MARINE MAMMAL COMMUNICATION
Sperm whale acoustics: the clicking machine and its output.

Bertel Møhl

Dept. Zoophysiology, University of Århus, and CSC, The Danish National Research Foundation.

Findings from a study of sound transmission within the spermaceti complex of a fresh sperm whale cadaver is related to free field recordings of clicks. The size-determined multi-pulsed structure, peculiar to sperm whale clicks, was reproduced. New data on source levels are presented, showing that sperm whale clicks are the most intense, biologically generated sound so far reported. Also, some quantitative information about directionality is given.

INTRODUCTION

The complicated anatomy of the gigantic nose of the sperm whale has led to different hypotheses on its function. The Norris and Harvey (1972) hypothesis of a sound generating function has the merit of explaining quantitative properties of the regularly spaced, multi-pulsed click, peculiar to the species (Fig. 1).

Figure 1. Waveform of sperm whale click, selected to show the fixed interval repetition pattern. Doublets are due to sea surface reflected pulses, identified by ‘s#’. Directly received pulses are identified by ‘p#’. 

The basic principle of the Norris and Harvey hypothesis (N&H) is that of multiple reflections of a single pulse by two air filled sacs at each end of the spermaceti organ (Fig. 2, with caption).

Figure 2. Proposed sperm whale click generator. A, phonic lips. B, distal sac + blow hole. C, spermaceti bag. D, muscle/tendon layer. E, frontal air sac. F, brain. G, ‘junk’. The site of generation is at the phonic lips (A). The primary event is seen in the far-field as the low-amplitude p0-pulse (Fig. 1), traveling directly from the generation site. Most of the energy, however, is channeled in the spermaceti (C) towards the frontal sac (E) and reflected forward through the ‘junk’, a body of connective tissue with lens-shaped bodies of spermaceti. The sound is proposed to exit from the flat, frontal surface of the junk as p1. Higher numbered pulses represent fractional, stray energy traveling back and forth inside the spermaceti complex (consisting of the spermaceti bag, the ‘junk’, and the air sacs). The main fraction of whatever energy left is released at each round trip. This results in the pulse amplitude decay pattern, seen in Fig. 1.

Pinging the spermaceti complex

Direct, physiological tests of the N&H hypothesis have been lacking until 1997, where a mass stranding at Rømø, the Wadden sea, gave us the opportunity of making sound transmission studies on a fresh cadaver. We injected FM-pulses, sweeping from 26 to 10 kHz in 26 ms into the spermaceti
complex and generated the autocorrelation function (ACR) of the returning echo pattern (Fig. 3).

![Figure 3. ACR of FM-pulse excitation of spermaceti complex.](image)

This resulted in a repetitive, decaying pattern with interpulse intervals similar to those of clicks from live animals of the same size. The main findings are 1, that a regularly spaced, multi-pulse pattern can be generated from internal reflections of an externally applied, single sound pulse, 2, that the junk is sound transparent and communicating with the spermaceti organ, and 3, that there is no sound transmission laterally into the spermaceti complex. Details of his work are reported in J. Comp. Physiol. 2001, http://dx.doi.org/10.1007/s003590100205

**Far-field recordings**

Field studies with large-aperture hydrophone arrays in 1997, 1998 [2] and 2000 off Northern Norway have accumulated evidence, showing that the sonic output of this whale is as extraordinary as is its sound generator. Recordings in July 2000 were based on a large aperture array of independent, dGPS-located receivers [3], deployed from 7 crafts with a spacing of approx. 1 km. This allowed for acoustic localization of the diving sperm whales (Fig. 4), a prerequisite for derivation of source levels (SL).

Clicks with SL rms-intensities above 230 dB re 1 µPa were measured. Such levels occurred rarely, and only on hydrophones close to the general 3-D course of the whale. The preliminary results show directionality in the order of 10° at half angle, half-power points. Such directionality and the record high intensities indicate a function of the clicks for long-range biosonar.

![Figure 4. Example of sperm whale localization, using time-of-arrival differences for the same click at 6 different receivers. The position of each receiver (open circles) is obtained independently via dGPS with a horizontal precision of 2.5 m. SL seen at receiver #6 is 233 dB peRMS re 1 µPa (on-axis), against 193 dB at receiver 3 and 185 dB at receiver 4.](image)

On a more general level, it shows that the acoustic output of the sperm whale matches the mechanics and size of the spermaceti complex, suggesting long-range biosonar to be the driving force in the evolution of the spermaceti complex.

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**REFERENCES**

Pinniped Vocal Communication: Form and Function

R. J. Schusterman, B. L. Southall, D. Kastak, and C. Reichmuth Kastak

University of California Santa Cruz, Long Marine Laboratory, 100 Shaffer Road, Santa Cruz, CA 95060 USA
(email rjschust@cats.ucsc.edu)

Our study of pinniped vocal signaling emphasizes that an individual’s vocalizations primarily operate to capture the attention of other individuals in the group. For example, the most basic function of a pup attraction call produced by a female is to draw the pup’s attention to its mother’s voice. Through its association with subsequent suckling behavior this vocalization eventually evokes a strong approach response when the pup is hungry. Conversely, threats typically arouse fear or aggressive responses in others due to their abrupt onset and their pairing with behavioral events such as pushing and biting. These observations, combined with our findings that the production and structure of vocalizations of pinnipeds can be altered with food reinforcement, suggests that non-imitative learning plays an important role in the vocal behavior of pinnipeds.

APPROACHES TO ANIMAL VOCAL COMMUNICATION

During the first three quarters of the past century animal vocal communication emphasized the delineation of stimulus variables influencing the emotional and aroused state of the signaling animal and a search for the neurophysiological mechanisms related to signal production. In contrast, the last quarter century has seen research and theory about animal vocal communication being greatly influenced by human information processing theory, particularly in terms of the human linguistic model (that is, semantics and syntactics). In particular, some primatologists and some marine mammalogists have tended to focus their efforts on the cognitive state of both the actors or senders and the recipients; they have emphasized the importance of the meaning of the signal while de-emphasizing the importance of signal structure and the identity of the signaler. However, with the advent of selfish gene theory, interest has been renewed in how the actors’ signals function to govern the behavior of recipients to the benefit of the actor (and possibly, but not necessarily, to the benefit of the recipient as well). At the turn of the twenty-first century we are seeing a renewed emphasis on ethological principles and receiver psychology in the evolutionary and ecological study of animal signaling, including sound production [1, 2]. Our approach to the study of pinniped vocal communication looks at the identity of the individual producing the signal (sex, age, emotional state within a social context, experience, etc.), the structure of the signal, and how the signal exerts an influence and guides the behavior of the recipient.

Pinniped Vocalizations

Natural Settings

Pinnipeds are among the most vocal of all mammalian taxa. Of the pinnipeds, the sea lions and fur seals vocalize most in air, the seals underwater, and walruses in both media. Sea lion females leave their pups to forage and then reunite with their pups after exchanging signature vocalizations at long range. Calls attracting females to their pups and visa versa are diverse, but are marked by sharp onsets and are frequency and amplitude modulated. Figure 1 shows a California sea lion mother-pup reunion; upon returning to shore, the mother emits her characteristic pup attraction call while simultaneously guiding her pup vocally around a physical barrier. Like sea lions, seals that breed on land in crowded rookeries also

FIGURE 1. California sea lion mother and pup exchanging calls while the mother controls the pup’s locomotory behavior. The interaction terminates in a ritualized nose-to-nose greeting.
vocalize more in air. However, with the exception of elephant seals, there is no evidence of mutual vocal recognition between mother and pup in seals. In all pinnipeds, threats and alarm calls are structurally similar across sexes and species. Pinniped males have individually recognizable calls that they produce in the context of aggressive exchanges. They are repetitive, broadband pulses with rapid onset. The main function of pinniped vocalizations appears to be to elicit the attention of recipients and to guide their behavior in a way that is most beneficial to the signaler.

**Artificial Settings**

A variety of experimental approaches show that although pinniped vocal behavior is likely under strong hormonal control, the calls also have some degree of plasticity. For example, we have repeatedly found in the laboratory that male California sea lions, male harbor seals, and a female elephant seal are highly vocal during the breeding season and relatively quiet at other times of the year. Despite these strong annual cycles, it is relatively easy to condition the vocalizations of these and other captive pinnipeds [3]. Figure 2 shows spontaneous vocalizations produced in captivity during the breeding seasons of two seals. Although these calls were not spontaneously produced outside of the breeding season, we were able to control the production of these sounds by a trainer’s gestural and vocal cues via food reinforcement. Once the sounds had been conditioned to the cues, they could be reliably produced at any time during the animal’s annual cycle. Further, Figure 3 shows vocalizations produced by several adolescent walruses in captivity. These observations lead us to believe that the vocal behavior of pinnipeds is somewhat malleable, and can be controlled by a variety of environmental conditions including social situations and conditioning contexts.

**Conclusions**

By concentrating on the attention-getting characteristics of pinniped signals, the ability of the signaler to control its vocal output, and the degree to which these signals influence the behavior of recipients, new insights into the form and function of pinniped vocal communication emerge. For example, pairing vocal signals with emotion inducing behaviors, such as touching, nursing, posturing, pushing, biting, locomoting, and chasing, places signalers in an advantageous position within a variety of social contexts including mother-pup reunions, male-male competition, and sexual displays.

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**REFERENCES**

Strategies of Communication in the Wild: Sounds and Associated Behavior of Free-Ranging Atlantic Spotted dolphins (Stenella frontalis) and Bottlenose dolphins (Tursiops truncatus) in the Bahamas.

D. L. Herzing

Biological Sciences, Florida Atlantic University, Boca Raton, FL USA 33431

Understanding the social sounds and associated behavior of free-ranging delphinids has historically been limited by lack of access to animals and poor underwater viewing conditions. There are significant gaps in understanding how dolphins detect, decode, and decipher both their environmental and social signals in the wild. Resident groups of Atlantic spotted dolphin, (Stenella frontalis) and bottlenose dolphin (Tursiops truncatus) have been the focus of a long-term, underwater natural history study in the Bahamas every summer since 1985. Individuals, families, and subpods have been video taped underwater (sound and behavior) in multiple behavioral contexts including intra and interspecific activities. The relationship between basic behavioral categories and acoustic characteristics of social sounds, vocal and non-vocal repertoires, will be described including vocalizations associated with 1) contact/reunions/broadcasting, 2) excitement/distress/alarm, 3) pursuit/herding/discipline, 4) agonistic/aggressive behavior, 5) group synchrony/cohesion, 6) interspecific interactions, 7) foraging/feeding/targeting, 8) non-vocal activity with behavior, and 9) predator surveillance and monitoring. Sensory envelopes, potential transmission mechanisms, and conspecific reactions to vocal activity will be discussed.

INTRODUCTION

Understanding the characteristics and features of the social sounds and associated behavior of free-ranging delphinids has been limited by lack of access and poor underwater viewing conditions. Communication studies of delphinids have been undertaken in both captivity (Herman and Tavolga 1980) and in the wild (Connor and Smolker 1996; Norris et al. 1994). The basic life history, age class categories, and behavior for S. frontalis have recently been described (Herzing 1996, 1997). A sympatric species, T. truncatus, also shares the same habitat (Herzing and Johnson 1997; Rossbach and Herzing 1997). The following is a detailed account of sounds and associated underwater behavior of S. frontalis in various age classes, relationships, and during interspecific interactions with bottlenose dolphins.

Since 1985 a resident group of free-ranging Atlantic spotted dolphins have been observed. Underwater video camera with hydrophone input (flat to 22kHz) was used to document behavior and associated sounds. Behavior included 1) contact, reunions, broadcasting, 2) excitement, distress, alarm, 3) pursuit, herding, discipline, 4) agonistic, aggressive behavior, 5) group synchrony, 6) interspecific interactions, 7) foraging, feeding, 8) non-vocal activity with behavior, and 9) predator surveillance and monitoring. Sounds were digitized on a computer (MacDSP Spectral Innovations and Canary software) and categorized by sound type.

RESULTS

Contact/Reunions/Broadcasting

Frequency-modulated whistles (8-18 kHz) were the predominant sounds heard during behavioral contexts including a) mother/calf reunions - mothers produced their own signature whistles after calves departed and until they rejoined her, b) alloparental care - older conspecifics produced their own signature whistles prior to the retrieval of younger dolphins, c) courtship behavior - females and males repetitively broadcast their signature whistles during courtship and mating, and d) individual separation from the group - solitary dolphins took a position near the bottom and emitted their signature whistles while rotating their head.

Excitement/Distress/Alarm Sounds

The "whistle-squawk" and sharp clicks were the predominate sounds produced during alarm and distress. S. frontalis produced an "excitement vocalization", a combination burst- pulsed sound (4-8 kHz range) and signature whistle of the vocalizer (8-18 kHz). The duration of this vocalization ranged from 2.0 to 30 seconds. During production dolphins were highly erratic in their swimming and emitted a bubble stream. After a conspecific made tactile contact with the excited dolphin, the sound ceased.
Pursuit/Herding/Discipline Sounds

During the pursuit and herding of conspecifics the predominant sound produced was the "buzz" or "genital buzz" (1.2 - 2.5 kHz and repetition rates 8 – 2000 Hz). This sound is a low frequency, high-repetition rate echolocation train directed towards the genital or mid-section of a conspecific, often by a male to a receptive female during courtship behavior and during mother/calf or larger group discipline. This behavioral sequence was observed both intraspecifically within and between all age classes of *S. frontalis*, and interspecifically between juvenile and young adult spotted dolphin and *T. truncatus*. The "buzz" was also used when chasing sharks.

Agonistic/Aggressive Sounds

The predominant sounds produced during agonistic and aggressive behavior were burst-pulsed sounds. Squawks were the dominant sounds during head-to-head confrontations, body charges, and open-mouth posturing. Squawks are broad-band, burst-pulsed sounds (0.2 - 12 kHz with main energy 1.1-2.4 kHz, 0.2 - 1.0 sec, repetition rates 200 - 1200 Hz).

Barks, low-frequency, burst-pulsed sounds (0.2 to 2.0 kHz, 0.5 to 1.0 sec) and screams, overlapping frequency-modulated whistles (5.8 - 9.4 kHz, 2.5 - 4.0 sec), were produced during highly escalated aggressive behavioral sequences.

Group Synchronizing Sounds

Predominant sounds produced during synchronized activity included the coordinated production of squawks. In highly escalated aggressive activity, male *S. frontalis* coordinated their swimming behavior, postures, and production of squawks. Synchronized squawks are a highly coordinated burst-pulsed sound (0.1 to 15 kHz, main energy 0.1-2.2 kHz, 0.9-1.0 sec.

Interspecific Interaction Sounds

During mixed-species sexual play, agonistic, or aggressive interactions, squawks and synchronized squawks were the predominant sound. The scream and bark were also produced during highly escalated aggression between male dolphins of both species.

Foraging and Feeding Sounds

Predominant sounds produced during hunting, foraging, and targeting were echolocation clicks. *S. frontalis* and *T. truncatus* echolocated while scanning and digging for buried prey in sandy bottoms, increasing the repetition rate of clicks (200-500 Hz) as they directed their sound into the sand. *T. truncatus* used an echolocation train termed the "razor buzz" (2.0 - 6.0 kHz, repetition rates 200 Hz), trills (repetitive series of discrete tonal beeps below 5.0 kHz) and upswept whistles (4.8 - 16.0 kHz) during feeding. Similar echolocation trains were observed during the targeting of inanimate objects during play (i.e. seaweed) or conspecifics.

Non-Vocal Sounds

*S. frontalis* used a) tail-slaps as attention getting mechanisms or in annoyance, b) jaw claps in escalated aggression, c) aerial displays during play behavior and also during intra and interspecific aggressive chases, d) bubble displays in the production of whistles (bubble trails) and in annoyance (full and half bubbles), and bubble rings during annoyance or aggressive contexts, and e) in-air vocalizations, including the chuff (an explosive exhalation) during annoyance, and the raspberry (a constricted exhalation) in interspecies affiliative contexts.

Predator Surveillance and Monitoring

Various surveillance strategies were observed for *Stenella* during rest and travel. These included underwater observation of echolocation activity and behavior such as age-class specific reactions to sharks. Dolphins monitored their environment by listening in both clear and murky waters. During twilight hours and in deep water (> 30 m), dolphins were observed underwater and did not employ active, audible (<15 kHz), echolocation until an apparent cue was detected and warranted inspection. Post-detection behavior included slow rate echolocation clicks (8-20 Hz), close, physical contact within the dolphin group, and coordinated head scanning towards the bottom.

REFERENCES

Geographic variations in the whistles of Hawai`ian spinner dolphins (*Stenella longirostris*)

C. Bazúa-Durán and W.W.L. Au

*Hawai`i Institute of Marine Biology, University of Hawai`i, P.O. Box 1106, Kailua, HI 96734, USA. bazua@soest.hawaii.edu*

Spinner dolphin whistles from five main Hawai`ian Islands were analyzed for microgeographic variations and then combined with those of Midway and Mo`orea to search for macrogeographic variations. Frequency and time information from spectrograms show that micro- and macrogeographic variations exist in the whistles and that macrogeographic variations are larger than microgeographic variations. In addition, microgeographic variations were larger within than between islands in Hawai`i, suggesting that the whistles from the main Hawai`ian islands are part of whistle-specific subgroups. Whistle-specific subgroups presumably consist of individuals having similar whistles that may spend time together. It is possible that more mixing occurs between main Hawai`ian Islands than what was previously thought. Spinner dolphins off Kaua`i may be more isolated from those of the other main Hawai`ian islands.

**INTRODUCTION**

In some animals geographically separated groups can be identified by differences in their acoustic emissions. The existence of such differences may indicate that “vocal” learning is the likely mechanism for adopting a particular sound repertoire. Differences in the acoustic repertoire may develop so as to discourage the intermixing of groups of a species that have adapted to local ecological conditions.

In this study, “microgeographic variation” was used to describe differences between whistles of spinner dolphins in the main Hawai`ian Islands, while “macrogeographic variation” was used to describe differences occurring over long distances. Spinner dolphin whistles from the main Hawai`ian islands were compared to Midway Atoll and Mo`orea to search for macrogeographic variations. Spinner dolphins from Mo`orea do not intermix with Hawai`ian spinner dolphins, and spinners from Midway Atoll presumably do not intermix with dolphins from the Hawai`ian islands. Spinners in Hawai`ian waters have the potential for intermixing, however, the term dialect was not used due to the limited information on intermixing in Hawai`i. Differences in the whistle repertoire should be inversely correlated with the degree of mixing. Geographic variations have been found for killer whales, sperm whales and bottlenose dolphins.

**MATERIALS AND METHODS**

From 1998 to 2000 spinner dolphin whistles from the locations shown in Figure 1 were recorded using a spherical hydrophone and a portable DAT recorder. The frequency response of the recording system was flat to 24 kHz. Canary© software 1.2.4 was used to obtain the spectrogram of each whistle and to extract 10 whistle parameters: 1) beginning frequency, 2) ending frequency, 3) peak frequency, 4) maximum frequency, 5) minimum frequency, 6) duration, 7) peak time, 8) center time, 9) number of inflection points, and 10) number of steps. These parameters were used in a discriminant function analysis (DFA) in STATISTICA®. Canonical correlation was also calculated to obtain the relative degree of distances between groups. The Mahalanobis distance ($D^2$) between each pair of areas was used to evaluate the differences in the whistles of several areas. The larger the $D^2$ value the more different the groups are.

**FIGURE 1.** Map of the Pacific Ocean showing the locations where spinner dolphin whistles were recorded: Midway Atoll, main Hawai`ian Islands, Mo`orea, French Polynesia.
RESULTS AND DISCUSSION

A total of 9074 whistles were selected for analysis; 925 for Midway, 1112 for Kaua‘i, 2646 for O‘ahu, 1905 for Lāna‘i, 1062 for Maui, 961 for Hawai‘i, and 463 for Mo‘orea. Statistically significant differences were found between the whistles of Midway, the five main Hawai‘ian Islands combined, and Mo‘orea (p<0.001), however, the differences found in the whistles from each area by the DFA are very small (0.29<D²<0.75; in 2D).

Statistically significant differences were also found in the whistles of the five main Hawai‘ian Islands (p<0.001), however, the differences found by DFA are again very small (0.13<D²<0.42; in 4D). Microgeographic variations seem to be larger within than between main Hawai‘ian Islands and the differences found tended to agree with the geographic distance and possible movement of spinner dolphins between islands. Hawai‘ian whistles could be categorized by whistle-specific subgroups and some of the whistle-specific subgroups of an island are similar to those of other islands. The concept of whistle-specific subgroup was created to explain the similarities found between groups of spinners dolphins within an Island. A whistle-specific subgroup could consist of individuals having similar whistle repertoires that may regularly spend some time together. Kaua‘i whistle-specific subgroups seem to be more unique than those of the rest of the main Hawai‘ian Islands, indicating that the movement of spinners could be greater between O‘ahu-Lāna‘i-Maui-Hawai‘i than between Kaua‘i (the furthest island) and the rest of the main Hawai‘ian Islands. The home range of Hawai‘ian spinner dolphins does not seem to be limited to a single island and the dolphins do not seem to belong to different populations but may be part of a “super population”. It seems that more mixing occurs than previously thought and that the movement of spinner groups is somewhat reflected in their whistles.

Whistles from Midway were very different from those of both Mo‘orea and the main Hawai‘ian islands (D²>0.59; in 6D) (see Fig. 2). Differences in the whistles from Mo‘orea and each Hawai‘ian island (0.47>D²>0.37; in 6D) were larger than the differences between the Hawai‘ian islands, with the exception of Mo‘orea versus Hawai‘i (D²=0.16; in 6D), O‘ahu versus Hawai‘i (D²=0.40; in 6D), and Lāna‘i versus Maui (D²=0.42; in 6D). Therefore, macrogeographic differences in the whistle repertoire of spinner dolphins seem to be larger than microgeographic differences, suggesting that spinner dolphins develop changes in their whistles characteristics as a result to the adaptation to their habitat or due to isolation.

CONCLUSIONS

The results of the DFA suggest that macro- and microgeographic variations exist in the whistles of spinner dolphins, but that they are very small. It seems that more than 75% of the whistle types of spinner dolphin whistle repertoire are shared between geographically separated areas. The existence of differences in the whistles of different populations of spinner dolphins suggests that “vocal” learning is the possible mechanism for the acquisition of these acoustic emissions.

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Potential Use of Low-Frequency Sounds by Baleen Whales for Probing the Environment: Evidence from Models and Empirical Measurements

C. W. Clark\textsuperscript{a}, W. T. Ellison\textsuperscript{b} and L. Hatch\textsuperscript{c}

\textsuperscript{a}Bioacoustics Research Program, Cornell Lab of Ornithology, 159 Sapsucker Woods Rd., Ithaca, NY 14850, USA
\textsuperscript{b}Marine Acoustics, Inc. PO Box 340, Litchfield, CT 06759 USA
\textsuperscript{c}Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14850 USA

Natural variability within a population is the fodder for selection, and an organism with traits best adapted to its environment is most likely to transfer genes to the next generation. Here we take the simplistic view that acoustic characteristics shared broadly across multiple species are considered more ancestral than features only shared at the species level. This conceptual framework is the basis for gauging the degree to which, and the approximate order in which the physical environment has effected the features of baleen whale (mysticetes) sounds. Comparison of mysticete sound characteristics and evaluation based on several predictions of sonar equations support the hypothesis that sounds from shallow water and deep water species are matched to their respective environments so as to optimize underwater sound transmission for long-range communication. We propose that in the marine environment the influences of physical acoustics imposed strong selective pressures on the acoustic features of whale sounds. In some species for which selection has favored very long-range communication signals, we propose a secondarily derived function, that animals use reflections of their sounds as a simple form of echo-ranging to navigate and orient relative to physical features of the ocean.

WHALES AND SOUND PROPAGATION

Within the group of whales known as mysticetes, bowhead and right whales are considered the least evolutionarily derived, while blue and fin whales are considered to have evolved more recently. All mysticete species produce calls, while blue, bowhead, fin and humpback whales also produce long, patterned sequences of sounds referred to as songs which are sung by males. The primary function of calls and songs is assumed to be for communication between individuals.

In the marine habitat, the physical environment strongly influences acoustic transmission range. From an evolutionary perspective, and assuming that many mysticete whale sounds function for long-range communication, we propose that the physical environment would have imposed strong selective pressures on the acoustic features of whale sounds. Given the dramatic differences between sound propagation in shallow and deep water environments, we predict major differences between the acoustic characteristics for species that spend significant portions of their lives in coastal versus pelagic habitats. These concepts are developed by careful consideration of the broadband sonar equation, with particular attention to signal features that increase transmission range and signal detection [1,2].

SIGNAL FEATURE PREDICTIONS

The implications from these considerations indicate that selection should favor whales that produce signals matched to a frequency band with low transmission loss and low ambient noise. In biological terms, center frequency and bandwidth are predicted as two signal features that selection should act upon to increase detection probability and recognition. Further advantages would be gained by increased signal intensity, redundancy and stereotypy, and by auditory thresholds matched to low level ambient noise conditions in the signal frequency band. Signal bandwidth is an enormously beneficial factor as it offers the possibility for a receiver to successfully detect and recognize the signal in environments where portions of the signal are lost due to such factors as frequency dependent multi-path effects or masking. Bandwidth removes peaks and nulls that would otherwise be present in a pure tone transmission. The result is a more well behaved signal and one that is easier to detect and recognize. Therefore, selection should favor animals with sensory perception and processing mechanisms that take advantage of signal bandwidth within a frequency band window of low transmission loss and low ambient noise.
RESULTS

In shallow coastal habitats (<100m), empirical and modeled physical acoustic transmission loss and ambient noise evidence predict that selection should favor whale sounds in the intermediate, 100-500Hz frequency band. In deep (>1000m) water, similar considerations indicate that selection should favor whale sounds in the low frequency, 10-100Hz band. Phylogenetic evidence supports the working assumption that early mysticetes were shallow water grazers that later moved offshore into deeper water where they could exploit major food resources that occur seasonally along up-sloping edges as found around seamounts and along continental shelves. At such locations, the ocean temperature varies dramatically with depth, and refraction, in combination with extremely low levels of absorption, can lead to exceptionally low levels of transmission loss and extremely long ranges of acoustic transmission [3]. Low-frequency, ambient noise in the deep ocean is probably dominated by wind from high latitudes, while the present-day dominant source is from commercial shipping. In general, ambient noise level in the deep ocean is inversely related to frequency. However, there appears to be a plateau in ambient noise in the 10-100 Hz band.

A comparison of mysticete sound characteristics shows that signal features are well matched to the acoustic constraints of the shallow and pelagic habitats. Bandwidths and peak frequencies for calls and songs of the three coastal species, are between 25-600 Hz, and 150-400 Hz, respectively, while bandwidths and peak frequencies for the two pelagic species are between 3-25 Hz and 18-35 Hz, respectively. Both these sets of acoustic characteristics are well matched to the acoustic transmission properties and ambient noise conditions of the respective environments. Further pronounced differences between songs for species in these two environments are found in signal redundancy and stereotypy. We conclude that the most sounds of baleen whale have acoustic characteristics that are well adapted for long-range communication within a species’ predominant breeding and feeding environment.

SECONDARY HYPOTHESIS

Through further consideration of a more speculative nature, but grounded in basic principles, we propose that in some species for which selection has favored extremely low-frequency, stereotypic and redundant signals, a secondary function for these sounds has evolved. This secondary function is a form of echo detection and ranging. We propose that some species use the reflections of their sounds from natural ocean boundaries to navigate and orient. An empirical example for a blue whale approaching Bermuda shows that in this scenario physical acoustics is not a limiting factor in the detection of a reflection off the base of Bermuda. We conclude that there is no a priori reason, based on transmission properties of the environment and other physical acoustic considerations, to reject the hypothesis that certain baleen whales could use sounds for echo-ranging. However, there are presently no direct, unequivocal data to support this hypothesis. Despite this lack of evidence, we propose the following mechanism for the evolution of an echo-detection and echo-ranging function. As low-frequency signals became increasingly better adapted for very long-range communication within the deep-sea environment, selection favored signals that were infrasonic, intense, stereotypic and redundant. These last three features are also advantageous for detection of reverberation and reflection. Thus, there was a secondary selective advantage to individuals producing and perceiving these signals as an aide in long-range navigation and orientation along the shelf edge and in the deep ocean.

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Phylogenetic and ecological influences on the vocal patterns of aquatic mating pinnipeds.

Sofie M. Van Parijs

Norwegian Polar Institute, Tromsø, N – 9296, Norway. Sofie@npolar.no

Underwater vocalizations of males serve as an invaluable tool for studying the reproductive strategies of aquatic mating pinnipeds. The relative influences of ecology on reproductive strategies were studied by comparing male vocal behavior in species with ‘predictable’ and ‘unpredictable’ female distribution. Female harbor seals travel from pupping sites along predictable foraging routes. Female bearded seals pup on ice floes, which change location continuously, rendering female distribution less predictable. Distinctive vocal clusters of male harbor seals were apparent in areas where female density was greatest. In contrast, male bearded seals vocalized in higher densities around fjord entrances, which suggests that they may use ‘geographical bottlenecks’ to intercept passing females. Varying influences of tidal and diel cycles on female movements were reflected in male vocal patterns. In both species males vocalized more during the period when females were more likely to be in the water. Male strategies reflect variability in female distribution between species. Phylogenetic influences on male harbor seal vocalizations from ten sites around the globe were explored. Variation in spectral parameters and seasonal patterns of vocalizations were similar to the global population structure. Males exhibited both geographical and vocal dialects. Aquatic mating pinnipeds exhibit plasticity in vocal behavior influenced by varying ecological constraints, but evolutionary history also influences several aspects of male reproductive strategies.

INTRODUCTION

In this study, I examine how phylogeny and ecology has influenced the evolution of vocal patterns in aquatic mating pinnipeds. Evolutionary and ecological relationships vary in their influence on the development of mammalian behavioral traits and strategies. Vocal behavior can serve as a useful indicator for exploring varying effects of phylogeny and ecology on the behavior of a species (e.g. 1).

Pinnipeds show considerable diversity in breeding habitats, group size and sexual dimorphism. They are highly vocal taxa, with vocalization predominantly used during the breeding season for the purpose of mother-infant recognition (e.g. 2) and male/male competition or attraction of females (e.g. 3). In most aquatic mating species, energetic constraints force females to forage during late lactation. Therefore, females are widely dispersed at sea during the mating season, and it is unlikely that males are able to monopolize females. Males produce stereotypic underwater vocal and dive displays for male/male competition and/or for attracting females (e.g. 4, 5).

METHODS

Firstly, the relative influences of ecology on male reproductive strategies were explored. Comparisons were made between two aquatic mating species, one with a predictable and another with an unpredictable female distribution. Female harbor seals, Phoca vitulina, haul out at known locations and travel along predictable routes from their pupping haul out sites to forage at sea (6). In contrast, female bearded seal, Erignathus barbatus, distribution is highly variable or ‘unpredictable’ and is strongly related to the availability of suitable ice for hauling out (e.g. 7). Harbor seal vocal distribution and patterns (8, 9, 10) were compared to that of bearded seals (11). All vocalizations were recorded using an SSQ 906A navy sonobuoy hydrophone (sensitivity: - 170dB re. 1µPa, frequency response: 5Hz - 15kHz ± 3dB), a custom built pre-amplifier (sensitivity: - 130dB re. 1µPa, frequency response: 5Hz - 13kHz ± 3dB) and a Sony digital audio tape recorder, TCD-D8 (frequency response: 5Hz - 22kHz). Vocal densities of males and tidal and diurnal patterns of vocalizations were contrasted with female movement patterns.

Secondly, the importance of phylogeny on male harbor seal vocal patterns at ten sites around the globe was explored. Harbor seals are generally believed to be philopatric, returning to the same areas each year to breed. Consequently, seals from different areas are genetically differentiated, with levels of genetic divergence increasing with distance (12, 13). Recordings were made of male harbor seal roar vocalizations from ten sites around the globe (Scotland, 2 sites; Norway, 1 site; Sweden, 1 site; E. Canada, 2 sites; W. Canada, 1 site; California, 3 sites). Recordings were made using a variety of different hydrophones and audio cassette recorders. and were analyzed as spectrograms using BatSound (Pettersson Elektronik AB; 1996). Vocalizations
were separated into three different quality categories, poor, medium and good, based on their spectrogram quality (Fast Fourier Transforms, dt: 10 ms, df: 102 Hz, FFT size: 512). Only good signals, where all spectral contours were distinctly measurable were used for these analyses. Four standard vocal parameters were measured (9), the lowest measurable frequency (kHz), the frequency with the greatest energy (kHz), the total duration, (seconds) and the pulse duration, (seconds). Comparative analyses were made using Sorensen (Bray-Curtis) principal coordinates analyses within the program PC-ORD 4.0 for windows.

RESULTS/DISCUSSION

Vocal clusters of male harbor seals were apparent in areas where female density was greatest. In harbor seals, male densities were reflective of variation in female distribution, with the highest densities of males occurring in areas where female density is greatest (3, 8). In contrast, male bearded seals vocalized in higher densities around fjord entrances, which suggests that they may use ‘geographical bottlenecks’ to intercept passing females (11). This strategy appears to be a consequence of the unpredictable nature of female distribution. Varying influences of tidal and diel cycles on female movements were reflected in male vocal patterns (8, 11). In both species males vocalized more during the period when females were more likely to be in the water (14, 15, 16). These fine-scale variations observed in the temporal patterns of male bearded and harbor seal display behavior appear to reflect differences in the ecological constraints on female haul-out patterns and foraging behavior.

Global analyses of male harbor seal vocal patterns showed that variation in underwater roar vocalizations reflected the phylogenetic differentiation in this species, with significant variation occurring between Eastern Pacific (Phoca v. richardsi), Western (Phoca v. concolour) and Eastern (Phoca v. vitulina) Atlantic populations. Geographical variation in vocal patterns was observed between discrete populations, while vocal dialects were apparent between mixing sub populations. The seasonal occurrence of underwater vocalizations also appears to be influenced by phylogenetic variation, with vocalizations from Eastern Atlantic populations restricted within the mating season, while year round vocalizations were observed in Eastern Pacific populations.

Male mating strategies in aquatically mating pinnipeds are considerably more variable than previously envisaged. These results show that phylogenetic and ecological influences affect vocal patterns at the level of the species, sub species, population and even at the level of local haul-out groups. These findings suggest that vocal patterns, and therefore reproductive strategies, in aquatic mating pinnipeds are clearly influenced both by evolutionary history and adaptive plasticity to current conditions.

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REFERENCES

Testing the Perception of Bottlenose Dolphin Signature Whistle Variations Using a Habituation-Dishabituation Paradigm

V. M. Janik\textsuperscript{a} and S. Rey\textsuperscript{b}

\textsuperscript{a}SMRU, School of Biology, University of St Andrews, Fife KY16 8LB, U.K.
\textsuperscript{b}CREAF, Fac. de Ciències, Universitat Autònoma de Barcelona, 08193 Bellaterra, Barcelona, SPAIN

Bottlenose dolphins (\textit{Tursiops truncatus}) produce individually distinctive signature whistles. However, subtle variations can be found in different behavioural contexts. This study investigated whether other individuals can perceive these variations. We used a habituation/dishabituation procedure in which one variant of a whistle was played 15 times while the final test playback was of another variant. Stimuli were prepared from dolphin whistles by tracking the frequency contour over time and then resynthesizing the whistle using its original amplitude envelope. The main stimulus used had a wave-shaped frequency spectrogram stretching from 4 to 10.5 kHz and a duration of 133 ms. Playbacks were conducted at Hagenbeck Zoo in Germany to a group of 5 dolphins. Swimming speed of each individual was used as a measure of habituation to a stimulus. The group showed the strongest dishabituation to a test stimulus that had a 3.2 kHz lower start and a 3.7 kHz higher end frequency than the habituation stimulus. The overall frequency contour of the whistle remained the same in the test stimulus. Our results suggest that dolphins perceive and may be able to extract context-specific information from variations in signature whistles.

Bottlenose dolphins (\textit{Tursiops truncatus}) have been found to produce individually-distinctive signature whistles while they are in isolation \cite{1, 2}. Inter-individual variability of these whistles is much greater than it is known from other animals \cite{1}. However, intra-individual variation has received much less research attention. Janik et al. \cite{3} found that a bottlenose dolphin produced context-specific variants of its signature whistle. While the overall frequency modulation of the whistle remained constant, subtle parameters like frequency range and the duration of parts of the whistle varied according to whether the animal received food after performing a visual discrimination task. Such parameter variations occur in many sound-producing animals and reflect the motivational state of the animal. However, in many cases it is not clear whether parameter variations can be perceived by other animals. Therefore, the first step to establish whether motivational information is available to other individuals is to investigate whether variations can be perceived. To test perception we used a habituation/dishabituation paradigm on a group of five captive bottlenose dolphins. The tested signature whistle variation was within the range of variations found by Janik et al. \cite{3}.

The study was conducted at the Hagenbeck Tierpark dolphinarium in Hamburg, Germany, on a group of four female and one male bottlenose dolphins. A signature whistle and an upsweep whistle of a female bottlenose dolphin from another zoo were used to prepare playback stimuli. Whistles were digitized at a sampling rate of 50 kHz using SIGNAL software (Engineering Design, Belmont, MA, USA). From each whistle we extracted the amplitude envelope and the frequency modulation over time (FFT size: 1024, df: 49 Hz, dt: 20.5 ms). Using this information we re-synthesized computer whistles of different types of whistles of the same unknown female but with the exact same amplitude envelope and duration. In the first experiment (three sessions), the habituation stimulus was a re-synthesized signature whistle variation while the test stimulus was the re-synthesized signature whistle. The variation had a higher start (7.2 versus 4 kHz) and a lower end frequency (6.8 versus 10.5 kHz) than the re-synthesized original signature whistle (Fig. 1). In the second experiment (2 sessions), the habituation stimulus was the re-synthesized signature whistle while the test stimulus was a re-synthesized upsweep whistle (Fig. 1). To test perception of whistle variations one whistle was played as a habituation stimulus (15 times in a total of 30 minutes, one whistle every 2 minutes), while the 16th playback was of a test stimulus. Playback equipment consisted of a Casio DAT-Recorder DA-R100, a Klein & Hummel Telewatt P240 power amplifier and an Atlantic Research LC54M1 transducer. The transducer was placed out of sight of the dolphins in a separate pool. We observed swimming speed and direction in the 15 sec before and after each playback as a behavioural indicator of habituation and dishabituation. These swimming responses were measured by counting how often and in which sequence each animal crossed 9 different sections of their pool system.
All dolphins showed a strong swimming response to the first playback in each session. In the first experiment, we could observe a habituation to the signature whistle variation and a dishabituation to the signature whistle (Fig. 2). However, in the second experiment that used the upsweep whistle as a test stimulus we could not observe a significant dishabituation. This can be explained by the lack of a habituation to the signature whistle stimulus. Strong reactions of the group to playbacks could be observed throughout the entire time of each session.

Our results suggest that bottlenose dolphins can perceive signature whistle variations like the ones found by Janik et al. [3]. We think that the habituation-dishabituation paradigm is a promising tool to investigate whistle perception in dolphins. However, in future experiments one should try to keep the habituation period more flexible and only use the test stimulus once habituation has been achieved. It is obvious that this can be much longer than the period used in this study. Furthermore, animals showed a general decrease in responses between sessions. Thus, methodology should be adjusted accordingly in future studies.

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Australian research in marine mammal vocalisations

Cato, Douglas H., McCauley, Robert D., Noad, Michael J., Rogers, Tracey, and Schultz, Ken W.

More than 20 years of Australian research into marine animal sounds has revealed a wide diversity of sounds and acoustic environments around Australian and in the Antarctic. These have included studies of vocalisations from several species of baleen whales, dolphins and seals. Humpback whale songs over 20 years have usually shown the well structured, evolving song typical of the species, though with some anomalies. Recently, there was a remarkable replacement of the east coast song by west coast song in a way that appears to be unprecedented in animal communication. In the last year, a large set of diverse sounds have been recorded from blue whales off the west coast. Leopard seals studied in captivity and in the Antarctic have shown a range of vocalisations correlated with both close contact communication and with breeding. Studies of dolphin sounds in the wild have shown significant differences between four species in communication whistles and relation to behaviour and the use of low frequency harmonic sounds during social activity in bottlenose dolphins.

INTRODUCTION

Although marine mammal sounds have been heard on occasions in Australian waters for more than 30 years, research on vocalisations did not commence until about 1980. This was mainly because of the scarcity of baleen whales prior to 1980 and the significant recovery of stocks that has been observed since then. This recovery has resulted in a substantial increase in vocal activity in Australian waters, with a significant impact on the background ambient noise. Whereas it was difficult to find and record baleen whale sounds in 1980 due to scarcity of vocalisations, there are now substantial areas around the continent where vocalisations are audible for much of the year. With increasing success in studies of baleen whale vocalisations, work has expanded to include vocalisations of dolphins and seals. This paper summarises observations and knowledge of marine mammal vocalisations in Australian waters.

HUMPBACK WHALE SONG

The first baleen whale stock to show signs of recovery was that of the humpback whale in the early 1980s [1]. At the termination of whaling on the east coast of Australia in 1962, the humpback whale stock size there may have been no more than 100 [2], whereas today it is estimated to be around 4000 [2]. Humpback whale songs have been recorded off east Australia since 1979 and off western Australia since 1983 [3] and vocalisations have increased generally in proportion to the stock size. Whereas it was rare to hear a song even during the peak of the migration in 1981, it is now usual to hear several singers simultaneously.

Studies of humpback whale songs [3] have usually shown a well structured sequence of themes and repeating phrases following song "rules" similar to those observed in the northern hemisphere [4, 5]. Change has usually been gradual and evolutionary, but there was at least one occasion of rapid change over the course of a year leading to a poorly structured song which eventually returned to a more typical structure [3]. Songs off east and west coasts have usually been unrelated [3,6], whereas east coast songs have shown significant similarities to those east across the Pacific Ocean near New Caledonia, New Zealand, and Tonga [7]. In 1996, however, a new song was observed concurrently with the existing song in the east coast stock. Originally from only a small percentage of singers, this new song replaced the old song within two years. The new song was in fact the west coast song, and the rapid replacement is an example of "cultural revolution" not previously observed in animal vocal tradition [8].
BLUE WHALES

Although there have been odd sightings of blue whales, it is only in the last five years that significant numbers have been noticed off the south west and south east corners of the continent [9, 10]. A variety of sounds have been recorded. A series of three powerful, long, low frequency tonal signals spread over 78 s, predominate [9]. Initial propagation modelling suggests these signals can carry long distances, perhaps into several hundred kilometres. Another sound type is believed related to feeding.

LEOPARD SEALS

Studies of leopard seals in captivity (Taronga Zoo in Sydney) and in the Antarctic have shown two distinctively different types of vocalisations correlated with different behaviours. A repertoire of high source level vocalisations observed in the breeding season from both males and females appear to be used to advertise breeding receptivity and condition [11]. There appears to be geographical variation in these vocalisations. A set of lower source level, shorter duration vocalisations appear to be used by animals during close interaction throughout the year have been termed “local sounds” [11].

DOLPHINS

Comparisons of vocalisations of four species of dolphin (Tursiops truncatus, T. aduncus, Dephinis delphis and Sousa chinensis) in the wild have shown significant differences in whistles. Vocalisations of Tursiops aduncus have shown frequent use of low frequency harmonic sounds during social activity, which have not been observed from this species elsewhere [12].

RIGHT WHALE SOUNDS

Southern right whale numbers have been very low since about 1840 [13] but have recently shown significant recovery [14]. Vocalisations were first recorded in 1979, from a mother and new born calf, and were similar to those reported for this species off South America [15]. Low frequency pulses have also been recorded from a pygmy right whale [16], a species which appears to be limited to latitudes 31° and 52° S.

REFERENCES

An Acoustic System for Tracking Cetaceans around a Trawl

B. Woodward

Department of Electronic and Electrical Engineering, Loughborough University, LE11 3TU, UK

The paper presents an outline of an acoustic system for tracking echo-locating cetaceans in three-dimensional space in the vicinity of a pelagic trawl. The system has been used during trials in the Atlantic with a Dutch fisheries research vessel. Preliminary results show that positions could be calculated, although the precision was limited by having to attach hydrophone streamers to a working trawl and by using bandwidth-limited coaxial cables instead of fibre-optic cables for data transmission. The technique has been developed to gain a better understanding of how cetaceans react to the presence of obstacles.

INTRODUCTION

The aim of the research is to develop a real time acoustic system for tracking small echo-locating cetaceans (dolphins, porpoises and whales) in the vicinity of a pelagic trawl in order to study their behaviour as a contribution to reducing the by-catch of these animals by European fisheries, a problem highlighted by the International Whaling Commission [1]. The system is based on an array of hydrophones, attached to the trawl, which detect the animals’ echo-location clicks. These clicks are sent as shaped electrical signals along a co-axial cable to a receiver on the ship towing the trawl. The function of the receiver is to measure the propagation delays between the arrivals of the clicks at the hydrophones and convert them into a position fix. This is normally achieved by applying a tracking algorithm [2, 3], but the bandwidth limitations of the coaxial cable led to the use of a look-up table as an alternative to determine positions.

POSITION-FIXING PRINCIPLES

With four hydrophones that are not in the same plane, positions can be determined unambiguously in three-dimensional space. On the trawl, owing to hydrodynamic constraints, four hydrophones were mounted in two parallel streamers and hence in the same plane. To avoid positional ambiguities, a fifth hydrophone was mounted on the towing warp out of the plane of the streamers (Fig. 1). Since click rates can be variable from a few hertz up to several hundred hertz and swimming speeds can be up to 10 m/s, this presents the problem of a high repetition rate combined with a high velocity of the acoustic source. If more than one animal is echo-locating at the same time, a large number of pulses may arrive at the hydrophones in a short time, requiring some complicated unscrambling by the receiver.

For tracking in three-dimensional space, a click has to be received unambiguously on all the hydrophones. In principle, a tracking algorithm can then be applied to the measured relative arrival times to compute an instantaneous \((x,y,z)\) position. The algorithm initially used here was developed for tracking a diver carrying a pinger and produces two estimates of a position, corresponding to the two roots of a quadratic equation [2]. One of these estimates is the true location of the animal being tracked; the other may be discounted by observing that the times corresponding to such a position do not match the times actually measured. A further test is performed to ensure that the estimated position is attainable by the animal, given its maximum possible speed and its previously calculated position. If this is not the case, there remain two possibilities: either the new position is due to some inaccuracy in the tracking system, or a new acoustic source, such as another echo-locating dolphin, has been detected.

Owing to the computational load necessary for applying a real-time tracking algorithm, this approach was abandoned. A quick and simple position-fixing technique was therefore needed, so a look-up table was adopted whereby the area around the array was divided into discrete zones. For each zone a time difference was calculated for each pair of hydrophones. These were then sorted to reduce the delay between the arrival of the clicks and the position calculation, allowing the system to work in near real-time. On the arrival of a click the timings were compared with the table and the corresponding position was plotted. The disadvantage of this method was the time needed to calibrate the array and create the look-up table. Using multi-tasking programming the effect of this calibration was minimised, thereby allowing tracking to continue even while re-calibrating.

HARDWARE AND SOFTWARE

To produce a relatively stable array in turbulent water flow required the use of two high technology hydrophone streamers and adjustments to the pelagic trawl to which they were attached. Each streamer consisted of two hydrophones, with associated pre-amplifiers and a calibration pinger. The hydrophones were connected to an underwater electronics unit that extracted the arrival time information from the click patterns. The digitised data were then transmitted along a 2 km co-axial cable to the ship, where they...
were stored on an instrumentation recorder and on a PC-based data-logger. Finally, the data were sent, via an RS232 link, to another PC that controlled the calibration of the hydrophone system and applied the tracking algorithm.

It was known from simulations that small relative movements of the hydrophones in an array can produce large errors in position fixes. The array therefore needed to be re-calibrated frequently because it could be in any of a range of configurations depending on the shape and movement of the trawl. The calibration system periodically pinged from streamer to streamer, allowing the inter-hydrophone spacings to be calculated. If the array and fifth hydrophone were stable, the fifth hydrophone could be used as part of the array to increase the accuracy of the look-up table method. Two sets of streamers were produced and tested. The accuracy of the timing data from the arrays was limited by the co-axial cable transmission link, with a bandwidth capability of 100 kHz, giving a maximum timing accuracy of 10 μs. This was a severe limitation and resulted in the computation of several possible locations for each click. These locations tended to lie in a line between the source and the array, and meant that source positions were defined in terms of vectors, rather than points. Multi-tasking software was written using Borland Delphi 2 and Borland C++ Builder to produce the look-up table and update and re-sort it whenever a calibration pulse was detected.

CONCLUSION

The system has been fully deployed during two sea trials in the Atlantic, mainly along the continental shelf west of Ireland. Data is still being analysed, but the small numbers of cetaceans encountered limited the scope of the testing. Problems with the self-calibration system reduced the accuracy of the system, and these were exacerbated by the detection of click-like noise sources on the trawl itself, particularly the Netsonde headrope depth instrumentation.

The outcome of the research so far is that the system shows promise for behavioural studies and should provide information contributing to the design of nets that are more easily detected by cetaceans and lead to a reduction in by-catches.

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REFERENCES

Beyond bottlenoses: a comparative study of the sounds produced by sympatric delphinids.

Peter J. Corkeron\textsuperscript{a} and Sofie M. Van Parijs\textsuperscript{b}

\footnotesize \textsuperscript{a}Norwegian Institute of Fisheries and Aquaculture Ltd., Tromsø N - 9291, Norway. \textsuperscript{b}Norwegian Polar Institute, Tromsø N - 9296, Norway.

Comparative studies provide one method of assessing selective forces acting on species inhabiting similar habitats. Previous comparisons of delphinid sound production have focused on echolocation. Comparisons of the suite of sounds produced by free ranging delphinids remain uncommon. We studied the sound production of two species of inshore dolphins: Irrawaddy dolphins, \textit{Orcaella brevirostris}, and Pacific humpback dolphins, \textit{Sousa chinensis}, in northern Australia. Both species occur in shallow turbid tropical waters and have apparently similar social structures. Irrawaddy dolphins’ repertoire consists of broad-band clicks, pulsed sounds and two simple whistles. In contrast, humpback dolphins produce broad band clicks, barks, quacks, grunts and at least 17 different whistles. Humpback dolphins’ repertoire is similar to that of the other Delphinines studied to date, particularly \textit{Tursiops} and \textit{Stenella}. Irrawaddy dolphins’ repertoire does not resemble that of their nearest taxonomic relative, the killer whale, \textit{Orcinus orca}, but resembles that of \textit{Sotalia}. Humpback dolphins appear to have adapted the Delphinine repertoire to their inshore habitat, while Irrawaddy dolphins’ repertoire is closer to the primitive Odontocete state. Expanding this approach will provide further insight into the evolution of cetacean communication.

INTRODUCTION

The impressive communicative faculties and complex social behaviour of bottlenose dolphins, \textit{Tursiops} sp., are being revealed through research on free-ranging animals [e.g. 1,2]. However, with a few exceptions [e.g. 3] the acoustic repertoires of most other delphinids remain poorly described. Comparative studies within mammalian families have improved our understanding of many aspects of mammalian biology. No comparisons of been delphinids’ communicative behaviour have been attempted to date.

Recently, we have described the acoustic repertoires of two species of dolphins sympatric in shallow inshore tropical waters: Pacific humpback dolphins, \textit{Sousa chinensis}, and Irrawaddy dolphins, \textit{Orcaella brevirostris} [4,5]. A recent phylogeny [6] places both species in the Delphinidae, but in separate subfamilies. Here we compare the acoustic repertoires of the two species, and point to the relative importance of phylogeny and ecology in delphinid vocal communication.

METHODS

This study was conducted between March 1999 and January 2000, at sites in northeastern and southeastern Queensland, Australia. Recordings of groups of each dolphin species were made using a High Tech Inc. hydrophone (model HTI-96-MIN, sensitivity: -170db, frequency response: 5 Hz - 30 kHz ± 1.0dB, -165 dB re: 1 V/uPa) and a digital audio tape recorder, SONY TCD-D8 (frequency response: 20Hz – 22 kHz ± 1.0dB). Recordings when only one species was in the vicinity were used for analyses.

Recordings were played back and analysed as spectrograms using BatSound (Pettersson Elektronik AB; 1996). Vocalisations were categorised as, poor, medium and good, based on their spectrogram quality (Fast Fourier Transforms, dt: 10ms, df: 102Hz, FFT size: 512). Poor signals were discarded from analyses. Measurements of the maximum frequency range were restricted by the upper limit (22 kHz) of the recording equipment. Vocalisations were separated into four categories: broad band clicks, burst pulses, narrow band FM sounds (whistles) and other sounds. Whistle types were further categorised by their spectral contours by visual assessments carried out by both authors. Concurrent behavioural data were recorded also [see 4,5, for details]

RESULTS

The humpback dolphins recorded produced broad band clicks, two distinct burst-pulse sounds (barks and quacks), a low frequency, narrow band grunt, and whistles. Broad band clicks were high in frequency (8 kHz to > 22 kHz), were directly related to foraging behaviour and may play a role in social behaviour. Barks and quacks (frequency: 0.6 kHz to > 22 kHz, duration: 0.1 to 8 seconds) were recorded during foraging and socializing. Grunts (frequency:
The details of both species’ social structure remain unclear, but humpback dolphins appear to have a fission-fusion society similar to that of *Tursiops*. Irrawaddy dolphins’ social structure remains completely unknown. We suggest that comparing the contexts in which these two species use social communication will provide new insights into how delphinids mediate their social interactions. Further, we hypothesize that Irrawaddy dolphins live in less complex societies than do *Tursiops* or *Sousa*.

Further comparisons of this sort across the Delphinidae will improve our understanding of how the acoustic faculties within the group have evolved. Achieving this will require researchers to look beyond studies of *Tursiops*. To date, bottlenose dolphins have been the study animals of choice for field studies by delphinid behaviourists. This is probably because they are the species most accessible to members of academic institutions in the USA and Europe. Expanding work to include less well studied species is sure to improve this branch of science.

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Estimated Active Space of Killer Whale Sounds

P. J. O. Miller

Department of Biology, Woods Hole Oceanographic Institution

Estimates of the range of signal detectability, or “active space”, are useful to predict the ranges over which animals communicate, to describe the function of a repertoire, and to explore the effects of background noise on communication. Here the active space of 819 killer whale calls and 24 whistles was estimated using source spectra obtained with two hydrophone arrays towed in series. Transmission loss was calculated at 0.1km steps, and active space estimated as the range at which energy in all 1/3-octave bands from 1-20kHz fell below auditory threshold or 6dB below noise levels at sea states 0 and 6. In sea-state 0, active space ranged from 1.9-25.8 km with stereotyped calls exceeding variable calls and whistles. Among stereotyped calls, active space fell into two clusters. Types containing a separately-modulated high-frequency component had a greater active space than types without such a component. The same pattern was observed at threshold-limited and sea-state 6 noise levels, but active space was reduced by ~80% for all sound classes in sea-state 6 conditions. This suggests that killer whales communicate over large distances, that the repertoire consists of long- and shorter-range sound classes, and that natural environmental noise can dramatically reduce communication ranges.

METHODS

Active space was estimated for each sound for which I measured a source spectra from 1-20kHz as described below. Based upon their frequency structure, sounds were classified as whistles, variable calls or stereotyped calls of a type described by Ford [3]. Active space was calculated as the maximum range at which \( SL(f) + TL(f,r) > NL(f) + DT(f) \) for energy summed in any 1/3-octave band. SL is source spectra, TL is transmission loss, NL is the background noise level, and DT is the receiver’s detection threshold.

Source level (SL) of killer whale sounds was measured using recordings of sounds on two calibrated 8-element (2.6 m) hydrophone arrays towed in series separated by 100m. Range from the rear array to the signaler was calculated by intersecting the angles-of-arrival of the sound on the two arrays, and never exceeded 300m. Source level was calculated by adding hemispherical spreading loss of 20log(r)-3dB [4] to the received spectra of the loudest portion (>100ms in duration) of each sound. Calibration trials demonstrated that range errors should contribute no more than 3dB of error to the SL value.

Transmission loss (TL) was calculated in 0.1km range steps using the shallow-water equations of Marsh and Shulkin [4] assuming water depth of 100m and a sand bottom. Noise levels (NL) were generated using Knudsen et al.’s 5dB per octave rule for sea states 0 and 6 [5]. A no-noise model in which detection was assumed to be limited by the auditory threshold of killer whales was also used. The detection threshold (DT) was -6dB SNR or the auditory threshold of killer whales, whichever was higher for each 1/3-octave band. Beluga whales reliably detect conspecific signals at ~6dB SNR [6].

RESULTS

Source levels were measured for 819 calls and 24 whistles from 5 hours of recordings on two days in September, 1998 in Johnstone Strait, BC (Fig. 1). Conditions were calm during both days, and whales from A-pod were present both days. As predicted, the choice of NL had a significant influence on active space estimates. In sea-state 0 conditions, active space estimates ranged from 1.9 to 25.8km, while in the quietest noise conditions in which hearing is threshold limited, active space ranged from 4.5 to 26.2 km. The maximum ranges closely match those of bottlenose dolphin whistles described by Janik [2]. In all noise conditions, stereotyped calls had a greater active space...
FIGURE 1. Spectrograms of a whistle and the eight most common call types recorded. Note the high-frequency component in types N1, N2, N4, N5 & N9. than variable calls and whistles (Fig. 2). Stereotyped calls contained two clusters by active space, where all of the longer-range types are known to contain a separately-modulated high-frequency component, while the short range types do not (Figs. 1 and 3).

FIGURE 2. Mean (±2 s.e.) estimated active space of whistles, variable and stereotyped calls in threshold-limited, seas-state 0 and sea-state 6 noise conditions.

DISCUSSION

The results of this study suggest that killer whales communicate over large ranges relative to terrestrial animals, and that the repertoire consists of long- and shorter-range sound types. Long-range sounds are stereotyped calls with two frequency contours, while shorter-range signals consist of calls without a high-frequency component, variable calls, and whistles. Natural levels of noise due to rough seas appear to cause a significant reduction in communication ranges. This is likely to also apply to anthropogenic noise caused by vessels, but suggests that killer whales may have existing adaptations to compensate for noise.

While this technique seems useful to describe a signal repertoire, many input parameters are likely to vary regularly. TL is strongly dependent on local conditions, so actual ranges could be greater or less than those estimated here. Likewise, individual variability in SL or DT would affect detection ranges, and directional signal transmission and reception cause active space to vary depending on the orientation of both the signaler and receiver. Further refinements accounting for these effects will improve our ability to estimate actual communication ranges.

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