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## Most 'flight' baleen whale species are acoustically cryptic to killer whales, unlike 'fight' species

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INTERNATIONAL WHALING COMMISSION

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# Most ‘flight’ baleen whale species are acoustically cryptic to killer whales, unlike ‘fight’ species

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## ABSTRACT

Baleen whales can be divided into ‘fight’ and ‘flight’ species based on their reactions to killer whale attacks. Flight species are slow-moving, maneuverable, displaying group or single defense against attacks on their calves, and migrating and breeding in denser aggregations in shallow coastal waters. Flight species are sleek, fast-swimming, flee on contact with killer whales, and migrate and breed while dispersed in pelagic waters. One corollary to this hypothesis is that male singing in fight species should involve competition among groups with more colorful and interesting singing, while in flight species, males should sing loudly and more monotonously to attract distant mates. Since fight species rely somewhat on group defense and return reliably to the same areas to calve and mate, they do not need to hide acoustically from killer whales; but loud-singing flight species would be more susceptible to being located by killer whales. This suggests a possible role for acoustic crypsis, which has been reported for some species of toothed whales that only call at frequencies that are too high for killer whales to hear. Here I examine whether the calls of baleen whale flight species (unlike fight species) call at low frequencies that are difficult (<1500 Hz) or impossible (<100 Hz) for killer whales to hear. A review shows that five out of six fight species call at higher frequencies (≥4000 Hz) and with high source levels (>175 dB re 1 μPa at 1 m) and can be heard by killer whales from at least 100 km away, while sixth fight species (gray whales), frequently attacked by killer whales on migration, call at quieter source levels (157 dB) and can be heard only within 15 km. For flight species, the opposite pattern is clear: six out of eight flight (or likely flight) species call with some combination of low frequencies (<1000 Hz) or low source levels (≤175 dB), such that they are either acoustically invisible to killer whales or can only be heard by nearby (<10 km) killer whales.


## INTRODUCTION

Killer whales (*Orcinus orca*) routinely attack and kill baleen whales throughout the world’s oceans, as evidenced by rake-like scars on surviving whales and direct observation of successful attacks (e.g., Jefferson et al. 1991, Mehta et al. 2007, Pitman et al. 2014, Corsi et al. 2022, McInnes et al. 2024). The degree to which baleen whales form part of the regular diet of killer whales has long been debated, although it is certainly true that smaller species and the calves of larger species are targeted more frequently. Gray whales in particular are routinely targeted both in Monterey Bay (McInnes et al. 2024) and off Unimak Island (Barrett-Lennard et al. 2011) on their migration routes between Mexico and the Bering Sea. Similarly, common minke whales (*Balaenoptera acutorostrata*) and Antarctic minke whales (*Balaenoptera bonaerensis*) are also frequently targeted and successfully killed by mammal-eating killer whales (e.g., Pitman & Ensor 2003, Ford et al. 2006). For the larger baleen whales, predation is usually confined to calves (e.g., Steiger et al. 2008, Pitman et al. 2014), and even blue whales (*Balaenoptera musculus*) are not immune to successful attacks (e.g., Tarpy 1979, Pitman et al. 2007, Totterdell et al. 2022).

Three major hypotheses have been proposed for how killer whale predation has shaped the ecology of baleen whales and broader ecosystems. The *migration hypothesis* holds that baleen whales migrate between high latitude feeding grounds and low-latitude calving grounds to reduce the risk of killer whale predation on their calves (Corkeron & Connor 1999). While initially debated (Clapham 2001, Connor & Corkeron 2001), further evidence led to a more general acceptance of this hypothesis (Clapham 2017). The *sequential megafaunal collapse hypothesis* (Springer et al. 2003) proposed that the decline of large whales due to whaling in the North Pacific led to reduced prey availability for killer whales, which then sequentially targeted and depleted seals, sea lions, and otters, leading to further trophic cascades. The lengthy ensuing debate over the validity of this hypothesis remains unresolved (e.g., Wade et al. 2007, Springer et al. 2008, Estes et al. 2009). Finally, the *fight or flight hypothesis* divides baleen whale species into two groups, those that stay and defend their calves when confronted by killer whales (the ‘fight’ club) and those that instantly flee (the ‘flight’ club) (Ford & Reeves 2008). The known members of the fight club are North Atlantic right whales (*Eubalaena glacialis*), southern right whales (*Eubalaena australis*), bowhead whales (*Balaena mysticetus*), humpback whales (*Megaptera novaeangliae*), and gray whales (*Eschrichtius robustus*); while the flight club includes blue whales, fin whales (*Balaenoptera physalus*), sei whales (*Balaenoptera borealis*), common minke whales, Antarctic minke whales, and Bryde’s whales (*Balaenoptera edeni*).

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The fight or flight hypothesis (Ford & Reeves 2008) seeks to explain a wide variety of behavioral, morphometric, and ecological adaptations that differ among baleen whale species. The fight species include active defense against killer whale attacks, including coordinated group defense. Fight species are slow-swimming and maneuverable, with chunky bodies, callosities and encrustations on their bodies, and usually migrate and calve close to the coast in shallow water, allowing for more shelter and easier defense against killer whale attacks. In contrast, flight species flee rapidly (20–40 km.h$^{-1}$) in a straight line for sustained periods of time, and if overtaken and attacked by killer whales do little defend themselves. Flight species have streamlined and slender bodies adapted for speed, and usually migrate and calve in open ocean waters with plenty of space to flee in all directions. These two strategies take different paths to increasing targeting costs to killer whales: fight species increase handling time and the risk of injury, while flight species increase energetic costs through prolonged high-speed pursuit (Ford & Reeves 2008).

In addition to these key aspects covered in the original fight or flight hypothesis (Ford & Reeves 2008), there are a number of deeper implications for calving and breeding. Fight species often congregate in shallow waters for calving and breeding, for example southern right whales in Peninsula Valdés, Argentina (Sueyro et al. 2018), humpback whales in Hervey Bay, eastern Australia (Forestell et al. 2011), and gray whales in Magdalena Bay, Mexico (Scammon 1874). Aggregations allow for easier group defense in shallow waters but prevent foraging during winter, since there is seldom enough food in shallow bays to support large groups of baleen whales. For example, no food was found in the stomachs of any of the 2037 humpback whales taken in just 96 days in summer 1937 in Shark Bay (western Australia) by the US-flagged *Ulysses* (Walsh 2010). During the open boat whaling era, the presence of large aggregations of slow-moving fight species (right, bowhead, gray, and humpback whales) without doubt contributed to their early targeting by whalers and widespread depletion in the 1700s to early 1900s (Smith et al. 2012). Conversely the flight species could only be targeted by faster steam-powered boats during the modern whaling revolution starting in the late 1800s (Tønnessen & Johnsen 1982). Fight species have a major advantage over flight species in finding a mate, since most individuals are aggregated in shallow water during mating season. Flight species have to work hard at attracting or finding a mate while widely dispersed over pelagic regions. Breeding success obviously depends on finding a mate, convincing them to mate, and reducing mortality while doing so. I argue that all three of these steps play a critical role in the singing behavior of baleen whales.

While both males and females of baleen whales do produce social and feeding calls, it is generally accepted that only males produce long, loud, and sustained songs (e.g., Clark & Garland 2022). When considering fight and flight species, the fight species do not need to travel far to find mates since they are often nearby, but they do need to convince females of their attractivity. Thus sexual selection for elaborate songs is expected for fight species, and indeed humpback whales famously have lengthy and intricate song sequences (Cholewiak & Cerchio 2022, Dunlop 2022); bowhead whales are the jazz singers of the ocean with as many as 184 unique song types over three years off Spitsbergen (Stafford et al. 2018); and southern right whales also produce a wide array of different songs (e.g., Clark 1982). Conversely, flight species need to focus on finding a mate while widely scattered in the open ocean, which presumably involves singing until a female locates the attractively singing baritone voice and mating ensues. Flight species therefore need to sing loudly to maximize the number of females that hear them, to sing simple and repeated song structures so that it is easier to locate them, and to sing over a prolonged period of time to allow females time to track them down. This kind of singing is seen most prominently in Antarctic blue whales and southern fin whales, which sing so loudly and longingly that they form a continuous background chorus of sound audible throughout the Southern Hemisphere (e.g., Letsheleha et al. 2022, Širović & Oleson 2022).

Given loud and continuous singing by both fight and flight species, why do killer whales not home in on their song and attack them? For fight species, this is less of a mystery: they are congregated predictably from year to year in areas with low food availability, and rely on group defense against killer whales. There is no mystery about where the aggregations of fight species are, should a pod of killer whales specialize on hunting them, and therefore little adaptive reason for their songs to be cryptic. However, flight species face a dilemma: they need to call as loudly as possibly to attract a mate, but they cannot afford to attract killer whales to their mating region (and especially to areas with mother-calf pairs). One option would be spatial separation between vulnerable mother-calf pairs and the calling males and receptive females, but at least in blue whales, sex ratios are similar in summer and winter areas (Branch & Monnahan 2021). Instead, flight species could alter their calls so that they sing at a frequency that is impossible for killer whales to hear, or at a marginal frequency such that their songs could only be detected if the killer whales are so close that they could be detected visually or by the sound of their blows and splashes.

The possibility of acoustic crypsis is not confined to baleen whales. Among the toothed whales, there is also a wide range of group sizes, social behavior, and differences in calls. Members of four separate families (Phocoenidae, Pontoporiidae, Kogiidae, Delphinidae) include species that lack whistles, and produce only low-energy, very high frequency clicks that are above the hearing range for killer whales, or at frequencies where killer whales hear poorly, which they defined to be <2 kHz and >100 kHz (Morisaka & Connor 2007). Subsequent research on captive killer whales has further refined the audible ranges for killer whales (Szymanski et al. 1999, Branstetter et al. 2017, Branstetter et al. 2023).

Here I reviewed calling frequency ranges for a variety of different populations and species of baleen whales in both the fight and flight groups and compare these ranges to the frequency ranges that killer whales can hear, to see if there is evidence supporting acoustic crypsis in baleen whales. I predicted that fight species should have upper frequencies that are easily audible to killer whales, while flight species should call at frequencies below killer whale hearing range or at frequencies where killer whale hearing is impaired. While investigating this frequency hypothesis I discovered further that some species sing much more loudly than others, and this also tended to differ between fight and flight species. I found that while all except one fight species was audible to killer whales, most flight species were either inaudible or could only be heard at close range.

## METHODS

I conducted a literature search for scientific papers on the calling frequency of all species of baleen whales, including the recently described Omura's whale, *Balaenoptera omurai* (Wada et al. 2003), and Rice's whale, *Balaenoptera ricei* (Rosel et al. 2021). The review was intended to compile sufficient data to establish the range of calling frequencies for each species, rather than being a comprehensive review for every whale population. No calling information could be found about pygmy right whale (*Caperea marginata*) which has rarely been seen in the wild due to its rarity and cryptic behavior, although its baleen plates were found in a killer whale caught off South Africa (Best et al. 2010). Species were divided into fight and flight groups based on Ford and Reeves (2008). Their classification did not include North Pacific right whales (*Eubalaena japonica*), which I classified as a fight species based on similarities with North Atlantic right whales and southern right whales; the newly described Omura's and Rice's whales, which I classified as likely flight species given their morphological and genetic similarities to Bryde's whales and sei whales (Wada et al. 2003, Rosel et al. 2021); or pygmy right whales, which have unknown affinities.

Information about killer whale auditory range comes from aquarium experiments conducted with trained animals (Szymanski et al. 1999, Branstetter et al. 2017, Branstetter et al. 2023) but are not available for free-swimming wild individuals. The resulting behavioral audiograms show a typical U-shaped pattern, where sounds at the lowest and highest frequency need to be much louder to be heard than sounds at their preferred frequency. The best-fit model from Branstetter et al. (2017) was used, as this relates the threshold received level (dB re 1 µPa at 1 m, hereafter "dB") required for a killer whale to detect a sound at a particular frequency (*f*, in kHz):

$$\text{Threshold} = 0.00927e^{4.38x} - 32.7x + 91.8\text{, where } x = \log_{10} f$$

It should be noted that this model was fitted only to data from killer whales that could hear the sounds. Experimental testing was conducted at lower and lower frequency levels, and not conducted below the frequency at which an individual killer whale failed to respond at all. Thus while all eight individuals responded to tones at 5000 Hz, only five individuals responded at 500 Hz, and one individual at 100 Hz. Thus at low frequency levels (100–500 Hz), the modeled received level is actually quieter than the average for all killer whales if non-responding individuals had been included.

Since baleen whales call at a range of frequencies and source levels (not received levels), simple calculations were made to estimate the distance at which a particular source level (dB) and frequency (Hz) could be heard by killer whales assuming either spherical spreading transmission loss (TL, in dB): $TL = 20\log_{10}(r)$ or cylindrical spreading $TL = 10\log_{10}(r)$, where *r* is distance in meters. The resulting predictions were compared with received levels at known distances (Miller et al. 2014, Miller et al. 2021) to select the spreading model that best matched the observed data.

## RESULTS

Frequency ranges were obtained from the literature search, although it was not always possible to find reports based on data from acoustic receivers that spanned the range of interest (10–5,000 Hz). Some species were much better studied than others, with humpback whales being particularly well studied, and therefore only a representative sample of humpback populations were included in the review (Table 1).

In the fight species, data were obtained for 14 populations of 6 species, all except one of which produced calls below 50 Hz at the lower end, and all except one also produced calls above 1,000 Hz at the upper end (Figure 1). Many (11 of 14) of the populations produced calls above 4,000 Hz, and the gunshot sounds of southern right whales in New Zealand and North Atlantic right whales in the Bay of Fundy exceeded 20,000 Hz. Every fight species contained at least one population that produced calls above 4,500 Hz (Table 1).

In the flight species, data were obtained for 25 populations of 6 species, with complete coverage for blue whale populations, but less complete coverage for other species. Most populations included evidence of calling at or below 50 Hz at the lower range (19 out of 25), but few populations called at higher frequencies: only 6 populations called above 1000 Hz, and only 4 above 4,000 Hz (Figure 1). Blue and fin whale calls were generally below 100 Hz and always below 500 Hz; Bryde's and Antarctic minke whale calls were under 1,000 Hz; but both sei whales and common minke whales included higher frequency calls exceeding 4,000 Hz, and up to 9,400 Hz for common minke whales in the northern Great Barrier Reef, Australia (Table 1).

The two probable flight species produced only lower frequency calls: up to 208 Hz for Rice's whales and up to 90 Hz for Omura's whales. One report on a captive Rice's whale from the gulf coast of Florida (Edds et al. 1993) included sounds from 250 to 950 Hz, but since the individual was stressed, in captivity, and a juvenile, these were not considered to be part of their regular repertoire and were excluded from the analysis.

Killer whale auditory range is only available from captive specimens under carefully controlled conditions. In short, individuals are trained to respond to noise pulses, and experiments are conducted to determine how loud (dB) those pulses need to be at different frequencies (Hz) for detection to occur (Szymanski et al. 1999, Branstetter et al. 2017). The most pertinent of these experiments (Branstetter et al. 2017) found that best hearing occurred at 34,000 Hz, good hearing was in the range 5,000–81,000 Hz, and that hearing cutoffs (requiring >100 dB received levels) were 600–114,000 Hz. One individual (labeled H) was tested at the most extreme frequency levels and this individual detected a 123 dB pulse at 100 Hz at the low end and a 122 dB pulse at 160,000 Hz at the upper end.

For a source level of 189 dB, typical of Antarctic blue whales and fin whales, transmission loss would need to be 66 dB for the received level to be 123 dB (the detection threshold at 100 Hz). Spherical spreading transmission loss implies a detection distance of 2.0 km for this scenario, while cylindrical spreading transmission loss implied a detection distance of 3981 km. Tracking of Antarctic blue whales (source level 188–191 dB) using hydrophone arrays revealed that received levels only exceeded 123 dB when the whales were within 0.9 km of the hydrophone array (Miller et al. 2014); and later studies with tracked blue and fin whales at distances of 2–50 km almost never exceeded received levels of 120 dB (Miller et al. 2021). Therefore cylindrical spreading gave predictions of received distance more than three orders of magnitude too high, while spherical spreading gave predictions close to the observed data. All further calculations therefore assumed spherical spreading.

Assuming spherical spreading transmission loss, and a source level of 190 dB, killer whales could detect baleen whale calls at 100 Hz at a distance of 2 km, 500 Hz at 26 km, and 2000 Hz at 251 km (Figure 2, Table 2). With lower source levels, detectable distances at those frequency levels declined rapidly: at 180 dB, killer whales could detect baleen whale calls at 0.6 km, 8 km, and 79 km respectively; for 170 dB at 0.2, 2.6, and 25 km; and for 160 dB at 0.06, 0.8, and 8 km.

## DISCUSSION

All the fight species produce calls that are easily detectable by killer whales, and many have broad frequencies over which they produce loud calls. Notably, North Atlantic right whales and southern right whales exceed 20,000 Hz in their loud 'gunshot' calls, and North Atlantic right whales, bowhead whales, and humpback whales all produce calls in the 184–189 dB range. Calls of all fight species except gray whales should be detectable by killer whales at ranges exceeding 100 km. Gray whales produce relatively quiet calls at 157 dB compared to the other fight species (≥176 dB), so that although they do call at up to 4,520 Hz, they are only audible to killer whales within about 15 km. The low detection range of gray whale vocalizations may reflect their need to avoid killer whale predation during their northward migration when calves are particularly vulnerable to killer whale predation (Barrett-Lennard et al. 2011, McInnes et al. 2024), given that this is a small species with relatively small calves even after they leave the safety of their wintering aggregations in Mexican lagoons.

Conversely, flight species are more acoustically cryptic, with the largest two species, blue and fin whales, being barely audible to killer whales. Blue whales produce their loudest sounds below 80 Hz for all populations except the Sri Lanka acoustic population (95–105 Hz), and are likely acoustically invisible to killer whales, or at best only detectable within 2 km. Blue whale populations in the northeast Pacific and Chile do produce sounds up to 500 Hz and 390 Hz, but these faint precursor calls can only be detected on nearby hydrophones, unlike their loud song components at lower frequencies. Fin whales call even lower than blue whales, never exceeding 99 Hz (Shabangu et al. 2020), and produce their loudest calls below 30 Hz. Killer whales are more likely to sight blue and fin whales, or hear their blows and splashing than detect their songs.

Intermediate-sized flight species are more mixed in terms of killer whale detection ranges. Sei whales call up to 900 Hz in the Antarctic (McDonald et al. 2005) and over 5,000 Hz in the Falkland Islands (Cerchio & Weir 2022). Even though their source levels are reported to be only 156 dB (McDonald et al. 2005, Cerchio & Weir 2022), they can be heard by killer whales from >20 km away. Bryde's whales typically call at levels below 245 Hz, except for one study recording pulses up to 900 Hz in the Gulf of California, but at their source levels of 152–175 dB, even a 900 Hz call could only be heard within 10 km.

The smallest flight species are common minke and Antarctic minke whales. Antarctic minke whales produce bioduck and pulse calls with peak energy at 50–250 Hz but harmonics up to 1000 Hz, but their calls are not particularly loud, only likely up to 165 dB, including only 140–147 dB from tags on calling individuals (Risch et al. 2014). Assuming loud calls at a high of 250 Hz and 165 dB, killer whales could only hear them within distances of 0.3 km. Common minke whales, however, make higher frequency 'boing' sounds at up to 5000 Hz in the northeast Chukchi Sea (Delarue et al. 2013) and up to 9000 Hz off Oahu

(Oswald et al. 2011), and 'star wars' sounds up to 9400 Hz off the northern Great Barrier Reef (Gedamke et al. 2001). Even though they are much quieter than blue and fin whales, with source levels around 150–165 dB, common minke whales should be audible from more than 100 km away. Both Antarctic minke whales and common minke whales are targeted by killer whales in different parts of the world, but Antarctic minke whales likely have higher predation pressure since they are the preferred prey for Type A killer whales in the Antarctic (Pitman & Ensor 2003), perhaps explaining their more acoustically cryptic songs compared to common minke whales.

No interactions have been observed between killer whales and Omura's, Rice's or pygmy right whales, and thus it is less clear whether these should be considered fight or flight species. Given the phylogenetic links and body shape similarities to Bryde's whales, though, it is likely that Omura's and Rice's whales are flight species. Rice's whales call at up to 208 Hz (Rice et al. 2014), but their calls are relatively quiet at only 155 dB (Širović et al. 2014), and thus they are unlikely to be heard by killer whales at more than 0.04 km away. Omura's whales have their peak calling at 15–53 Hz, with a range up to 90 Hz (Cerchio et al. 2015) and are acoustically invisible to killer whales. Pygmy right whales are seldom observed in the wild, and their calls have not been characterized. While they are eaten by killer whales (Best et al. 2010), no behavioral interactions have been observed, and they are not closely related to other baleen whale species, thus it is not possible to assign them to a fight or flight category at present.

These data show substantial, although not complete, support for the hypothesis that flight species are more acoustically cryptic than fight species (Table 3). Five out of six fight species can be detected by killer whales at ranges of more than 100 km, while the sixth, gray whales, is detectable to 15 km. It may be no coincidence that the most acoustically cryptic flight species is also the species most preyed upon by killer whales. Conversely, only one of eight flight (and likely flight) species are detectable beyond 100 km, and six (blue, fin, Antarctic minke, Bryde's, Rice's and Omura's whales) are undetectable at ranges beyond 10 km. Among the flight species, only sei whales (>20 km) and common minke whales (>100) are easily detected acoustically by distant killer whales.

The data and analyses here come with a wide range of caveats relating to the simplifying assumptions made in this analysis. First, the compilation of data for each population and species is not comprehensive, thus there may be populations of each species that call outside the frequency ranges listed, or that call louder or more softly than the source levels listed. Second, many hydrophones are designed only to capture a limited range of frequencies of calls, and thus some calls at higher frequencies may have been missed when compiling the information. Third, the assumption of spherical spreading for transmission loss is only a first approximation of detection range, which depends on a much wider variety of factors than the simple calculations here. Fourth, killer whale hearing range is obtained from a relatively small sample of captive individuals, all of which are fish-eating killer whales. It is possible that mammal-eating killer whales have a wider auditory range; conversely, free-living killer whales would have to contend with different background noise levels in the ocean. These factors may increase or decrease the detection ranges for each population and species, but are unlikely to change the overall pattern of acoustic detectability of fight compared to flight species.

Given these findings, it is worth venturing further into the realm of speculation to address why only male baleen whales produce loud repeated songs. If calling is indeed under selective pressure from killer whale predation, this makes sense: calves are most vulnerable to killer whale predation, and thus females should be more acoustically cryptic than males, for the same reason that many birds have brightly colored loudly singing males, but camouflaged quiet females. In the flight species acoustic crypsis ensures that males can sing extremely loudly (like blue and fin whales) to attract females from hundreds of kilometers away, yet simultaneously avoid the development of killer whale specialists that could hop from one male meal to the next, while also searching for associated females and calves. The flaw to this argument is that receptive females looking for mates are unlikely to have just given birth and hence be accompanied by calves vulnerable to killer whale predation. Perhaps this contradiction is addressed by considering that flight species frequently forage in winter months since they have no need to concentrate in food-poor shallow-water mating and calving areas. In such cases, ephemeral concentrations of flight species containing males, females, and calves would remain cryptic to killer whales.

It is also worth speculating whether the differences between fight and flight species may influence changes in songs over time. In fight species, long, complex, ever-changing songs with many types of patterns may be most attractive to females in denser aggregations of males and females. Indeed, in New Caledonia humpback whales, 20 years of paternity data showed that males who sired offspring had greater song complexity than those with no offspring (Garland et al. 2023). In flight species, simpler, monotonous, and louder songs would be needed to prove attractiveness, or perhaps just to reach a broader audience, in the same way that all too many humans use social media. Speculating even further, there might be adaptive pressure to call at lower frequencies over time among the flight species, that could explain the mystery of the deepening of blue whale calls in all populations worldwide over a period of many decades (McDonald et al. 2009). This pattern can be mathematically reproduced by assuming that there are two driving forces for the frequency of blue whale songs: a tendency to sing lower over time, and a tendency to sing at the same frequency as the rest of the whales in the population (Malige et al. 2022). Thus the tendency to sing lower over time could be a ghost from the evolutionary past where blue whales who sang lower to reduce detection by killer whales produced more offspring—engendering a female preference for courtship activities uninterrupted by killer whales.

The hypothesis presented here, that fight species should sing at higher frequencies and be more easily detected by killer whales, while flight species should be acoustically cryptic, does appear to hold for most species. However, given the caveats about data gathering and the simple modeling assumptions used to derive detection ranges, follow-up studies are needed to confirm this hypothesis. One possibility is direct play-back experiments to determine at what received levels killer whales can hear baleen whale songs, instead of using simple tonal sounds as in recent experiments. Work could also be done to characterize the source levels of baleen whales at different frequency bands, to better estimate the distances at which killer whales could detect their calls. Finally, behavioral studies are needed on Rice's, Omura's and pygmy right whales to determine if these three species should be classified as fight vs. flight species.

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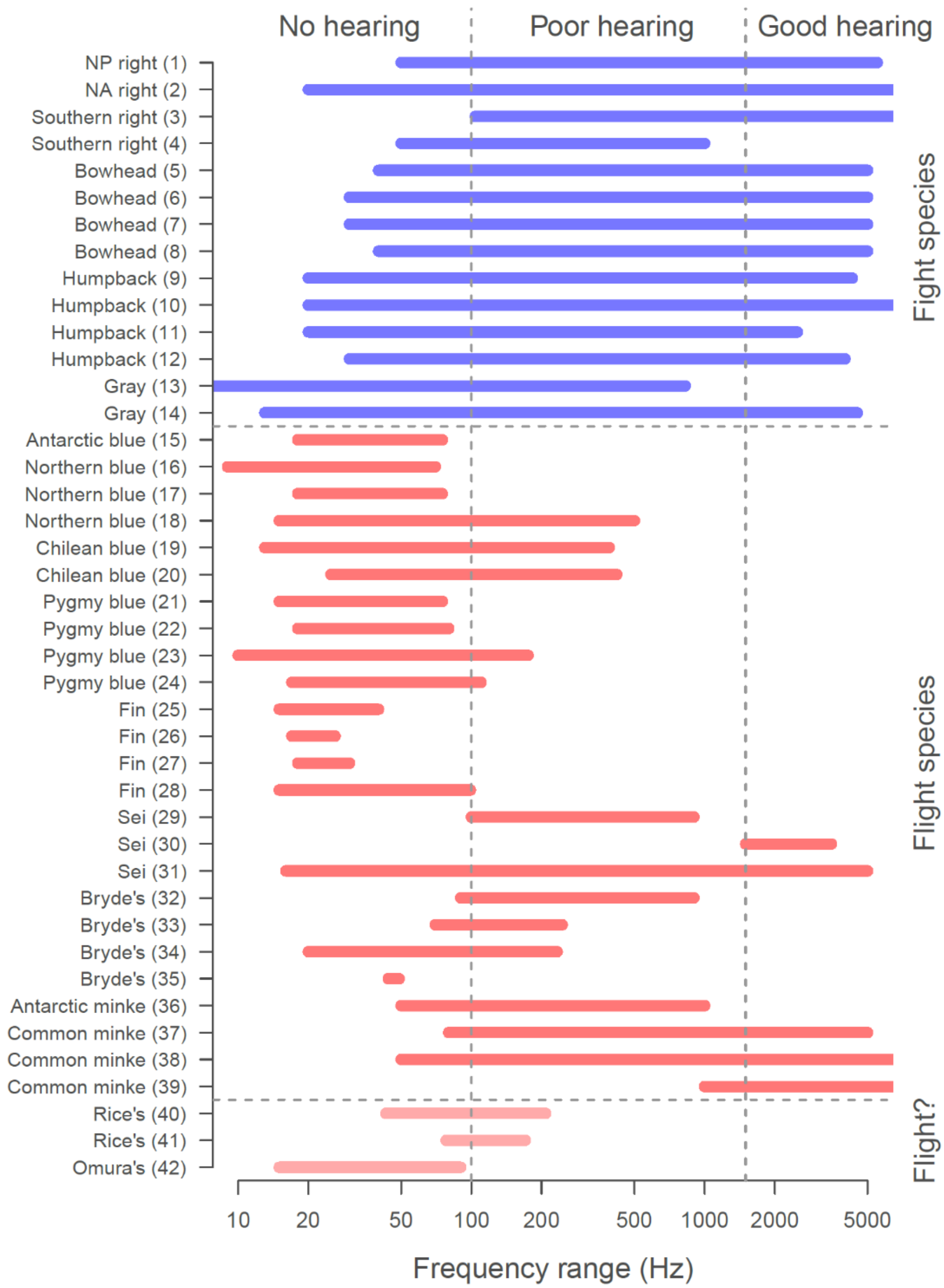


**Fig. 1**. Frequency range of calls made by different populations of baleen whales, divided into 'fight' species (blue), 'flight' species (red) and those that are likely flight species (lighter red). The approximate auditory range of killer whales is indicated as no hearing (<100 Hz), poor hearing (100–1500 Hz), and better hearing (>1500 Hz). Geographic locations of each population numbered 1–42 are given in Table 1.

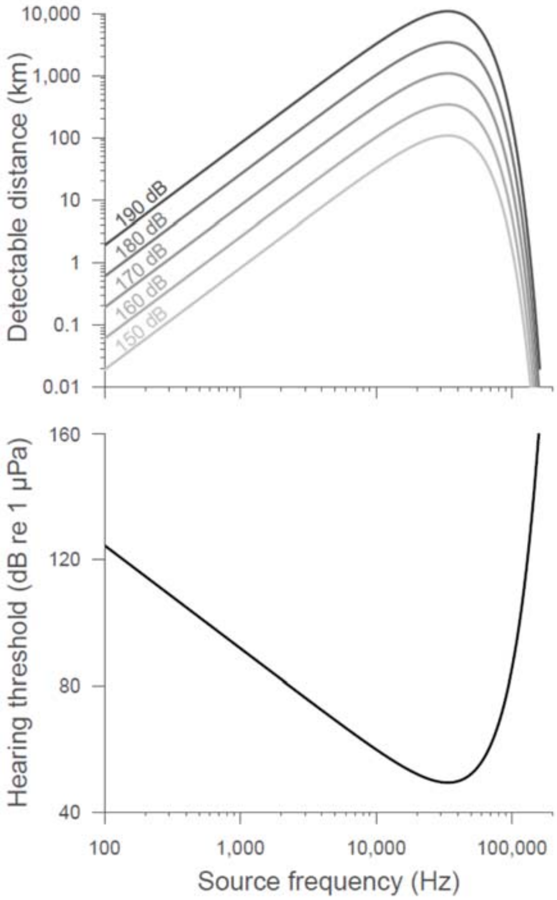


**Fig. 2**. Approximate distance within which calling baleen whales could be heard by killer whales (upper panel) for calls between 150 and 190 dB, at a range of source frequencies (Hz), given average hearing thresholds (dB) of captive killer whales (lower panel). Hearing thresholds are from the best fit model of Branstetter et al. (2017), and distances are calculated assuming spherical spreading for transmission loss.

**Table 1**. Calling frequency ranges for a sample of the populations within each species, divided into ‘fight’, ‘flight’ and likely flight species.

| Code | Category | Family | Species or subspecies | Region or population | Frequency peak (Hz) | Source level (dB) | Frequency range (Hz) | Citations |
|---|---|---|---|---|---|---|---|---|
| 1 | Fight | Balaenidae | North Pacific right | NE Bering Sea | – | 176–178 | 50–5,500 | Crance et al. (2017) |
| 2 | Fight | Balaenidae | North Atlantic right | Bay of Fundy | – | 189–196 | 20 to >20,000 | Parks et al. (2005) |
| 3 | Fight | Balaenidae | Southern right | New Zealand | – | – | 104 to >24,000 | Webster et al. (2016) |
| 4 | Fight | Balaenidae | Southern right | Argentina | – | – | 50 to >1000 | Clark (1982) |
| 5 | Fight | Balaenidae | Bowhead | Pt. Barrow, northern Alaska | 50–500 | 189 | 40–5,000 | Cummings and Holliday (1987) |
| 6 | Fight | Balaenidae | Bowhead | Fram Strait, western Greenland | 30–500 | – | 30–5,000 | Stafford (2022) |
| 7 | Fight | Balaenidae | Bowhead | Northern Bering Sea | 30–500 | – | 30–5,000 | Stafford (2022) |
| 8 | Fight | Balaenidae | Bowhead | Spitzbergen | – | – | 40–5,000 | Stafford et al. (2018) |
| 9 | Fight | Balaenopteridae | Humpback | East Australia | 40–2,000 | 184 | 20–4,300 | Dunlop (2022) |
| 10 | Fight | Balaenopteridae | Humpback | Hawai’i | 3,300–7,200 | – | 20 to >7,200 | Cerchio et al. (2001) |
| 11 | Fight | Balaenopteridae | Humpback | Oman | – | – | 20 to >2,500 | Cholewiak and Cerchio (2022) |
| 12 | Fight | Balaenopteridae | Humpback | Mexico | 1,900–3,600 | – | 30 to >4,000 | Cerchio et al. (2001) |
| 13 | Fight | Eschrichtiidae | Gray | Vancouver Island | 44–258 | 157 | 2–826 | Burnham et al. (2018) |
| 14 | Fight | Eschrichtiidae | Gray | Monterey Bay | 40–2,740 | – | 13–4,520 | Crane and Lashkari (1996) |
| 15 | Flight | Balaenopteridae | Antarctic blue | Australia (Antarctic song) | 18–27 | 189 | 18–75 | Balcazar et al. (2017), Miller et al. (2021) |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 16 | Flight | Balaenopteridae | Northern blue | North Atlantic | 16–21 | – | 9–70 | Edds (1982), Mellinger and Clark (2003), Delarue et al. (2022) |
| 17 | Flight | Balaenopteridae | Northern blue | Gulf of Alaska (Central/Western song) | 18–20 | – | 18–75 | Stafford (2003) |
| 18 | Flight | Balaenopteridae | Northern blue | California | 43–60 | 186 | 15–500 | McDonald et al. (2001), Rice et al. (2022) |
| 19 | Flight | Balaenopteridae | Chilean blue | Chile (SEP1 song) | 20–25 | 188 | 13–390 | Cummings and Thompson (1971) |
| 20 | Flight | Balaenopteridae | Chilean blue | Chile (SEP2 song) | 80 | – | 25–420 | Buchan et al. (2010) |
| 21 | Flight | Balaenopteridae | Pygmy blue | Southern Madagascar | 25–35 | 174–177 | 15–75 | Ljungblad et al. (1998) |
| 22 | Flight | Balaenopteridae | Pygmy blue | Australia | 65–71 | 179 | 18–80 | Balcazar et al. (2015) |
| 23 | Flight | Balaenopteridae | Pygmy blue | New Zealand | 17–20 | – | 10–175 | Branch et al. (2023) |
| 24 | Flight | Balaenopteridae | Pygmy blue | Seychelles (Sri Lanka song) | 95–105 | – | 17–110 | Stafford et al. (2023) |
| 25 | Flight | Balaenopteridae | Fin | Washington, Oregon | 20–21 | 189 | 15–40 | Weirathmueller et al. (2017) |
| 26 | Flight | Balaenopteridae | Fin | NW Atlantic | 17–26 | – | 17–26 | Delarue et al. (2009) |
| 27 | Flight | Balaenopteridae | Fin | Fram Strait and Svalbard | 18–25 | – | 18–30 | Ahonen et al. (2021) |
| 28 | Flight | Balaenopteridae | Fin | Maud Rise, Antarctica | 18–27 | 189–190 | 15–99 | Shabangu et al. (2020) |
| 29 | Flight | Balaenopteridae | Sei | Antarctic | – | 156 | 100–900 | McDonald et al. (2005) |
| 30 | Flight | Balaenopteridae | Sei | Nova Scotia | – | – | 1500–3500 | Knowlton et al. (1991) |
| 31 | Flight | Balaenopteridae | Sei | Falkland Islands | – | – | 16 to >5000 | Cerchio and Weir (2022) |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 32 | Flight | Balaenopteridae | Bryde's | Gulf of California | – | – | 90–900 | Edds et al. (1993) |
| 33 | Flight | Balaenopteridae | Bryde's | Gulf of California | 124 | 152–175 | 70–245 | Cummings et al. (1986) |
| 34 | Flight | Balaenopteridae | Bryde's | Eastern Tropical Pacific | 26–208 | – | 20–233 | Oleson et al. (2003) |
| 35 | Flight | Balaenopteridae | Bryde's | Japan | 44 | – | 44–49 | Oleson et al. (2003) |
| 36 | Flight | Balaenopteridae | Antarctic minke | Western Antarctic Peninsula | 146–165 | – | 50–1,000 | Risch et al. (2014) |
| 37 | Flight | Balaenopteridae | Common minke | NE Chukchi Sea | – | – | 80–5,000 | Delarue et al. (2013) |
| 38 | Flight | Balaenopteridae | Common minke | Northern Great Barrier Reef | – | 150–165 | 50–9,400 | Gedamke et al. (2001) |
| 39 | Flight | Balaenopteridae | Common minke | Oahu, USA | 1200–1600 | – | 1,000–9,000 | Oswald et al. (2011) |
| 40 | Flight? | Balaenopteridae | Rice's | Northern Gulf of Mexico | – | – | 43–208 | Rice et al. (2014) |
| 41 | Flight? | Balaenopteridae | Rice's | Northern Gulf of Mexico | – | 155 | 78–170 | Širović et al. (2014) |
| 42 | Flight? | Balaenopteridae | Omura's | NW Madagascar | 15–53 | – | 15–90 | Cerchio et al. (2015) |

**Table 2**. Estimated maximum distance (km) for killer whales to detect sounds at a particular source frequency and source level, assuming spherical spreading loss, and the best fitting model for hearing in killer whales in Branstetter et al. (2017).

| Source | Source level (dB) | | | | |
|---|---|---|---|---|---|
| frequency (Hz) | 150 | 160 | 170 | 180 | 190 |
| 100 | 0.0 | 0.1 | 0.2 | 0.6 | 1.9 |
| 200 | 0.1 | 0.2 | 0.6 | 1.8 | 5.9 |
| 300 | 0.1 | 0.4 | 1.1 | 3.6 | 11.4 |
| 400 | 0.2 | 0.6 | 1.8 | 5.7 | 18.2 |
| 500 | 0.3 | 0.8 | 2.6 | 8.3 | 26.2 |
| 600 | 0.4 | 1.1 | 3.5 | 11.1 | 35.2 |
| 700 | 0.5 | 1.4 | 4.5 | 14.3 | 45.3 |
| 800 | 0.6 | 1.8 | 5.6 | 17.8 | 56.4 |
| 900 | 0.7 | 2.2 | 6.8 | 21.6 | 68.4 |
| 1000 | 0.8 | 2.6 | 8.1 | 25.7 | 81.2 |
| 1100 | 0.9 | 3.0 | 9.5 | 30.0 | 94.9 |
| 1200 | 1.1 | 3.5 | 10.9 | 34.6 | 109.3 |
| 1300 | 1.2 | 3.9 | 12.5 | 39.4 | 124.6 |
| 1400 | 1.4 | 4.4 | 14.1 | 44.5 | 140.6 |
| 1500 | 1.6 | 5.0 | 15.7 | 49.8 | 157.4 |
| 1600 | 1.7 | 5.5 | 17.5 | 55.3 | 174.8 |
| 1700 | 1.9 | 6.1 | 19.3 | 61.0 | 193.0 |
| 1800 | 2.1 | 6.7 | 21.2 | 67.0 | 211.8 |
| 1900 | 2.3 | 7.3 | 23.1 | 73.1 | 231.3 |
| 2000 | 2.5 | 8.0 | 25.1 | 79.5 | 251.4 |
| 2100 | 2.7 | 8.6 | 27.2 | 86.1 | 272.2 |
| 2200 | 2.9 | 9.3 | 29.4 | 92.9 | 293.6 |
| 2300 | 3.2 | 10.0 | 31.6 | 99.8 | 315.6 |
| 2400 | 3.4 | 10.7 | 33.8 | 107.0 | 338.2 |
| 2500 | 3.6 | 11.4 | 36.1 | 114.3 | 361.4 |
| 2600 | 3.9 | 12.2 | 38.5 | 121.8 | 385.1 |
| 2700 | 4.1 | 12.9 | 40.9 | 129.5 | 409.5 |
| 2800 | 4.3 | 13.7 | 43.4 | 137.3 | 434.3 |
| 2900 | 4.6 | 14.5 | 46.0 | 145.4 | 459.7 |
| 3000 | 4.9 | 15.4 | 48.6 | 153.6 | 485.7 |
| 3100 | 5.1 | 16.2 | 51.2 | 162.0 | 512.1 |
| 3200 | 5.4 | 17.0 | 53.9 | 170.5 | 539.1 |
| 3300 | 5.7 | 17.9 | 56.7 | 179.2 | 566.6 |
| 3400 | 5.9 | 18.8 | 59.5 | 188.0 | 594.6 |
| 3500 | 6.2 | 19.7 | 62.3 | 197.0 | 623.1 |
| 3600 | 6.5 | 20.6 | 65.2 | 206.2 | 652.0 |
| 3700 | 6.8 | 21.5 | 68.1 | 215.5 | 681.4 |
| 3800 | 7.1 | 22.5 | 71.1 | 224.9 | 711.3 |
| 3900 | 7.4 | 23.5 | 74.2 | 234.5 | 741.7 |
| 4000 | 7.7 | 24.4 | 77.2 | 244.3 | 772.5 |

**Table 3**. Overall summary by species of maximum killer whale detection range estimated from source level and frequency of calls, for fight vs. flight species. Species in bold are almost acoustically undetectable to killer whales.

| Category | Common name | Scientific name | Maximum size (m) | Frequency peak (Hz) | Source level (dB) | Frequency range (Hz) | Maximum killer whale detection range (km) |
|---|---|---|---|---|---|---|---|
| Fight | North Pacific right | *Eubalaena japonica* | 19.8 | – | 176–178 | 50–5,500 | >100 |
| Fight | North Atlantic right | *Eubalaena glacialis* | 18.5 | – | 189–196 | 20 to >20,000 | >100 |
| Fight | Southern right | *Eubalaena australis* | 18.0 | – | – | 50 to >24,000 | >100 |
| Fight | Bowhead | *Balaena mysticetus* | 18.0 | 30–500 | 189 | 30–5,000 | >100 |
| Fight | Humpback | *Megaptera novaeangliae* | 17.0 | – | 184 | 20 to >7,200 | >100 |
| Fight | Gray | *Eschrichtius robustus* | 15.0 | 40–2,740 | 157 | 2–4,520 | 15 |
| Flight | **Blue** | *Balaenoptera musculus* | 30.5 | 16–105 | 189 | 9–500 | **2** |
| Flight | **Fin** | *Balaenoptera physalus* | 27.0 | 17–27 | 189–190 | 15–99 | **2** |
| Flight | Sei | *Balaenoptera borealis* | 19.5 | – | 156 | 100 to >5,000 | >20 |
| Flight | **Bryde's** | *Balaenoptera edeni* | 15.5 | 26–208 | 152–175 | 20–900 | **10** |
| Flight | **Antarctic minke** | *Balaenoptera bonaerensis* | 11.5 | 146–165 | 165? | 50–1,000 | **0.3** |
| Flight | Common minke | *Balaenoptera acutorostrata* | 10.0 | 1,200–1,600 | 150–165 | 50–9,400 | >100 |
| Flight? | **Rice's** | *Balaenoptera ricei* | 12.7 | – | 155 | 43–208 | **0.04** |
| Flight? | **Omura's** | *Balaenoptera omurai* | 11.5 | 15–53 | – | 15–90 | **<2** |
| Unknown | Pygmy right | *Caperea marginata* | 6.5 | – | – | – | unknown |