Narrow Acoustic Field of View Drives Frequency Scaling in Toothed Whale Biosonar

Highlights

- Toothed whales have evolved four different biosonar signals for echolocating prey
- Larger whales echolocate with higher output levels and at lower click rates
- Inverse frequency scaling leads to a highly narrow field of view across species

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In Brief

Jensen et al. analyze scaling of echolocation parameters in toothed whales. They show that large species use lower frequency and higher source levels for longer prey detection range. In contrast, species have converged on remarkably similar beamwidth, suggesting that a narrow field of view drives inverse frequency scaling in cetacean biosonar.
Narrow Acoustic Field of View Drives Frequency Scaling in Toothed Whale Biosonar

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SUMMARY

Toothed whales are apex predators varying in size from 40-kg porpoises to 50-ton sperm whales that all forage by emitting high-amplitude ultrasonic clicks and listening for weak returning echoes [1, 2]. The sensory field of view of these echolocating animals depends on the characteristics of the biosonar signals and the morphology of the sound generator, yet it is poorly understood how these biophysical relationships have shaped the evolution of biosonar parameters as toothed whales adapted to different foraging niches. Here we test how biosonar output, frequency, and directivity vary with body size to understand the co-evolution of biosonar signals and sound-generating structures. We show that the radiated power increases twice as steeply with body mass (P ∝ M1.47 ± 0.25) than expected from typical scaling laws of call intensity [3], indicating an evolutionary hyperallometric investment into sound production structures that may be driven by a strong selective pressure for long-range biosonar. We find that biosonar frequency scales inversely with body size (F ∝ M−0.19 ± 0.03), resulting in remarkably stable biosonar beamwidth that is independent of body size. We discuss why the three main hypotheses for inverse frequency scaling in animal communication signals [3–5] do not explain frequency scaling in toothed whale biosonar. We instead propose that a narrow acoustic field of view, analogous to the fovea of many visual predators, is the primary evolutionary driver of biosonar frequency in toothed whales, serving as a spatial filter to reduce clutter levels and facilitate long-range prey detection.

RESULTS AND DISCUSSION

Toothed whales comprise 75 species of apex predators that have adapted to a highly diverse set of feeding niches ranging from flooded forests and river systems to mesopelagic depths of the deep ocean. These echolocating predators depend on a pneumatic sound generator in their nasal passages to generate ultrasonic biosonar signals for finding and catching prey [6, 7]. While the origin of toothed whale echolocation suggests that echolocation evolved shortly after the split between toothed and baleen whales [8, 9], the diversification of toothed whale biosonar clicks and its consequences for sonar performance in different foraging niches has received much less attention. Extant toothed whales use four types of biosonar search clicks (Figure 1). Sperm whales (Physeteridae) produce broadband clicks that reverberate within the head to produce a multi-pulsed (MP) click [11]. Beaked whales (Ziphiidae) produce frequency-modulated (FM) clicks [12, 13]. Most delphinoids and river dolphins rely on a simple broadband (BB) click [14], whereas porpoises, franciscana dolphins, pygmy and dwarf sperm whales, and six species from the Lagenorhynchus and Cephalorhynchos genera generate narrowband high-frequency (NBHF) clicks [15–17] (Figure 1; Table S1). Despite large-scale differences in frequency and bandwidth, it remains poorly understood how evolution has shaped biosonar parameters in parallel with changes in body size. Sound source parameters of communicating terrestrial animals have been better studied, showing that larger animals generally produce communication signals at higher source levels [3] and at lower frequencies [4] compared to small animals, leading to a number of proposed scaling rules for animal communication signals. However, none of these mechanistic explanations accounted for directional sound emission, most likely because directional signals are beneficial for communication to a much lesser degree than for echolocation. Since signal frequency directly affects both sound directivity and attenuation, and therefore the sensory volume in which echolocating predators can detect prey [18], such traditional scaling laws may work differently for echolocating animals. Here we use phylogenetic regression of biosonar parameters of toothed whales to identify the evolutionary drivers of biosonar operation and to examine whether predictions from scaling of animal communication signals hold for echolocating toothed whales.

Hyperallometric Scaling of Sound Production Structures Lead to Increasing Biosonar Output for Large Whales

Toothed whales produce sound using a specialized set of nasal sound generators termed the phonic lips [6]. Sound production is driven by air pressure in the lower nasal passages set up by

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Figure 1. Evolution and Diversification of Biosonar Signal Types in Toothed Whales

(A) Biosonar signal types mapped onto the molecular phylogeny of odontocetes (adapted from [10]). Rectangles represent the ten families of extant toothed whales and have been color coded by biosonar signal type (red, multi-pulsed; blue, frequency modulated; purple, narrow band high frequency [NBHF]; orange, broadband). Note that a subset of Delphinidae species has evolved NBHF signals (purple box within Delphinidae).

(B–E) Waveforms of on-axis biosonar search signals for four representative species: Physeter macrocephalus (B; red), Ziphius cavirostris (C; blue), Phocoena phocoena (D; purple), and Tursiops aduncus (E; orange).

(F) Normalized power spectra corresponding to waveforms.

(G) Quality factor $Q_{\text{rms}}$ (defined as the centroid frequency divided by the root-mean-square [RMS] bandwidth) as a function of click centroid frequency for on-axis biosonar signals demonstrates the different clusters formed by broadband delphinid and narrowband high-frequency signals.

See also Table S1.
muscular activation of the nasopharyngeal pouch [7]. The radiated acoustic power is most likely limited by both the muscles responsible for driving air pressure and by the size of the vibrating phonic lips. Both of these scale with the size of the animal [7], resulting in increasing biosonar output with body size (Figure 2A). If toothed whales invest a constant fraction of their metabolic energy into sound production, then we expect the radiated acoustic power to scale with body mass to the power of three-quarters following studies of terrestrial animals [3]. In toothed whales, this assumption does not seem to hold: the radiated acoustic power per click (P, in watts) increases twice as steeply with body size (Figures 2B–2D), as expected from the three-quarter power scaling rule (phylogenetic generalized least squares [pGLS]: P \propto M^{1.47 \pm 0.25}; Data S1), indicating an evolutionary hyperallometric investment into sound-producing structures. This is most likely closely tied to increasing cranial asymmetry. Most toothed whales have two sets of phonic lips, with the right pair typically used for echolocation [19, 20]. Both delphinids and ziphiids exhibit significant cranial asymmetry [21], with a larger right compared to left set of phonic lips [6]. However, porpoises and other NBHF species, which are generally small, show little to no cranial asymmetry [22] and employ a relatively low peak-power biosonar [15–17] that they partially compensate for by producing longer echolocation signals with higher total energy. On the other
end of the size scale, sperm whales have a uniquely enlarged nasal complex with only a single hypertrophied right pair of pholic tips that in turn allows them to produce extremely powerful biosonar clicks [11]. This hyperallometric investment in sound-generating structures means that toothed whale biosonar signals do not abide by the same scaling laws as animal call intensity [3].

**Biosonar Search Range Increases with Body Size**

As a consequence of increasing sound source levels, larger animals greatly increase their prey detection range and sensory volume under noise-limited conditions (Figure 2E). Prey detection range for an echolocating animal can be estimated either through acoustic modeling that account for differences in frequency and directivity [23, 24] or by using biosonar click rates as a proxy for the maximum inspection range [14, 25]. Across toothed whales, estimated target detection range, assuming identical prey and spectral noise, increases from tens of meters for NBHF species up to hundreds of meters for large ziphiids and sperm whales (Figure 2E). Although prey size and background noise certainly differ across species, these increases in detection range are mirrored by systematic differences in maximum inspection range of free-ranging animals (Figure 2F). Since echolocating predators typically wait for echoes to return before emitting the next click, the slower click rate of larger animals suggests that they are searching for prey at greater distances. The systematic increase in maximum prey detection range and inspection range relative to body length results in larger animals being able to probe a greater volume of water for prey. This may be extremely important for species that traverse large distances in search of patchy prey, such as deep-diving sperm whales [26] or beaked whales [27], and where foraging performance depends on the time it takes to find patches or evaluate patch quality. In contrast, the short detection range of shallow-water or riverine species is most likely an adaptation to habitats where reverberation or clutter [28], rather than noise, may limit effective prey detection [29, 30].

Thus, although it remains to be specifically tested whether animals in open, deep-water environments use higher biosonar output levels compared to animals in coastal habitats, it seems likely that peak output levels and biosonar sampling rates reflect large-scale sensory adaptations to different foraging niches that are themselves tied into the size of the animal.

**Inverse Scaling of Biosonar Frequency Driven by Narrow Acoustic Field of View**

Large terrestrial animals generally vocalize at lower sound frequencies compared to smaller animals [31], and many studies have sought to identify the underlying principles behind frequency scaling in animal communication. Fletcher et al. [4], Ben-net-Clark [32], and Bradbury and Vehrenkamp [31] have argued that call frequency should be inversely proportional to body length (thereby resulting in $F \propto M^{-1/3}$) to ensure efficient sound production, since efficiency decreases sharply when the wavelength of emitted sound becomes larger than the circumference of the sound source [4]. Fletcher [5, 33] developed a more general model integrating sound production, propagation, and reception to estimate the sound frequency that maximizes communication range. With this functional approach, optimum frequency should scale with a slightly steeper power law for terrestrial animals ($F \propto M^{-0.40}$) and a much steeper power law for aquatic animals due to more efficient sound propagation ($F \propto M^{-0.65}$). Finally, Gillooly and Ophir [3] examined the possibility that maximum sound frequency is constrained by the rate of individual muscle contractions and concluded that frequency should therefore scale with a lower coefficient ($F \propto M^{-0.26}$) [3].

Our results for toothed whales show a clear frequency scaling with size (Figure 3A) that initially seems to support the muscle contraction model given very similar power law coefficients (pGLS: $F \propto M^{-0.19 \pm 0.03}$, Data S1). However, the biosonar frequencies of toothed whales are orders of magnitude higher than predicted from the frequency scaling relationship of communicating terrestrial mammals [32]. Furthermore, echolocation clicks are produced pneumatically [7], meaning that the muscle contraction hypothesis is a poor mechanistic explanation for inverse frequency scaling in toothed whales. The higher frequency compared to terrestrial animals of similar body size partially relates to the higher sound speed in water, meaning that efficient sound pressure radiation requires approximately 4.5 times higher sound frequency for the same sound generator size. However, Fletcher’s [4] sound production efficiency hypothesis also does not seem applicable since echolocating toothed whales use frequencies that are 10–30 times higher than required for efficient sound production.

An alternative ecological driver that might explain the high biosonar frequencies relates to the reflectivity of small prey [34, 35]: to achieve efficient backscatter, the dominant wavelength of the biosonar pulse should be less than the circumference of the target [36], meaning that minimum biosonar frequencies could be determined by the smallest prey of interest. In addition, if prey discrimination for target selection is required, frequencies must be well above this limit to generate detailed spectral information about target properties in the returning echo. An argument against the prey-backscatter hypothesis is that NBHF species show no scaling of frequency with size. These four groups of animals have independently evolved NBHF biosonar signals with centroid frequency around 130 kHz, most likely to avoid killer whale predation [37, 38]. Although small NBHF species use biosonar frequencies close to those predicted by scaling of frequency with body size, larger NBHF species use frequencies that are much higher than predicted for their size (Figure 3A), and we find no significant scaling of frequency within NBHF species (Figure 3B). It remains to be tested whether this lack of frequency scaling also means that NBHF species target approximately the same size of prey.

Finally, biosonar frequency also has consequences for other aspects of echolocation. Frequency, biosonar directivity, and the size of the sound emitter are tightly coupled in echolocating animals [39] so that transmitting directivity increases with the product of sound frequency and emitter size (i.e., the size of the melon). This makes it imperative to consider the implications of frequency choice on the directivity and therefore the field of view. We find a remarkable convergence on a narrow biosonar beam with a high directivity index ($DI = 26 \pm 2$ dB; Figure 3D) for wild toothed whales covering two orders of body mass (pGLS: $R^2 = 0.01, F_{1,17} = 0.16, p = 0.69$). This convergence mirrors similar patterns observed for trained bats [39] and raises the question of whether selection pressures are acting primarily on frequency or field of view. Paradoxically, NBHF species that show no scaling of biosonar frequency with body size still use
biosonar beams with similar directivity [15–17], meaning that transmitter aperture or melon size needs to be disproportionally small for larger NBHF species. Thus, at least in NBHF species, a narrow acoustic field of view does not seem to be a passive consequence of improving reflectivity of prey. In these species, a narrow field of view may have driven co-evolution of smaller transmitting apertures along with increasing biosonar frequency for larger NBHF species, suggesting that the acoustic field of view by itself may have evolutionary benefits.

The Evolutionary Benefits of a Narrow Acoustic Field of View

Our finding that free-ranging toothed whales spanning three orders of magnitude in body mass have converged on a high biosonar directivity (Figure 3D) suggests that the resulting narrow field of view may confer direct fitness advantages that can drive the co-evolution of biosonar parameters and structures associated with sound production and beam focusing in toothed whales. Several advantages of a narrow acoustic field of view may explain this sensory convergence either individually or in parallel:

1. For a power-limited biosonar system, an increase in transmitting directivity results in a longer and narrower field of view ahead of the echolocating whale (biosonar-detection hypothesis). This enables longer detection range of individual or patchy prey under conditions where ambient noise limits echo detection [23].
(2) The spatial filtering realized by a narrow acoustic field of view simultaneously reduces the generation of unwanted echoes from other objects in the environment [40], easing the cognitive demands [41] required to process complex acoustic scenes (spatial filtering hypothesis). This further facilitates biosonar operation in acoustically complex, cluttered, or highly reverberant areas such as coastal or riverine environments or in polar pack ice. However, although we see very high directivity for both beluga and narwhal [42], riverine species seem to use similar directivity compared to marine delphinids [29, 30].

(3) A narrow field of view may also help in tracking prey (prey-tracking hypothesis) by providing rapid changes in echo level as the narrow sonar beam is used to scan across the prey, as proposed for bats [43]. However, this also does not seem to explain the very high directivity seen here, since toothed whales generally increase the field of view with decreasing range [44–46].

Given these potential benefits, it is reasonable to ask why toothed whales do not have even narrower fields of view than the observed 5 to 10 degrees beamwidth. Several tradeoffs may be at work. First, although a narrow field of view increases source level and on-axis detection range, the total volume ensonified per click decreases with increasing directivity (since the ensonified volume is proportional to the square root of the biosonar beamwidth). Animals might partly compensate for this through movements that sequentially scan a wider swath, thus gaining the benefit of a long detection range and a large search volume [47]. A narrow field of view and correspondingly high source level also results in an average detection distance that increases with directivity (since detection distance is inversely proportional to the square root of beamwidth). Consequently, the time to intercept prey increases, thereby potentially reducing the number of prey captures per unit time but providing longer time for planning approaches and prey capture. A final problem posed by a narrow biosonar beam is analogous to the “homicidal chauffeur” problem from game theory [48]; during close-quarter prey tracking, prey only have to make relatively small excursions perpendicular to the axis of a narrow beam to escape the field of view. To some degree, toothed whales may have already addressed this problem since phocoenids [46], inids [30, 45], and delphinids [44] all demonstrate some level of dynamic control over their field of view by increasing beamwidth during target approach.

Conclusions
In conclusion, we have shown that size is an important factor shaping the biosonar output and detection range of toothed whales, but not their acoustic field of view. Hyperallometric investment in sound production organs in toothed whales means that the scaling coefficient of biosonar power to body mass is significantly higher than that for animal communication signals. Consequently, larger whales can detect prey at longer range, and they click more slowly to inspect these more distant regions. Conversely, there is a remarkable convergence on narrow biosonar beams across species independent of body size that mirrors similar patterns in bats [59] and may be analogous to the optical foveae of visual predators. We argue that the ecological advantages of a narrow field of view for biosonar-based prey search may drive both an inverse scaling of biosonar frequency with size, at frequencies much higher than typical animal communication signals, and the co-evolution of sound transmitter morphology. An optimal acoustic field of view, independent of body size, may be a tradeoff between long-range prey detection and clutter reduction, balanced against an increasingly small ensonified volume and larger risk of prey escaping the sensory field.

STAR★METHODS
Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION
Supplemental Information includes one table and one data file and can be found with this article online at https://doi.org/10.1016/j.cub.2018.10.037.

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AUTHOR CONTRIBUTIONS

DECLARATION OF INTERESTS
The authors declare no competing interests.
REFERENCES


STAR METHODS

KEY RESOURCES TABLE

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CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Frants Jensen (frants.jensen@gmail.com).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Data collection and synthesis

Acoustic data

We extracted and summarized data from 45 studies of free-ranging toothed whale biosonar signal parameters. Published data covered 39 out of some 80 known toothed whale species, and included representatives from 9 out of 10 toothed whale families. Primary acoustic parameters used for testing scaling predictions included the apparent source level (back-calculated to 1 m distance on the acoustic axis) measured as energy flux density (dB re. 1 Pa²s); the centroid frequency (kHz), defined as the half-power frequency that divides the power spectrum into two halves with equal energy; and the transmission beam directivity index (DI, in dB), the difference between on-axis source level and the source level of an omni-directional source of equal total energy. In addition, key descriptors of signal type included the duration, the root-mean-square (RMS) bandwidth (defined as the normalized second moment of the power spectrum) and the RMS quality factor Q (defined as the centroid frequency divided by the RMS bandwidth). We used the mean of reported values rather than extremes to reduce the influence of small sample sizes and make comparisons across species more reliable. Data were preferentially extracted from studies of wild animals, with up to three references per species, and removing the two studies of trained animals did not affect results. When source parameters were only available from studies using non-standardized source parameter definitions, not reporting values directly, or only reporting extremes rather than means, attempts were taken to estimate standardized parameters and these were indicated using superscript letters. For multiple studies of the same species or for studies reporting multiple measures (e.g., same species in different habitats), the average mean and standard deviations and the pooled range was calculated. All data can be found in Table S1 and in the online repository https://osf.io/2px9b/.

Body mass data

We collected approximate data on minimum and maximum weight for adult species preferentially from Jefferson and colleagues [53], and supplemented when needed with data from Arkive.org. For analyses, the mean of the reported extremes was calculated as our best estimate of approximate body mass of recorded animals. Since body mass was subsequently log-transformed for analyses, small errors in mass likely have only a minor effect on final results. All data from body mass is included in the online repository https://osf.io/2px9b/.

METHOD DETAILS

Biosonar output power

The biosonar output for each species was characterized by the total radiated acoustic power per click (in Watts, or J/s). We used the mean RMS source level (SLRMS, in dB re 1µPa² at 1 m), which is the radiated sound intensity per unit area at a distance of 1 m on...
the acoustic axis. Since echolocation signals are directional, we subtracted the transmission beam directivity (DL; in dB) to get a measure of what the source level would have been for an omni-directional signal with the same power. For species where transmission DL had not been empirically measured, we used a median value of 25.9 dB. The source power (in Pa²) was then divided by the specific acoustic impedance of water (calculated as density ρ multiplied by sound speed c) to quantify the radiated power per unit area (Wm⁻²). We finally calculated the total output power by multiplying by the total surface area of a sphere with 1 m radius. These steps are combined in Equation 1, noting that the correction 10⁶ is applied to change from the decibel reference sound pressure in water (μPa) to SI units of Pa.

\[ P = 4 \pi \frac{10^{0.1\text{SL}_{\text{ref}} - \text{DL}}/10}{10^9 \rho c} \quad \text{[units of W]} \]  

\text{(Equation 1)}

### Acoustic modeling of biosonar detection range

To evaluate how changing biosonar parameters affect potential detection range and acoustic depth of view, we modeled approximate prey detection range using the active sonar equation [14]:

\[ EL = SL - 2x TL + TS \]  

\text{(Equation 2)}

In Equation 2, all parameters are expressed in dB: EL is the received echo level; SL is the source level measured in energy flux density; 2x TL is the two-way transmission loss back and forth to the prey; and TS is the target strength, i.e., the amount of energy reflected back from the target. We estimated transmission loss as the combination of spherical spreading loss and frequency dependent absorption, so that TL = 20 log₁₀(R) + αR, with R signifying range to the target, and the absorption coefficient α calculated using the centroid frequency of each species [54].

Detection range was modeled under a noise-limited scenario, which assumes that detection occurs when the received echo energy exceeds the noise energy within the same frequency band (i.e., EL > NL). The masking noise energy is normally estimated as the spectral noise level N₀ (in dB re 1 μPa²Hz⁻¹, i.e., noise intensity per Hz bandwidth) integrated over the auditory filter bandwidth of the animal. Since we do not have reliable estimates of hearing sensitivity, let alone filter bandwidth, for many of the species here, we estimated the masking noise energy as the spectral noise level evaluated at the center frequency of the biosonar click and adjusted for the RMS bandwidth of on-axis signals:

\[ NL = N_0(F_c) + 10\log_{10}(BW_{\text{RMS}}) \]  

\text{(Equation 3)}

The spectral noise level (in dB re 1 μPa²Hz⁻¹) for centroid frequency Fc (in Hz) was estimated from the Wenz [55] Sea State 2 deep-water noise levels (approximately 58 dB at 1 kHz, with a decrease of 17 dB per 10-fold increase in frequency: Equation 4) plus thermal noise [56] for frequencies above 6 kHz (Equation 5) (equations from [57]):

\[ N_0, \ \text{wind}(F_c) = N_0(1kHz) - 17\log_{10}\left(\frac{F_c}{1kHz}\right) \]  

\text{(wind generated noise)}

\[ N_0, \ \text{thermal}(F_c) = -75 + 20\log_{10}(F_c) \]  

\text{(thermal noise)}

\text{(Equation 4)}

\text{(Equation 5)}

We solved the set of equations (EL = NL) numerically to find the maximum detection range, i.e., the range where the returning echo level was equal to the masking background noise level for three targets: a broadside cod (TS: −29 dB [58]); a tail aspect cod or small squid (TS: −36 dB [24]); and an intermediate target resembling a large squid (TS: −43 dB [58]).

### Quantification and Statistical Analysis

**Phylogenetic regression analysis**

The objective of scaling analyses was to test how body size affects biosonar signal parameters. To do this, we conducted a phylogenetic Generalized Least-squares analysis (pGLS) [59] to account for the differing degrees of trait similarity according to distances on a branching phylogeny. pGLS analyses were implemented in R version 3.3.1 [49] using the pgls function in the caper package [50]. We used phylogenetic data produced by McGowen et al. [10] downloaded as a Nexus file from TreeBase. The tree was edited in Mesquite [52] to remove species without data on biosonar signals, and to add timing of diversification of branches based on data published in McGowen et al. [10]. Finally, 95% confidence intervals (ignoring phylogeny) around the regression lines were calculated using the gls.ci function in the evomap package [51].

We used pGLS to quantify scaling relationships in the form \( Y \propto M^b \), where M is body mass, b is the scaling coefficient, and Y is the response variable. As independent variable, we used log-transformed body mass and as dependent variable we used back-calculated energy flux density (already on a log scale), log-transformed power, log-transformed centroid frequency or transmission DL (already on a log scale). For each pGLS model, species without measurements in the response variable were excluded from the analysis. For each relationship, we used Pagel’s λ estimated by the pgls::caper function using the maximum likelihood approach and bounding the value of λ between 0 and 1, to understand the amount of phylogenetic signal in the data.
Individual PGLS analyses were done for all odontocetes combined, as well as for the two big signal groups, broadband transient (BB) species [including *Platanistidae*, *Monodontidae*, * Iniidae*, and most species from *Delphinidae*], and narrow-band high-frequency (NBHF) specialists [including *Kogiidae*, *Pontoporiidae*, *Phocoenidae*, and six species from *Delphinidae*]. All results are included in Data S1.

**DATA AND SOFTWARE AVAILABILITY**

The data compiled for this paper are available in Table S1 and on OSF.io using the link: https://osf.io/2px9b/.
Supplemental Information

Narrow Acoustic Field of View Drives
Frequency Scaling in Toothed Whale Biosonar

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<td>1000</td>
<td>15</td>
<td>12&lt;sup&gt;d&lt;/sup&gt;</td>
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<td>4.1</td>
<td>3.3</td>
<td>27&lt;sup&gt;d&lt;/sup&gt;</td>
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<td><em>Platanista gangetica</em> [S5]</td>
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<td>127 ± 3</td>
<td>173 ± 3</td>
<td>22 ± 2</td>
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<td>59 ± 7</td>
<td>44 ± 7</td>
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<td>3.1 ± 0.3</td>
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<td><em>Ziphius cavirostris</em> [S6]</td>
<td>214</td>
<td>164</td>
<td>201&lt;sup&gt;f&lt;/sup&gt;</td>
<td>200</td>
<td>400</td>
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<td>5.3</td>
<td>&gt;25</td>
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<td><em>Hyperoodon ampullatus</em> [S7]</td>
<td>203 ± 9</td>
<td>169 ± 10</td>
<td>186 ± 9</td>
<td>276&lt;sup&gt;b&lt;/sup&gt;</td>
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<td>43</td>
<td>54&lt;sup&gt;f&lt;/sup&gt;</td>
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<td>18.3</td>
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<td>6.2&lt;sup&gt;i&lt;/sup&gt;</td>
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<tr>
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<td>211&lt;sup&gt;b&lt;/sup&gt;</td>
<td>165&lt;sup&gt;b&lt;/sup&gt;</td>
<td>200&lt;sup&gt;h&lt;/sup&gt;</td>
<td>301&lt;sup&gt;h&lt;/sup&gt;</td>
<td>333 ± 66&lt;sup&gt;b&lt;/sup&gt;</td>
<td>33&lt;sup&gt;b&lt;/sup&gt;</td>
<td>32&lt;sup&gt;b&lt;/sup&gt;</td>
<td>12.4&lt;sup&gt;b&lt;/sup&gt;</td>
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<td>132 ± 6</td>
<td>181 ± 6</td>
<td>14 ± 3</td>
<td>35 ± 18</td>
<td>101</td>
<td>96 ± 12</td>
<td>50 ± 17</td>
<td>29 ± 4</td>
<td>3.5 ± 0.5</td>
<td>25.9</td>
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<td><em>Monodon monoceros</em> [S15-18]</td>
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<td>155&lt;sup&gt;f&lt;/sup&gt;</td>
<td>201&lt;sup&gt;e&lt;/sup&gt;</td>
<td>28 ± 6&lt;sup&gt;b&lt;/sup&gt;</td>
<td>53 ± 13</td>
<td>69 ± 14</td>
<td>30 ± 11</td>
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<td><em>Delphinapterus leucas</em> [S19-21]</td>
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<td>163 ± 5</td>
<td>209&lt;sup&gt;e&lt;/sup&gt;</td>
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<td>23 ± 33</td>
<td>41 ± 6</td>
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<td><em>Neophocaena phocaenoides</em> [S22]</td>
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<td>130 ± 7&lt;sup&gt;b&lt;/sup&gt;</td>
<td>167 ± 8&lt;sup&gt;b&lt;/sup&gt;</td>
<td>44 ± 11&lt;sup&gt;b&lt;/sup&gt;</td>
<td>41 ± 42&lt;sup&gt;b&lt;/sup&gt;</td>
<td>129 ± 4&lt;sup&gt;b&lt;/sup&gt;</td>
<td>129 ± 4</td>
<td>21 ± 7</td>
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<tr>
<td><em>Phocoena phocoena</em> [S23]</td>
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<td>133 ± 6&lt;sup&gt;b&lt;/sup&gt;</td>
<td>175 ± 7&lt;sup&gt;b&lt;/sup&gt;</td>
<td>62 ± 21&lt;sup&gt;h&lt;/sup&gt;</td>
<td>-</td>
<td>137 ± 4&lt;sup&gt;b&lt;/sup&gt;</td>
<td>138 ± 5&lt;sup&gt;b&lt;/sup&gt;</td>
<td>15 ± 6&lt;sup&gt;b&lt;/sup&gt;</td>
<td>10 ± 2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>15 ± 4&lt;sup&gt;b&lt;/sup&gt;</td>
<td>25.3&lt;sup&gt;b&lt;/sup&gt;</td>
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<td><em>Phocoena dalli</em> [S23]</td>
<td>183 ± 7</td>
<td>132 ± 7</td>
<td>172 ± 7</td>
<td>104 ± 37</td>
<td>-</td>
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<td>137 ± 4</td>
<td>11 ± 5</td>
<td>8 ± 2</td>
<td>17 ± 4</td>
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Notes:
- <sup>a</sup>: Data taken from [S1-3].
- <sup>b</sup>: Data taken from [S4].
- <sup>c</sup>: Data taken from [S5].
- <sup>d</sup>: Data taken from [S6].
- <sup>e</sup>: Data taken from [S7].
- <sup>f</sup>: Data taken from [S8].
- <sup>g</sup>: Data taken from [S9].
- <sup>h</sup>: Data taken from [S10].
- <sup>i</sup>: Data taken from [S11].
- <sup>j</sup>: Data taken from [S12].
- <sup>k</sup>: Data taken from [S13].
- <sup>l</sup>: Data taken from [S14].
- <sup>m</sup>: Data taken from [S15].
- <sup>n</sup>: Data taken from [S16].
- <sup>o</sup>: Data taken from [S17].
- <sup>p</sup>: Data taken from [S18].
- <sup>q</sup>: Data taken from [S19].
- <sup>r</sup>: Data taken from [S20].
- <sup>s</sup>: Data taken from [S21].
- <sup>t</sup>: Data taken from [S22].
- <sup>u</sup>: Data taken from [S23].

单位：µPa, kHz, dB re 1µPa, degrees, µs, ms, MHz, kHz, dB.
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<th>Species (continued)</th>
<th>SL_{ap}</th>
<th>SL_{eff}</th>
<th>SL_{rms}</th>
<th>Duration</th>
<th>ICI</th>
<th>F_{c}</th>
<th>F_{p}</th>
<th>BW_{3dB}</th>
<th>BW_{rms}</th>
<th>Q_{RMS}</th>
<th>DI</th>
<th>HPBW</th>
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<tr>
<td>Orcinus</td>
<td>203 ± 10</td>
<td>149 ± 10</td>
<td>193 ± 10</td>
<td>41 ± 14</td>
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<td>37 ± 7</td>
<td>29 ± 9</td>
<td>25 ± 10</td>
<td>12 ± 2.6</td>
<td>2.7</td>
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<td><em>orca</em> [S24-26]</td>
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<td>130-171</td>
<td>176-217</td>
<td>27-86</td>
<td>7.5-12</td>
<td>21-56</td>
<td>16-49</td>
<td>9-43</td>
<td>7-20</td>
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<td><em>Lagenorhynchus albirostris</em> [S27, S28]</td>
<td>204^m</td>
<td>148^d</td>
<td>195^s</td>
<td>20^m</td>
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<td>120</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>29</td>
<td>8</td>
</tr>
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<td><em>Lagenorhynchus obscurus</em> [S29]</td>
<td>191 ± 7^f</td>
<td>134^d</td>
<td>182^a</td>
<td>16^f</td>
<td>&lt;70^d</td>
<td>-</td>
<td>81 ± 9</td>
<td>74 ± 27</td>
<td>67 ± 27</td>
<td>34 ± 9</td>
<td>2.4</td>
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<td>121 ± 4</td>
<td>166 ± 6</td>
<td>57 ± 6</td>
<td>-</td>
<td>128 ± 3</td>
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<td>20 ± 3</td>
<td>18 ± 5</td>
<td>8 ± 2</td>
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<td>165-190</td>
<td>111-137</td>
<td>153-180</td>
<td>52-138</td>
<td>-</td>
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<td>132 ± 6</td>
<td>21 ± 3</td>
<td>12 ± 3</td>
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<td>126 ± 2</td>
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<td>120 ± 5</td>
<td>161 ± 5</td>
<td>74 ± 9</td>
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<td>133 ± 6</td>
<td>173 ± 6</td>
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<td>126 ± 3</td>
<td>15 ± 4</td>
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<td>146 ± 3</td>
<td>186 ± 4</td>
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<td>95 ± 10</td>
<td>101±20</td>
<td>64 ± 16</td>
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<td>3.2 ± 0.3</td>
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<td>40^b</td>
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<td>75</td>
<td>49</td>
<td>27</td>
<td>25</td>
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<td>26.6 ± 1.5</td>
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<td>42-110</td>
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<td>26-79</td>
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<td>141 ± 3</td>
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<td>SL&lt;sub&gt;efd&lt;/sub&gt;</td>
<td>SL&lt;sub&gt;rms&lt;/sub&gt;</td>
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<td>F&lt;sub&gt;c&lt;/sub&gt;</td>
<td>F&lt;sub&gt;p&lt;/sub&gt;</td>
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<td>BW&lt;sub&gt;rms&lt;/sub&gt;</td>
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<td>83 ± 17</td>
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<td>80 ± 36</td>
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<td>193&lt;sup&gt;b&lt;/sup&gt;</td>
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<td>16 ± 5&lt;sup&gt;b&lt;/sup&gt;</td>
<td>67 ± 40&lt;sup&gt;b&lt;/sup&gt;</td>
<td>99 ± 15&lt;sup&gt;b&lt;/sup&gt;</td>
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<td>62 ± 17</td>
<td>35 ± 3&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2.7 ± 0.6&lt;sup&gt;b&lt;/sup&gt;</td>
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<td>Tursiops aduncus [S41, S44]</td>
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<td>122-160</td>
<td>183-204</td>
<td>8-48</td>
<td>3-255</td>
<td>45-129</td>
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<td>25-43</td>
<td>1.6-4.3</td>
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<td>146 ± 8&lt;sup&gt;bb&lt;/sup&gt;</td>
<td>193&lt;sup&gt;b&lt;/sup&gt;</td>
<td>22 ± 8&lt;sup&gt;bb&lt;/sup&gt;</td>
<td>91 ± 84&lt;sup&gt;b&lt;/sup&gt;</td>
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<td>32 ± 6&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2.4 ± 0.6&lt;sup&gt;b&lt;/sup&gt;</td>
<td>26</td>
<td>9</td>
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**Table S1. Biosonar click parameters for toothed whales (Related to Figures 1-3)**

**Abbreviations:**
- **SL<sub>pp</sub>:** Peak to peak source level; **SL<sub>rms</sub>:** RMS source level within -10 dB endpoints of amplitude envelope; **SL<sub>efd</sub>:** Energy flux density source level within -10 dB endpoints of amplitude envelope; **Duration:** Click duration defined as length between -10 dB endpoints of amplitude envelope; **ICI:** Interclick interval; **F<sub>c</sub>:** Centroid frequency; **F<sub>p</sub>:** Peak frequency; **BW<sub>3dB</sub>:** -3 dB bandwidth; **BW<sub>rms</sub>:** RMS bandwidth; **Q<sub>rms</sub>:** Quality factor defined as F<sub>c</sub> to BW<sub>rms</sub> ratio; **DI:** Directivity index; **HPBW:** Symmetrical half-power beamwidth.

Listed values are preferentially given as means along with ± s.d. and minimum-maximum ranges when possible. Exceptions are signified by superscript letters:
- **a:** Value inferred from the sine wave relationship: peak-peak = peak + 6 dB = RMS + 9 dB;
- **b:** Mean of means (multiple values provided for the same species within a paper or values from several papers combined);
- **c:** Duration defined as length between -3 dB endpoints of amplitude envelope;
- **d:** Approximate value mentioned within main text;
- **e:** Q<sub>3dB</sub> (quality factor defined as F<sub>c</sub> to BW<sub>3dB</sub> ratio);
- **f:** From figure data;
- **g:** Value inferred from the equation SL<sub>efd</sub> = SL<sub>rms</sub> + 10*log<sub>10</sub>(duration) [S45];
- **h:** Duration defined as 95% or 97% energy window within some larger window around signal;
- **i:** Median value (used if no means are provided);
- **j:** Teager-Kaiser energy click duration;
- **k:** Value estimated from the approximate relationship: half-power beamwidth = 185° * 10<sup>(DI/20)</sup> [S6];
- **l:** Recalculated using raw data recordings;
- **m:** Mean value taken as midpoint between reported minimum and maximum.
Supplemental References


