Environmental constraints on sound transmission by humpback whales

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Singing humpback whales in Hawaii produce a variety of sounds at high source levels (ca. 185 dB *re*: 1 μPa), in coastal waters 15–500 m deep. These sounds are attenuated and distorted as they propagate away from a singer, limiting the utilizable range of the sounds. In the current study, simulations based on normal-mode theory were used to investigate how the effects of shallow-water propagation constrain humpback whales' use of sound. It is shown that humpbacks can greatly affect transmission range by adjusting their positions and sounds in response to environmental factors. Source depth, in particular, is shown to be a major determinant of which frequencies propagate the farthest. A preliminary analysis of range-dependent distortion suggests that spectral cues can potentially provide listening whales with information about how far a sound has traveled. © *1999 Acoustical Society of America.* [S0001-4966(99)01211-4]

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INTRODUCTION

An animal's ability to use sound is strongly constrained by environmental factors. In particular, the medium(s) through which sounds propagate determine not only where the sounds will travel, but also to what extent they will be transformed (e.g., through distortion) as they travel. Such constraints are clearly reflected in the sound repertoires used by various species. For example, animals that use acoustic signals to communicate over short distances tend to use graded repertoires, composed of sounds that vary continuously along one or more dimensions; graded vocal signals are often supported by concurrent visual signals. In contrast, animals that communicate over long distances typically use discrete repertoires, consisting of highly stereotyped sounds that differ along many dimensions;[1] such signals remain discriminable even after significant distortion. Echolocating species must contend with huge environmental constraints. Bats vary their sonar signals continuously as a function of their environment when they are searching for and capturing prey.[2–4] When foraging in open spaces, bats tend to produce stereotyped sequences of constant-frequency sonar signals.[5–8] By narrowing the frequency bandwidth and lengthening the duration of their sonar signals, bats are able to put more energy into each frequency band, allowing them to overcome the relatively high attenuation of sound in air and to optimize their long-range detection of targets.[8,9] When bats are echolocating in more cluttered spaces, or are closing in on a target, they tend to shift to shorter duration, broadband signals that are more limited in range. Because environmental properties play such a critical role in shaping how animals use sound, it is important to carefully consider such factors when examining the vocal behaviors of a particular species. This is especially true for species that vocalize in shallow-water environments.

Shallow-water sound propagation has received much attention from ocean acousticians in the last 50 years, both theoretically and experimentally (for reviews, see Refs. 10–14). The problem is highly complex because it involves multiple reflections from the surface and bottom. Propagation in shallow water depends on signal frequency, source and receiver depth, sound-speed profiles (SSPs) in the water and in the bottom, water depth, biomass, bottom variability as a function of range, surface roughness, and so on. The large number of interacting variables makes predicting how sounds will propagate in shallow water extremely difficult. This high level of complexity may explain why so few researchers have incorporated analyses of propagation effects into their investigations of the vocal behaviors of shallow-water species. Shallow-water environments place unique constraints on sound transmission. These constraints have undoubtedly affected the ways in which vocal marine species (e.g., cetaceans) use sound.

Although investigators recognized early on that the transmission properties of underwater environments played an important role in shaping the acoustic abilities of cetaceans,[15,16] few studies attempted to rigorously account for these factors. The few analyses of propagation that were attempted were primarily theoretical and based on highly simplified models.[17] Initially, studies of the range and directionality of delphinid echolocation signals[18–21] provided the only data with which to address questions related to propagation. The complexities of propagation in real-world environments inhabited by cetaceans have only recently begun to be examined more closely.[22–29] Similarly, the constraints on cetacean sound use resulting from environmental factors

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[a)] Electronic mail: mercado@pavlov.rutgers.edu (e.g., ambient noise levels) are only now being broadly considered.[12]

Effects of propagation become most relevant when sounds are transmitted over long distances. No animals transmit sounds over longer distances than baleen whales (the mysticetes). Empirical research on the propagation of blue and fin whale sounds has shown that they can be detected from as far away as 1600 km.[30,31] Although it is doubtful that whales actually use sounds over such long ranges, it is clear that the sounds are produced to travel. For whales producing sounds in shallow water (e.g., less than 200 m deep), effective long-range transmission cannot be efficiently achieved simply by increasing the intensity of sounds. In such an environment, the spectral and temporal features of sounds critically determine how far the sounds will propagate and their discriminability after distortion. The current study uses computational methods to examine how shallow-water environments constrain sound transmission by a notably vociferous whale, the humpback (*Megaptera novaeangliae*).

I. SOUND TRANSMISSION BY HUMPBACK WHALES

A. Characteristics of sounds

In terms of sound production, humpback whales have few rivals. Their vocalizations can be extremely loud (up to 190 dB *re* 1 μPa,[12,32,33]) and are detectable from long distances (as far away as 160 km[30]). When ''singing,'' humpbacks may produce sounds for as long as 10–20 h nonstop,[34,35] and can be heard day and night for several months.[36,37] Additionally, humpback whales' sound repertoire is subjectively more variable than that of any other baleen whale. The sound-producing behaviors of humpback whales have been observed to vary as a function of gender, season, year, social context, geographic location, and individual.[22,38–42] Humpback whale sounds have typically been classified based on context and production mode.[41,43–46] For example, distinctions are made between songs (produced rhythmically, typically by lone males), social sounds (produced sporadically in competitive groups/pods of whales), and feeding sounds (produced in groups of foraging whales).

Humpback whale sounds can generally be divided into two main types: vocal and nonvocal sounds.[45,47] Nonvocal sounds include sounds produced by breaching, slapping body parts on the surface of the water, and blowing. Humpback whales produce vocal sounds internally using mechanisms that are poorly understood. Most of the spectral energy in humpback whale vocalizations falls between 50–4000 Hz,[41,48,49] with peak energy typically lying below 1500 Hz. Sounds range in duration from 0.1 to 10 s.[48,49] The majority of vocalizations is pulsed sounds. Many are constant in pitch with only brief periods of modulation; higher-pitched sounds tend to be modulated more extensively. Gradual or rapid frequency upsweeps are prevalent, with downsweeps being much less common.[48,49] The sound repertoire used by humpback whales is not fixed, but gradually changes over time.[41,49–51] This is most clearly evident for sounds produced within songs. Subjectively, specific sound types used within songs tend to be comparable between consecutive years, but less so over longer periods of time. Sound types may also be continuously modulated along one or more dimensions within a song.[41] Thus, the repertoire of sounds used by humpbacks appears to be graded rather than discrete. Although the sounds used by humpbacks are continuously and progressively changing, they appear to modulate within the boundaries of strict constraints that are stable across years.[49,51] For example, distributions of many sound characteristics (e.g., duration) were found to be highly stable over a 14-year span.[49] Interestingly, the distribution that varied the most across years was that of the frequency with peak energy (i.e., bandwidths appeared to be used differentially across years). It is important to note, however, that many other factors other than time may account for this variability, including variability in recording locations across years.

B. Acoustic environment

Humpback whales are globally distributed, inhabiting relatively shallow waters. During the summer, humpbacks can be found in high latitudes near continental shelves[52,53] where they spend much of their time feeding. In late fall and early winter, whales begin migrating towards lower-latitude subtropical areas where they spend the winter in shallow coastal waters. Most mating activities are believed to occur in the winter. During late winter and early spring, the whales begin migrating back to the summer feeding areas. Whales have been observed vocalizing during all stages of this annual cycle. The majority of humpback whale vocalizations, however, has been recorded in the wintering grounds.

Vocalizing humpbacks have been studied most extensively in the Hawaiian Islands and the West Indies. Whitehead[53] reported that most vocalizing (i.e., singing) whales located on Silver, Navidad, and Mouchoir Banks were in water between 15 to 60 m deep. Singers acoustically located along the coast of Hawaii were found in waters 19 to 558 m deep; mean water depth was 230 m.[22,23] Whales in the Penguin Bank region were located in areas with a mean water depth of 94 m.[54] Major concentrations of humpback whales are known to occur in the coastal waters near Maui, Lanai, and Molokai, and around Penguin Bank. Water depth between Maui and Lanai ranges between about 30 to 80 m deep, and water depth over Penguin Bank ranges between 50 to 200 m deep.[52] The bathymetry in Hawaiian coastal waters has not been extensively studied. Recent reports indicate that the bottom consists primarily of silty sand and clay, with occasional outcrops of coral, limestone, and rocks.[22,52]

Sound speed in the ocean environment determines not only how rapidly sounds can be transmitted, but also how sounds will propagate. The speed of sound in water increases with increasing temperature, salinity, and pressure (which typically vary with depth). Numerous techniques have been developed to estimate sound speed using these three variables (for a review, see Ref. 10). In Hawaiian coastal waters, temperatures range between 21 and 29 °C and salinity ranges between 34.2 to 35.5 ppt.[52,55,56] A similar temperature range (24–28 °C) has been reported in the Caribbean.[53] In oceans, water near the surface is constantly mixed by wind and waves. This mixing stabilizes the temperature and salinity of near-surface water at a relatively constant value. Sound speed in this ''mixed layer'' of water slowly increases as a function of depth due to increasing pressure. The depth of the mixed layer in Hawaii varies between 50 to 140 m.[52] Below the mixed layer is a layer of water in which temperature changes with depth; this layer is called the thermocline. Temperature decreases with depth in the thermocline, leading to a decrease in sound speed. The thermocline in Hawaii extends to depths of 275 to 365 m.[52] Detailed analyses of variations in sound speed as a function of depth have not been performed for shallow-water coastal environments in Hawaii or the Carribean. Recently, Frankel *et al.*[57] reported sound speeds between 1530 and 1535 m/s in the coastal waters off the island of Hawaii. They noted little change in sound speed down to 60 m, where a moderate thermocline began (-3 m/s gradient). Measurements taken at Silver Bank showed that the water was at a constant temperature from the surface to the seafloor.[53] The seafloor acts as a lower boundary on sound propagation. Bottom features (e.g., composition and smoothness) affect how sound propagates in the water above.[11] For example, soft bottom sediments such as mud are penetrable and remove significant fractions of energy; sandy bottoms tend to be much more reflective. Whitehead[53] found that singers were concentrated over regions with smooth bottoms. In such environments, the interaction between propagating sounds and the bottom depends primarily upon the materials that make up the bottom.

How well sounds propagate underwater is primarily determined by the properties of the environment (e.g., water temperature, salinity, and depth, bottom type, surface roughness) within which they are produced. A final feature of humpback whales' acoustic environment that constrains their use of sound, but that is somewhat independent of propagation effects, is ambient noise. Ambient noise in shallow-water coastal environments is quite variable depending on season, location, time of day, wind speed, bottom conditions, and the extent of biological and manmade sound production in the area; noise levels can vary by 10–20 dB from one day to the next.[12] In general, levels of ambient noise are influenced by the same factors that control transmission loss. Thus, regions of high transmission loss tend to have lower noise levels, and vice versa. Measurements of ambient noise levels in the humpback whale wintering grounds in Hawaii range from 58–95 dB *re* $1 \mu\mathrm{Pa}^2/\mathrm{Hz}$ in the 100- to 4000-Hz band.[24,58–62] These values are comparable with those reported from other shallow-water environments.[10,16,63–65] When whales are present in an area, their vocalizations contribute significantly to ambient noise levels.[53,60,66,67] Large boats also generate considerable noise.[12,62] Although ambient noise levels do not physically constrain sound transmission, they may mask sounds produced by humpback whales, limiting the range at which they can be detected.

C. Sound-field control

Humpbacks have some control over the factors that affect how well their sounds will propagate. First, and probably most importantly, they can control when and where they produce sounds. Thus, they could choose an area or time period within which to vocalize based on its ''acoustic potential'' (e.g., propagation characteristics and noise levels). Note that knowledge of the relative propagation potential of different locales need not be explicit. Whales could implicitly learn what locales are effective based on experience and/or could be genetically predisposed to favor sites that are effective. Evidence suggestive of such site selection is provided by observations of increased singer densities in areas with smooth bottoms.[53]

Other important factors affecting maximum range, that are more physiologically constrained, include the source level, beam pattern, and frequency range used by humpbacks. Source level refers to the relative intensity of sound radiated by a projector (in this case, the whale), at a standard distance from the source. The term beam pattern refers to the directional variability of projected sounds. Of these three factors, only the frequency range of produced sounds is known with any certainty for humpbacks. Individual sounds within songs can vary greatly in intensity.[41,48,68–70] Source levels of between 144 and 190 dB *re* 1 μPa at 1 m have been reported.[12,22,32,60,66,71,72] These source levels have generally been derived using estimated ranges, theoretical models of propagation based on geometrical spreading, and a relatively small number of measurements of received levels. Because of the many potential sources of error, current estimates of humpback whale source levels should be taken as points within the range of possible values (see Ref. 73 for a detailed discussion of this issue). Consider that estimates of *average* source levels have ranged from 155 to 185 dB over the last 20 years (30 dB corresponds to a 1000% increase in estimated average intensity).

Even less information is available regarding humpback whale beam patterns. Levenson[71] reported greater differences in received levels at different positions along a linear array than would be expected if humpback whales projected sounds omnidirectionally, and Clark[47] noted similar differences in levels received from vocalizing bowheads based on their relative orientation. These observations may reflect fluctuations in transmission loss resulting from varying source–receiver configurations (i.e., their depths relative to the surface and distances between one another) or other parameters. It is more likely, however, that they are due to directional properties associated with whales' beam patterns. Although low-frequency sounds will generally be less directional than higher-frequency sounds,[74] the common assumption that humpback whales project sounds omnidirectionally[17,22,69] seems unlikely given that most vocal mammals produce sounds directionally, and that omnidirectional sound production would be highly inefficient in a sound channel bounded by the bottom, surface, and shoreline.

II. ASSESSING ENVIRONMENTAL CONSTRAINTS

A. Models of shallow-water propagation

Early models of shallow-water propagation focused on characterizing transmission loss (a parameter describing how a sound weakens as a function of distance from the source). These techniques integrated models of geometrical spreading with measurements of transmission loss (TL) in shallow water. For example, Marsh[75] developed three equations for modeling transmission loss in terms of different spreading conditions. Sound energy was modeled as spherical spreading near the source ($\mathrm{TL}=20\log r$, where r is range in m), spreading between spherical and cylindrical at ''medium'' ranges ($\mathrm{TL}=15\log r$), and cylindrical spreading at longer ranges from the source ($\mathrm{TL}=10\log r$). Such formulas work reasonably well when the bottom is uniform. Frankel *et al.*[59] reported a close correspondence between measured transmission losses and the losses predicted by the Marsh equations in environments frequented by humpback whales. These equations do not, however, account for variables such as source and receiver depth or complex bottom interactions. This may explain why empirically based estimates of transmission loss in Hawaiian coastal waters (derived using spreading loss models) have ranged from $\mathrm{TL}=10\log r$[57] to $\mathrm{TL}=17\pm2.38\log r$.[22,24]

More recent models of sound transmission in shallow water are based on solutions of the wave equation (for reviews, see Refs. 10, 11, 13, and 14). The wave equation is a partial differential equation that relates acoustic pressure to spatiotemporal coordinates. The acoustic field emitted from a point source can be calculated by solving the wave equation, given a set of initial conditions or boundary values corresponding to environmental parameters; such calculations are typically performed using a computer. Several theoretical approaches have been developed for solving the wave equation including ray theory, normal-mode theory, spectral methods, and the parabolic equation model.[11,13] The choice of theoretical approach depends on the propagation ranges of interest, computational power, and sound channel variability. Normal-mode theory is well suited for modeling sound propagation in the environments frequented by humpback whales because bottom properties are only moderately variable and the propagation ranges of interest are between 0.1 and 60 km.[11] Additionally, previous studies have found good agreement between measurements and predicted values based on normal-mode theory.[11,76–79] Normal-mode solutions have the advantage that once they are solved for a particular environment, the solution can be used for all possible source and receiver configurations.

The computations in this paper used Westwood *et al.*'s normal-mode model, ORCA.[80–82] ORCA calculates the field parameters for an acoustoelastic environment with a multilayered bottom. As ORCA is a plane-layered range-independent model, the effects of scattering due to variable bathymetry or a rough ocean surface are not included in the computation. The main effect of scattering is to increase transmission loss, whereas bathymetric changes with scale length much greater than a wavelength cause more fundamental changes in the signal. In general, the problem of determining optimal frequencies for environments with variable bathymetry must be considered on a case-by-case basis, and is beyond the scope of this paper.

B. Optimum frequencies

By optimum frequency, we mean the frequency that achieves the maximum propagation range, given a particular environment and source depth. In any real shallow-water environment, there is likely to be an optimum frequency.[11,13,83] This follows from the fact that different features of the environment affect transmission loss differently at different frequencies. For example, at low frequencies fewer modes propagate, and so transmission loss may be dominated by the effects of water depth. At higher frequencies, on the other hand, transmission loss may be dominated by intrinsic absorption of energy in seafloor sediments. Ignoring temporarily the effects of other variables, which can be equally important, one sees that there is likely to be an intermediate frequency at which neither effect dominates and transmission loss is minimized. However, the number of variables affecting transmission loss is so large that one cannot predict their relative effects without actual numerical simulations of the propagation process.

In addition to optimum frequency, there is also a cutoff frequency below which sound will not propagate at all in shallow water.[10,11,14] The cutoff frequency (f_c) for a shallow-water environment can be approximated by

$$f_c=\frac{c_w/4h}{\sqrt{1-c_w^2/c_s^2}},$$

where c_w is the sound speed in water, c_s is the sound speed in the bottom, and h is the water depth.[14] For the water depths and bottom types encountered by vocalizing humpback whales, f_c ranges between about 1 to 100 Hz (estimated from Ref. 14, Fig. 5.8). The optimum frequency (f_o) depends on several variables including SSPs for the water and the bottom, and the depths of the water, source, and receiver.[11] Optimum frequencies can be calculated theoretically, using normal-mode methods, or empirically. Jensen and Kuperman[11] compared these two approaches and found that they produced similar results. They found that water depth was a primary determinant of f_o, and that f_o decreased with increasing water depth. Optimum frequency increased when either the source or receiver was not halfway between the bottom and the surface. They also noted that the effects of bottom properties on transmission led to different maximum propagation ranges at different water depths. The results of Jensen and Kuperman suggest that for humpbacks to maximize their propagation range in shallow water, they would need to produce sounds (1) with frequencies between 50 to 800 Hz, (2) at mid-depth in water between 30 to 300 m deep, and (3) over bottoms consisting primarily of sand and silt. These criteria correspond closely to the scenario that has been described for singing humpback whales.

Previous studies of humpback whale vocalizations have often suggested that lower-frequency vocalizations will propagate longer distances than higher-frequency vocalizations and that vocalizing humpbacks should therefore produce low frequencies to achieve the maximum propagation range.[69,84] It has also been suggested that low-frequency sounds might be used for long-distance communication, while higher-frequency sounds would be more appropriate for short-range communication.[41,69] Such suggestions appear to be based on (1) the fact that attenuation of sound by seawater increases with increasing frequency, (2) the assumption that lower-frequency signals are produced at levels equal to or greater than higher-frequency signals, and (3) the assumption that attenuation in the water channel is the primary

TABLE I. ORCA input files for full geoacoustic models: (a) 60-m water depth, without a thermocline; (b) 200-m water depth, with a thermocline starting at a depth of 70 m. Row 1 defines the physical properties of the upper boundary (air) for each environment, and row 4 defines the lower boundary (a basalt basement). The remaining rows define the physical properties of the channels through which sound propagates (i.e., the water and the bottom). cp=compressional speed in m/s, cs=shear speed in m/s, rho=density in g/cm^3, ap=compressional wave attenuation, as=shear wave attenuation, z=depth in m, nsvp=number of sound-speed profile points in the ocean, ctol=tolerance used in fitting SSP to eliminate layers (ctol=0 keeps all layers), nbot=number of layers in ocean bottom, ii=type of compressional speed profile (ii=1 is linear), h=layer thickness, cs1=compressional speed at the top of layer 1, cs2=compressional speed at the bottom of layer 1 (similarly for rho1 and rho2, ap1 and ap2, as1 and as2). Note that all environmental parameters are fixed across simulations except for nsvp, z, and cp in the ocean profile, and cp1 in the bottom profile; changes in these parameters reflect changes in SSPs. For further details, see Refs. 70 and 116 and Fig. 1.

(a) Hawaiian humpback whale environmental model without thermocline

(1) For upper halfspace: cp=350, cs=0.0, rho=0.001 21, ap=0.0, as=0.0
(2) Ocean profile: nsvp=2, ctol=0, z=0, cp=1534.3, rho=1.05, ap=0; z=60, cp=1535.2
(3) Bottom profile: nbot=1, ii=1, h=50, cp1=1565.9, cp2=1600, cs1=100, cs2=400, rho1=1.7, rho2=1.7, ap1=−0.5, ap2=−0.5, as1=0, as2=0
(4) For lower halfspace: cp=5250, cs=2500, rho=2.6, ap=−0.04, as=0

(b) Hawaiian humpback whale environmental model with thermocline

(1) For upper halfspace: cp=350, cs=0.0, rho=0.001 21, ap=0.0, as=0.0
(2) Ocean profile: nsvp=3, ctol=0, z=0, cp=1534.3, rho=1.05, ap=0; z=70, cp=1535.4, z=200, cp=1519.6
(3) Bottom profile: nbot=1, ii=1, h=50, cp1=1550, cp2=1600, cs1=100, cs2=400, rho1=1.7, rho2=1.7, ap1=−0.5, ap2=−0.5, as1=0, as2=0
(4) For lower halfspace: cp=5250, cs=2500, rho=2.6, ap=−0.04, as=0

determinant of how far different frequencies will propagate in shallow water. Effects of water depth, source depth, receiver depth, bottom type, and SSPs do not appear to have been considered in these previous analyses. The results of Jensen and Kuperman indicate that such factors can strongly affect which frequencies propagate best, and that in some environments higher-frequency vocalizations should propagate longer distances than lower frequency vocalizations of equal energy. The following simulations examine this possibility in greater detail.

III. ENVIRONMENTAL EFFECTS ON PROPAGATION

To investigate how shallow-water propagation effects might constrain how humpback whales use sound, simulations were run to calculate optimum frequencies in environments similar to those frequented by singing whales in Hawaii, and to assess whether there might be predictable, range-dependent, spectral distortion effects in these environments. To a certain extent, a subset of these analyses can be viewed as a replication of the analyses performed by Jensen and Kuperman.[11] It is thus useful to review the nature of their simulations, and how they compare with the ones performed in the current study.

Jensen and Kuperman looked at the effects of three main environmental parameters in their study: water depth, bottom type, and sound-speed profiles in the water channel. To simplify the analysis, they used a single, homogeneous bottom layer, always placed the source at mid-depth, and averaged the propagation loss over the water column for each receiver range. Jensen and Kuperman calculated optimum frequencies for (1) water depths between 25 to 400 m, (2) bottom types ranging from clay–silt to chalk–limestone; representative values obtained from the literature were used for porosity, relative density, relative speed, compressional speed, shear speed, compressional attenuation, and shear attenuation for each bottom type, and (3) two sound-speed profiles; one corresponding to typical winter profiles, with a surface speed of 1490 m/s and a constant gradient of 1.8 m/s, and the other corresponding to typical summer profiles, with a surface speed of 1535 m/s, a surface channel of 20 m, followed by a drop in sound speed to 1500 m/s, and then a constant gradient identical to the winter profile. The source depths they simulated ranged from 12.5 to 200 m, depending on the water depth, and transmission loss was calculated out to a range of about 85 km.

In the current study, environmental parameters for Hawaiian coastal waters (in particular, shallow-water regions near Maui) were estimated based primarily on measurements reported in previous studies or in computer databases maintained at the University of Hawaii. Effects of the following parameters on optimum frequency were investigated: water depth, source depth, receiver depth, and sound-speed profiles in the water channel. Water depths of 20, 40, 60, 100, 200, and 350 m were simulated. Because humpbacks only sing in Hawaii during the winter, and because previous reports indicate that a surface channel is not present, the ocean was modeled as a mixed layer over a thermocline. The mixed layer was modeled as being either 70 or 120 m deep. For water depths of 60 m or less, a thermocline layer was not included (see Table I and Fig. 1). SSPs were calculated using an empirically derived formula,[85] based on water temperature, salinity, and depth. A constant salinity of 35 ppt was used for all simulations. Temperature was constant at 25° above the thermocline and decreased at −0.052°/m within the thermocline (based on slopes from data presented in Ref. 55). Sound velocities calculated using this formula were consistent with measurements (e.g., $c=1534$ m/s near the surface). The bottom was modeled as a 50-m layer of sand and silt over basalt. Sound speed at the water-bottom boundary was set at $1.02c$ (after Ref. 11). Bottom SSP estimates were chosen to emulate the bottom properties particular to waters in Maui coastal regions. Source depths of 5, 15, and 30 m were chosen based on past reports of singer depths.[86] Sample ORCA input files for typical environments used in simulations

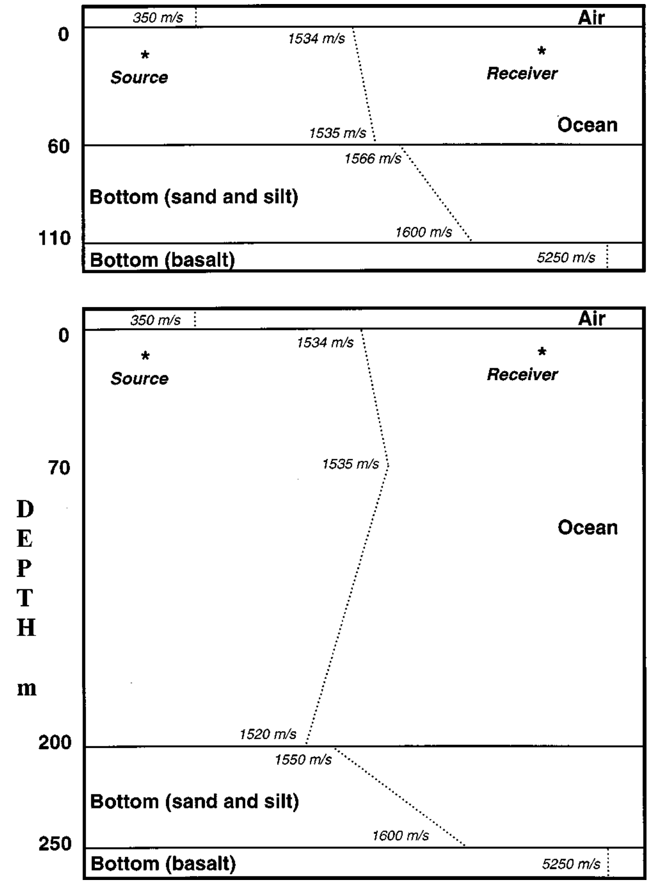

FIG. 1. Example environmental models used for ORCA simulations. The top figure corresponds to a 60-m water depth with no thermocline [see (a) in Table I], and the bottom figure corresponds to a 200-m water depth with a thermocline starting at 70 m [see (b) in Table I]. Solid lines show boundaries between channels, and dotted lines show how sound speed changes as a function of depth and material (where sound speed increases from left to right). Ocean sound-speed profiles varied as a function of water depth and thermocline depth. Bottom sound speed changed as a function of the sound speed in water at the interface. There are discrete jumps in sound speed at the air interface, bottom interface, and where the bottom changes to basalt. Only SSPs for the ocean channel and the first bottom layer were varied across simulations. Note that the figures are to scale vertically, but not horizontally. In a typical scenario (e.g., with a singer in 60-m deep water, and a receiver 6 km away), the range to depth ratio is about 100 (i.e., the ocean channel is a very thin disc).

are given in Table I; Fig. 1 illustrates these environments.

It is important to note from the outset that the results of these simulations should not be interpreted as precise estimates of the optimum frequencies in environments frequented by humpback whales. Jensen and Kuperman[11] had to manipulate shear-speed and compressional attenuation parameters in order to closely match theoretical results with measurements (these parameters are held constant in the current analysis; see Table I). Their calculated optimum frequencies were, however, roughly comparable to measured optimum frequencies even before such manipulations. The important data gained from the current simulations are the relative effects of changes in environmental parameters, rather than the absolute values of calculated optimum frequencies *per se*. Field measurements are needed to assess how accurately the model predicts actual optimum frequencies.

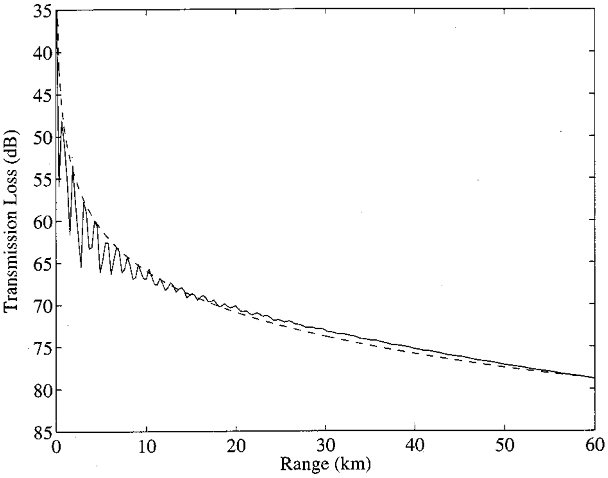

FIG. 2. Fitted transmission loss curve. The solid line is an example TL curve calculated by ORCA, and the dotted line is a logarithmic fitted curve calculated using MATLAB. Note that this estimation of transmission loss is conservative in that a listening whale exposed to varying received levels will detect the maximum received level in a given region (assuming it is above some perceptual threshold), as opposed to the average received level. Additionally, horizontally smoothed curves are more biologically relevant than averages calculated across vertical water columns (as in Ref. 11), because listening whales are more likely to be moving approximately parallel to the surface than to be bobbing up and down at a fixed range.

A. Dependence of optimum frequency on source depth, water depth, and thermocline depth

For the current analyses, optimum frequencies were calculated for a number of different scenarios using continuous-wave techniques. Simulations were initially run for 20 frequencies evenly spaced between 20 to 4000 Hz. Each simulation calculated the transmission loss (TL) at 200 distances from the source, evenly spaced between 50 to 60 000 m, and at 50 receiver depths evenly spaced between the surface and the bottom (resulting in a 50×200 matrix of TL values). A logarithmic curve of the form $\mathrm{TL}=a\log r$, was fit to each row of the matrix to provide an estimated transmission loss curve for each depth (see Fig. 2). The receiver depth corresponding to the minimum value of a for a single simulation was taken to be the ''optimal receiver depth'' (r_o) for that simulation. The optimum frequency (f_o) for a given scenario was found by comparing values of a across simulations (i.e., the frequency that led to the minimum overall value of a, thereby minimizing TL, was taken to be the optimum frequency). Table II summarizes the results of these analyses for the different scenarios considered.

Some of the data presented in Table II can be compared with the results reported by Jensen and Kuperman.[11] For example, for a water depth of 60 m and a source depth of 30 m, they report an optimum frequency between 400 and 800 Hz. The current simulations yielded an optimum frequency of 650 Hz. For simulations with a water depth of 40 m and a source depth of 20 m, Jensen and Kuperman report an optimum frequency of about 1600 Hz. The current analysis found an optimum frequency of 1700 Hz when the source was 15 m deep in 40-m-deep water. The current simulations showed that optimum frequencies increased as the source moved away from the mid-depth position, as noted in Ref. 11. Interestingly, water depth did not appear to strongly af-

TABLE II. Optimum frequencies for humpback environments in Hawaii, d_w = water depth, d_t = thermocline depth, d_s = source depth, f_o = optimum frequency, r_o = optimal receiver depth, $a_m = \min_i[a_i]\log r$, and $\overline{a}$ and σ_a are the mean and standard deviation over all a_i.

d_w (m)	d_t (m)	d_s (m)	f_o (Hz)	r_o (m)	a_m	$\overline{a}$	σ_a
20	NA	5	4000+	7.6	15.7	21.1	10.1
	NA	15	2740	8.4	16.5	21.2	9.6
40	NA	5	4000+	6.6	15.7	17.6	3.0
	NA	15	1700	13.7	15.7	16.9	2.5
	NA	30	3370	28.1	16.4	17.4	2.2
60	NA	5	4000+	8.2	15.7	17.4	2.9
	NA	15	1700	13.0	15.8	16.7	2.4
	NA	30	650	22.7	16.1	16.9	2.0
100	NA	5	4000+	7.1	15.7	17.2	2.3
	NA	15	1700	13.1	15.7	16.5	1.7
	NA	30	650	25.2	16.1	16.7	1.5
	70	5	4000+	7.1	15.7	17.4	2.5
	70	15	1700	13.1	15.7	16.7	1.9
	70	30	650	25.2	16.2	16.9	1.6
200	70	5	4000+	9.1	15.7	17.2	1.9
	70	15	1700	13.2	15.7	16.6	1.6
	70	30	1910	29.4	16.3	16.8	1.9
	120	5	4000+	9.1	15.7	17.1	1.3
	120	15	1910	13.2	15.7	16.4	0.8
	120	30	650	25.4	16.1	16.6	2.1
350	70	5	4000+	8.1	15.7	17.4	2.1
	70	15	1490	15.2	15.7	16.7	1.5
	70	30	1910	29.5	16.3	16.9	1.0
	120	5	4000+	8.1	15.6	17.0	1.6
	120	15	1490	15.2	15.8	16.4	0.9
	120	30	650	22.4	16.1	16.6	0.6

fect optimum frequencies ($r = -0.12$; where r is the correlation coefficient between the two variables), in contrast to previous reports. Rather, source depth appeared to be the main factor determining the optimum frequency ($r = -0.80$). This apparent discrepancy may be explained by the fact that Jensen and Kuperman always positioned the source at mid-depth, such that water depth and source depth were always covarying.

The mean optimum frequency across all simulations was 2400 Hz ($\sigma = 1300$ Hz), somewhat higher than what might be expected given the data presented in Ref. 11 and the frequencies used by humpback whales. The optimum receiver depth was closely correlated with the source depth ($r = 0.96$) and with transmission loss (as represented by a, $r = 0.79$). The variability of transmission loss as a function of frequency (estimated by σ_a) appeared to decrease with increasing water depth ($r = -0.51$). Variability also seemed to decrease with increasing source depth ($r = -0.33$). The presence of a thermocline and its position led to some subtle changes in optimum frequencies and estimated transmission loss curves. For example, simulations where the source was 30 m deep and a thermocline was present at 120 m (vs 70 m) yielded lower optimum frequencies, shallower optimum receiver depths, and slightly lower a values.

Propagation contour maps provide a clearer picture of how transmission loss changes as a function of source depth and frequency. Figure 3 shows contour plots for simulations in 60-m-deep water. When the source is 5 m deep [Fig. 3(a)], there is no evidence of an optimum frequency. When the source is 15 m deep [Fig. 3(b)], the 74-dB contour shows a clear bulge near the optimum frequency of 1700 Hz. This indicates that signals near 1700 Hz will travel a longer distance before decreasing by 74 dB. When the source is 30 m deep [Fig. 3(c)], the 74-dB contour shows evidence of alternating near-optimum and suboptimum frequencies. The lowest bulge extends the farthest along the range axis and is centered on the optimum frequency of 650 Hz. Note that the optimum frequency for the source 30 m deep does not propagate as well as the optimum frequency for the source 15 m deep. In general, Fig. 3 looks the way it does because the depth of the source determines which normal modes are excited. Optimal propagation occurs for those normal modes that interact least with the lossy bottom, which typically are the lowest-order modes. Similarly, optimal propagation oc-

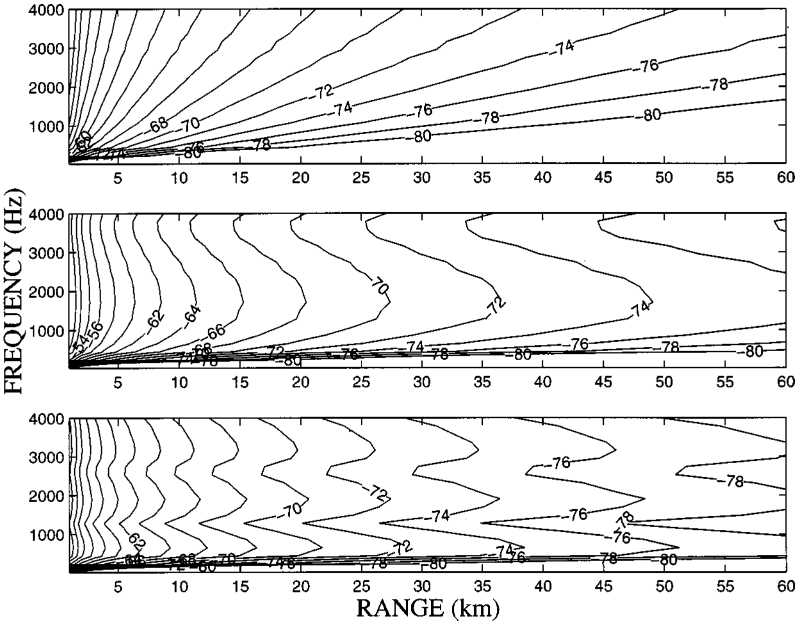

FIG. 3. Contour plots of transmission loss. Plots are based on fitted TL curves with the receiver at the optimal depth. Simulated scenario is for 60-m deep water (as described in Fig. 1 and Table I), with a source at (a) 5-m deep (top plot), (b) 15-m deep (middle plot), and (c) 30-m deep (bottom plot). The numbers on the contours indicate a particular transmission loss value, and the shapes of the contours show the range where signals at different frequencies will have decreased by this amount. The contours graphically illustrate how source depth and signal frequency can dramatically affect propagation. The high optimum frequencies computed for a 5-m deep source may in part reflect surface decoupling.[117] In real environments, scattering would likely attenuate higher frequencies preferentially, shifting the optimum to some mid frequency below 4000 Hz.

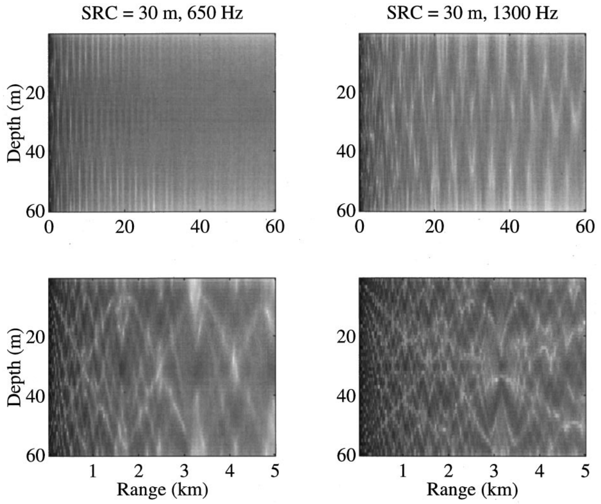

FIG. 4. Plots of transmission loss before smoothing. Simulated scenario is again for 60-m deep water (as described in Fig. 1 and Table I), with a 30-m deep source (the smoothed contour plot for this simulation is shown in Fig. 3). Bottom plots show a zoomed portion (the first 5 km) of the plots above them. Lighter coloration indicates greater losses. Note the complex range and depth-dependent variations in loss and how they vary with frequency. Also note the periodic interference patterns over longer distances. The optimum frequency for this scenario was found to be 650 Hz. At shorter distances, however, regions of high loss are larger for 650 Hz than for 1300 Hz.

curs when the source and receiver are at the same depth because then the receiver is optimally positioned to receive those normal modes most effectively excited by the source.

It should be kept in mind that the data displayed in Table II and Fig. 3 are based on simplifications of the data generated by the ORCA simulations. Propagation loss varies greatly as a function of range and depth from the source. Figure 4 shows visual representations of the original 50×200 matrices for simulations with $d_w = 60\,\mathrm{m}$, $d_s = 30\,\mathrm{m}$, for two frequencies (650 and 1300 Hz); lighter areas indicate a larger transmission loss. Although overall propagation losses are clearly reduced for the optimum frequency (650 Hz) at long ranges, there appear to be larger regions of high loss at shorter ranges than for the suboptimum frequency (1300 Hz). Clearly, optimum frequencies are not optimal for all points within the sound channel, but rather are optimal for achieving the maximum range ‘‘on the average.’’ There is no frequency that will propagate optimally to every point in the sound channel.

B. Range-dependent spectral damping

Although knowledge of transmission loss is important for determining how far sounds will travel, such knowledge is only moderately useful for predicting how features of a signal other than amplitude will change as a signal propagates. One way to address this problem is to model the ocean channel using linear systems theory.[27,87] Propagation through an ocean channel can then be modeled as transmission of a signal through a set of linear, spatiotemporal-varying filters. The effect of propagation on any signal, for every source–receiver configuration, can be described in terms of a set of filter characteristics (specifically, a set of impulse response functions, also known as Green’s functions). Once this set of filter characteristics is known (either through measurements or theoretical calculations), the signal properties that will be received at any point in the channel can be determined for arbitrary signals. In practice, it is extremely difficult to precisely determine the Green’s functions across a wide band of frequencies for real-world environments. Reasonable approximations to these functions can, however, be obtained based on solutions of the wave equation (e.g., using wideband normal-mode techniques).

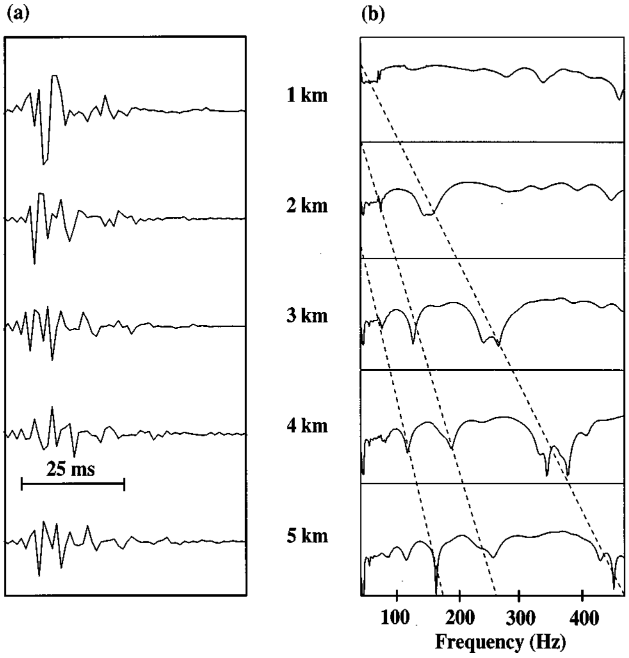

FIG. 5. Green’s functions for a humpback’s environment (60-m water depth, 15-m source and receiver depth). Waveforms in (a) show from top to bottom, Green’s functions at ranges of 1, 2, 3, 4, and 5 km; peaks in these waveforms correspond to various ray paths. Spectra in (b) are of these waveforms. These spectra can be interpreted as the frequency responses of channel filters; i.e., the effects of propagation on a signal can be simulated by passing the signal through a filter with bandpass/stop features matching these spectra. Note the systematic, range-dependent spread of spectral peaks and troughs. It can be seen that the behavior of the Green’s function becomes increasingly complex as the ratio of range to water depth increases. Dotted lines indicate trends in spectral distortion that appear to be correlated with range.

Preliminary calculations of Green’s functions for a prototypical humpback whale environment were performed using ORCA’s wideband analysis capabilities. Environmental parameters were identical to those used in the previous simulations. Water depth was fixed at 60 m. The source and receiver were both 15 m deep and at ranges between 1 to 5 km from one another. The bandwidth considered in the analyses was between 50 to 475 Hz (i.e., the Green’s functions are valid for signals with spectral components limited to this range of frequencies). Figure 5 shows the Green’s functions at ranges of 1, 2, 3, 4, and 5 km along with their spectra. These spectra, denoted as $G(w)$, reveal how signal features will likely be affected by transmission. For example, at 2 km, a clear trough is evident in $G(w)$ near 180 Hz. This indicates that, for this source–receiver configuration, the channel acts as a band-stop filter, significantly damping spectral energy near 180 Hz. At 3 km, two troughs are evident, one near 150 Hz and one near 280 Hz (with two minima). At 4 km, three troughs can be seen. Visually, these separate troughs can be correlated across spectra. The single trough in $G(w)$ at 2 km appears to move to the right (increase in frequency) and develops two deep minima with increasing distance from the source. The 150-Hz trough at 3 km moves to the right and becomes shallower, and a smaller 90-Hz trough (at 3 km) moves to the right and becomes deeper. It appears that in this scenario, the distance a sound has traveled can be determined based on the spectral content of the received signal (independent of source amplitude), assuming the source signal is relatively broadband. Note that this result is not an artifact of the simplifying assumptions (e.g., flat bottom and surface) used in the simulations. A more complex environment would provide even more potential cues for determining the distance a sound has traveled.[88,89] The specific effects of the channel on a particular signal can be derived either by convolving the source waveform with the Green's function (for a particular range) or, equivalently, by multiplying the source spectrum times $G(w)$.[27]

IV. CONCLUSIONS

The simulations of sound propagation described in this paper have revealed several intrinsic constraints on humpback whales' use of sound that have not been previously noted. First, the results strongly suggest that humpback whales cannot increase the distances their sounds travel in shallow water simply by using lower frequencies. In contrast, all of the simulations indicate that maximum propagation ranges would actually be decreased for lower frequencies (below 200 Hz) and that humpback whales should typically produce higher frequencies rather than lower frequencies if they want their sounds to go farther. Second, source depth was found to be a critical determinant of the optimum frequency, optimum receiver depth, and maximum propagation range. Other factors such as water depth appear to be more relevant in determining the bandwidth of near-optimal frequencies. For example, transmission loss appears to vary less as a function of frequency in deeper water, whereas very shallow-water environments (20 m deep) strongly constrain long-range propagation to higher frequencies. Third, the large spatial variability in transmission loss as a function of range and receiver depth (see Fig. 4) suggests that propagation models based on geometrical spreading give a misleading impression of how sounds attenuate as they propagate away from a whale vocalizing in shallow water. It is possible (and even likely) that a whale 2 km from a singer would, at certain times and positions, experience higher received levels than a whale 1 km away from the same singer. Finally, the results seem to suggest that most humpback whale sounds are not acoustically optimal for long-range propagation. Although humpbacks do produce sounds within the range of optimum frequencies, most of their sounds are below this range. Possible reasons for this discrepancy are discussed below in more detail.

The current model is limited in that it does not account for the effects of scattering by the ocean surface or bottom, or the effects of bottom gradients (e.g., the model assumes a constant water depth and sound-speed field). Such factors undoubtedly affect transmission loss. For example, measurements and theoretical analyses of transmission loss in Hawaiian shallow-water environments, that take into account basic slope profiles (e.g., up-slope versus down-slope versus cross-slope), suggest that transmission loss is greatest for sounds propagating up-slope[24] (see also Ref. 90). Transmission loss in down-slope and cross-slope conditions was found to be significantly reduced in comparison to the up-slope condition; loss in the down-slope and cross-slope conditions was comparable. Past studies (e.g., Refs. 11, 76–79) have shown a close correspondence between transmission loss values predicted by simulations based on normal-mode theory and measured values, despite the simplifying assumptions made regarding the ''flatness'' of surface and bottom features. In some cases, the effects of a sloping bottom may be balanced by other factors. For example, sound traveling from shallow water to deeper water spreads out, but suffers less reflection loss, so that transmission loss may actually be decreased relative to an environment with a flat bottom.[12]

Although more advanced environmental models, which can simulate range-dependent water depths and bottom properties (e.g., parabolic equation models), can potentially allow more realistic scenarios to be investigated, it is not clear that this would clarify the constraints faced by humpback whales given the dearth of relevant data. Many of the critical environmental variables needed to develop more veridical models have yet to be measured, including the bathymetry, bottom composition, and sound-speed fields of areas frequented by vocalizing whales. Other important factors that are currently unknown are source directivity, the relative intensities of different frequencies produced by humpbacks, and the ranges at which humpbacks make use of sounds. Future studies can provide important tests of the current results as well as better estimates of environmental parameters. For example, recordings could be made simultaneously at multiple distances and depths from a vocalizing humpback, and the spectra of these recordings compared to look for predictable propagation effects and average transmission loss values. Alternatively, manmade sources could be placed in environments frequented by humpback whales (projecting broadband signals at various depths) to assess how different frequencies propagate and which frequencies propagate the farthest. As more precise measurements of environmental conditions are reported, the accuracy with which propagation effects can be predicted will obviously improve. Despite its limitations, the current model represents a significant advance over the purely geometric models that have been used in the past to assess environmental constraints on sound transmission by humpback whales. Previous computational studies of sound transmission by fin[27] and blue whales[28,29,91] indicate that consideration of such constraints is a crucial prerequisite for analyses of mysticete sounds.

The preliminary calculations of Green's functions described in this paper illustrate how the distorting effects of propagation through particular environments can be quantitatively predicted (see also Ref. 27). Empirically measured Green's functions can also be used for this purpose.[28,29,91–93] Currently, recorded vocalizations are often analyzed as if they were the ''true'' signals produced by whales, even though this is essentially never the case. If the Green's functions for an environment are known, then features attributable to propagation effects can be more readily identified. Knowledge of the Green's functions associated with a particular sound channel can also allow information that otherwise might not be available (such as distance from the source) to be extracted from recorded signals. In theory, such knowledge allows the exact position of the source to be determined from a recording made with a single receiver (assuming the channel is sufficiently complex[88,94]). Knowledge of Green's functions for a particular environment can also be used to enhance signal processing.[28] Propagation effects can cause identical signals to appear to have different features depending on where they are received. Studies that attempt to analyze the variability of sounds across individuals thus need to consider the variability due to propagation effects. This can be accomplished either by making sure recordings from individuals are made from various locations, or by finding the Green's functions for the channel of interest.

The natural history of humpback whales suggests that they should have highly developed acoustic abilities. It would be surprising to find that they use sounds that are not well suited for their intended purpose. The mismatch between calculated optimum frequencies and those actually produced by humpbacks suggests that (1) the environmental model may not accurately simulate the environmental constraints encountered by vocalizing humpbacks, (2) factors other than maximum propagation potential may constrain the frequencies used by humpback whales, and/or (3) humpbacks may only use a subset of the frequencies they produce for long-range transmission. As noted previously, the optimum frequencies computed in the current analysis are only an initial estimate, so possibility (1) alone may account for this discrepancy. There have been previous reports, however, indicating that blue whales[91] and other mammalian species[95,96] do not always produce frequencies that propagate optimally over long ranges. Possibilities (2) and (3) should thus be considered more closely.

Anatomical and functional constraints undoubtedly limit the frequencies used by humpback whales. If the function of a sound does not require long-range propagation, then sounds with optimum frequencies for propagation may not be functionally optimal. Wiley and Richards[96] suggest that maximum range of detection is probably not the primary selection pressure on most animals' vocal repertoires, and that features that degrade predictably with range are more important. Physical properties of production mechanisms also limit the frequencies a whale can optimally produce (however, the wide range of frequencies produced by humpbacks seems to suggest that this is not a strong constraint). Finally, the spectrum of environmental noise will constrain the range of frequencies that will be maximally discriminable over long ranges. For example, in shallow water, low-frequency noise levels may be lower than in deeper water.[12] Consider also that if many animals in a localized region are producing similar sounds that propagate optimally, then the signals may begin to ''optimally'' interfere with one another. Consequently, the effective utilizable range of a sound may not be reflected by its maximum propagation range;[97] maximum range only provides an upper bound on utilizable range.

Whereas environmental constraints may not account for why humpbacks produce energy at lower frequencies, they may explain why they are capable of producing such a wide band of frequencies. Humpbacks produce frequencies that are much higher than many other smaller mammals. For example, professional sopranos seldom produce frequencies above 1200 Hz, and then only at relatively low intensities, for short periods of time.[98] In contrast, male humpbacks may produce frequencies between 1000–4000 Hz, at high intensities, hundreds of times a day. Other mysticetes have not demonstrated such abilities. It is also important to note that when humpback whales produce lower frequencies, they typically also produce a large number of harmonically related higher-frequency bands that can extend up to 8000 Hz. In some cases, the energy in these higher-frequency harmonics can be more intense than the energy in the low-frequency fundamental.[99] Such tone complexes likely include frequencies that are optimum or near optimum.

We noted earlier that vocalizing humpback whales can potentially reduce the limitations on propagation imposed by environmental constraints by properly positioning themselves. For example, to maximize their range and the predictability of propagation effects, singers could select an acoustic channel based mainly on water depth, bottom properties, and the presence or absence of a thermocline. Given known environmental conditions, they could then dive to an ''optimum'' depth and produce optimum frequencies. Humpback whales could also attempt to match their depth to that of potential receivers (assuming this information is known or can be predicted). To maximize propagation through positioning, whales would need feedback on how far their signals are traveling. If the utility of sounds is a function of how far they travel, then this ''feedback'' could be provided by natural selection. For example, individuals that frequently vocalized in environments/positions with good propagation characteristics would gain a selective advantage. A second potential source of feedback is echoes from structures in the environment. It is well-known that humpback song sounds generate strong echoes off the ocean floor, as well as banks and pinnacles, that are clearly detectable in recordings.[69,100] Other potential sources of echoes include schools of fish or other whales.[32,69,70,101–105] Such echoes provide information about how sounds are propagating in particular contexts. Whether humpback whales use this information to maximize propagation ranges is currently unknown. It is known that various other species do position themselves such that long-range propagation is enhanced.[96,106–109]

Humpback whales could also affect propagation range by modulating the spectral and energetic properties of the sounds they produce. Although there is currently little evidence suggesting that humpbacks or other whales change sound features to accommodate different nonbiological environmental features (e.g., topology, water depth), this lack of evidence may simply reflect the limited attention given to the issue. Au *et al.*[110] found that belugas used different echolocation signals when faced with different ambient noise levels; differences between signals were highly correlated with signal amplitude. Singing humpback whales have also been observed to change their signals in response to changes in noise levels.[62] Humpbacks sang at a faster rate when noise levels increased moderately. When larger increases occurred (e.g., when large ships passed nearby), they sang faster and shifted to higher frequencies. Norris[62] suggested that these changes reflected increased stress levels rather than attempts by the whales to optimize their signals with respect to noise levels. Other species have been shown to dynamically manipulate the sounds they produce to match a particular environment or situation. Most notably, bats use different echolocation signals depending on the environment, target range, and sounds of other bats in the area.[2–4,111] Given the complexities of shallow-water propagation, it would be to a humpback whale's advantage to attend to the acoustically relevant physical features of the environment, and to modify his signals accordingly.

It has been shown previously that some birds can use the degradation of spectral features of known songs to determine the proximity of other vocalizing birds, and that such cues are more salient than intensity differences.[112,113] The results of the current analysis suggest that humpback whales could also potentially extract range information from the vocalizations of conspecifics. Although the sound-localization abilities of humpback whales are essentially unknown, the fact that singers space themselves apart[22,23] shows that they can at least roughly determine their distance from a source. Singing humpback whales appear to mimic the songs of other humpbacks,[114,115] suggesting that they are attending closely to the properties of sounds produced by other whales. Experimental playback studies analogous to those used with birds may clarify whether singers are relying more on spectral cues or intensity cues to maintain spacing. Given the variability of transmission loss in shallow water (as illustrated in Fig. 4), we expect that spectral cues will be found to be much more salient.

In summary, simulations based on normal-mode theory predict (1) that how far a singing humpback whale's sounds will propagate will be a function of the frequencies produced, the depth of the singer, and several environmental features such as water depth and bottom type, (2) that the optimal receiving depth (on average) will be approximately equal to the source depth, (3) that the bandwidth of near-optimum frequencies will increase with increasing water depth, and (4) that distortions caused by propagation can potentially provide useful information about the position of the source. Given the long evolutionary history of humpback whales, it seems likely that such factors are ''taken into account'' by vocalizing humpbacks, through genetic predispositions and/or behavioral adaptability. Computational models, such as the one used in this study, provide powerful tools for investigating the physical limits on cetaceans' use of sound and for assessing how propagation effects influence the sounds they produce.

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