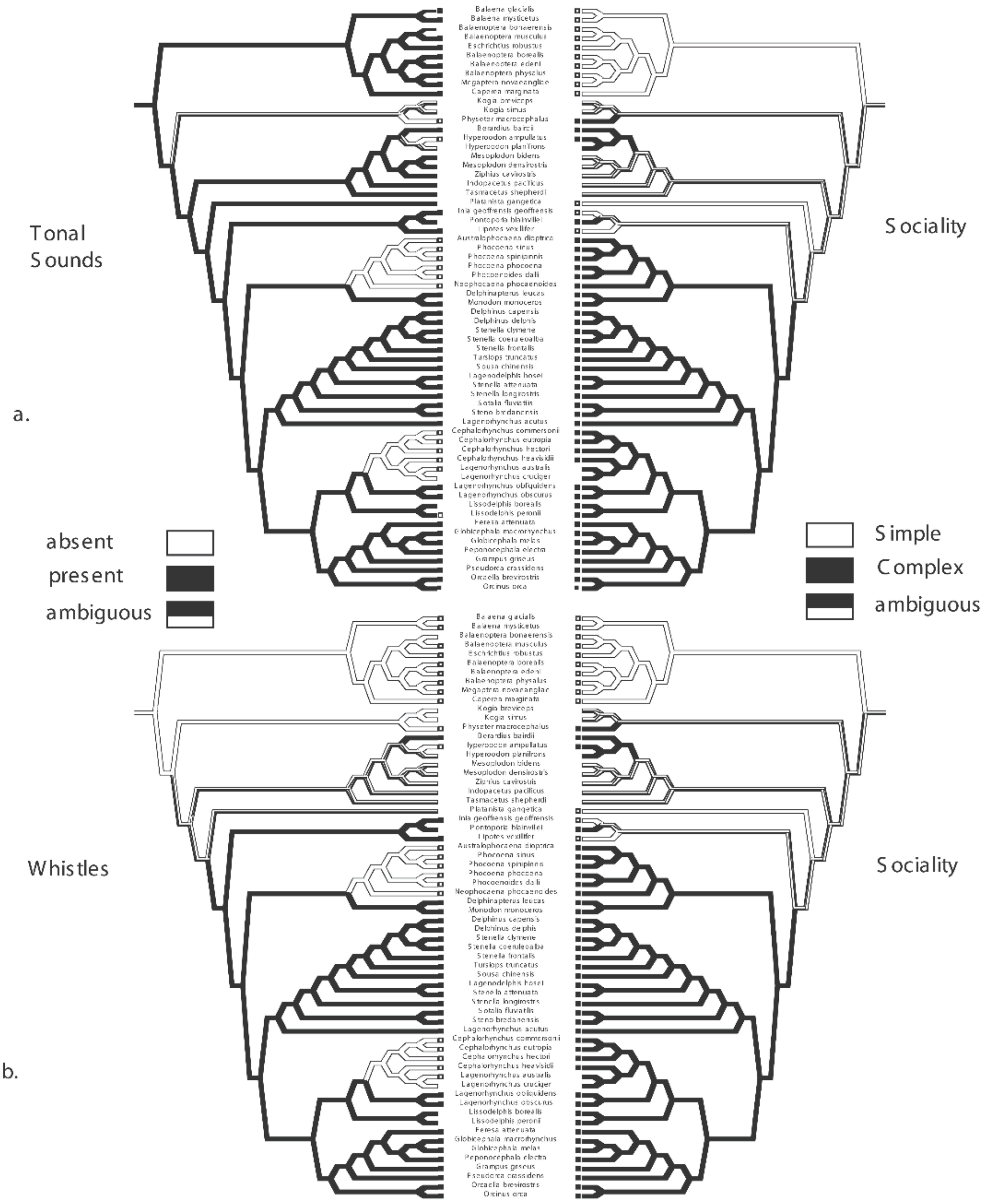
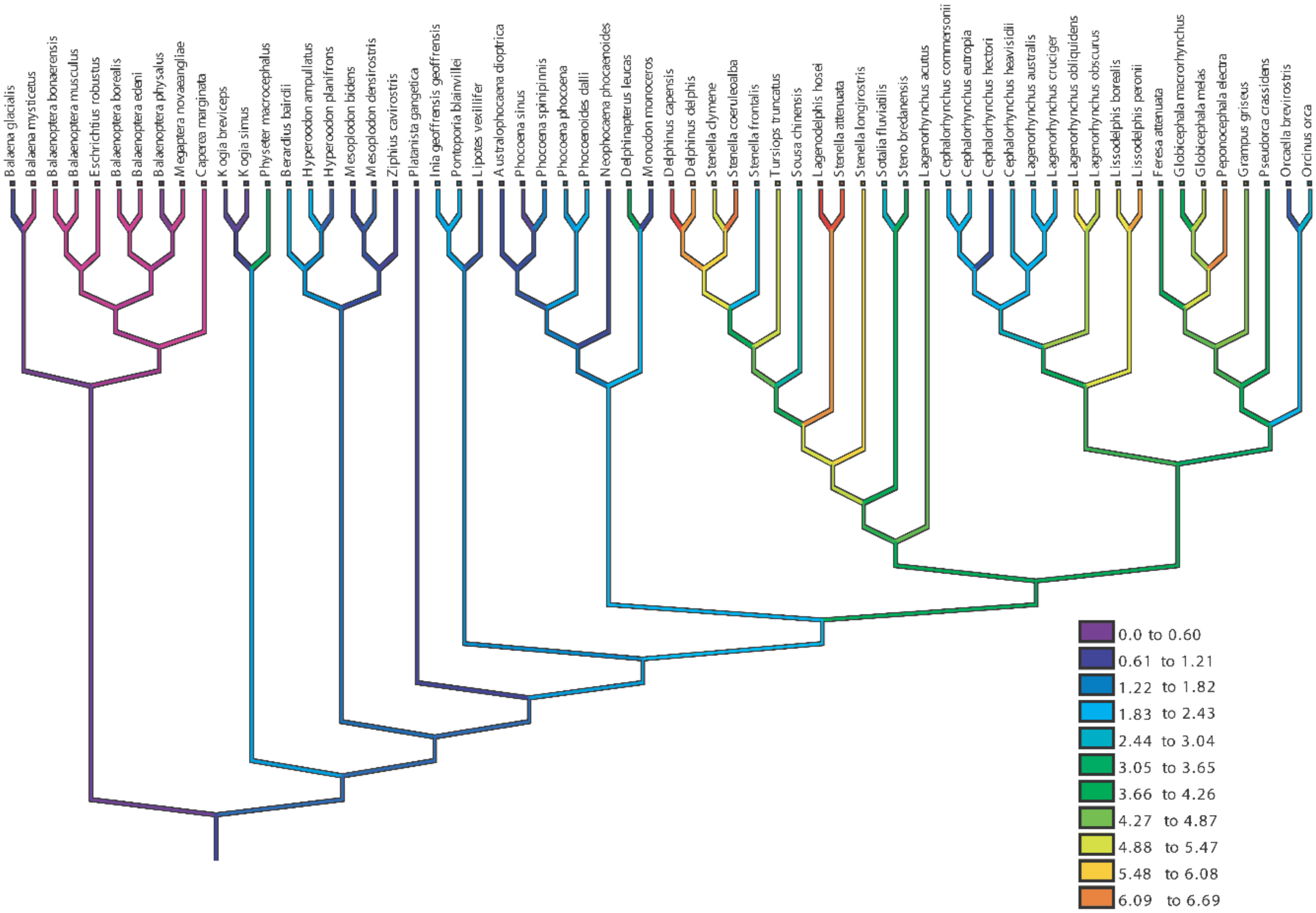

Tonal Sounds
Sociality
a.
absent
present
ambiguous
Simple
Complex
ambiguous
Balaena glacialis
Balaena mysticetus
Balaenoptera bonaerensis
Balaenoptera musculus
Eschrichtius robustus
Balaenoptera borealis
Balaenoptera edeni
Balaenoptera physalus
Megaptera novaeangliae
Caperea marginata
Kogia breviceps
Kogia simus
Physeter macrocephalus
Berardius bairdii
Hyperoodon ampullatus
Hyperoodon planifrons
Mesoplodon bidens
Mesoplodon densirostris
Ziphius cavirostris
Indopacetus pacificus
Tasmacetus shepherdi
Platanista gangetica
Inia geoffrensis geoffrensis
Pontoporia blainvillei
Lipotes vexillifer
Australophocaena dioptrica
Phocoena sinus
Phocoena spinipinnis
Phocoena phocoena
Phocoenoides dalli
Neophocaena phocaenoides
Delphinapterus leucas
Monodon monoceros
Delphinus capensis
Delphinus delphis
Stenella clymene
Stenella coeruleoalba
Stenella frontalis
Tursiops truncatus
Sousa chinensis
Lagenodelphis hosei
Stenella attenuata
Stenella longirostris
Sotalia fluviatilis
Steno bredanensis
Lagenorhynchus acutus
Cephalorhynchus commersonii
Cephalorhynchus eutropia
Cephalorhynchus hectori
Cephalorhynchus heavisidii
Lagenorhynchus australis
Lagenorhynchus cruciger
Lagenorhynchus obliquidens
Lagenorhynchus obscurus
Lissodelphis borealis
Lissodelphis peronii
Feresa attenuata
Globicephala macrorhynchus
Globicephala melas
Peponocephala electra
Grampus griseus
Pseudorca crassidens
Orcaella brevirostris
Orcinus orca
Whistles
Sociality
b.
Balaena glacialis
Balaena mysticetus
Balaenoptera bonaerensis
Balaenoptera musculus
Eschrichtius robustus
Balaenoptera borealis
Balaenoptera edeni
Balaenoptera physalus
Megaptera novaeangliae
Caperea marginata
Kogia breviceps
Kogia simus
Physeter macrocephalus
Berardius bairdii
Hyperoodon ampullatus
Hyperoodon planifrons
Mesoplodon bidens
Mesoplodon densirostris
Ziphius cavirostris
Indopacetus pacificus
Tasmacetus shepherdi
Platanista gangetica
Inia geoffrensis geoffrensis
Pontoporia blainvillei
Lipotes vexillifer
Australophocaena dioptrica
Phocoena sinus
Phocoena spinipinnis
Phocoena phocoena
Phocoenoides dalli
Neophocaena phocaenoides
Delphinapterus leucas
Monodon monoceros
Delphinus capensis
Delphinus delphis
Stenella clymene
Stenella coeruleoalba
Stenella frontalis
Tursiops truncatus
Sousa chinensis
Lagenodelphis hosei
Stenella attenuata
Stenella longirostris
Sotalia fluviatilis
Steno bredanensis
Lagenorhynchus acutus
Cephalorhynchus commersonii
Cephalorhynchus eutropia
Cephalorhynchus hectori
Cephalorhynchus heavisidii
Lagenorhynchus australis
Lagenorhynchus cruciger
Lagenorhynchus obliquidens
Lagenorhynchus obscurus
Lissodelphis borealis
Lissodelphis peronii
Feresa attenuata
Globicephala macrorhynchus
Globicephala melas
Peponocephala electra
Grampus griseus
Pseudorca crassidens
Orcaella brevirostris
Orcinus orca

FIG. 12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Balaena mysticetus
Balaenoptera bonaerensis
Balaenoptera musculus
Eschrichtius robustus
Balaenoptera borealis
Balaenoptera edeni
Balaenoptera physalus
Megaptera novaeangliae
Caperea marginata
Kogia breviceps
Kogia simus
Physeter macrocephalus
Berardius bairdii
Hyperoodon ampullatus
Hyperoodon planifrons
Mesoplodon bidens
Mesoplodon densirostris
Ziphius cavirostris
Platanista gangetica
Inia geoffrensis geoffrensis
Pontoporia blainvillei
Lipotes vexillifer
Australophocaena dioptrica
Phocoena sinus
Phocoena spinipinnis
Phocoena phocoena
Phocoenoides dalli
Neophocaena phocaenoides
Delphinapterus leucas
Monodon monoceros
Delphinus capensis
Delphinus delphis
Stenella clymene
Stenella coeruleoalba
Stenella frontalis
Tursiops truncatus
Sousa chinensis
Lagenodelphis hosei
Stenella attenuata
Stenella longirostris
Sotalia fluviatilis
Steno bredanensis
Lagenorhynchus acutus
Cephalorhynchus commersonii
Cephalorhynchus eutropia
Cephalorhynchus hectori
Cephalorhynchus heavisidii
Lagenorhynchus australis
Lagenorhynchus cruciger
Lagenorhynchus obliquidens
Lagenorhynchus obscurus
Lissodelphis borealis
Lissodelphis peronii
Feresa attenuata
Globicephala macrorhynchus
Globicephala melas
Peponocephala electra
Grampus griseus
Pseudorca crassidens
Orcaella brevirostris
Orcinus orca
0.0 to 0.60
0.61 to 1.21
1.22 to 1.82
1.83 to 2.43
2.44 to 3.04
3.05 to 3.65
3.66 to 4.26
4.27 to 4.87
4.88 to 5.47
5.48 to 6.08
6.09 to 6.69

FIG. 13

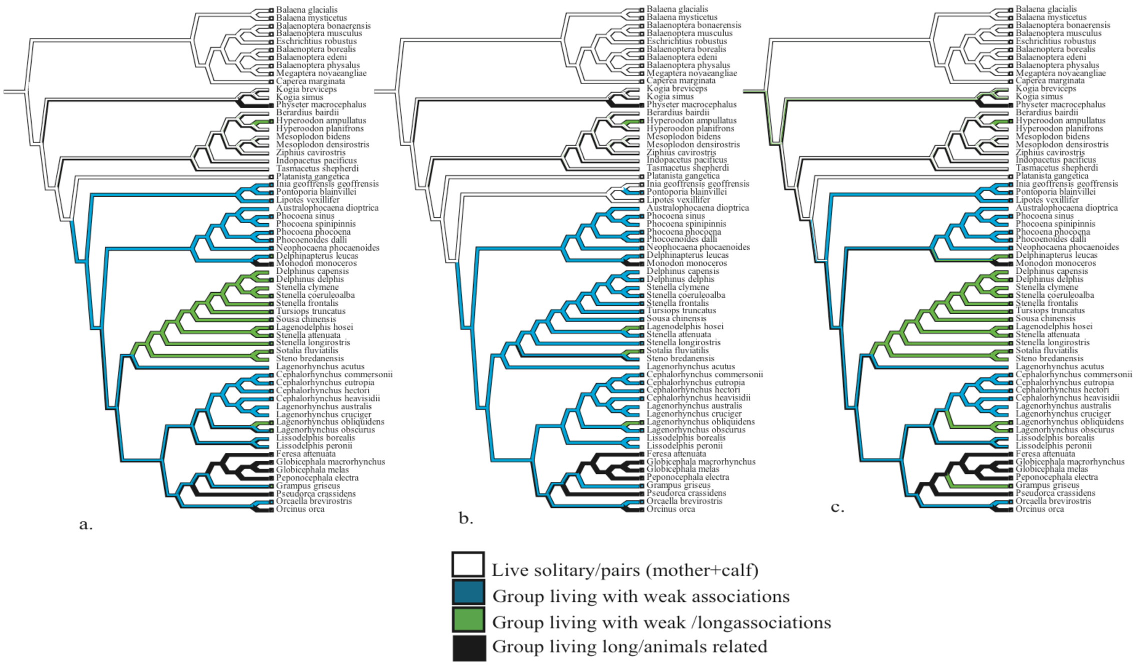

Balaena glacialis
Balaena mysticetus
Balaenoptera bonaerensis
Balaenoptera musculus
Eschrichtius robustus
Balaenoptera borealis
Balaenoptera edeni
Balaenoptera physalus
Megaptera novaeangliae
Caperea marginata
Kogia breviceps
Kogia simus
Physeter macrocephalus
Berardius bairdii
Hyperoodon ampullatus
Hyperoodon planifrons
Mesoplodon bidens
Mesoplodon densirostris
Ziphius cavirostris
Indopacetus pacificus
Tasmacetus shepherdi
Platanista gangetica
Inia geoffrensis geoffrensis
Pontoporia blainvillei
Lipotes vexillifer
Australophocaena dioptrica
Phocoena sinus
Phocoena spinipinnis
Phocoena phocoena
Phocoenoides dalli
Neophocaena phocaenoides
Delphinapterus leucas
Monodon monoceros
Delphinus capensis
Delphinus delphis
Stenella clymene
Stenella coeruleoalba
Stenella frontalis
Tursiops truncatus
Sousa chinensis
Lagenodelphis hosei
Stenella attenuata
Stenella longirostris
Sotalia fluviatilis
Steno bredanensis
Lagenorhynchus acutus
Cephalorhynchus commersonii
Cephalorhynchus eutropia
Cephalorhynchus hectori
Cephalorhynchus heavisidii
Lagenorhynchus australis
Lagenorhynchus cruciger
Lagenorhynchus obliquidens
Lagenorhynchus obscurus
Lissodelphis borealis
Lissodelphis peronii
Feresa attenuata
Globicephala macrorhynchus
Globicephala melas
Peponocephala electra
Grampus griseus
Pseudorca crassidens
Orcaella brevirostris
Orcinus orca
a.
b.
c.
Live solitary/pairs (mother+calf)
Group living with weak associations
Group living with weak /longassociations
Group living long/animals related

FIG. 14

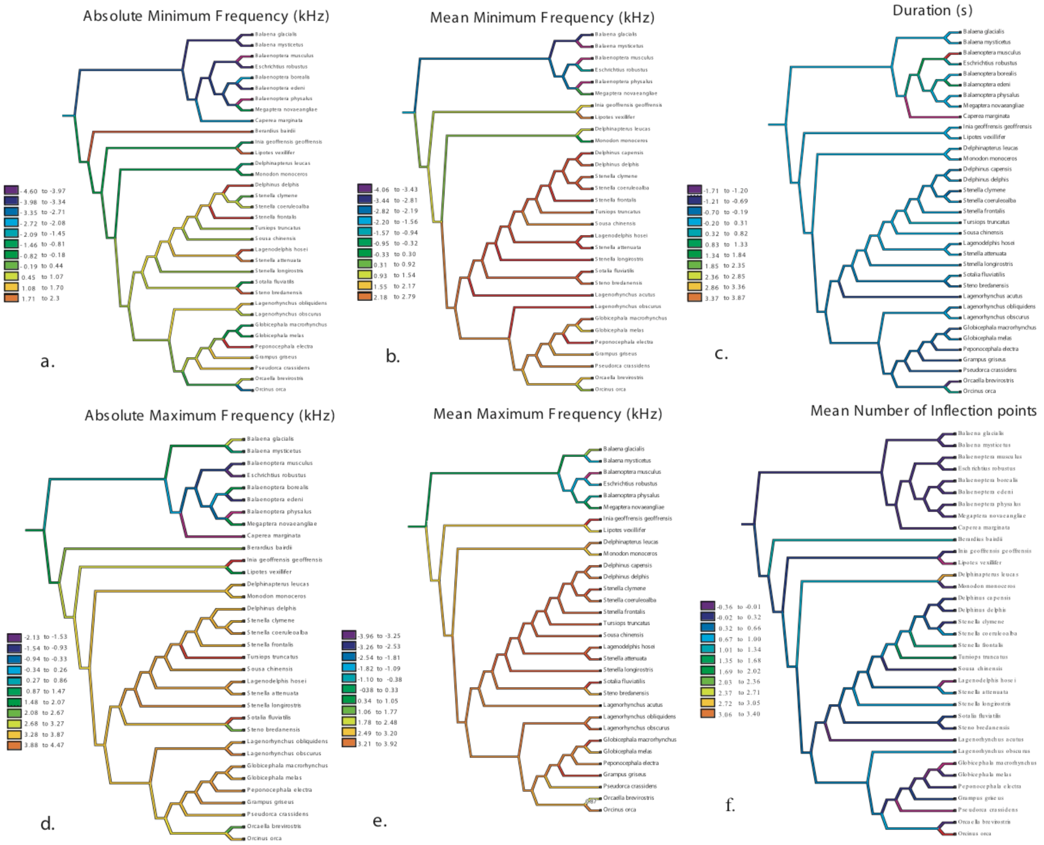
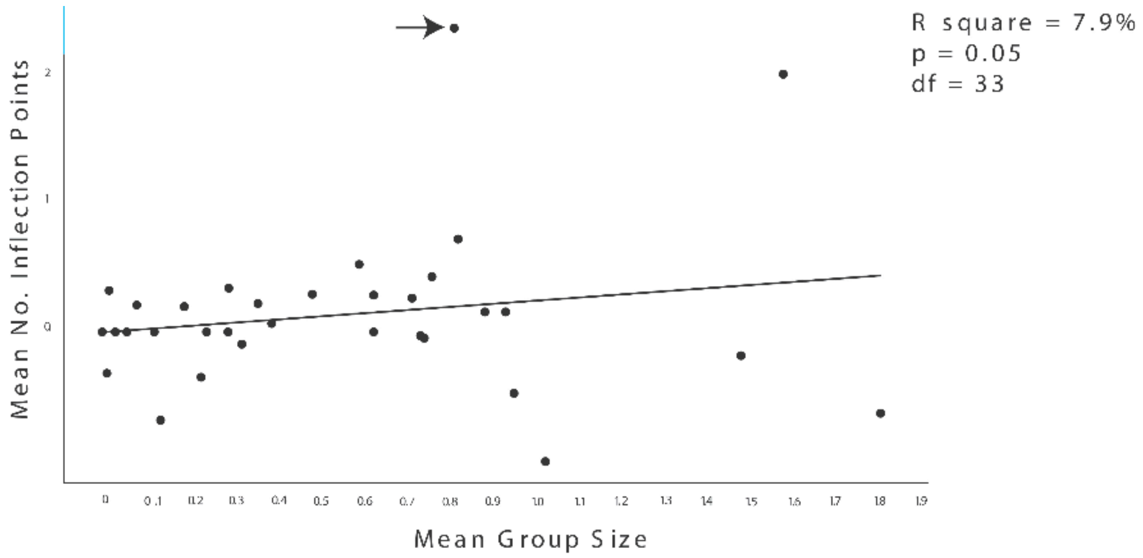

Absolute Minimum Frequency (kHz)
Balaena glacialis
Balaena mysticetus
Balaenoptera musculus
Eschrichtius robustus
Balaenoptera borealis
Balaenoptera edeni
Balaenoptera physalus
Megaptera novaeangliae
Caperea marginata
Berardius bairdii
Inia geoffrensis geoffrensis
Lipotes vexillifer
Delphinapterus leucas
Monodon monoceros
Delphinus delphis
Stenella clymene
Stenella coeruleoalba
Stenella frontalis
Tursiops truncatus
Sousa chinensis
Lagenodelphis hosei
Stenella attenuata
Stenella longirostris
Sotalia fluviatilis
Steno bredanensis
Lagenorhynchus obliquidens
Lagenorhynchus obscurus
Globicephala macrorhynchus
Globicephala melas
Peponocephala electra
Grampus griseus
Pseudorca crassidens
Orcaella brevirostris
Orcinus orca
- 4.60 to -3.97
- 3.98 to -3.34
- 3.35 to -2.71
- 2.72 to -2.08
- 2.09 to -1.45
- 1.46 to -0.81
- 0.82 to -0.18
- 0.19 to 0.44
0.45 to 1.07
1.08 to 1.70
1.71 to 2.3
a.
Mean Minimum Frequency (kHz)
Balaena glacialis
Balaena mysticetus
Balaenoptera musculus
Eschrichtius robustus
Balaenoptera physalus
Megaptera novaeangliae
Inia geoffrensis geoffrensis
Lipotes vexillifer
Delphinapterus leucas
Monodon monoceros
Delphinus capensis
Delphinus delphis
Stenella clymene
Stenella coeruleoalba
Stenella frontalis
Tursiops truncatus
Sousa chinensis
Lagenodelphis hosei
Stenella attenuata
Stenella longirostris
Sotalia fluviatilis
Steno bredanensis
Lagenorhynchus acutus
Lagenorhynchus obscurus
Globicephala macrorhynchus
Globicephala melas
Peponocephala electra
Grampus griseus
Pseudorca crassidens
Orcaella brevirostris
Orcinus orca
-4.06 to -3.43
-3.44 to -2.81
-2.82 to -2.19
-2.20 to -1.56
-1.57 to -0.94
-0.95 to -0.32
-0.33 to 0.30
0.31 to 0.92
0.93 to 1.54
1.55 to 2.17
2.18 to 2.79
b.
Duration (s)
Balaena glacialis
Balaena mysticetus
Balaenoptera musculus
Eschrichtius robustus
Balaenoptera borealis
Balaenoptera edeni
Balaenoptera physalus
Megaptera novaeangliae
Caperea marginata
Inia geoffrensis geoffrensis
Lipotes vexillifer
Delphinapterus leucas
Monodon monoceros
Delphinus capensis
Delphinus delphis
Stenella clymene
Stenella coeruleoalba
Stenella frontalis
Tursiops truncatus
Sousa chinensis
Lagenodelphis hosei
Stenella attenuata
Stenella longirostris
Sotalia fluviatilis
Steno bredanensis
Lagenorhynchus acutus
Lagenorhynchus obliquidens
Lagenorhynchus obscurus
Globicephala macrorhynchus
Globicephala melas
Peponocephala electra
Grampus griseus
Pseudorca crassidens
Orcaella brevirostris
Orcinus orca
-1.71 to -1.20
-1.21 to -0.69
-0.70 to -0.19
-0.20 to 0.31
0.32 to 0.82
0.83 to 1.33
1.34 to 1.84
1.85 to 2.35
2.36 to 2.85
2.86 to 3.36
3.37 to 3.87
c.
Absolute Maximum Frequency (kHz)
Balaena glacialis
Balaena mysticetus
Balaenoptera musculus
Eschrichtius robustus
Balaenoptera borealis
Balaenoptera edeni
Balaenoptera physalus
Megaptera novaeangliae
Caperea marginata
Berardius bairdi
Inia geoffrensis geoffrensis
Lipotes vexillifer
Delphinapterus leucas
Monodon monoceros
Delphinus delphis
Stenella clymene
Stenella coeruleoalba
Stenella frontalis
Tursiops truncatus
Sousa chinensis
Lagenodelphis hosei
Stenella attenuata
Stenella longirostris
Sotalia fluviatilis
Steno bredanensis
Lagenorhynchus obliquidens
Lagenorhynchus obscurus
Globicephala macrorhynchus
Globicephala melas
Peponocephala electra
Grampus griseus
Pseudorca crassidens
Orcaella brevirostris
Orcinus orca
-2.13 to -1.53
-1.54 to -0.93
-0.94 to -0.33
-0.34 to 0.26
0.27 to 0.86
0.87 to 1.47
1.48 to 2.07
2.08 to 2.67
2.68 to 3.27
3.28 to 3.87
3.88 to 4.47
d.
Mean Maximum Frequency (kHz)
Balaena glacialis
Balaena mysticetus
Balaenoptera musculus
Eschrichtius robustus
Balaenoptera physalus
Megaptera novaeangliae
Inia geoffrensis geoffrensis
Lipotes vexillifer
Delphinapterus leucas
Monodon monoceros
Delphinus capensis
Delphinus delphis
Stenella clymene
Stenella coeruleoalba
Stenella frontalis
Tursiops truncatus
Sousa chinensis
Lagenodelphis hosei
Stenella attenuata
Stenella longirostris
Sotalia fluviatilis
Steno bredanensis
Lagenorhynchus acutus
Lagenorhynchus obliquidens
Lagenorhynchus obscurus
Globicephala macrorhynchus
Globicephala melas
Peponocephala electra
Grampus griseus
Pseudorca crassidens
Orcaella brevirostris
Orcinus orca
-3.96 to -3.25
-3.26 to -2.53
-2.54 to -1.81
-1.82 to -1.09
-1.10 to -0.38
-038 to 0.33
0.34 to 1.05
1.06 to 1.77
1.78 to 2.48
2.49 to 3.20
3.21 to 3.92
e.
Mean Number of Inflection points
Balaena glacialis
Balaena mysticetus
Balaenoptera musculus
Eschrichtius robustus
Balaenoptera borealis
Balaenoptera edeni
Balaenoptera physalus
Megaptera novaeangliae
Caperea marginata
Berardius bairdi
Inia geoffrensis geoffrensis
Lipotes vexillifer
Delphinapterus leucas
Monodon monoceros
Delphinus capensis
Delphinus delphis
Stenella clymene
Stenella coeruleoalba
Stenella frontalis
Tursiops truncatus
Sousa chinensis
Lagenodelphis hosei
Stenella attenuata
Stenella longirostris
Sotalia fluviatilis
Steno bredanensis
Lagenorhynchus acutus
Lagenorhynchus obscurus
Globicephala macrorhynchus
Globicephala melas
Peponocephala electra
Grampus griseus
Pseudorca crassidens
Orcaella brevirostris
Orcinus orca
-0.36 to -0.01
-0.02 to 0.32
0.32 to 0.66
0.67 to 1.00
1.01 to 1.34
1.35 to 1.68
1.69 to 2.02
2.03 to 2.36
2.37 to 2.71
2.72 to 3.05
3.06 to 3.40
f.

FIG. 15


R square = 7.9%
p = 0.05
df = 33
Mean No. Inflection Points
2
1
0
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1.1
1.2
1.3
14
15
1.6
17
18
1.9
Mean Group Size

CHAPTER VI

GEOGRAPHICAL WHISTLE VARIATION BETWEEN ADJACENT BOTTLENOSE DOLPHIN POPULATIONS

LAURA J. MAY-COLLADO[1,2] AND DOUGLAS WARTZOK[1]

[1]Florida International University, Department of Biological Sciences, 11200 SW 8th Street, Miami, FL 33199, USA

[2]Universidad de Costa Rica, Escuela de Biología, Apto. 2060 San Pedro, Costa Rica

ABSTRACT

Whistles are narrowband and frequency modulated sound produced by many cetaceans. These sounds have been extensively studied in delphinids. Several factors have been proposed to explain between- and within-species variation in whistles. This study aims to bring insight in micro-geographic whistle variation of two bottlenose dolphin populations (Bocas del Toro, Panama vs. Gandoca Manzanillo, Costa Rica) by assessing several factors e.g., habitat acoustic characteristics (ambient and anthropogenic), sympatry with other dolphin species, and intrinsic differences between populations due to variation in behavioral activities and/or distance between populations in some cases leading to isolation. Our results show that the two adjacent populations are distinct in both frequency and temporal whistle parameters. The differences in the mean values of each whistle parameter between these adjacent populations were no smaller than differences between those and more distant populations in the north and south. There were no apparent trends in increasing or decreasing whistle frequency with latitude as shown for other dolphin species. We found that a combination of factors may contribute to the significant differences found between these two adjacent (~35 km apart) populations. Isolation or relatively low mixing of populations may be important. An ongoing photo-ID of these dolphins has hitherto not found any matches between populations. The acoustical structure of their habitat also may play a role. Bocas del Toro has a higher boat traffic rate but lower overall low frequency ambient noise levels. Dolphins produced whistles with characteristics that may help them to cope with their respective environmental noises. While dolphins from Bocas emit longer whistles (maybe to avoid masking by high-frequency boats), dolphins from Gandoca-Manzanillo emit high frequency whistles (perhaps to avoid masking by low frequency ambient noise levels). Sympatry with *Sotalia guianensis* also may be a factor. However, if this sympatry has an effect, it is in the opposite direction than predicted by the 'species hypothesis'. Bottlenose dolphins sympatric with *Sotalia* produce whistles that are more similar to *Sotalia* whistles than are the whistles of non-sympatric bottlenose dolphins. Finally, behavior may be an important source of within population variation. Populations may vary in their investment in different activities. The results of this study suggest that bottlenose dolphin whistles are plastic and influenced by a variety of factors. Isolated populations can be expected to be locally adapted and thus differ from other isolated populations.

KEY WORDS: ambient noise, isolation, boat traffic, behavior, zoogeography, sympatry

INTRODUCTION

Most toothed whales emit frequency modulated tonal sounds that are narrowband in frequency (with most of their energy below 20 kHz) (Au 2000, Richardson *et al.* 1995). These signals are produced under a variety of social contexts. In true dolphins (Delphinidae), tonal sounds are typically referred to as whistles, and are emitted especially during social interactions that involve group cohesion, individual recognition, and recruitment during feeding activities (e.g. Caldwell and Caldwell 1965, 1990, Sayigh *et al.* 1995, Janik *et al.* 1994, Janik 2000, Acevedo-Gutierrez and Stienessen 2004).

Whistle interspecific variation occurs primarily in frequency variables (e.g., Steiner 1981, Wang *et al.* 1995b, Rendell *et al.* 1999, Matthews *et al.* 1999). Several factors have been proposed to explain frequency variation across species, including phylogeny, sociality, zoogeography, and morphological constraints. Recent comparative phylogenetic studies May-Collado *et al.* (2007a-b) examined the evolution of some frequency components in Cetacean tonal sounds. Their findings suggest that the evolution of minimum frequency in Cetaceans appears to be influenced by body size and group size, whereas whistle complexity (measured in terms of mean number of inflection points) was influenced by social structure.

Whistle variation also occurs within species. Several studies have found variation in frequency modulation (mean number of inflection points) and whistle duration (e.g., Wang *et al.* 1995a, Azevedo *et al.* 2005, Morisaka *et al.* 2005a). However, recent studies have also found frequency parameters as key to discriminate between populations (e.g., Morisaka *et al.* 2005a, Azevedo *et al*. 2005, Rossi-Santos and Podos 2006). Such differences have been observed both at micro-geographic scales (between neighboring populations) and macro-geographic scales, between widely separated ones (e.g., Wang *et al.* 1995a, Barzua-Duran and Au 2002, 2004, Azevedo and Sluys 2005, Morisaka *et al.* 2005a, Rossi-Santos and Podos 2006, Azevedo *et al.* 2007, Camargo *et al.* 2007, dos Santos *et al.* 2007, May-Collado and Wartzok 2007). The general pattern suggests greater whistle variation between populations that are further apart (e.g., Wang *et al.* 1995a, Barzua-Duran and Au 2002, 2004, Azevedo and Sluys 2005, Rossi-Santos and Podos 2006). However, a recent study in spinner dolphins found that some populations from the Atlantic and Pacific where more similar than less distant populations (Camargo *et al.* 2007).

In many terrestrial animals (particularly birds) geographic variation in signal structure has provided insights into the dispersal capabilities of species (e.g., Mundinger 1982; McGregor *et al.* 2000), isolation and genetic divergence between groups or populations (e.g., Lemon 1966, McGregor *et al.* 2000, Ford 2002), and adaptation to ecological conditions (e.g., Marler 1960, Brumm 2006, Boncoraglio and Saino 2007, Gillam and McCracken 2007, Peters *et al.* 2007).

The causes of geographical variation in dolphins (and cetaceans in general) are still poorly known. However, recent studies suggest that the acoustic structure of the habitat (which is described in terms of ambient noise, known sources of anthropogenic noise, and the physical structure e.g., bottom substrate, currents, etc) may play an important role in the reported intra-specific whistle variation. Morisaka *et al* (2005b) found that Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) from three populations around Japan differ in their whistle frequency structure (adopted frequencies and coefficient of frequency modulation). Dolphins from the noisiest habitat tended to produce low frequencies whistles with little modulation as potential strategy to avoid masking and attenuation of higher-frequency signals (Morisaka *et al.* 2005b). In contrast, short-beaked common dolphins (*Delphinus delphis*) from the English Channel British Isles, whistled at higher frequency when compared with common dolphins from the Celtic Sea (Ansmann *et al.* 2007). In this case, dolphins emitted high-frequency whistles in the presumably noisiest site (no measurements of ambient noise were taken), the English Channel, where dolphins may avoid masking by the low-frequency ambient noise produced by the high vessel traffic of the area.

Other proposed factors for whistle intraspecific variation include recent isolation events (e.g., in spinner dolphins see Camargo et al. 2007), intra-specific variation in group fluidity or group stability in association patterns (e.g., in spinner dolphins of Hawaii see Barzua-Duran and Au 2002), and zoogeographical relationships (Steiner 1981). Steiner (1981) suggested that sympatric dolphin species would tend to be more different than when they occur separately.

The goal of this study is to evaluate the interaction of some of these factors and whistle acoustic variation between two adjacent populations of bottlenose dolphins (*Tursiops truncatus*) in the southern Caribbean of Central America. We tested the following factors: ambient noise levels, boat traffic, sympatry with the coastal Guyanese dolphin (*Sotalia guianensis*), and intrinsic population in terms of differences due to behavioral states and degree of isolation (distance) by comparing the whistle parameters of these populations with populations in the western north and southern Atlantic.

MATERIAL AND METHODS

Study areas and dolphin populations

The study took place in Gandoca-Manzanillo Wildlife Refuge from 2004 to 2007 and the Archipelago of Bocas del Toro in 2004, 2006, and 2007. Gandoca-Manzanillo Wildlife Reserve is located along the Caribbean coast of Costa Rica, about 35 km north of the Archipielago Bocas del Toro. The Refuge was established in 1985 and includes about 38.33 km of land and sea. It was primarily established to protect coral reefs, mangroves, swamps, and flooded forest. Boat traffic is relatively low. Powered boats are used in the Refuge for local fishing and tourism interested in sport fishing (at the mouth of the Sixaola River) and dolphin watching. Dolphin watching is boat based, and possibly the main reason for boat traffic during high tourist season. There are two small resident populations of dolphin species, the Guyanese dolphin (*Sotalia guianensis*) and the bottlenose dolphin (*Tursiops truncatus*). The species are sympatric within the limits of the Refuge, where they form mixed-species groups regularly (Acevedo *et al.* 2005, Gamboa-Poveda and May-Collado 2006). Preliminary photo-ID suggests that only a part of the identified bottlenose dolphins are resident to the Refuge, most appear to have a more offshore range (May-Collado *et al.* unpublished data).

The Province of Bocas de Toro, Panama covers about 8,745 km. The province consists of several islands including the main island Isla Colon the protected island of Bastimento (under the category of National Park), mainland of Almirante Bay, where the main port of the area is located, Bocas Torito, Tierra Oscura, Punta Laurel, and Cauchero. Some of the islands of the archipelago are somewhat interconnected with the mainland by islets of mangroves (Fig. 10). The main way of transportation between the islands and mainland are powered boats and canoes. In Bocas the resident bottlenose dolphin population is small. Unlike Gandoca-Manzanillo most of the identified dolphins are regularly seen in the area, and also show strong site fidelity within the Archipelago (May-Collado *et al.* unpublished data). No other dolphin species are found in the area. Despite the relatively short distance between the two study areas (35 km) there is no evidence of mixing between the two populations after four years of ongoing research (May-Collado personal observation).

Recordings

Signals were recorded using a broadband system consisting of a RESON hydrophone (-203 dB re 1V/µPa, 1 Hz to 140 kHz) connected to AVISOFT recorder and Ultra Sound Gate 116 (sampling rate 400-500 kHz 16 bit) that sent the signals to a laptop.

Ambient noise was recorded in five stations in Bocas del Toro and in three in Gandoca-Manzanillo (see Fig.16) at 500 and 384 kHz sampling rate. One-minute ambient noise files were recorded every five minutes in a period of 15 minutes at each station and at a known gain level. To calibrate ambient noise level recordings we used a calibrated ITC-1001 sound projector to send 2, 6, 10,14, 18, and 22 kHz sine waves to the recording system. Projector and hydrophone were at distance of 7.3 m. The rms voltage input to the ITC-1001 was measured at each frequency and the received sound level at 7.3 m was calculated based on spherical spreading. We randomly selected 1 sec of the ‘control’ (each of the above frequencies) and join it with 1 sec segment separately with each of the three recorded files with ambient noise (three 2 sec files) of same sampling rate (500 kHz). For ambient noise files with 384 kHz sampling rate we selected 1.3 sec, to compensate for differences in sampling rate with the control (500 kHz), so that both files had the same number of points rather than the same length of time. Each control 1 sec file was joined separately with 1 sec (or 1.3 sec) ambient noise using the software Media Join 1.0 (Mystik Media © 2004-2005). Later the joined files were opened in RAVEN PRO 1.3 beta version build 20 (Cornell Lab of Ornithology 2003-2007 ©). The average relative power in dB for the one second of control and one second of ambient noise were measured. Although RAVEN provides only relative, not absolute, power levels, we knew the actual recorded levels in the control segments and could then calculate the levels of ambient noise.

Dolphin whistles were recorded continuously with a sampling rate between 384-500 kHz. For accompanying behavioral observations, recording sessions were segmented into three-minute intervals. Behavioral observations were made every other interval (group scanning lasted two-three minutes as well) and the predominant behavior during that interval was recorded. The predominant behavior was decided based on the activity of most members in a group. A group was defined as all group members maintaining a distance no more than 10 times their body length and engaged in similar behavioral activities (Smolker *et al.* 1992). However, when several groups were present and relatively close to each other, these were considered the same 'acoustic' group for that particular recording session. This is because we could not associate the recorded signals with their respective group. In this case, the predominant behavior was assigned based on the most common behavior or behaviors in which all groups were engaged. When animals were performing a behavior difficult to assign to any of the below defined categories during a scanning period, the behavior was noted as unknown. Five behavioral categories were defined based on a combination of previous definitions (e.g., Lusseau and Higham 2004, May-Collado and Morales-Ramirez 2005):

(1) *Feeding/Foraging/Diving*: individuals actively searching, pursuing, and/or consuming prey were assigned to this category. Often diving periods were long and involved 'steep dives' where animals arched their backs and lifted the tail vertically before each dive. Direction and distance between animals varied depending on individual or apparent group feeding. (2) *Social activities*: dolphins interacted among themselves e.g., different types of body contact (aggressive and 'friendly'), tail slapping, and animals following the boat or other dolphins. Groups tend to split in small subgroups and sometimes spread over a larger area, or the opposite when small groups reunite in bays and form temporarily large groups. (3) *Traveling*: dolphins swimming either slowly or fast but always maintaining a steady direction, (4) *Resting:* dolphin swimming at a slow speed, surfacing regularly and often synchronically but always within a small area. Often but not always group members where close to each other. (5) *Milling:* group members spaced and showing random directionality during swimming, often slowly and within the same area. Surfacing patterns were variable. (6) *Unknown:* assigned to groups when several factors, such as weather condition, and uncertainty due to elusive behavior by the dolphins would not allow the predominant behavior to be clearly determined.

Whistles were analyzed in RAVEN 1.2 (Cornell Lab of Ornithology 2003-2007 ©) with a FFT size of 1024 points, an overlap of 50%, and using a 512-522 sample Hann window. Nine standard parameters were measured for every highly quality whistle (the entire contour was clearly seen): beginning frequency (Beg), ending frequency (End), minimum frequency (Min), maximum frequency (Max), delta frequency (MaxF—MinF), peak frequency (measured in the whistle contour were intensity was the highest), duration (s), number of inflection points, and number of harmonics. In addition, we followed Morisaka *et al.* (2005b) study by measuring adopted frequencies (McCowan 1995) in order to measure the frequency distribution of a whistle. Nineteen intervals equally distanced were set in every whistle by diving is duration by 20 frequency points (McCowan 1995). These same adopted frequencies were used to calculate a coefficient of frequency modulation (COFM) for each whistle (McCowan and Reiss 1995). The coefficient measures changes in complexity of whistle contour and represents the magnitude of frequency modulation in a whistle. High COFM indicate high frequency modulation (see Morisaka *et al.* 2005b).

$$\mathrm{COFM} = \sum_{(n=1,19)} |\mathrm{Y}_{n+1} - \mathrm{Y}_{n}|/10,000,$$

Where Y_n is the frequency at the *n*th frequency point.

Boat traffic

Boat sighting rate during dolphin encounters for Bocas and Gandoca-Manzanillo has been estimated as 0.66 and 0.21 boat/min (Taubitz 2007). In Bocas a boat is in sight every 1.5 minutes while in Gandoca-Manzanillo every 4.8 minutes (Taubitz 2007). In Bocas boats are used for local transportation, personal, fishing, and for dolphin watching activities and in Gandoca-Manzanillo for local fishing and tourist activities like sport fishing and dolphin-watching. The majority of boats in Bocas are powered with engines between 50-150 hp while in Gandoca-Manzanillo the majority of the boats use engines less than 50 hp (Taubitz 2007). The presence/absence of boats was noted during the recording sessions. When boats were present we also noted the number of boats present in each recording file. The absence of boats in this study refers to the presence of only our research boat. Boat presence was considered as such when a boat was in view within a maximum distance of 500 m or when it was acoustically detectable by our recording equipment (and thus possibly within the acoustic range of the dolphins).

Statistical analysis

The Median nonparametric test, run in JMP 7.0 (SAS Institute Inc. 2007) was used to compare the overall median noise levels between sites and within sites. Standard whistle parameters (Min, Max, Delta, Beg, End, Peak, duration, number of inflection pointes and harmonics), the coefficient of modulation and adopted frequencies were compared between populations using the nonparametric test Mann-Whitney U in SYSTAT 12.0 software (SYSTAT Software, Inc. 2007). With the exception of the variables number of inflection points and harmonics, all whistle parameters were Box-Cox transformed to adjust their distribution to nearly normal (Sokal and Rohlf 1995). Then we (1) compared the coefficient of frequency modulation considering the effect of population, whistle duration and their interaction, and (2) we tested population, behavior, boat presence, and site fidelity (in the case of Bocas dolphins) as factors and evaluate their explanatory power and their interaction when comparing all whistle parameters between populations by analysis of covariance (ANCOVA) in the JMP software (SAS Institute Inc. 2007). The transformed variables were also evaluated using a multivariate discriminant function analysis (with a discriminant linear method) to classify whistles within and between populations and between and within species (using the software JMP 7.0). Within population whistle variation was evaluated across behavioral states and boat presence/absence using the nonparametric tests Kruskal-Wallis and Mann-Whitney U, respectively. Because dolphins in Bocas appear to show strong site fidelity we evaluated if whistle parameters vary across sites using the above statistical tests. Finally, we test if the overlap in home ranges between the bottlenose dolphins and *Sotalia guianensis* from Gandoca-Manzanillo influences whistle variation. In other words is whistle variation between bottlenose dolphins and *Sotalia* from Gandoca-Manzanillo larger than the variation between *Sotalia* and bottlenose dolphins from Bocas. We tested if the differences in means were significantly different between sympatric and non-sympatric dolphins with a χ^2 test.

Finally, we compare the mean values of whistle parameters from our results with other studies by first testing for homogeneity of variances (Levene's F test) and then used a t-test (when variances were equal) or Welch t-test (when variances were unequal). We also tested if the differences in the mean of the various whistle parameters were significantly different between adjacent and the different distant populations with one-way χ^2 test. We tested for the two adjacent populations the hypothesis, Ho=no significant difference, and expected values were calculated dividing the total by the number of parameters being compared).

RESULTS

Comparisons between adjacent populations: A discriminant analysis misclassified only 25.37% of the whistles. A total of 103 out of 128 whistles were correctly assigned to the Bocas population, and 50 out of 77 whistles to Gandoca-Manzanillo. Whistle standard parameters differ significantly between dolphin populations, with the exception of minimum and peak frequency, mean number of harmonics, and the coefficient of modulation (see Table 10 for p-values). In general, Bocas dolphin whistled with lower maximum, delta, and ending frequencies and higher beginning frequency, producing longer whistles, and showing higher mean number of inflection points compared to dolphins from Gandoca-Manzanillo (Fig. 17a-b).

The difference in the Box-Cox transformed adopted frequencies between populations was marginally significant at the 0.05 level ($F=3.88$, $p=0.049$). However, when accounting for the effect of population, behavior, boat presence, and their interaction we found that all interactions affect adopted frequencies: population*behavior (ANCOVA $F=7.30$, $p=0.009$), population*boat presence (ANCOVA $F=7.64$, $p=0.006$), and behavior*boat presence (ANCOVA $F=7.46$, $p<0.0001$).

The coefficient of frequency modulation correlated with duration ($R^2=0.36$, $p<0.0001$, $F=101.84$, $p<0.0001$, Fig.18), but not with population or their interaction. When considering the effect of population, boat presence, behavior and their interactions on whistle standard parameters we found that behavior had a significant effect on the coefficient of frequency modulation (ANCOVA $F=4.93$, $p=0.0081$), duration (ANCOVA $F=4.93$, $p=0.0081$), delta and minimum frequency (ANCOVA $F=3.32$, $p=0.038$, $F=6.04$, p=0.003 respectively), and the interaction between population and behavior on ending frequency (ANCOVA F=3.44, p=0.034).

Comparisons between distant populations: Pairwise comparisons between populations indicate that there are significant differences between bottlenose dolphin whistles from Bocas and Gandoca-Manzanillo and other populations studied in Atlantic (see Tables 11 and 12, Fig. 19). The magnitude of the differences in whistle mean values between the adjacent populations of Bocas and Gandoca-Manzanillo are small ($p>0.05$). Interestingly the same pattern was found between Bocas and each of the distant populations ($p>0.05$). The magnitude of the differences, in whistle mean values were significantly higher (particularly in maximum and ending frequencies) between Gandoca-Manzanillo and Texas (χ^2= 45.91, $p<0.0023$, df=5), Brazil (χ^2= 35.38, $p<0.013$, df=5), and Argentina (χ^2= 40.43, $p<0.009$, df=5).

Factors promoting whistle variation

Sympatry: We tested the hypotheses that bottlenose dolphins living in sympatry with the *Sotalia guianensis* will show significantly greater differences in their whistle parameters mean values relative to *Sotalia guianensis* than will non-sympatric bottlenose dolphins, as predicted by the 'species hypothesis'. The differences in whistle frequency mean values between *Tursiops* and *Sotalia* are significantly larger between sympatric and non-sympatric species (χ^2=1593.8 $p<0.0001$, df=5). However, the trend is opposite as expected by 'species hypothesis'. The differences between *S. guianensis* and bottlenose dolphins from Gandoca-Manzanillo (sympatric) were significantly smaller than those between *S. guianensis* and bottlenose dolphins from Bocas (non-sympatric) (Fig.20).

Behavior: Bocas del Toro dolphins showed significant differences across behavioral states only in minimum frequency (χ^2=16.26, df=4, p=0.0027), ending frequency (χ^2=12.10, df=4, p=0.017), and in adopted frequencies (ANOVA F=10.35, $p<0.0001$). Minimum frequency was higher during foraging and resting, and ending frequency was higher during foraging (Fig. 21a). Adopted frequencies were significantly higher during foraging than during traveling and social activities, but not when the animals were milling or resting. No significant differences were found in other whistle parameters.

Gandoca-Manzanillo dolphins whistled with significantly greater modulation during traveling than foraging (ANOVA F=3.73, p=0.029). Dolphins emitted whistles with a greater mean number of harmonics (χ^2=10.43, df=2, p=0.005) during social activities, and when engaged in foraging activities they whistled with lower delta frequency than during social and traveling activities (χ^2=6.22, df=2, p=0.044) (Fig. 21b). No significant differences were found between other standard whistle parameters, adopted frequencies and behavioral states.

Site fidelity: Dolphins from different sites within Bocas showed significant differences in frequency whistle parameters. Dolphins recorded from Bocas Torito whistled with lower minimum (χ^2=11.80, p=0.02, df=4) and maximum frequency (χ^2=9.78, p=0.04, df=4), lower ending (χ^2=23.42, p=0.0001, df=4) and peak frequencies (χ^2=12.84, p=0.012, df=4) compared to the dolphins recorded from other sites (see Fig.22).

Ambient noise: Overall noise levels differ significantly between Gandoca-Manzanillo and Bocas (χ^2=5.41, p=0.020, Fig. 23a). Noise levels were significantly different across frequencies within each site. In Bocas noise levels were particularly high at 2, 10, and 14 kHz (Bocas χ^2=36.11, p<0.0001, df=5). Noise levels were higher at 2 kHz in Gandoca-Manzanillo (χ^2=22.47, p=0.0004, df=5). Sites were significantly different only at 2 kHz (χ^2=4.57, p=0.033, df=1). Ambient noise stations at each study site also varied in noise levels (Bocas: χ^2=35.23, df=5, p<0.0001, Gandoca-Manzanillo: χ^2=16.14, df=2, p=0.0003). In Bocas, the stations Drago, Torito, and Almirante Entrance and stations BEG and MID in Gandoca-Manzanillo had the highest noise levels (Fig. 23b-c). It is important to note that we did not assess directly the relationship between noise levels and whistle structure because our ambient noise data were not measured simultaneously with dolphin recording sessions.

Presence/absence of boats: Boat traffic has been found to be significantly higher in Bocas than in Gandoca-Manzanillo (Taubitz 2007). Because traffic is very low in Gandoca-Manzanillo the sampled size of interactions between dolphins and boats was too low for analysis. Therefore, the following results are just for Bocas. In Bocas dolphins in the presence of boats tended to emit whistles with higher maximum frequency (χ^2=5.02, p=0.025, df=1), greater delta frequency (χ^2=6.74, p=0.0009, df=1), longer duration (χ^2=5.14, p=0.023, df=1), and higher mean number of inflection points (χ^2=7.30, p=0.007, df=1) than when only the research boat was present. Adopted frequencies were also higher in the presence of boats (ANOVA F=5.08, p=0.024) and the coefficient of frequency modulation was slightly higher (ANOVA F=4.02, p=0.046) when only the research boat was present.

DISCUSSION

Dolphin whistles are important communicative signals used in a variety of contexts including, mother and calf recognition, formation of male alliances, group cohesion, etc (e.g., Caldwell and Caldwell 1965; Caldwell *et al.* 1990, Fripp *et al.* 2005, Herzing 2000, Janik 2000, Tyack 1997, 2000, Watwood *et al.* 2004). Because of their important role in social interactions, some of the variation in whistles may reasonably be assumed to facilitate transmission efficiency and avoid signal masking. In general animals are believed to produce signals that are adapted to their particular environment (Peters *et al.* 2007). Recent studies have found evidence that geographical variation in dolphin whistle acoustic structure may be largely due to local environmental conditions (e.g., Wang *et al.* 1995, Morisaka *et al.* 2005, Ansmann *et al.* 2007). However, other factors such as learning, genetic differentiation (Azevedo and Sluys 2005, Rossi-Santos and Podos 2006, Camargo *et al.* 2007), and zoogeographical relationships (Steiner 1981) may be important as well. This comparative study provides evidence that dolphin whistles are plastic and appear to be shaped by a combination of factors. The contribution of each of these factors to whistle variation may vary in accordance to local biological and abiotic conditions.

Wang *et al.* (1995) compared several populations of bottlenose dolphins and found that neighboring populations tended to show a smaller magnitude of whistle variation than distant populations. We found evidence of geographical variation in whistle structure between the adjacent populations of bottlenose dolphins from Bocas and Gandoca-Manzanillo. Bocas dolphins tended to produce lower frequency and longer whistles than Gandoca-Manzanillo dolphins. The significant differences in duration are expected, as it has been shown that duration varies the most within species (e.g., Ding *et al.* 1995, Barzua-

Duran and Au 2004, Rendell *et al.* 1999, Whitten and Thomas 2001). However, the differences in frequency are interesting since these are generally more ‘important’ in interspecific variation (Wang *et al.* 1995b, Rendell *et al.* 1999, May-Collado *et al.* 2007a).

Both populations also differ significantly in almost all standard whistle parameters with populations in north and south Atlantic. However, the magnitude of the differences between Bocas and Gandoca-Manzanillo were not necessarily smaller than their differences with each of the distant populations. In other words, we did not find evidence that differences in whistle structure were greater between far separated compared to closer populations as found by Wang *et al*. (1995). Dolphins from Bocas and Gandoca-Manzanillo are as different as other populations in the Atlantic. This may suggest that genetic isolation is important and that these adjacent populations are as isolated from each other as they are from more distant populations. An ongoing Photo-Id study (four years) in these two sites has not yet found evidence of mixing between these populations (May-Collado unpublished data). Until, genetic data are available we cannot estimate the contribution of population isolation to the overall differences in whistle structure between these two populations, but it appears to have a significant role.

Other factors that appear to be influencing whistle structure are local ambient and anthropogenic noise levels. Boat traffic is high in Bocas although low frequency (2 kHz ambient noise levels are higher in Gandoca-Manzanillo. Dolphins have been shown to respond acoustically to environmental noise in a variety of ways including whistle production rate (Van Parijs and Corkeron 2001, Buckstaff 2004), shifts in signal frequency (from low to high see Lesage *et al.* 1993), and an increase (Foote *et al.* 2004) or decrease (Buckstaff 2004) in signal duration. When comparing whistles recorded in presence and absence (not counting the research boat) of boats, particularly dolphin-watching boats, we found that Bocas dolphins tend to increase slightly their whistle maximum frequency from 15.35 kHz to 16.74 kHz, and duration from 1.05 to 1.30 sec., and their whistle modulation (measured as the mean number of inflection points) from 3.28 to 5.13. However, when accounting for site fidelity, dolphins from Bocas Torito (the area with the most intense dolphin-watching activities, up to 15 boats following a single group) had the lowest frequency parameters (except for beginning frequency) and longest whistles. These results contrast those by Buckstaff (2004) where bottlenose dolphin whistles did not change significantly in frequency range or duration.

Engine noise is due to air bubbles that collapse near the blades of the propellers, which is the most significant source of noise above 2 kHz (Evans et al. 1992). Increasing propeller rotation rate also shifts engine noise to higher frequencies (Richardson *et al.* 1995), which would have greater potential for masking cetacean signals (Bain and Dahlheim 1994) and may explain the general respond of dolphins to increase their maximum frequencies, like common dolphins in the English Channel were vessels are large with more noise at low frequencies compared with the small boats (with more noise at higher frequencies) in Bocas. In Bocas, for those dolphins that are continuously targeted by dolphin-watching boats, perhaps lowering frequency parameters to be below the noise level, may be a more adequate strategy to avoid masking (like the dolphins from Bocas Torito). While Beluga whales and common dolphins whales have been reported to use higher frequencies when ships are in the area (Lesage et al. 2003; Ansmann *et al.* 2007), other dolphin species like the Indo-Pacific bottlenose dolphin lower its frequency and modulation to overcome masking. Increased occurrence of long whistles to overcome signal interference, has also been reported in the calls of three populations of killer whales where whale-watching activities have become intense (Foote *et al.* 2004). Erber (2002) estimated whale-watching boat engine levels to be 145 to 169 dB re 1µPa @ 1m, more than sufficient to mask important signals such as the communicative whistles of dolphins (1 to 35 kHz) (Richardson *et al*. 1995). In general, dolphins can overcome signal masking or interference by increasing their frequency, amplitude, and duration (Foote *et al.* 2004). Dolphins from Gandoca-Manzanillo do not experience intense boat traffic, but overall ambient noise levels are relatively high, particularly at 2 kHz. High frequency whistles may help to cope with this. This is also supported by the fact that even in the presence of another dolphin species, *Sotalia guianensis*, bottlenose dolphins from Gandoca-Manzanillo produced high frequency whistles. According to the 'species hypothesis' sympatric species are expected to be more different than when found separately. Despite the overall differences between these two species, the magnitude of these differences in whistle structure between *Sotalia* and bottlenose dolphins of Gandoca-Manzanillo are smaller than the differences between *Sotalia* and bottlenose dolphins from Bocas.

Behavior also played a significant role in whistle variation, but its contribution to this variation is not clear. Overall, behavior and its interaction with population, explained the variation observed in several whistle parameters (duration, COFM, delta, minimum, and ending frequencies). In addition, whistle structure varied across behavioral states within each population. We did not find a common pattern between these two populations and their whistle structure in association with the different behavioral activities. In Bocas, frequency parameters (minimum, ending, and adopted frequencies) varied the most across behaviors, while in Gandoca-Manzanillo frequency modulation (measured as

COFM), and mean number of harmonics were the most variable parameters. Significant variation of whistle duration has been found in other dolphin species associated with behavioral states or context (Whitten and Thomas 2001), but this was not the case for these two populations. Unfortunately, most studies report whistle production rate but not the frequency and temporal parameters for each behavioral state (e.g., Van Parijs and Corkeron 2001, dos Santos et al. 2005, Nowacek 2005). In common dolphins, behavior was considered a small source of variation in whistle frequency and temporal parameters (Whitten and Thomas 2001, Barzua-Duran and Au 2004, Ansmann *et al.* 2007) but there were no common patterns between these studies.

Dolphins vary geographically in their whistle structures. The factors that influence these sounds may contribute differently according to local conditions. Furthermore, selection for individual plasticity in whistle structure may be key when living in a continuously changing environment. Our study shows that there are many sources that promote variability between and within populations, but dolphins appear to be plastic and respond differently to these factors.

CONCLUDING REMARKS

Whistles are key communicative signals in dolphin societies. These sounds show high inter and intra specific variation. Several factors have been proposed to influence this variation. This study finds that in the case of two adjacent populations both population isolation and environmental variables may contribute significantly to variation in both frequency and temporal parameters. Unlike a previous study, we do not find evidence that neighboring bottlenose dolphin populations are significantly more similar than more distant populations. Both adjacent populations live in contrasting habitats in terms of ambient noise and boat traffic and both factors appear to influence differently each population. Behavioral and zoogeographical relationships with other dolphin species may also have some part in the observed variation but at a much smaller scale.

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Table 10. Descriptive statistics of whistle acoustic parameters for both dolphin populations (see Fig. 16).

Acoustical Parameter	Mean ± SD	Range	C.V. %	Mean ± SD	Range	C.V. %
	Bocas del Toro (n=128)			Wildlife Refuge of Gandoca-Manzanillo (n=77)		
Minimum Frequency (kHz) *(p>0.05)*	5.27±1.76	1.6-11.9	0.334	5.68±2.24	1.61-10.85	0.393
Maximum Frequency (kHz)* *(Mann-Whitney U=12145, p=0.012)*	15.84±3.65	8.35-26.54	0.231	17.61±4.93	8.77-28.48	0.280
Delta Frequency (kHz)* *(Mann-Whitney U=4003, p=0.025)*	10.56±3.75	3.25-20.14	0.355	11.94±4.32	4.21-22.89	0.362
Beginning Frequency (kHz)* *(Mann-Whitney U=5984, p=0.010)*	9.95±3.78	3.43-19.63	0.380	8.43± 3.66	1.61-17.21	0.435
Ending Frequency (kHz)* *(Mann-Whitney U=2332.5, p<0.001)*	8.43±4.0	1.64-21.38	0.469	13.15±5.57	4.13-27.14	0.424
Peak (kHz) *(p>0.05)*	10.40-3.20	5.27-21.10	0.308	10.64±4.24	4.13-28.32	0.399
Duration (s)* *(Mann-Whitney U=6131.5, p=0.003)*	1.14-0.69	0.061-3.35	0.603	0.89±0.69	0.087-3.40	0.771
Number of Inflection Points* *(Mann-Whitney U=5800, p<0.031)*	3.93±4.10	0-20	1.04	2.64±3.41	0-19	1.295
Number of Harmonics *(p>0.05)*	1.47±2.05	0-15	1.399	2.34±1.16	0-13	1.157
COFM *(Mann-Whitney U=5473, p=0.185)*	4.96±4.11	0.32-20.31	0.828	4.80±6.53	0.439-48.725	1.360

Table 11. Bottlenose dolphin standard whistle parameters from this study and with other studied populations in the Atlantic

Study	***Population***	***N***	***Min (kHz)***	***Max (kHz)***	***Beg (kHz)***	***End (kHz)***	***Duration (s)***	***#IP***
This study	Bocas del Toro, Panama (CA)*	128	5.27±1.76	15.84±3.65	9.95±3.78	8.43±4.0	1.14-0.69	3.93±4.10
This study	Gandoca-Manzanillo, Costa Rica (CA)*	77	5.68±2.24	17.61±4.93	8.43± 3.66	13.15±5.57	0.89±0.69	2.64±3.41
This study	'Southern Central America' (both sites together)*	205	5.43±1.96	16.50±4.26	9.38±3.80	10.20±5.15	1.04±0.69	3.44±3.90
Azevedo et al. 2007	Patos Lagoon, Brazil (SA)*	788	5.96±2.15	12.21±3.20	8.28±3.11	8.37±3.7	0.553±0.394	1.42±1.85
Wang et al. 1995	Golfo San Jose, Argentina (SA)*	110	5.91±1.5	13.65±1.54	9.24±2.74	6.63±2.29	1.14±0.49	1.58±1.24
Wang et al. 1995	Texas, USA (NA)*	2022	5.77±1.84	11.32±3.31	8.01±2.81	8.16±3.78	0.68±0.40	2.09±2.54
Steiner	Western North Atlantic Ocean (NA)**	857	7.33±1.66	16.235±2.688	11.26±3.98	10.225±3.646	1.30±0.63	2.86±2.45

CA=Central Atlanctic (southern most area)
SA=Southern Atlantic
NA=Northern Atlantic
*Coastal populations
** Some appear to be oceanic and other two of the recording sites are in coastal waters of the Caribbean
Ω significantly higher value

Table 12. Pairwise comparison of whistle standard parameters between populations, significant values a the p-value level of p<0.05

COMPARISIONS	***MIN (KHZ)***	***MAX (KHZ)***	***BEG (KHZ)***	***END (KHZ)***	***DURATION (S)***	***#IP***
Bocas vs Brazil	t= 3.44, P<0.0006	t= 42.93, P<0.0001	t=5.40, P<0.0001	P>0.05	t= 13.78, P<0.0001	t= 11.46, P<0.0001
Bocas vs. Argentina	t= 3.26, P<0.001	t= 5.86, P<0.0001	P<0.005	t= 4.17, P<0.0001	P>0.05	t= 5.78, P<0.0001
Bocas vs Texas	t= 2.99, P<0.003	t= 14.88, P<0.0001	t= 7.35, P<0.0001	P>0.05	t= 11.94, P<0.0001	t= 7.59, P<0.0001
Bocas vs Western NA	t=13.10, P<0.0001	P>0.05	t= 3.48, P<0.0005	t= 5.13, P<0.0001	t= 2.64, P<0.0080	t= 4.10, P<0.0001
Gandoca-Manzanillo vs Brazil	P>0.05	t= 13.35, P<0.0001	P>0.05	t= 11.01, P<0.0001	t= 6.59, P<0.0001	t= 5.10, P<0.0001
Gandoca-Manzanillo vs. Argentina	P>0.05	t= 7.89, P<0.0001	P>0.05	t= 11.62, P<0.0001	t= 2.89, P<0.0043	t= 3.00, P<0.0031
Gandoca-Manzanillo vs Texas	P>0.05	t= 16.02, P<0.0001	P>0.05	t= 11.92, P<0.0001	t= 4.36, P<0.0001	P>0.05
Gandoca-Manzanillo vs Western NA	P>0.05	t= 3.94, P<0.0001	t= 6.01, P<0.0001	t= 7.17, P<0.0001	t= 5.43, P<0.0001	P>0.05
Bocas vs Gandoca-Manzanillo	See Table 10					
Southern Central America vs Brazil	t= 3.20, P<0.0014	t=15.88, P<0.0001	t= 4.30, P<0.0001	t= 5.78, P<0.0001	t= 14.17, P<0.0001	t= 10.65, P<0.0001
Southern Central America vs. Argentina	t= 2.24, P<0.0258	t= 6.78, P<0.0001	P>0.05	t= 6.91, P<0.0001	P>0.05	t= 4.86, P<0.0001
Southern Central America vs Texas	t= 2.51, P<0.012	t= 20.74, P<0.0001	t= 6.41, P<0.0001	t= 7.08, P<0.0001	t= 11.30, P<0.0001	t= 6.84, P<0.0001
Southern Central America vs Western NA	t= 14.22, P<0.0001	P>0.05	t= 6.10, P<0.0001	P<0.05	t= 5.13, P<0.0001	t= 2.61, P<0.0092
Argentina vs Brazil	P>0.05	t= 4.64, P<0.0001	t= 3.11, P<0.002	t= 4.80, P<0.0001	t= 14.17, P<0.0001	P>0.05
Texas vs. Brazil	t= 2.34, P<0.019	t=6.46, P<0.0001	t= 2.14, P<0.032	P>0.05	t= 7.59, P<0.0001	t= 6.74, P<0.0001
Western NA vs. Brazil	t= 14.56, P<0.0001	t= 27.70, P<0.0001	P>0.05	t= 10.24, P<0.0001	t= 28.05, P<0.0001	t= 13.10, P<0.0001
Argentina vs/ Texas	P>0.05	t= 7.33, P<0.0001	t= 3.36, P<0.0008	t= 4.20, P<0.0001	t= 11.60, P<0.0001	t= 2.10, P<0.0358
Argentina vs Western NA	t= 8.55, P<0.0001	t= 9.90, P<0.0001	t= 5.15, P<0.0001	t= 10.10, P<0.0001	t= 2.55, P<0.0109	t= 7.18, P<0.0001
Texas vs Western NA	t= 4.03, P<0.0001	t= 38.45, P<0.0001	P>0.05	t= 13.54, P<0.0001	t= 30.70, P<0.0001	P<0.0001

FIG. 16

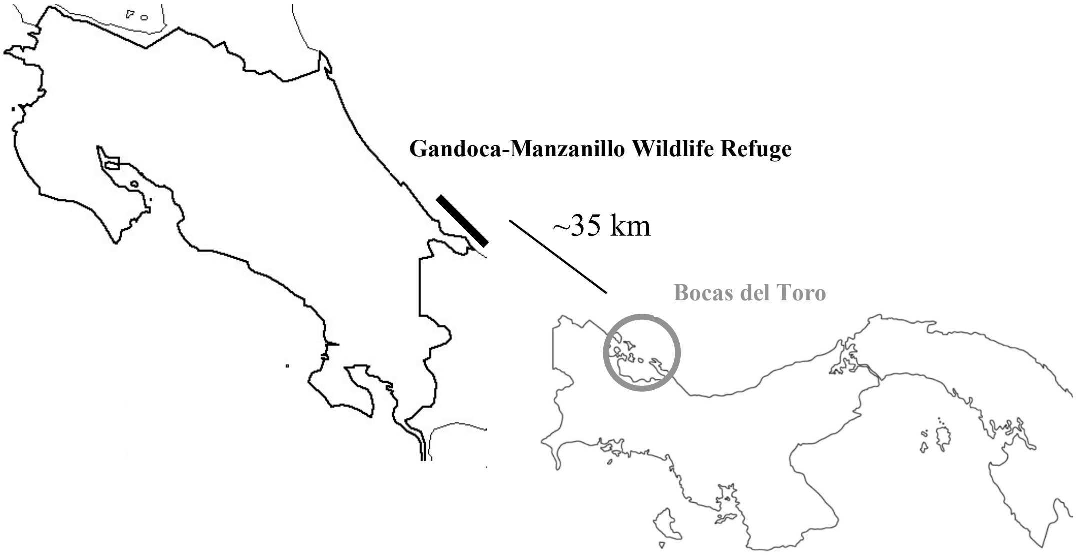
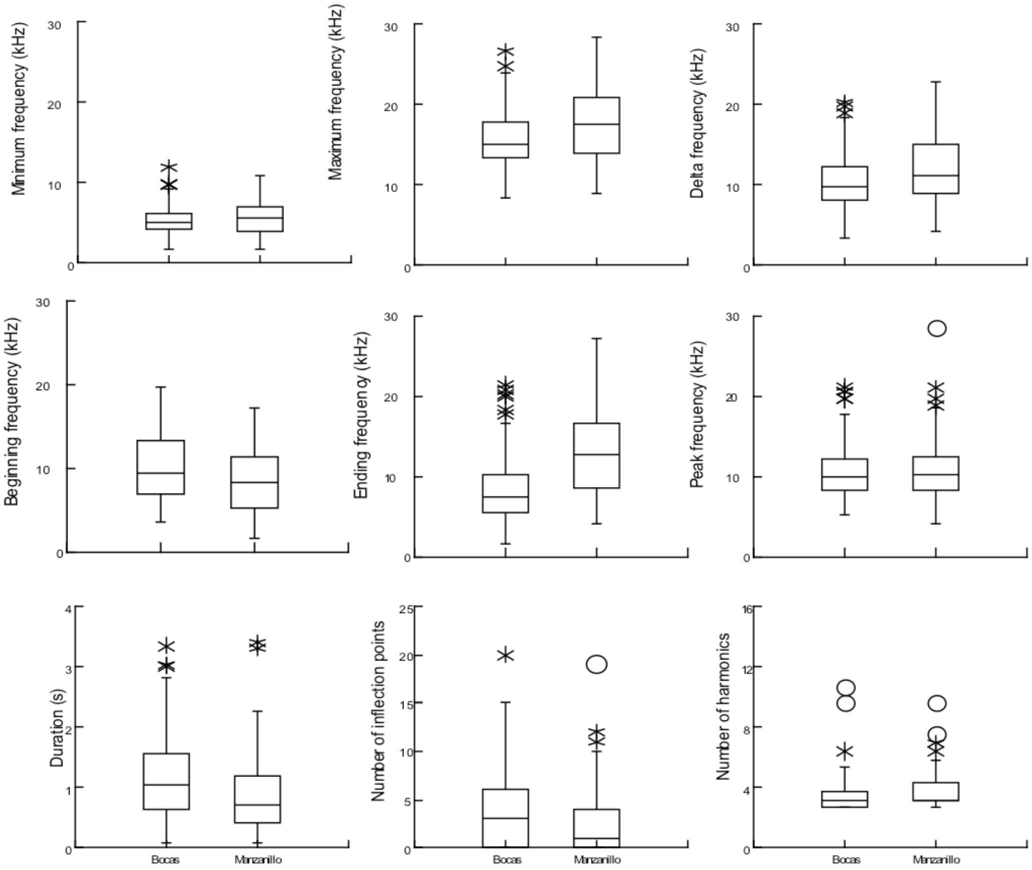


FIG. 17



Minimum frequency (kHz)
Maximum frequency (kHz)
Delta frequency (kHz)
Beginning frequency (kHz)
Ending frequency (kHz)
Peak frequency (kHz)
Duration (s)
Number of inflection points
Number of harmonics
0
10
20
30
0
1
2
3
4
0
5
10
15
20
25
0
4
8
12
16
Bocas
Manzanillo

FIG. 18

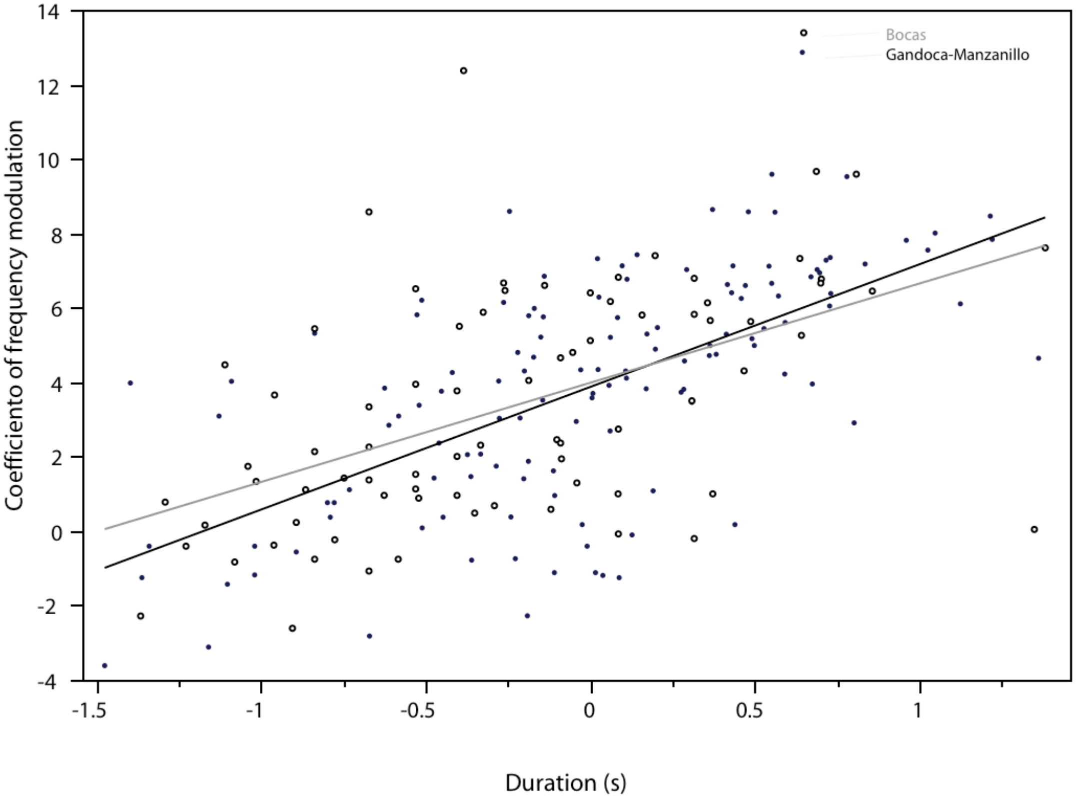
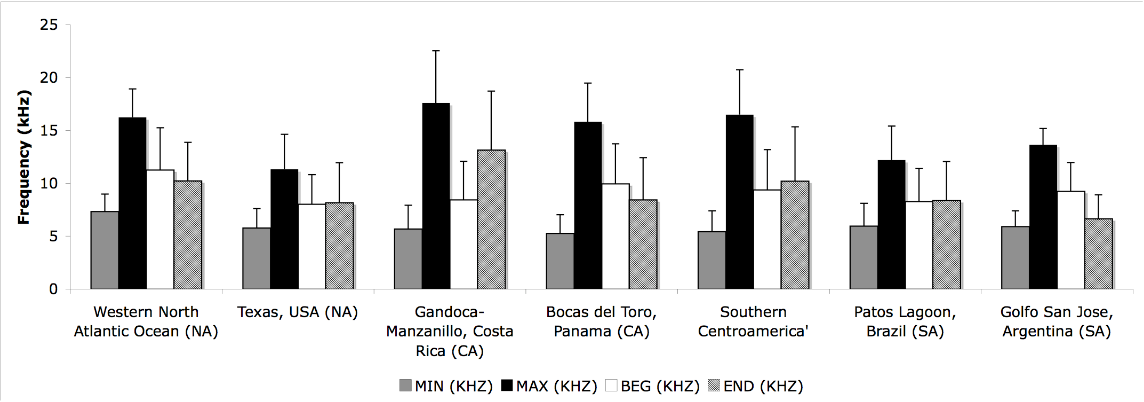
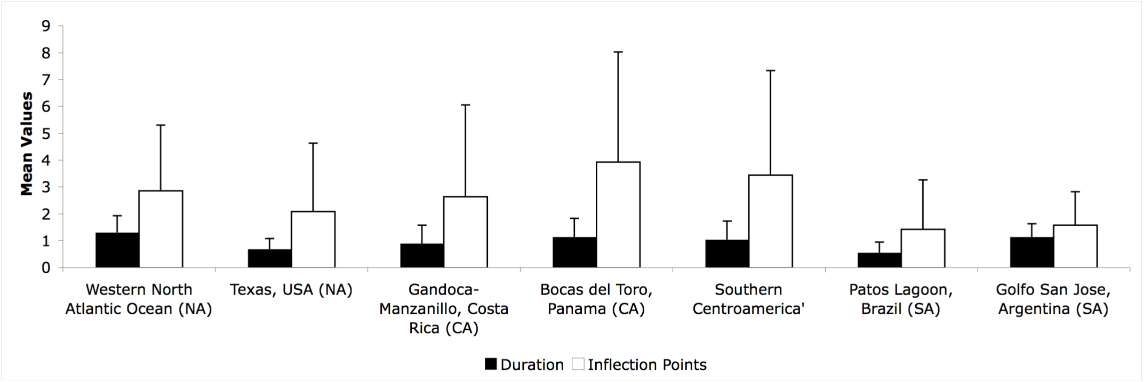

Bocas
Gandoca-Manzanillo
Coefficiento of frequency modulation
14
12
10
8
6
4
2
0
-2
-4
-1.5
-1
-0.5
0
0.5
1
Duration (s)

FIG. 19



Frequency (kHz)
25
20
15
10
5
0
Western North Atlantic Ocean (NA)
Texas, USA (NA)
Gandoca-Manzanillo, Costa Rica (CA)
Bocas del Toro, Panama (CA)
Southern Centroamerica'
Patos Lagoon, Brazil (SA)
Golfo San Jose, Argentina (SA)
MIN (KHZ)
MAX (KHZ)
BEG (KHZ)
END (KHZ)

a.



Mean Values
9
8
7
6
5
4
3
2
1
0
Western North Atlantic Ocean (NA)
Texas, USA (NA)
Gandoca-Manzanillo, Costa Rica (CA)
Bocas del Toro, Panama (CA)
Southern Centroamerica'
Patos Lagoon, Brazil (SA)
Golfo San Jose, Argentina (SA)
Duration
Inflection Points

b.

FIG. 20

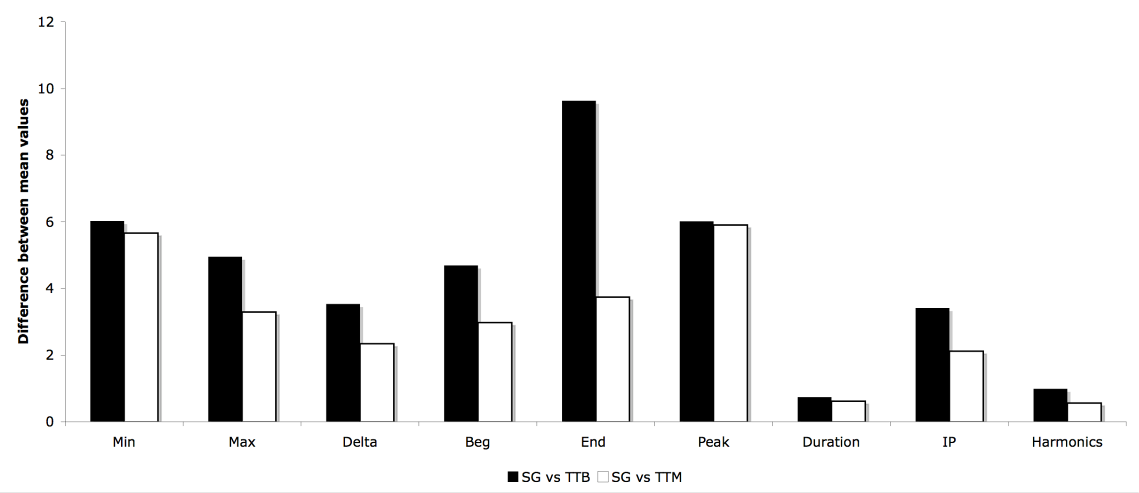
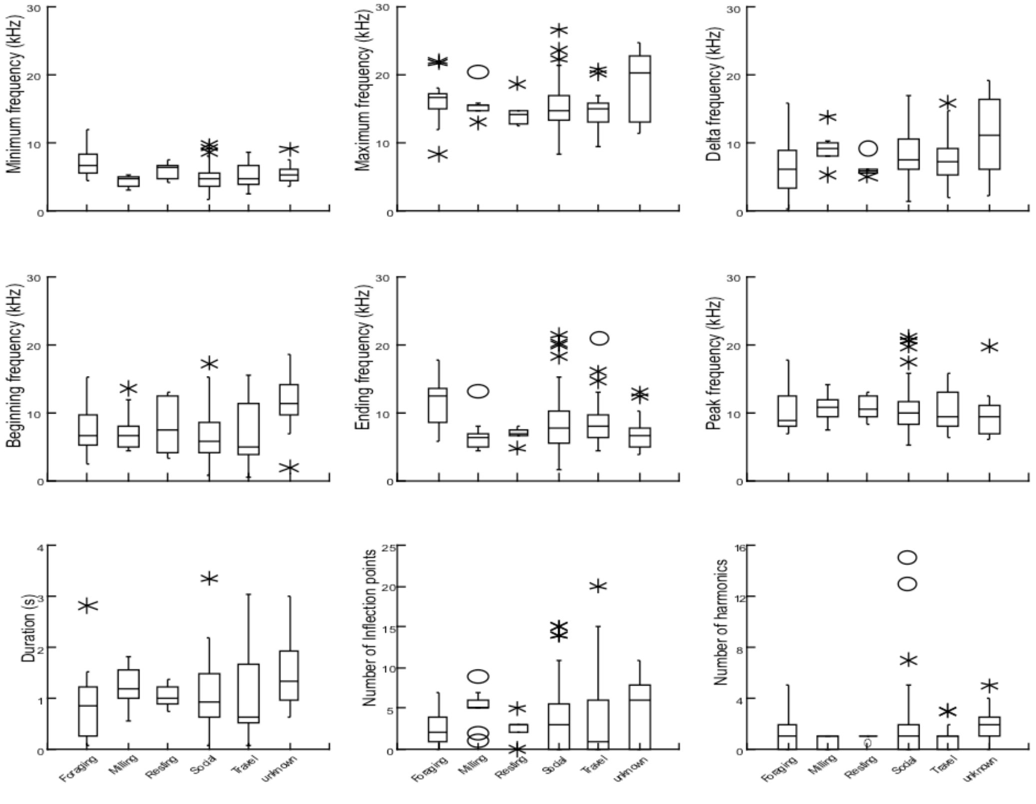
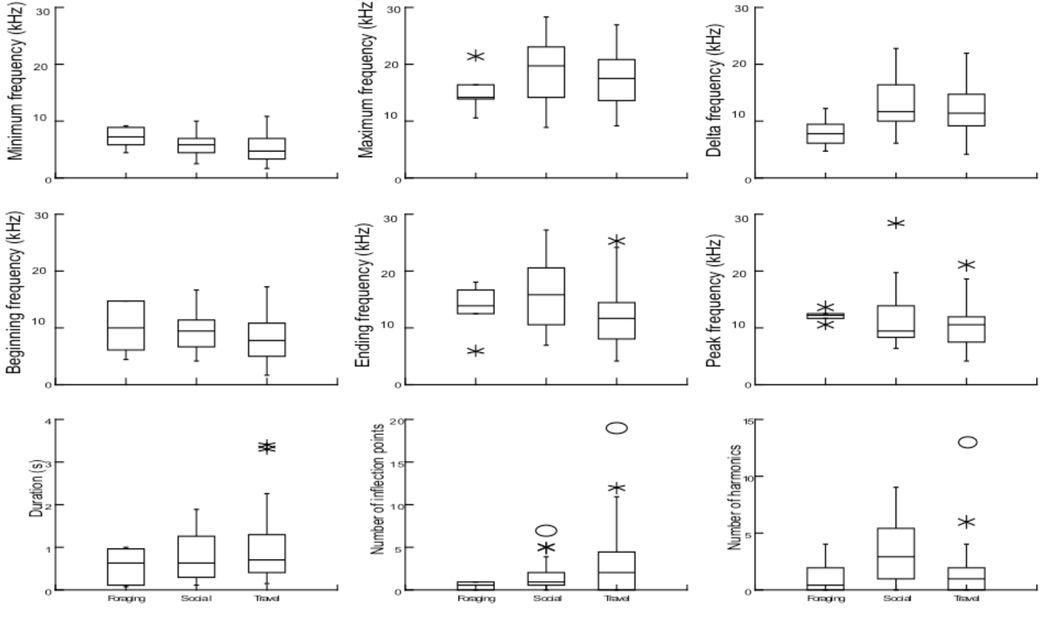

12
10
8
6
4
2
0
Difference between mean values
Min
Max
Delta
Beg
End
Peak
Duration
IP
Harmonics
■ SG vs TTB
□ SG vs TTM

FIG. 21



A. Bocas del Toro



B. Gandoca-Manzanillo

FIG. 22

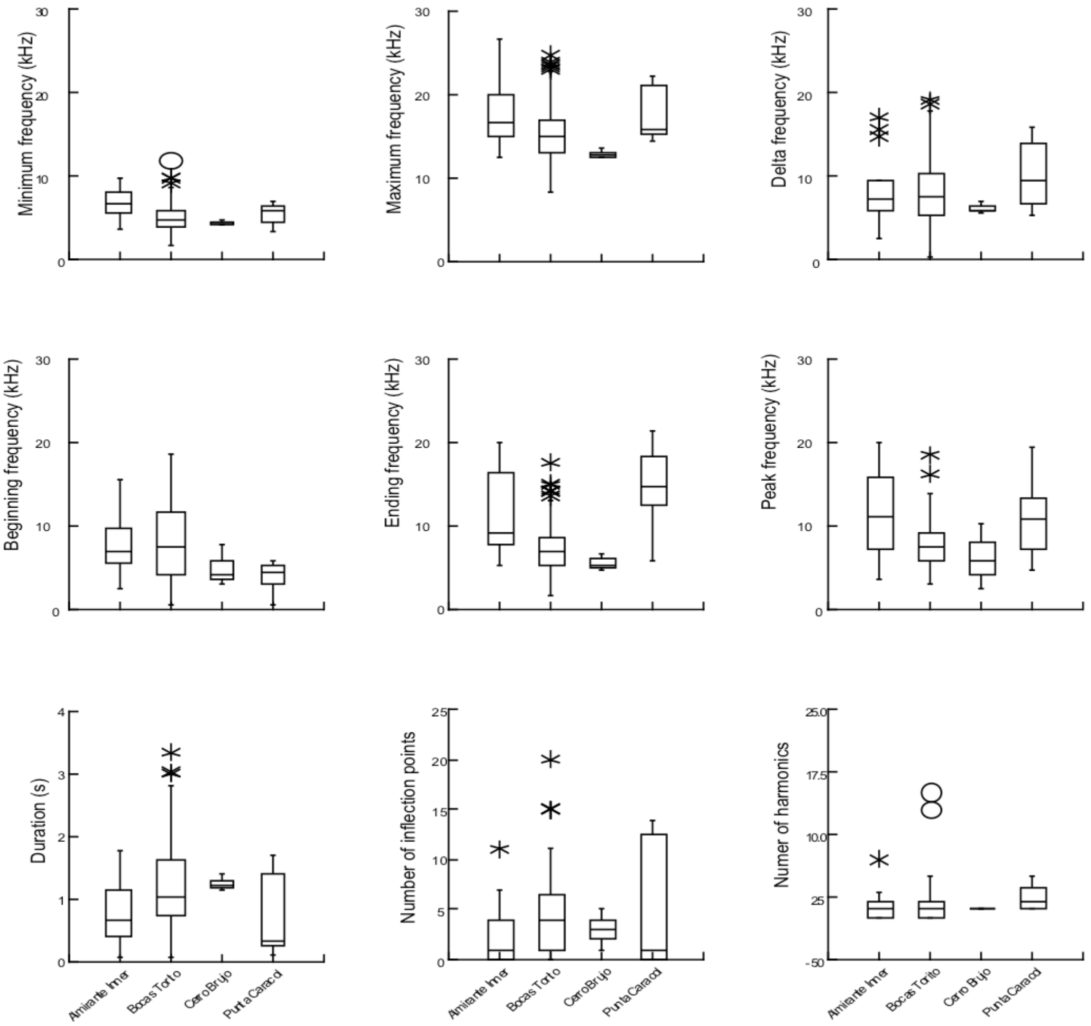
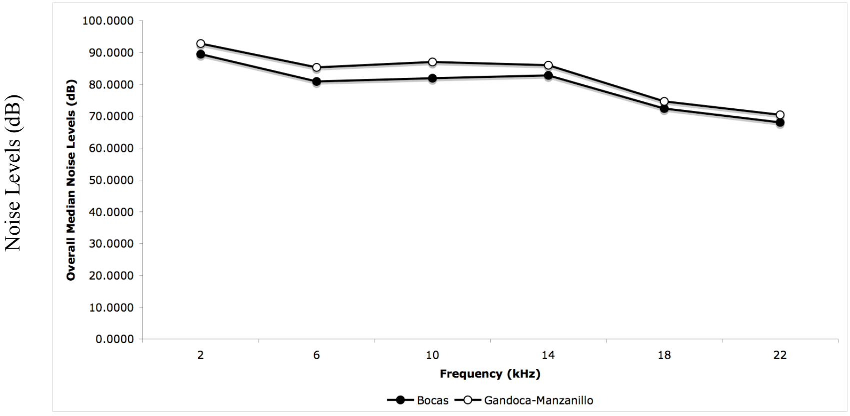
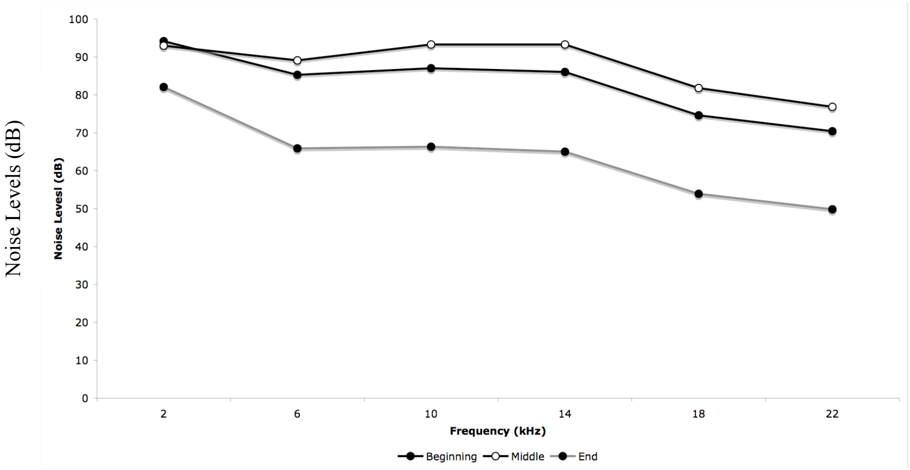

Minimum frequency (kHz)
Maximum frequency (kHz)
Delta frequency (kHz)
Beginning frequency (kHz)
Ending frequency (kHz)
Peak frequency (kHz)
0
10
20
30
Duration (s)
0
1
2
3
4
Number of inflection points
0
5
10
15
20
25
Numer of harmonics
-50
25
10.0
17.5
25.0
Amirante Inner
Bocas Torito
Cerro Brujo
Punta Caracol

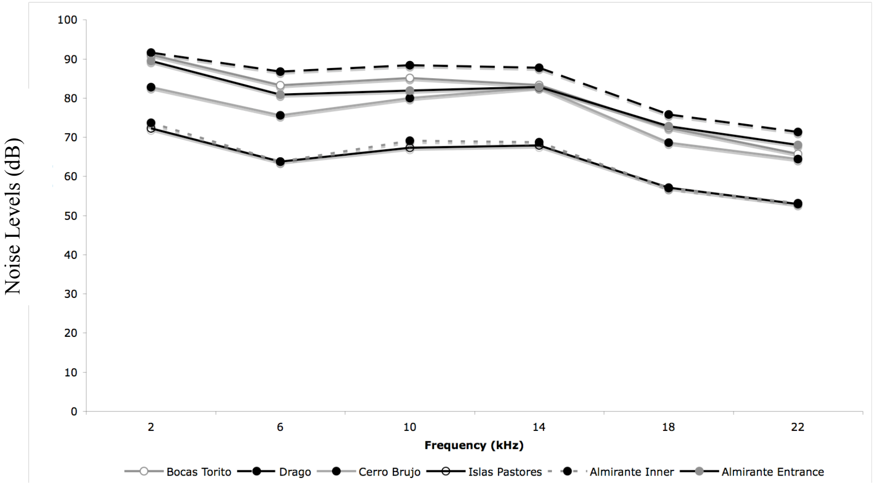
FIG. 23



a. Overall median values by study site



b. Median values for each ambient noise station in Wildlife Refuge of Gandoca-Manzanillo.



c. Median values for each ambient noise station in Bocas del Toro

CHAPTER VII

CONCLUSIONS AND FUTURE RESEARCH DIRECTIONS

- A detailed species-level cetacean phylogeny was reconstructed to test several evolutionary hypotheses regarding tonal sound evolution. This phylogenetic hypothesis is concordant with well establish benchmark clades previously supported by morphological and mitochondrial and nuclear DNA and thus seems appropriate for hypotheses testing. Both exhaustive taxon sampling and a Bayesian approach for analysis seem to have contributed to phylogenetic accuracy as judged by recovery of benchmark clades. Still, some key clades, most notably ziphiids, remain poorly resolved due to lack of data, and the phylogenetic placement of some lineages is still controversial, e.g. the river dolphin *Platanista*. My future research directions in this field aims to produce a comprehensive 'total evidence' Cetacean phylogeny by combining multiple datasets that are already available (morphology, nuclear DNA, mitochondrial DNA, SINE). We also aim to continue testing the utility of cyt-b for rapid, but reliable, estimates of phylogenies for other mammal groups, including Cetartiodactyla (Agnarsson and May-Collado in prep.).
- The freshwater dolphin *Inia geoffrensis* (Boto), emits tonal sounds that, although relatively short, closely resemble in several acoustical parameters the 'whistles' a category of sounds applied by some authors exclusively to social dolphin tonal sounds. Despite the general assumption that river dolphins are solitary, very little is known about their social structure. In some parts of their distribution, at least, they can be found in groups. However, the relationships between group members,

or the stability of these groups is unknown. Based on our behavioral observations and the distance at which their tonal signals can be detected in their environment, it is possible that at least the study population of the Boto in Ecuador use these tonal for social communication. However, instead of promoting social encounter, we suggest they may be used to maintain distance between individuals or groups. Finally, our results suggest remarkable whistle variation between botos from Ecuador and other populations (Colombia, Peru, and Brazil). Although, this may be largely a product of limitations of recording systems used by previous studies, it will be important to revisit these populations and obtain recordings using a broadband system as the one used in this dissertation. If the differences in whistle structure turn out not simply to be a product of recording limitations, they may represent one of the most remarkable geographical variation ever reported in toothed whales.

- Tonal sound acoustical structure varies across species particularly in frequency parameters. We tested two hypotheses that are believed to shape these frequency parameters through their evolutionary history: body size and sociality. The results of this dissertation find evidence that Cetacean body size has constrained the evolution of tonal sounds minimum frequency (although only a portion of the variation can be explained by body size). 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.

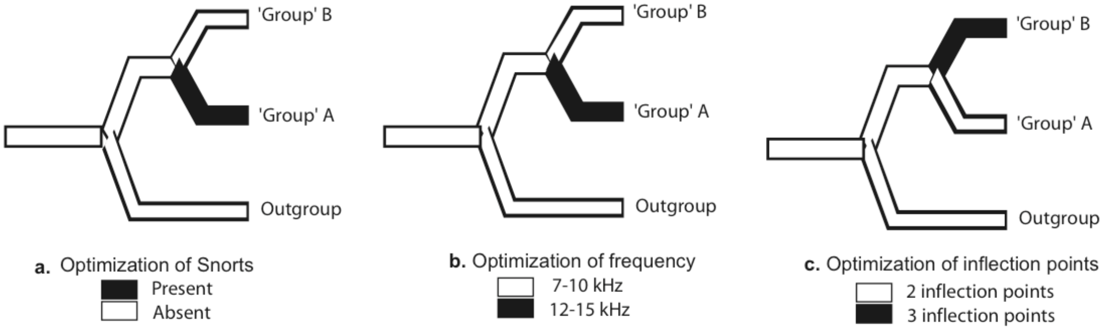
However, there is no evidence, that body size has constrained the evolution of any other frequency parameter and alternative hypotheses are required to explain their evolution.

- We find no evidence supporting the ‘dolphin hypotheses’ stating that ‘whistles’ evolved within Delphinidae in a social context. Whistles arose earlier in the evolutionary history of whales than hitherto appreciated, however, the evolutionary history of sociality in Cetaceans is complex and several alternative hypotheses are discussed in this dissertation. Nonetheless, sociality does seem to explain some of the variation observed in minimum frequency. Cetacean species that live in large groups tend to produce whistles with higher minimum frequency. In these group-living species, members are generally relatively close to each other so that sounds need not be transmitted over long distances. Furthermore, the evolution of tonal sound complexity seems to be intertwined with social structure: (1) increased tonal sound modulation (whistle ‘complexity’) significantly correlates with group size and social structure and (2) changes in tonal sound complexity were significantly concentrated on social branches. For future directions in the study of evolutionary history of sociality and sound communication in Cetaceans it will be important to obtain data on social structure and tonal sounds for a greater number of cetaceans, and to take into consideration the social structure and tonal sound production of outgroups.
- Studying the intraspecific variation of tonal sounds (‘whistles’) in bottlenose dolphins also proved to be complex. The observed variation appears to be product of a combination of factors that may influence differently each of the acoustical

parameters in a whistle. However, in the study populations, it appears that isolation and local adaptation to the acoustic characteristics of their habitat are important factors promoting intraspecific variation. Future, studies should assess the genetic isolation between these two populations, and directly measure the relationship between ambient noise levels and whistle frequency and duration by obtaining ambient noise levels from the same recordings from which whistles are extracted.

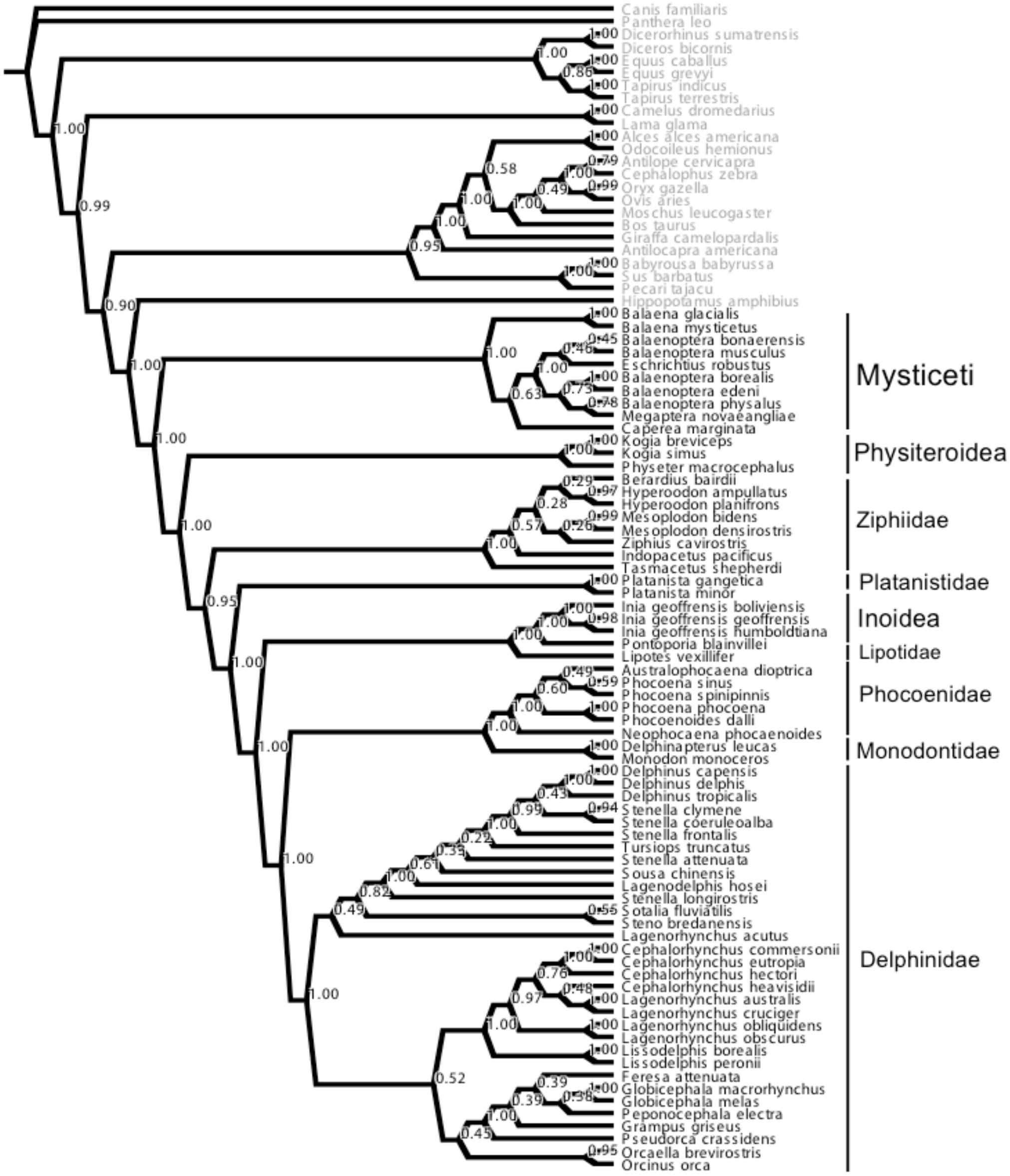
APPENDIXES

APPENDIX I



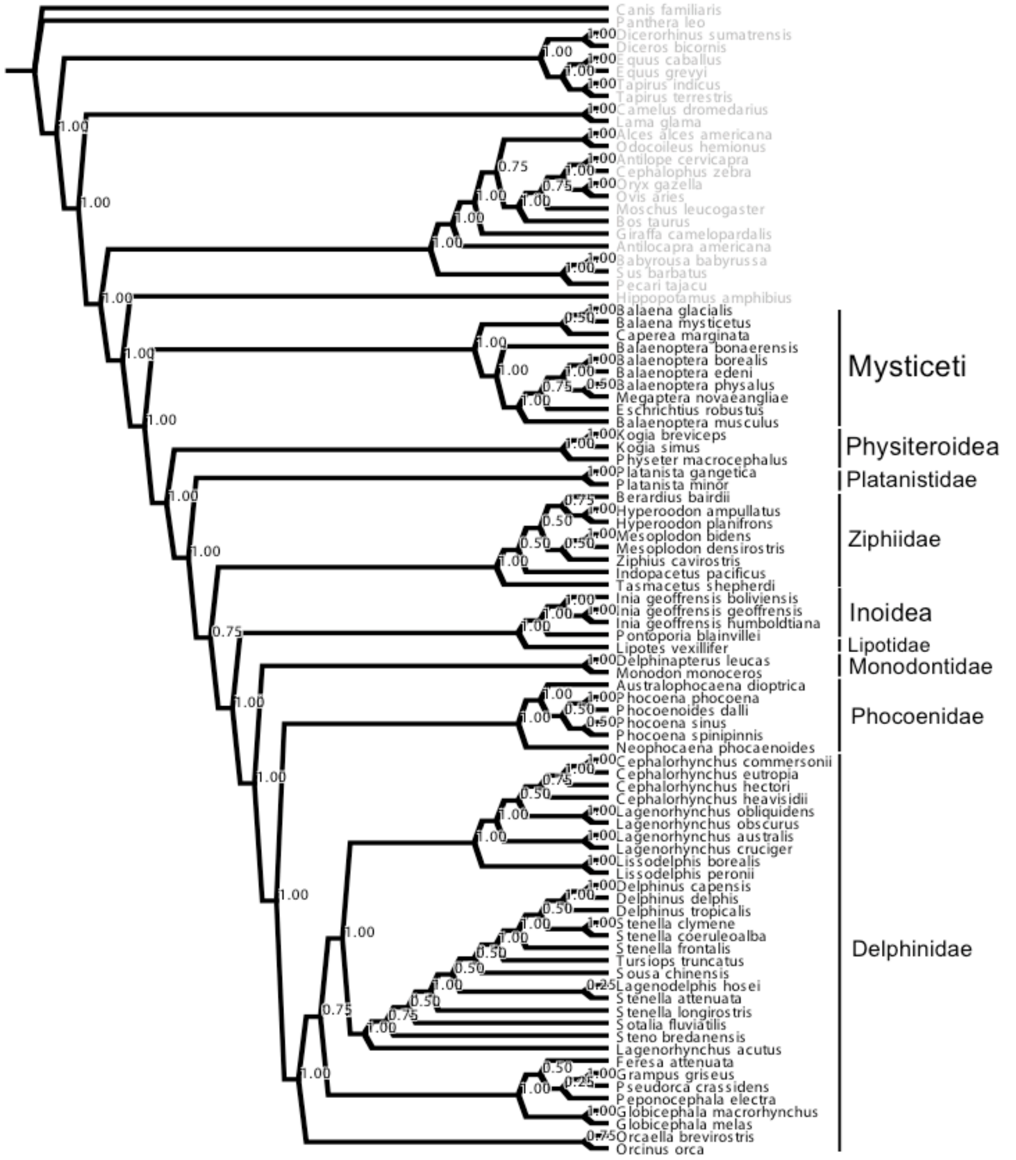
Whistles as a unit for evolutionary analyses. As noted above there are several reasons why using conglomerate concepts like 'whistles' as units of study can hinder progress in the understanding of sound evolution. Apart from being rather arbitrarily defined, and hence differently by different authors, 'whistles' represent a set of characters that may vary independently and may each have different phylogenetic distributions. As a thought experiment let us think of an example where sound production is being compared in two sister lineages. Let us assume that some authors are interested in the evolutionary origin of tonal sounds called 'snorts', and that snorts are defined as narrowband, frequency modulated sounds, with a contour containing at least two inflection points and frequency above 10 kHz. In group A it is noted that sounds are narrowband, frequency modulated, with three inflection points and frequency ranging from 12-15 kHz. In group B sounds are narrowband, frequency modulated, with a contour of two inflection points and frequency ranging from 7-9 kHz. Under a 'broad concept' analysis we would therefore conclude that 'snorts' were present in A, but absent in B, and might conclude that snorts originated in the common ancestor of A (diagram a). However, this belies both the similarities and differences that exist in sound production in the two groups. It denies homology of frequency modulation, contours etc, and even suggests that tonal sounds evolved independently in each group (as 'snorts' are 'different' tonal sounds from non-snorts). Under a 'component' analysis (diagrams b and c), traits like frequency modulation and band width would be scored as identical in the two groups—their similarity would be taken as evidence of common ancestry, i.e. homology. Instead of 'snorts' originating in A, we would more simply explain the differences between the two groups in terms of frequency, and if e.g., the outgroups shared the lower frequency (indicated by white branches) of B we would conclude that a switch to higher frequency (indicated by black branches) occurred in the common ancestor of A (diagram b). In other words, we would learn that the difference between what people call 'snorts' and what they don't call snorts may simply be a matter of sound frequency. In this latter case there is no indication of tonal sound production being non-homologous in A and B, and in fact they share most characteristics of the tonal sounds. Additionally we would learn (diagram c) that inflection points increased from two (white branches) to three (dark branches) in the lineage leading to B (supposing the condition in A was shared with the outgroups). This is information that the concept of 'snorts' obscured. By a component analysis we learn a lot more than by a concept analysis. If we now were interested in the association of sounds and sociality, and group A was social and group B (and outgroups) not, it might be claimed that 'snorts' and 'sociality' are associated and evolved in concert (following diagram a). However, a much more precise and informative conclusion would be that sociality and sound frequency (diagram b) might be related. Hence instead of explaining the social context of 'snorts' we would do well to examine how sound frequency might play an important role in social communication etc. We believe that 'whistles' are no better justified as a unit for evolutionary analysis than 'snorts' in the example above. We do use them in an attempt to test the dolphin hypothesis, but then we opt for a component approach for most of our analyses.

APPENDIX 2



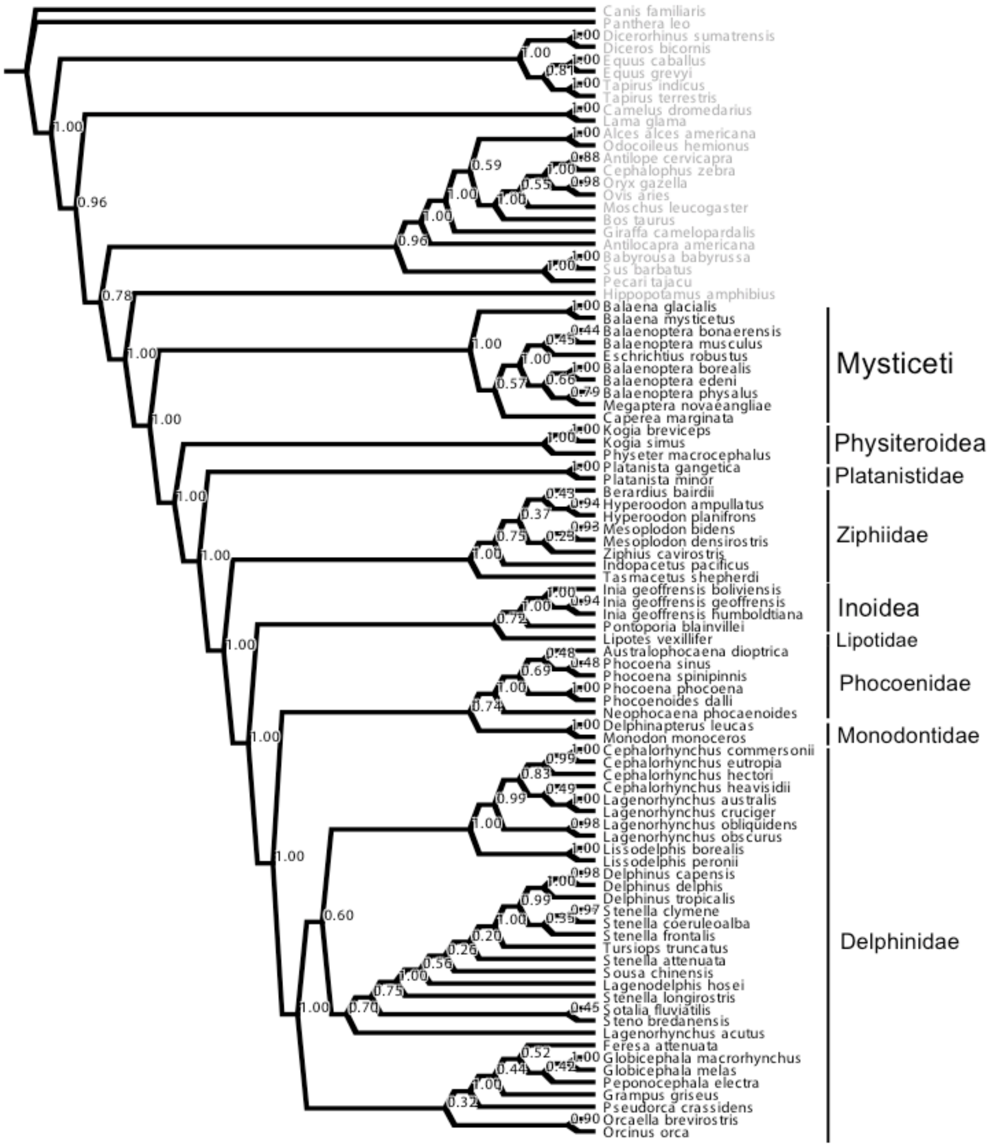
A cetacean phylogeny consistent with Arnason (2004). A majority rule consensus of all post-burnin trees from May-Collado et al. (2007) filtered to be congruent with the mitogenomic phylogeny of Arnason (2004). Numbers on nodes represent posterior probabilities.

APPENDIX 3



A cetacean phylogeny consistent with Messenger and McGuire (1998). A majority rule consensus of all post-burnin trees from May-Collado et al. (2007) filtered to be congruent with the combined morphological and molecular phylogeny of Messenger and McGuire (1998). Numbers on nodes represent posterior probabilities.

APPENDIX 4



A cetacean phylogeny consistent with Nikaido et al. (2001). A majority rule consensus of all post-burnin trees from May-Collado et al. (2007) filtered to be congruent with the SINE phylogeny of Nikaido et al. (2001). Numbers on nodes represent posterior probabilities.

APPENDIX 5. Cetacean social structure and group size. This table reviews published data on cetacean social structure and group size. Numbers in parenthesis correspond to state assigned to each characters as described in Table 1 (bold numbers represent the most common state reported for a particular species).

Species	Sociality 2-states Character	Sociality 4-states Character	Group Mean Size	Sociality components			References
Baleen Whales (Mysticeti) Balaenidae				Description of Group Size	Stability/ Associations	Composition	
*Eubalaena glacialis***	0	0	2.57	-Singly, Pairs, **(0)** -Breeding and feeding grounds aggregations, (3)	-Short (except for mother and calf) **(0)** - Weak associations when found in groups**(1)**	-Pairs Mother+ Calf **(0)** -Groups segregated by sex and age, Mixed (1,2)	1, 2,3
Balaena mysticetus	0	0	1	-Singly, Pairs, **(0)** -Breeding and feeding grounds aggregations, (3)	Short (except for mother and calf) **(0)** - Weak associations when found in groups**(1)**	-Pairs Mother+ Calf **(0)** -Groups segregated by sex and age, Mixed (1,2)	3, 4, 5
Balaenopteridae							
Balaenoptera borealis	0	0	1	-Singly, Pairs, **(0)** -Breeding and feeding grounds aggregations, (3)	Short (except for mother and calf) **(0)** - Weak associations when found in groups **(1)**	-Pairs Mother+ Calf **(0)** -Groups segregated by sex and age, Mixed (1,2)	3,6
B. bonaerensis	0	0	1	-Singly, Pairs, **(0)** - Breeding and feeding grounds aggregations, (3)	Short (except for mother and calf) **(0)** - Weak associations when found in groups **(1)**	-Pairs Mother+ Calf **(0)** -Groups segregated by sex and age, Mixed (1,2)	3,7
B. edeni/ B. brydei	0	0	1	-Singly, Pairs, **(0)** -Breeding and feeding grounds aggregations, (3)	Short (except for mother and calf) **(0)** - Weak associations when found in groups **(1)**	-Pairs Mother+ Calf **(0)** -Groups segregated by sex and age, Mixed (1,2)	3, 8, 9
B. musculus	0	0	1	-Singly, Pairs, **(0)** -Breeding and feeding grounds aggregations, (3)	Short (except for mother and calf) **(0)** - Weak associations when found in groups **(1)**	-Pairs Mother+ Calf **(0)** -Groups segregated by sex and age, Mixed (1,2)	3
B. physalus	0	0	1.55	-Singly, Pairs, **(0)** -Small groups, (1) -Breeding and feeding grounds aggregations, (3)	Short (except for mother and calf) **(0)** - Weak associations when found in groups **(1)**	-Pairs Mother+ Calf **(0)** -Groups segregated by sex and age, Mixed (1,2)	3, 9-13
Megaptera novaeangliae	0	0	1	-Singly, Pairs, **(0)** - Breeding and feeding grounds aggregations, (3)	Short (except for mother and calf) **(0)** - Weak associations when found in groups **(1)**	-Pairs Mother+ Calf **(0)** -Groups segregated by sex and age, Mixed (1,2)	3, 9, 14- 22
Eschrichtidae							
Eschrichtius robustus	0	0	1	-Singly, Pairs, **(0)** - Breeding and feeding grounds aggregations, (3)	Short (except for mother and calf) **(0)** - Weak associations when found in groups **(1)**	-Pairs Mother+ Calf **(0)** -Groups segregated by sex and age, Mixed (1,2)	3, 23-24
Neobalaenidae							

Capera marginata	0	0	1	-Singly, Pairs, **(0)** - Breeding and feeding grounds aggregations, (3)	Short (except for mother and calf) **(0)** **-** Weak associations when found in groups **(1)**	-Pairs Mother+ Calf **(0)** -Groups segregated by sex and age, Mixed (1,2)	3
TOOTHED WHALES (ODONTOCETI) KOGIIDAE							
*Kogia breviceps***	?	?	~2	-Singly, pairs (stranded animals) **(0)** -Small group **(1)**	Unknown (except for the mother and calf) **(?)**	-Segregated by sex and age (possibly) **(1)** -Mixed (possibly) **(2)**	25-26
K. simus	?	?	1.87	-Singly (stranded animals) (0) -Small groups **(1)**	Unknown (except for the mother and calf) **(?)**	-Segregated by sex and age (possibly) **(1)** -Mixed (possibly) **(2)**	25-31
PHYSETERIDAE							
Physeter macrocephalus	1	3	22.1	-Solitary adult males **(0)** -Small Female + calves (nursery groups) **(1)** -Immature males groups (1)	-Weak associations in immature male groups **(1)** -Long associations in Matrilineal groups **(3)**	-Segregated by sex and age **(1)**	27, 32-40
ZIPHIIDAE							
Berardius bairdii (B. anurxii)	1	?	7.2	-Small groups (male biased) **(1)** -Large Aggregations when traveling (3)	Unknown (except for the mother or father and calf in this case) **(?)** - Males possibly do parental care but it is not clear what kind of associations they have **(?)**	-Mixed **(2)**	41-48
Hyperoodon ampullatus	1	2	7	-Small groups **(1)**	Fluid associations except for long-term associations between males **(2)**	-Segregated by sex and age **(1)**	49-51
H. planifrons	?	?	3.61	-Small groups **(1)**	Unknown (except for the mother and calf) **(?)**	Unknown **(?)**	52
Mesoplodon bidens	?	?	3	-Small groups **(1)**	Unknown (except for the mother and calf) **(?)**	Mixed **(2)**	53-55
M. densirostris	?	?	3.7	-Singly (strandings data), pairs **(0)** -Small groups **(1)**	Unknown (except for the mother and calf) **(?)**	-Mother+calf **(0)** -Mixed **(2)**	54-58
Ziphius cavirostris	?	?	2.9	-Singly (strandings data), pairs **(0)** -Small groups **(1)**	Unknown (except for the mother and calf) **(?)**	-Mother+calf **(0)** -Mixed **(2)**	27, 28, 56, 59-62
PLATANISTIDAE							
Platanista gangetica gangetica *Platanista gangetica minor*	0	0	2.45	-Singly, pairs (Mother+calf) (most common) **(0)** -Aggregations (3)	-Relatively long for mother and calf **(0)** -**W**eak associations when found in groups **(1)**	Mother+calf **(0)** Unknown **(?)**	27, 63-71
INIIDAE							
Inia geoffrensis	0	0/1	6.22	-Singly (strandings data), pairs **(0)** -Small groups **(1)** -Aggregations in breeding and feeding grounds (3)	-Relatively long for mother and calf **(0)** -**W**eak associations when found in groups **(1)**	-Mother+ Calf **(0)** -Single sex **(1)** -Mixed **(2)**	27, 72-78
PONTOPORIDAE							
Pontoporia blainvillei	1	1	7.1	-Solitary animals are rare (0)	-Weak associations (described as ‘fluid’)	-Mixed **(2)**	79-82

				-Small groups (traveling, feeding, socializing) **(1)**	**(1)**		
LIPOTIDAE							
Lipotes vexillifer	0	0/1	3.4	-Singly, pairs (Mother+calf) (0) -Small (most common) **(1)** -Aggregations (3)	-Relatively long for mother and calf **(0)** -Weak associations when found in groups **(1)**	Mother+calf **(0)** Unknown **(?)**	27, 83-86
PHOCOENIDAE							
Phocoena dioptrica	1	?	3	-Singly (0) -Small groups **(1)**	-Unknown (except for the mother and calf) **(?)**	Mother+calf (0) Unknown **(?)**	87-89
Phocoena phocoena	1	1	5.7	-Single **(0)** -Pairs (most common) -Small groups (most common) **(1)** -Aggregations (3)	-Relatively long for mother and calf **(0)** -Weak associations when found in groups **(1) –described as 'fluid'**	Mother+calf **(0)** Unknown **(?)**	27, 90-94
P. sinus	1	1	2	-Single -Pairs (most common) **(0)** -Small groups (1)	-Relatively long for mother and calf **(0)** -Weak associations when found in groups **(1) –described as 'fluid'**	Segregated by sex and age (possibly) **(1)**	27, 95-97
P. spinipinnis	1	?	4.5	-Small (most common) **(1)** -Aggregations (3)	-Unknown (except for the mother and calf) possibly short **(?)**	Mother+calf (0) Unknown **(?)**	27
Phocoenoides dalli	1	1	7.4	-Single (sometimes) (0) -Small groups (most common) **(1)** -Large feeding aggregations (rare) (3)	-Relatively long for mother and calf **(0)** -Weak associations when found in groups **(1) –described as 'fluid'**	Segregated by sex and age (possibly) **(1)**	27, 98-99
Neophocaena phocaenoides	1	1	3	-Pairs (most common) **(0)** -Small groups (most common in Yangtzee) **(1)**	-Relatively long for mother and calf **(0)** -Weak associations when found in groups **(1) –described as 'undeveloped'**	Mother+calf **(0)** Unknown **(?)**	27, 100-104
MONODONTIDAE							
Monodon monocerus	1	3	3	-Small groups (most common) **(1)** -Large schools (2)	-Short and fluid assocaitons (possibly in large groups) **(1)** -Matrilineal (described as possibly 'matrifocal') **(3)**	-Segregated by sex and age (possibly) **(1)** -Mixed **(2)**	27, 105-110
Delphinapterus leucas	1	1/2	32.9	-Singly (0) -Small groups (most common in some areas) **(1)** -Schools (most common in some areas) **(2)** -Large Aggregations in breeding areas (3)	-Relatively long for mother and calf **(0)** -Weak associations when found in groups **(1) –described as 'fluid'**	Segregated by age and sex **(1)**	27, 111-119
DELPHINIDAE							
Cephalorhynchus commersonii	1	1	6.9	-Small groups **(1)**	-Weak (described as 'fission-fusion') **(1)**	Mother+calf **(0)** Unknown **(?)**	27, 120-121
C. eutropia	1	1	10	-Small groups **(1)**	-Weak (described as 'fission-fusion') **(1)**	Mother+calf **(0)** Unknown **(?)**	120,122
C. hectori	1	1	8	-Small groups **(1)**	-Weak (described as 'fission-fusion') **(1)**	Segregated by age and sex (possibly) **(1)**	123-127
C. heavisidii	1	1	3.2	-Small groups **(1)**	-Weak (described as 'fission-fusion') **(1)**	Mother+calf **(0)**	128, 120

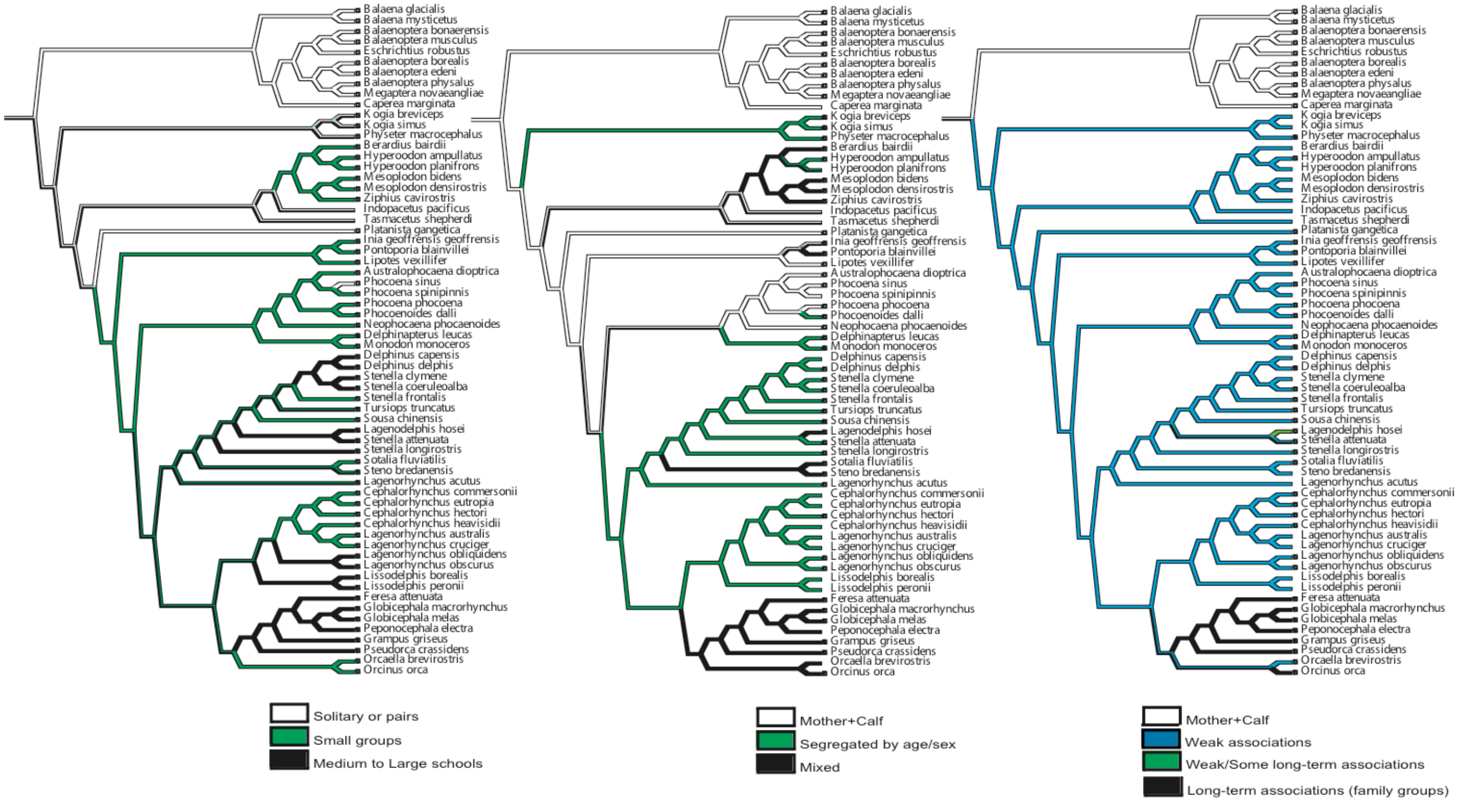
						Unknown **(?)**	
Lagenorhynchus australis	?	?	6.92	-Small groups **(1)** -Aggregations (rare) (3)	-Unknown (except for the mother and calf) **(?)** -Weak (described as 'fission-fusion') **(1)**	Mother+calf **(0)** Unknown **(?)**	129-131 131b
L.cruciger	?	?	7	-Small groups **(1)**	- Unknown (except for the mother and calf) **(?)**	Mother+calf **(0)** Unknown **(?)**	132-133
L. obliquidens	1	1	127.38	-Medium sized groups **(2)** -Large schools (small units within)	-Weak associations (possible strong male associations) **(1,2)**	Segregated by age and sex **(1)**	27, 129, 134-136
L. obscurus	1	1/2	86	-Small groups (1) -Medium sized groups (most common) **(2)** -Large schools	-Weak **(1) -described as 'fission-fusion'** -Some long term associations **(2)**	Segregated by age and sex **(1)**	27, 137-141
L. acutus	1	1	53.2	-Small groups (most common in some areas) **(1)** -Medium (most common in some areas) **(2)** -Large schools	-Unknown (except for the mother and calf) possibly short **(?)**	Segregated by age and sex (based on strandings) **(1)**	27, 142-144
Lissodelphins borealis	1	?	110.2	-Singly (0) -Large schools (most common) **(2)**	-Unknown (except for the mother and calf) possibly short **(?)**	Mother+calf **(0)** Unknown **(?)**	27, 145-147
L. peronii	1	?	210	-Singly (0) -Small groups (1) -Large schools (most common) **(2)**	-Unknown (except for the mother and calf) possibly short **(?)**	Mother+calf **(0)** Unknown **(?)**	146, 148-150
Delphinus delphis	1	1/2	230.38	-Small subunits (within large and Medium size schools) **(1)** -Medium sized groups (most common in some areas) **(2)** -Large schools (most common in some areas) -Large aggregations (3)	-Strong subunits with possible related animals **(3)** -Weak associations**-described as 'highly fluid fission-fusion social system' (1)**	Segregated by age and sex (possibly) **(1)**	28, 136, 151-155
Delphinus capensis	1	?	411.69	-Large schools **(2)**	-Unknown (except for the mother and calf) possibly short **(?)**	Mother+calf **(0)** Unknown **(?)**	136
Stenella attenuata	1	1/2	360	-Small groups (1) -Medium sized groups **(2)** -Large schools	-Strong associations (possibly within male groups) **(2)** -Weak associations (described as 'fluid') **(1)**	Segregated by age and sex **(1)**	27-28, 156-162
S. clymene	1	?	97.4	-Small groups (1) -Medium sized groups **(2)** -Large schools	-Unknown (except for the mother and calf) possibly short **(?)**	Segregated by age and sex (based on strandings) **(1)**	27-28, 136, 163-167
S. frontalis	1	1/2	10	-Small groups **(1)**	-Strong associations (within male groups) **(2)** -Weak associations (described as 'fluid') **(1)**	Segregated by age and sex **(1)**	27, 168-173
S. coeruleoalba	1	1/2	302	-Small (most common in some areas) **(1)** -Medium (most common in some areas) **(2)** -Large schools (most	-Strong associations (possibly within male groups) **(2)** -Weak associations (described as 'fluid') **(1)**	-Segregated by age and sex **(1)** -Mixed **(2)**	27-28, 136, 174-175

				common in some areas)			
S. longirostris	1	1/2	147.74	-Large schools **(2)**	-Weak associations (described as 'fluid') **(1)** -Strong (described as 'strongly bonded') for other group members not necessarily just males) **(2)**	-Segregation by sex and age **(1)**	27-28, 136, 177, 179, 180, 178, 176, 181,
Tursiops truncatus	1	1/2	92-2	-Small groups (most common in some areas) **(1)** -Medium sized groups (most common in some areas) **(2)** -Large schools (most common in offshore ecotype)	-Strong (males coalitions and alliances) **(2)** -Weak (described as 'fission-fusion') **(1)**	-Segregation by sex and age **(1)**	27-28, 136, 182-*199*
Lagenodelphis hosei	1	2	440.05	-Large schools **(2)**	-Strong (described as more strong than other social dolphins like *Stenella*) **(2)**	-Mixed (based on strandings) **(2)**	27, 136, 200-204
Sousa chinensis	1	1/2	14.9	-Solitary large adults (0) -Small groups (most common) **(1)** -Medium sized groups (rare)	-Weak (described as 'fluid with short-lasting associations') **(1)** -Strong mother +calf **(0)** -Strong (affiliations in stable groups from Mozambique) **(2)**	-Segregation by sex and age **(1)** -Mixed (all age classes) **(2)**	27, 205-210
Sotalia fluviatilis (riverine) *Sotalia guianensis (marine)*	1	2	13	-Singly (both species) (0) -Small (riverine) (most common) **(1)** -Medium (marine) (2) -Large feeding aggregations (marine) (3)	-Weak associations **(1)** -'Family' (2adults+calf) described in the marine species **(2)**	-Mixed **(2)**	211-218
Steno bredanensis	1	?	40	-Small (most common in some areas) **(1)** -Medium (most common in some areas) **(2)** -Large aggregations (3)	Unknown (except for the mother and calf) **(?)**	-Mixed (based on strandings but largely unknown) **(2)**	27-28, 136, 219-223
Feresa attenuata	1	?	30.12	-Small (more common in some areas) **(1)** -Medium sized groups (more common in some areas) **(2)** -Large schools (rare)	-Strong (possibly similar to other globicephaliinids were individuals are related) **(3)**	-Mixed (based on strandings but largely unknown) **(2)**	27, 136, 224-227
Globicephala macrorhynchus	1	3	41.1	-Small groups **(1)** -Medium sized groups **(2)**	-Matrilineal (natal philopatry, males live the group) **(3)**	-Mixed **(2)**	27-28, 45, 136, 228-234
G. melas	1	3	84.5	-Medium sized groups **(2)** -Large schools	-Matrilineal (natal philopatry, males live the group) **(3)** -Weak (some evidence of short term associations) **(1)**	-Mixed **(2)**	27, 228-229, 231-232, 234, 235-238
Grampus griseus	1	1/2	63	-Small (more common in some areas) **(1)** -Medium (more common in some areas)**(2)** -Large schools (rare)	-Possibly strong, calves tend to stay longer than non-globicephaliinids dolphins. **(2)** -Natal philopatry, males move between groups) **(3)**	-Mixed **(2)** -Maybe some segregation by age **(1)**	27-28, 136, 234, 239-243
Peponocephala electra	1	3	257.7	-Large schools (more common) **(2)**	-Strong (described as 'strong social bonds') **(2)**	Mother+calf **(0)** Unknown **(?)**	27, 136, 234, 244-246

Pseudorca crassidens	1	3	36.16	-Small groups (1) -Medium (more common in some areas) **(2)** -Large schools	-Strong (described as 'strong affiliative behavior' in stranded animals) **(2)**	-Mixed (based on strandings) **(2)**	27-28, 45, 136, 247-250
Orcaella brevirostris (riverine) *Orcaella heinsohni (marine)*	1	0	3.5	-Small (most common) **(1)** -Medium sized groups (rare) (2)	-Weak (described as 'frequency mixing' **(1)**	Mother+calf **(0)** Unknown **(?)**	251-254
Orcinus orca	1	3	12	-Single (mainly males are infrequent) (0) -Small to Medium ('fish eating') **(1)** -Small ('mammal eating') **(1)** -Large aggregations (3)	-Matrilineal with natal philopatry in fish eating orcas **(3)** -Two generation matrilineal in mammal eating orcas (3)	-Mixed **(2)**	27-28, 136, 234, 255-266

**Species which part of information comes from the sister species

APPENDIX 6



a. Group Size

b. Group Composition

c. Group Stability/Associations

Optimization of components of sociality. This figure shows social components optimization (a=group size, b=group composition, c=group stability/association patterns) on the preferred phylogeny. Note that this optimization contains polymorphic species and thus family based group like *Physeter* and *Monodon* and species with long-term associations between non-related group members are all optimized using the lowest state of sociality.

APPENDIX 7. Cetacean tonal sound acoustic parameters. This table reviews published data on cetacean tonal sound acoustic parameters. Numbers in bold correspond to the preferred value used in the optimizations (see Methods).

SPECIES	MAX (KHZ)	MMAX (KHZ)	MIN (KHZ)	MMIN (KHZ)	MAXD (S)	MD (S)	MIND (S)	COMPLEXITY [INFLECTION POINTS-IP]			REFERENCES
								MEAN	IP-TWO STATE	IP-FOUR STATE	
BALEEN WHALES (MYSTICETI)											
BALAENIDAE											
Eubalaena glacialis	11.23	3.14	0.02	0.05	2.08	0.99	0.26	1≤*	0	0	267
B. mysticetus	**2**	0.165	0.09	**0.02**		1.1		1≤*	0	0	268
	1	**0.3**	**0.02**	0.05							269
BALAENOPTERIDAE											
Balaenoptera bonaerensis	?	?	?	?	?	?	?	?	?	?	
B. borealis	**3.5**	?	1.5	?		0.04		1≤*	0	0	270
	1		**~0.1**			**1.1**					271
B. edeni/ B. brydei	**0.245**		0.07			0.42		1≤*	0	0	272
	0.180		0.09								273
	0.079		**0.0207**			**2.3**					274
B. musculus	0.0185		0.0157			11		1≤*	0	0	275
	0.0202		0.0182			10					276
	0.122					**29**					277
			0.011			0.80					278
	0.052		0.050		10	8					279
	0.0277		0.0189			16	3				280
		0.0189		0.0172	**28.2**	22.8					281
	0.242	**0.0883**	0.0143	**0.0166**			**1**				282
B. physalus	**0.118**		**0.010**					1≤*	0	0	283
		0.023		**0.018**		**1**					284
	0.058	**0.042**	0.017	0.020		0.7					285
Megaptera novaeangliae	4	1.315	0.25	0.925		0.96		1≤*	0	0	286
ESCHRICHTIDAE											
Eschrichtius robustus	**0.2**		**0.02**			1.54		1≤*	0	0	287
	0.2		0.1								288
		0.3		0.25							289
NEOBALAENIDAE											
Capera marginata	0.135	?	0.06	?		0.18		1≤*	0	0	290
TOOTHED WHALES (ODONTOCETI)											
KOGIIDAE											

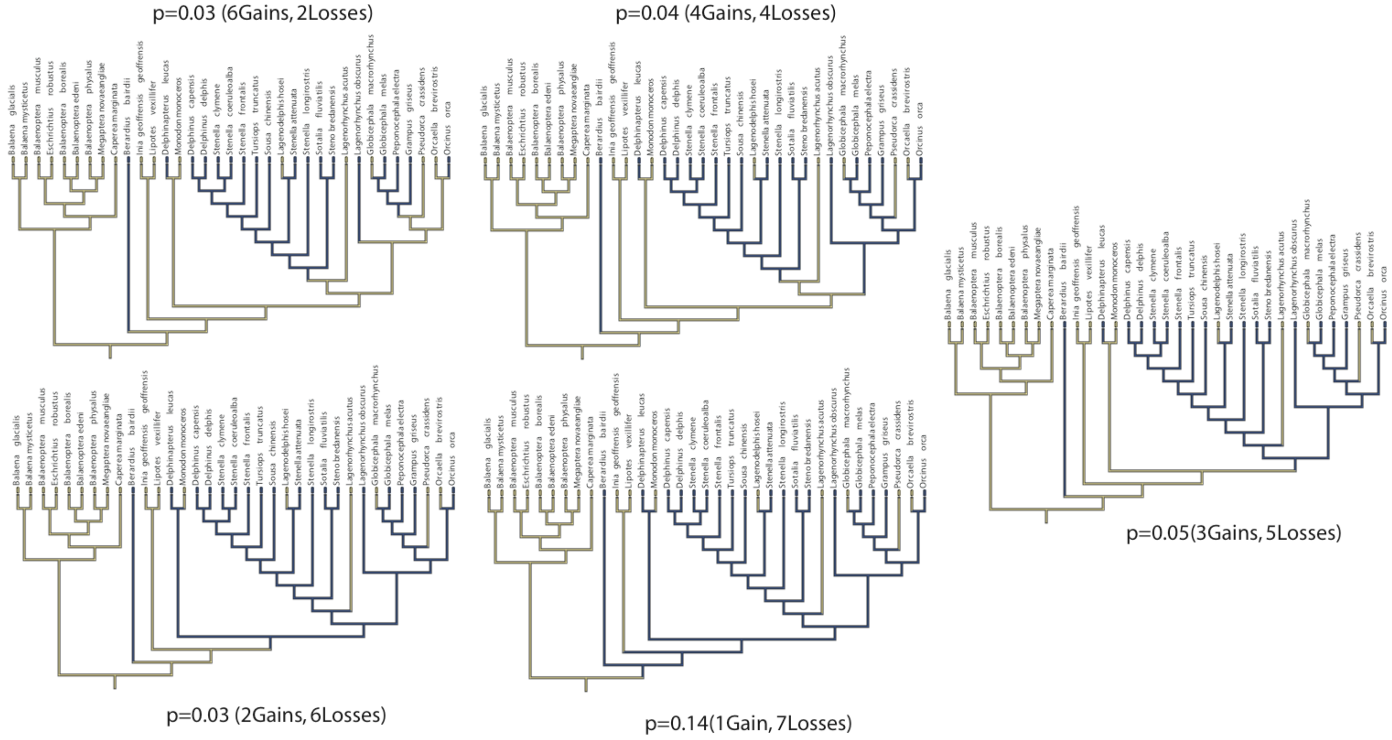
Kogia breviceps	?	?	?	?	?	?	?	?	?	?	
K. simus	?	?	?	?	?	?	?	?	?	?	
PHYSETERIDAE											
Physeter macrocephalus	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
ZIPHIIDAE											
Berardius bairdii (B. anurxii)	8.0	?	4	?	~3.5		~2	~3	1	2	46
Hyperoodon ampullatus	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
H. planifrons	?	?	?	?	?	?	?	?	?	?	
Mesoplodon bidens	?	?	?	?	?	?	?	?	?	?	
M. densirostris	?	?	?	?	?	?	?	?	?	?	
Ziphius cavirostris	?	?	?	?	?	?	?	?	?	?	
PLATANISTIDAE											
Platanista gangetica	?	?	?	?	?	?	?	?	?	?	
INIIDAE											
Inia geoffrensis	**48.10** 5.16 13	**24.71** 2.97	5.03 **0.22** 3	15.06 **2.54**	0.080 **4.42**	0.009 **1.14**	**0.002** 0.16	 1.05	1	1	291 292-293 294
PONTOPORIDAE											
Pontoporia blainvillei	?	?	?	?	?	?	?	?			
LIPOTIDAE											
Lipotes vexillifer	4.5 **4.6**	5.84 **6.1**	3.8 3.8	5.0 **4.9**	**1.8** 1.6	1 1	**0.4** 0.5	0.72	1	0	295 296
PHOCOENIDAE											
Phocoena dioptrica	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
Phocoena phocoena	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
P. sinus	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
P. spinipinnis	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
Phocoenoides dalli	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
Neophocaena phocaenoides	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
MONODONTIDAE											
Monodon monocerus	**18** 10 8.84	 7.18	**0.3** 5 0.360	 0.718	**6** 0.85 1.26	 1.19	**0.05** 0.1 0.68	1≤* 1≤* 1≤*	0	?	297 298 299
Delphinapterus leucas	**19.6** 15.8	6.8 4.33 **11.65**	**0.2** 0.4	3.8 3.38 **1.99**	**3.92** 3.2	1.06 0.75 **1.12**	**0.01** 0.05	1>* 1>* **13.5**	1	3	300 301 302
DELPHINIDAE											
Cephalorhynchus commersonii	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	

C. eutropia	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
C. hectori	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
C. heavisidii	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
Lagenorhynchus australis	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
L.cruciger	?	?	?	?	?	?	?	?	?	?	
L. obliquidens	~13	~10	~1	?	0.2	0.7	1.2	~>1	1	0	303
L. obscurus	27.3	**16.49**	1.04	**8.11**	**3.14**	**1.03**	0.18	1.97	1	1	292
		13.22		8.15	1.04	0.535	**0.014**				304
L. acutus	?	12.14	?	8.21		0.5		0.92	1	0	305
Lissodelphins borealis	?	?	?	?	?	?	?	?	?	?	
L. peronii	?	?	?	?	?	?	?	?	?	?	
Delphinus delphis	19.8	11.65	4.8	**6.42**				1>*	1	1	306
		13.6		7.4		0.8		**1.2**			307
Delphinus capensis	?	15.5	?	7.7		0.70		1.3	1	1	307
Stenella attenuata	21.4	15.72	3.13	8.73	1.95	0.53	0.09	0.70	1	1	292
		18.7		**8.2**		**0.9**		**1.9**			307
S. clymene	?	**19.2**	?	**6.33**		**0.61**		1>*	1	?	308
		13.62		9.25		0.41					309
S. frontalis	19.8	16.04	5	7.91	2.07	0.82	0.08	3.43	1	3	292
S. coeruleoalba	22.99	11.53	1.1	**6.84**		0.54		1.3	1	1	310
		14.8		8.1		**0.8**		**1.9**			307
S. longirostris	22.5	15.2	3.91	9.03	1.82	**0.75**	0.10	1.07	1	1	292
		13.7		9.1		0.6		**1.9**			307
	24	16.5		9.99		0.72	0.016				311
	25.25	**17.56**	**0.85**	9.66	3.35	0.49	0.013				312
	23.04	16.8	4	10.19	**4.49**	0.61	**0.040**				313
		14.32		**8.76**	1.87	0.43		0.55			305
Tursiops truncatus	**41**					0.86			1	3	314
		17.2		7.4		**1.4**		**3.7**			307
	21.6	11.35	1.86	**5.46**	3.20	0.70	0.05	1.86			292
		11.95	**0.94**		3.20	0.75	0.05	2.14			315
		16.24		7.33		1.3		2.86			305
Lagenodelphis hosei	24.0	**16.9**	4.3	9.36		**0.77**			1	0	316
	18.3	14.9	6.6	11		0.46		0.80			317
	13.4			**7.64**	0.5		0.4				318
Sousa chinensis	**22**	16.3	**0.9**	4.5	1.3	**1.1**	0.01	1>*	1	?	319
			3			0.2					320
	20		1.2			0.13					321
*Sotalia fluviatilis***		19.95	1.34	**7.21**	**1.064**	0.381	0.038	0.77	1	1	322
	23.9	15.41	3.65	10.2	1.04	0.41	0.06	**1.38**			292, 293

	38.25	**21.32**	2.714	13.14							Authors unpublished data
		13	**0.5**	7.6	0.852	0.103	0.01	0.7			
	18	13.312	1.031	10.521	2.2	**0.79**	**0.009**	1.3			
	17.49	15.65		9.18		0.63					323
											324
											325
Steno bredanensis	7.0		4						1	1	326
		9.1		6.03		0.6		1.3			307
Feresa attenuata	?	?	?	?	?	?	?	?	?	?	
Globicephala macrorhynchus	23.6	**10.87**	0.24	6.25		**0.56**		0.69	1	0	327
		6.1		**3.6**		0.4		**0.7**			307
G. melas	21.2	**8.86**	0.32	**3.48**		**0.72**		0.98			327
		4.716		2.82		0.71		**1.01**			305
Grampus griseus		**20**		**3.9**		4.9		1>*	1	1	328
	23.8	13.44	1.90	8.83		**0.53**		**1.37**			327
Peponocephala electra		12.14		8.381		0.54		**1.05**	1	1	317
	24.5		5.5		0.9		0.1	0.04			329
Pseudorca crassidens	18.1	**8.29**	1.87	5.43		**0.56**		**0.75**	1	0	327
		6.1		**4.7**		0.4		0.5			307
*Orcaella brevirostris***	6.0	4.2	1.1	3.2	0.3	0.3	0.1	~1≤	1	0	330
Orcinus orca	**18**			**1.5**					1	3	331
		6.61		4.27							332
			0.05								333
	8.9	9.9	2.4	5.4		**1.8**		1>			334
	16.7	**12.64**		3.36	18.3	1.11	0.06	**21.14**			335

**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 references 115 and 116)

APPENDIX 8


p=0.03 (6Gains, 2Losses)

p=0.04 (4Gains, 4Losses)

p=0.05(3Gains, 5Losses)

p=0.03 (2Gains, 6Losses)

p=0.14(1Gain, 7Losses)

Optimization of tonal sound complexity and the association between sociality and tonal sound complexity. Most parsimonious optimizations of tonal sound complexity (based on mean number of inflection points, MIP) and results from the concentrated changes test for sociality and tonal sound complexity (yellow= state 0, tonal sounds with MIP≤1, blue=state 1, tonal sounds with MIP>1).

APPENDIX 9. Association between components of sociality and tonal sound complexity. This table summarizes results from SIMMAP analyses of character associations between social components (selecting the highest social state for polymorphic species) and components of tonal sound complexity on the preferred phylogeny.

Tonal Sound Complexity	Group size (p<0.027, p>0.973)			
Four states	0	1	2	3
0 (0-1) *Dij*	0.079	0.0090	-0.028	
p-value	0.91	0.86	0.001*	
1 (1.1-2) *Dij*	-0.036	0.0023	0.123	
p-value	0.005*	0.79	0.92	
2 (2.1-3) *Dij*	-0.0049	0.052	-0.022	
p-value	0.015*	0.90	0.007*	
3 (>3.1) *Dij*	-0.0051	0.026	-0.0025	
p-value	0.021*	0.89	0.013*	
Tonal Sound Complexity	Group associations/stability (p<0.027, p>0.973)			
Four states	0	1	2	3
0 (0-1) *Dij*	0.080	0.0098	-0.031	0.0012
p-value	0.93	0.88	p<0.0001*	0.84
1 (1.1-2) *Dij*	-0.036	0.023	0.061	0.042
p-value	0.005*	0.89	0.91	0.89
2 (2.1-3) *Dij*	-0.062	0.014	0.023	-0.054
p-value	0.009*	0.92	0.92	0.010*
3 (>3.1) *Dij*	-0.0057	0.020	0.0054	-0.00069
p-value	0.009*	0.94	0.87	0.027*
Tonal Sound Complexity	Group Composition (p<0.027, p>0.973)			
Four states	0	1	2	3
0 (0-1) *Dij*	0.087	-0.024	-0.0069	0.0049
p-value	0.94	0.004*	0.021*	0.86
1 (1.1-2) *Dij*	-0.017	0.075	0.031	-0.0007
p-value	0.004*	0.93	0.91	0.04
2 (2.1-3) *Dij*	-0.0014	-0.0043	0.029	0.003
p-value	0.033	0.021*	0.91	0.84
3 (>3.1) *Dij*	0.0089	0.014	-0.0016	0.0055
p-value	0.84	0.90	0.015*	0.56

*Significant negative associations, **significant positive associations

D=0.394, p<0.0001, $n_{p\text{-value}}$=510, n_D=2000 Group Size and Tonal Sound Complexity
D=0.364 p<0.0001, $n_{p\text{-value}}$=553, n_D=2000 Group Association/Stability and Tonal Sound Complexity
D= 0.306 p<0.0001 , $n_{p\text{-value}}$=832, n_D=2000 Group Composition and Tonal Sound Complexity

APPENDIX 10. Association between sociality and tonal sound complexity. This table summarizes results from SIMMAP analyses of character associations between social structure (categorized as 1-4) and tonal sound complexity on the preferred phylogeny across reference phylogenies (see Methods)

Tonal Sound Complexity **Four states** D=0.375 p<0.001* (2states) D=0.356 p<0.001* (4states)	Social Structure (p<0.027, p>0.973) **Arnasson *et al.* 2004 filtered (n=325)**			
	0	1	2	3
0 (≤ 1 mean inflection point) *D-statistic* *p-value*	0.081 0.73	0.053 0.75	-0.041 0.003*	-0.0052 0.006*
1 (≤ 1 mean inflection point) *D-statistic* *p-value*	-0.044 p<0.001*	0.002 0.95	0.111 0.99**	0.036 0.98**
0 (0-1) *Dij* *p-value*	0.082 0.94	0.016 0.84	-0.033 p<0.001*	0.0094 0.90
1 (1.1-2) *Dij* *p-value*	-0.037 0.006*	0.026 0.91	0.077 0.95	0.022 0.93
2 (2.1-3) *Dij* *p-value*	-0.0036 0.009*	0.010 0.87	0.020 0.92	-0.0024 0.006*
3 (>3.1) *Dij* *p-value*	-0.0045 0.006*	0.016 0.88	0.005 0.84	0.0025 0.86
Tonal Sound Complexity **Four states** D=0.382 p<0.001* (2states) D=0.358 p<0.001* (4states)	**Nikaido *et al.* 2001 filtered (n=341)**			
	0	1	2	3
0 (≤ 1 mean inflection point) *D-statistic* *p-value*	0.083 0.75	0.053 0.72	-0.043 p<0.001*	-0.0047 0.003*
1 (≤ 1 mean inflection point) *D-statistic* *p-value*	-0.046 p<0.001*	0.0004 0.91	0.1156 0.99**	0.036 0.99**
0 (0-1) *Dij* *p-value*	0.082 0.91	0.00006 0.74	-0.033 0.005*	0.0090 0.85
1 (1.1-2) *Dij* *p-value*	-0.037 p<0.001*	0.0234 0.91	0.0776 0.92	0.0235 0.92
2 (2.1-3) *Dij* *p-value*	-0.0044 0.005*	0.0133 0.92	0.0223 0.87	-0.0032 0.020*
3 (>3.1) *Dij* *p-value*	-0.0050 0.011*	0.0165 0.93	0.0054 0.89	0.0026 0.90

TONAL SOUND COMPLEXITY **FOUR STATES** D=0.442/0.269 p<0.001* (2states) D=0.360/0.217 p<0.001* (4states)	**Messenger and McGuire 1998 (n=4) filtered/ Bayesian (n=2001)**			
	0	1	2	3
0 (≤ 1 mean inflection point) *D-statistic* *p-value*	0.085/0.072 p>0.999**/0.86	0.064/0.016 0.5/0.65	-0.050/-0.027 p<0.001*/0.004*	-0.015/-0.007 p<0.001*/0.025*
1 (≤ 1 mean inflection point) *D-statistic* *p-value*	-0.044/-0.053 p<0.001*/0.004*	-0.015/0.015 p<0.001*/0.96	0.12/0.048 p>0.999**/0.98**	0.05/0.031 p>0.999**/0.95
0 (0-1) *Dij* *p-value*	0.081/0.052 p>0.999**/0.94	0.0062/0.013 0.75/0.85	-0.032/-0.014 p<0.001*/0.04	-0.026/-0.009 p<0.001*/0.06
1 (1.1-2) *Dij* *p-value*	-0.036/-0.033 p<0.001*/0.021*	0.023/0.0007 p>0.999**/0.81	0.072/0.037 p>0.999**/0.93	0.038/0.025 p>0.999**/0.92
2 (2.1-3) *Dij* *p-value*	-0.0041/0.0011 p<0.001*/0.78	0.0060/0.012 0.75/0.87	0.026/-0.0032 0.75/0.064	-0.0032/0.003 p<0.001*/0.81
3 (>3.1) *Dij* *p-value*	-0.0057/-0.0019 p<0.001*/0.09	0.018/0.006 0.5/0.85	0.0028/0.0015 0.75/0.77	0.0037/0.005 p>0.999**/0.87
TONAL SOUND COMPLEXITY **FOUR STATES** D=0.378 p<0.001* (2states) D=0.355 p<0.001* (4states)	**May-Collado et al. 2007 filtered (n=1069)**			
	0	1	2	3
0 (≤ 1 mean inflection point) *D-statistic* *p-value*	0.082 0.74	0.053 0.73	-0.041 0.007*	-0.006 p<0.001*
1 (≤ 1 mean inflection point) *D-statistic* *p-value*	-0.045 p<0.001*	0.0012 0.92	0.112 0.99**	0.037 0.97**
0 (0-1) *Dij* *p-value*	0.082 0.92	0.0018 0.83	-0.033 p<0.001*	0.009 0.89
1 (1.1-2) *Dij* *p-value*	-0.037 0.0009*	0.025 0.93	0.077 0.93	0.023 0.90
2 (2.1-3) *Dij* *p-value*	-0.0037 0.021*	0.013 0.91	0.020 0.90	-0.003 0.012*
3 (>3.1) *Dij* *p-value*	-0.0043 0.013*	0.014 0.89	0.007 0.89	0.002 0.84

*Significant negative associations, **significant positive associations

APPENDIX 11. Regression between group size and tonal sound characteristics. This table summarizes results from PDAP regressionbetween group size and mean minimum frequency (MMinF) and mean number of inflection points (IP) across reference phylogenies (see Methods)

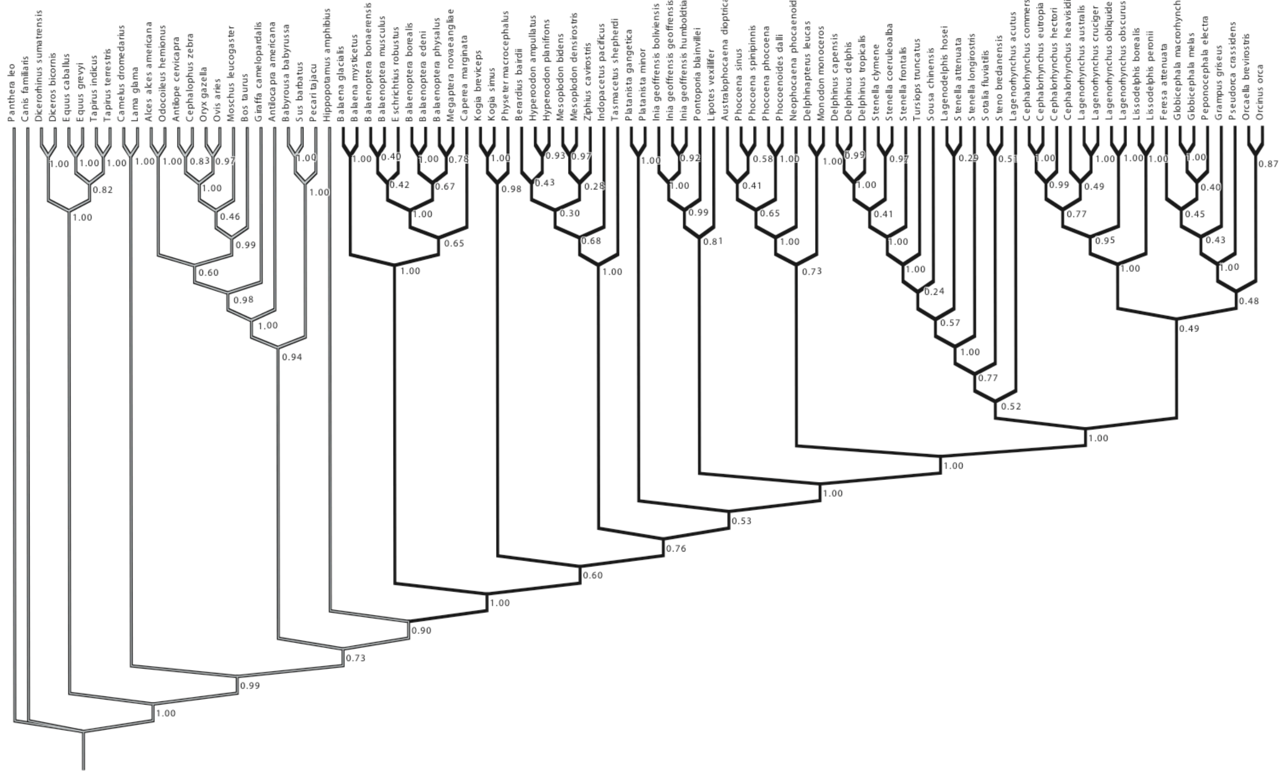
Acoustic Parameters vs Group Size	May-Agnarsson 2000 trees burnin	May-Collado filtered	Messenger and McGuire (1998) filtered	Messenger and McGuire (1998) Parsimony on their nuclear/morphology data	Messenger and McGuire (1998) Bayesian on their nuclear/morphology data	Arnasson et al (2003) Filtered	Nikaido et al. (2001) filtered
All Cetaceans							
MMinF R-square Df p-value	3.5 29 0.31	3.2 29 0.33	1.9 29 0.24	2.8 21 0.44	2.9 21 0.43	3.7 29 0.30	3.1 29 0.17
IP R-square Df p-value	7.5 33 0.05*	7.4 33 0.05*	10.2 33 0.03*	<1 22 0.86	<1 22 0.85	5.1 33 0.09	3.7 33 0.13
Toothed-Whales							
MMinF R-square Df p-value	13.8 23 0.03*	13.2 23 0.03*	5.8 23 0.12	11.4 16 0.08	9.7 16 0.21	15.4 23 0.03*	13.5 23 0.03*
IP R-square Df p-value	7.3 24 0.09	7.1 24 0.09	10 24 0.06	<1 17 0.92	<1 17 0.93	4.7 24 0.14	3.5 24 0.17

*Significant results

APPENDIX 12. Regression between duration and other acoustic variables. This table summarizes results from PDAP regression analyses between duration (s) and absolute (AbsMinF) and mean minimum (MMin) frequency and mean number of inflection

Acoustic Parameters vs Group Size	May-Agnarsson 2000 trees burnin	May-Collado filtered	Messenger and McGuire (1998) filtered	Messenger and McGuire (1998) Parsimony on their nuclear/morphology data	Messenger and McGuire (1998) Bayesian on their nuclear/morphology data	Arnasson et al (2003) Filtered	Nikaido et al. (2001) filtered
All Cetaceans							
Abs MinF R-square Df p-value	17 31 0.017	16.5 31 0.018	19.4 31 0.01	29.7 20 0.008	37 20 0.002	16.5 31 0.02	16.6 31 0.018
MMinF R-square Df p-value	17.5 29 0.019	19 29 0.014	12.5 29 0.05	Not significant	Not significant	19 29 0.014	19 29 0.014
IP R-square Df p-value	11.9 32 0.05	11.7 32 0.04	9.4 32 0.07	35.6 21 0.002	42.3 20 0.001	11.9 32 0.04	12.2 32 0.04
Toothed-Whales							
Abs MinF R-square Df p-value	37.8 22 0.001	39 22 0.001	38.7 22 0.001	43.9 15 0.003	45.9 15 0.002	39.2 22 0.001	38.1 22 0.001
MMinF R-square Df p-value	23.8 23 0.013	26.7 23 0.008	24.6 23 0.01	25.8 16 0.03	23.9 16 0.03	26.4 23 0.008	26 23 0.009
IP R-square Df p-value	44.8 23 p<0.001	44.1 23 P<0.001	44.2 23 p<0.001	38.3 16 0.006	46 15 0.002	45 23 p<0.001	46.1 23 p<0.001

APPENDIX 13



Phylogeny of Cetacea. This figure reproduces the preferred phylogenetic hypothesis of May-Collado et al. (2007), used here for all main analyses. Numbers on nodes represent posterior probabilities

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VITA

LAURA JOHANNA MAY-COLLADO

May 6th 1971	Born, Puntarenas, Costa Rica
1991-1995	B.S. Biology University of Costa Rica San Jose, Costa Rica
1992-1996	Teaching Assistant/Museum of Zoology Curator Assistant (Mammalogy/Ornithology) University of Costa Rica San Jose, Costa Rica
1997-1998	Visitor Scholar Portland State University Portland, USA
2001-2002	Teaching Assistant Organization for Tropical Studies San Jose, Costa Rica
1998-2001	M. Sc. Biology University of Costa Rica San Jose, Costa Rica
1998-2003	Research Assistant Centro de Investigaciones del Mar y Limnologia, University of Costa Rica, San Jose, Costa Rica
2003-2007	Doctoral Candidate in Biology, Dept. of Biological Sciences, Florida International University Miami, Florida, USA
2003-2005	Head Teaching Assistant Teaching Assistant, Dept. of Biological Sciences, Florida International University Miami, Florida, USA

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