Factors Affecting the Responses of Marine Mammals to Acoustic Disturbance

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ABSTRACT

The issues surrounding marine mammals and noise cannot be managed effectively without an understanding of the effects of that noise on individual mammals and their populations. In the spring of 2003 the National Research Council released *Ocean Noise and Marine Mammals*, a report that reviewed sources of ocean noise (natural and anthropogenic), the effects of noise on marine mammals, patterns and long-term trends in ocean noise, and included recommendations intended to improve understanding of the sources and impacts of anthropogenic marine noise. This paper provides a brief summary of observed effects of ocean noise on marine mammals and the factors that can change the response of the animal to the noise exposure. It introduces the reader to short- and long-term behavior changes that have been observed in marine mammals in response to ocean noise, and discusses future directions for marine mammal research.

Public recognition of issues concerning coastal water quality, global warming, and the survival of threatened species appears to be increasing. Perhaps one of the most controversial and least understood impacts humans have on the marine environment results from the effects of human-generated ocean noise on marine mammals and other marine organisms. Ocean research, national defense, shipping, resource discovery, and many other activities result in the introduction of sound into the ocean, but the effects these noises have on marine mammals and other marine organisms are poorly understood. Mammals are of particular concern because they include a number of threatened and endangered species, they rely on acoustic communication to sense their environment and communicate with each other, and their disturbance is regulated by the Marine Mammal Protection Act. Although many other marine organisms use sound and thus increasing levels of anthropogenic sound are also likely to affect them as well, this article focuses on the issue as it relates to marine mammals.

Marine mammals use acoustic signals to expand their sensory environment to distances well beyond the range provided by vision or chemical senses. Acoustic signals can be transmitted over great distances, while light is rapidly attenuated in ocean waters, and chemicals diffuse only slowly and in unpredictable ways. The evolution of an auditory system that can discriminate different sounds, determine the direction of a sound source, and detect sounds even when the environment is reasonably noisy, greatly increases the survival potential of aquatic animals. It has been argued that humans and animals glean a great deal about their environment from the "acoustic scene," and that this scene provides an immense amount of subtle information about the environment around an animal that is necessary for survival (e.g., sounds of a reef or a shore line) (see Bregman, 1990; Fay and Popper, 2000).

To describe and summarize the sources of ocean noise, and review what is known of the effect of noise on marine mammals, the National Research Council convened a panel of experts and produced the report *Ocean Noise and Marine Mammals* (2003). This paper summarizes some of the effects of ocean noise that were discussed by the committee and is intended as a complement to the papers in this volume that delve into individual sources or specific observed effects on marine organisms. Additional impacts of noise on the marine ecosystem that were included in the report such as the effects on fish that make up the marine food web upon which marine mammals depend and the effects of noise-induced stress on the animals are not discussed here. For more complete reviews of general and specific behavioral reactions, the reader is referred to both Richardson et al. (1995) and the NRC report (2003) from which much of this material is drawn.

In this paper we discuss a wide range of species of marine mammals. The seals and sea lions constitute the pinnipeds and these species are adapted to an amphibious life style with hearing accommodations enabling them to hear both above and below water. Their ears are not as adapted to underwater hearing as are those of the cetaceans. Among the whales, there are two major groups to which we make reference. One, the odontocetes or toothed whales, includes dolphins, porpoises, killer whales, other relatively small species, and the much larger sperm whale. The other group, the baleen whales or mysticetes, includes what are generally the large species including humpback, fin, and right whales. We know far more about hearing and acoustic behavior of the smaller odontocetes since, because of their size, only these animals can be kept in captivity for experimental research. In contrast, far less is known about the mysticetes. It is clear, however, that whereas odontocetes often can hear and use sounds to over 100 kHz, mysticetes appear to only hear and use sounds to somewhat less than

10 kHz. Virtually nothing is known about the beaked whale family of odontocetes.

Factors Affecting Marine Mammal Responses to Acoustic Disturbance

Internal, Animal-specific Modifiers of Behavior

Generalizations about the effects of ocean noise on marine mammals are complicated by a host of factors. After detection of a sound, behavioral responses of marine mammals are highly variable and depend on a suite of internal and external factors. Internal, animal-specific factors include:

- individual hearing sensitivity, activity pattern, and motivational and behavioral states at the time of exposure;
- past exposure of the animal to the noise, which may have led to habituation or sensitization;
- individual noise tolerance; and
- demographic factors such as age, sex, and presence of dependent offspring.

These factors are obviously very difficult to determine in wild, free-ranging populations, and so a few examples are included here to illustrate how these factors may affect animal responses.

In general, it appears that resting animals are more likely to be disturbed by noise than are animals engaged in social activities. Würsig (Richardson et al., 1995) summarized the responses of several species of dolphins to boats as "resting dolphins tend to avoid boats, foraging dolphins ignore them, and socializing dolphins may approach." Migrating bowhead (*Balaena mysticetus*) and gray (*Eschrichtius robustus*) whales divert around sources of noise, whether the noise originates from industrial activities or recorded playbacks of industrial activities (Richardson et al., 1995). Almost all bowheads reacted at received levels of 114 dB re 1 μPa. However, if no other option is available, migrating bowhead whales will pass through an ensonified field to continue their migration. During spring migration, when the only available open water lead through the ice was within 200 m of a projector playing sounds associated with a drilling platform, the bowheads continued through the sound field despite received levels of 131 dB re 1 μPa (Richardson et al., 1991).

Some age and sex classes are more sensitive to noise disturbance, and such disturbance may be more detrimental to young animals. Age and sex classes can be most clearly identified and observed among pinnipeds that are on land or ice, so most of the data come from responses of these pinnipeds to noise. In northern sea lions (*Eumetopias jubatus*), dominant, territory-holding males and females with young are less likely to leave a haul-out site in response to an aircraft overflight than are juveniles and pregnant females (Calkins, 1979). Walrus (*Odobenus rosmarus*) sometimes stampede into the water in response to aircraft overflights and this has the potential to result in the death of calves (Loughrey, 1959). Vessel approaches to walrus on ice may cause the herd to enter the water and in some cases leave calves stranded in slippery depressions on the ice where they are vulnerable to predation by polar bears (Fay et al., 1984). Mother–calf gray whale pairs appear to be particularly sensitive to disturbance by whale-watching boats (Tilt, 1985). Humpback whale (*Megaptera novaeangliae*) groups containing at least one calf were more responsive to approaches by small boats on several behavioral measures of respiration, diving, swimming, and aerial behaviors than were groups without a calf (Bauer et al., 1993).

External Behavior Modifiers

External factors that influence the response of marine mammals to acoustic disturbances include:

- non-acoustic characteristics of the sound source, such as whether it is stationary or moving;
- environmental factors that influence sound transmission;
- habitat characteristics, such as being in a confined location; and
- location, such as proximity of the animal to a shoreline.

Behavioral responses range from subtle changes in surfacing and breathing patterns, to cessation of vocalizations, to active avoidance or escape from the region of the highest sound levels.

The responses of whales to noise sources often depend on the perceived motion of the sound source as well as on the nature of the sound itself. For a given source level, fin (*Balaenoptera physalus*) and right (*Eubalaena glacialis*) whales are more likely to tolerate a stationary source than they are one that is approaching them (Watkins, 1986). Humpback whales are more likely to respond at lower received levels to a stimulus with a sudden onset than to one that is continuously present (Malme et al., 1985). These startle responses are one reason that many seismic surveys are required to "ramp up" the signal so fewer animals will experience the startle reaction and so that animals can vacate the area of loudest signals. There is, however, no experimental evidence that this action reduces mammal disturbance. The ramp-up of a playback signal or a seismic air gun array takes place over a short timescale (a few tens of minutes maximum) compared to the changing received levels an animal experiences as it swims toward a stationary signal source. Bowheads react to playback levels of drill ship noise at levels they apparently tolerate quite well when they swim close to operating drill ships. Richardson et al. (1995) provide two explanations for these behavioral differences. First is the speed of ramp-up, as noted. Second, the whales observed near an operating drill ship may be the ones that are more tolerant of noise; the sensitive whales seen responding to the playback levels may have already avoided the actual drill ship at ranges that were undetected by observers near the drill ship.

Responses of animals also vary depending on where the animals are when they encounter a novel noise source. Pinnipeds generally show reduced reaction distances to ships when the animals are in the water compared to when they are on ice or on land. Swimming walrus move away from an approaching ship that is tens of meters away, whereas walrus on the ice react at ranges of hundreds of meters (Fay et al., 1984). Similar differences in avoidance ranges have been seen in California sea lions (*Zalophus californianus*) and harbor seals (*Phoca vitulina*). Visual and olfactory cues may also be important contributors to the responses of animals on land or ice.

Bowhead whales that are at the surface in shallow water are more responsive to the overflights of aircraft than are surfaced bowheads in deeper water habitat (Richardson and Malme, 1993). Beluga whales (*Delphinapterus leucas*) respond to ship noise at lower received levels when they are confined to open water leads in the ice in the spring than when they are in open, ice-free water (Burns and Seaman, 1985). Migrating gray whales diverted around a stationary sound source projecting playbacks of the U.S. Navy's Low Frequency Active (LFA) sonar when the source was located in the migratory path but seemed to ignore the sound source when it was located seaward of the migratory path. When the source was in the path, received levels of 140 dB re 1 μPa were sufficient to cause some path deflection. However, when the source was located seaward of the migratory path, the whales ignored received levels greater than 140 dB re 1 μPa (Tyack and Clark, 1998).

Vocalization Changes in the Presence of Noise

Changes in vocalizations include reductions in or cessation of calling as observed in: right whales responding to boats (Watkins, 1986); bowhead whales in response to playbacks of industrial sounds (Wartzok et al., 1989); sperm whales (*Physeter catodon*) in response to short sequences of pulses from acoustic pingers (Watkins and Schevill, 1975); and sperm and pilot whales (*Globicephala melaena*) in response to the Heard Island Feasibility Test source (Bowles et al., 1994). Humpback whales, which appeared in all other behavioral measures to have habituated to the presence of whale-watching boats, still tended to cease vocalizations when boats were near (Watkins, 1986).

Not all cetaceans respond to ocean noise with a decrease or cessation of calls. Sperm whales continued calling when encountering continuous pulsing from echosounders (Watkins, 1977) and when exposed to received sound levels of 180 dB re 1 μPa (RMS) from the discharge of a detonator (Madsen and Møhl, 2000); humpback whales moved away from low-frequency (3-kHz range) so-

nar pulses and sweeps but did not change their calling (Maybaum, 1993); and a fin whale continued to call with no change in rate, level, or frequency components as a container ship went from idle to full power within a kilometer of the whale (Edds, 1988). However, sperm whales in the Caribbean became silent in the presence of military sonar signals (3-8 kHz range; Watkins et al., 1985).

In addition to changing the frequency of occurrence of calls in the presence of noise, some species are able to change the source level and output frequency and duration of their signals. Beluga whales adjust their echolocation clicks to higher frequencies and to higher source levels in the presence of background noise (Au et al., 1985). Miller et al. (2000) found that humpback whales exposed to low-frequency active sonar signals increased the duration of their songs by 29 percent on average, but with a great deal of individual variation.

Masking of Acoustic Cues by Marine Noise

One of the most pervasive and significant effects of a general increase in background noise on most vertebrates, including marine mammals, may be the reduction in an animal's ability to detect relevant sounds in the presence of other sounds—a phenomenon known as auditory masking. Masking, which might be thought of as acoustic interference, occurs when both the signal and masking sound have similar frequencies and either overlap or occur very close to each other in time. Noise is only effective in masking a signal if it is within a certain "critical band" (CB) around the signal's frequency (Scharf, 1970). If the masker is within the critical band of a signal of importance to the animal, the noise will affect detection of the signal. The actual degree of masking depends upon the amount of noise energy within this critical frequency band. Thus, a noise with low energy within the critical band of a signal or with greater energy outside of the critical band of the signal will have little impact on detection, whereas a noise within the critical band will show increased effects on detection of the signal as the level of the noise increases.

CBs have been measured both directly and indirectly in a number of marine mammals. In cases where data are available over a wide range of frequencies, critical bandwidth as a proportion of the frequency at the center of the bandwidth is lower for odontocetes than for most mammals at frequencies above 1 kHz. This means that relative to the frequency of interest, at higher frequencies only the noise energy within a bandwidth that is a small percentage of that frequency will be effective in masking it, while at lower frequencies sound energy within a bandwidth that is a much larger percentage of that frequency will cause masking.

Directional Hearing

When noise and a signal arrive at a receiver from different directions, two mechanisms can function to reduce masking. The first relates to the receiving beam pattern of the animal; that is, the extent to which its auditory system is more sensitive to sound on a particular bearing. Normally the direction of greatest sensitivity is ahead, and an animal will typically orient toward a sound source so that the absolute level of the sound at the receiver is increased and, provided the noise and signal are on different bearings, the signal-to-noise ratio is also improved. Animals can also determine the direction from which a sound arrives based on cues, such as differences in arrival times, sound levels, and phases at the two ears. The ability that this provides to resolve the signal and noise to different directions can further reduce masking. Thus, an animal's directional hearing capabilities have a bearing on its vulnerability to masking. The bottlenose dolphin (*Tursiops truncatus*) has good directional hearing above 1 kHz (Renaud and Popper, 1975) but directional hearing at lower frequencies has been less completely studied. The shielding effects of head structures that are important for both the receiver beam and for causing the sound level differences at the two ears that contribute to directional hearing are wavelength dependent. This is reflected by a general trend for a less acute directional hearing ability for lower frequency sounds. The directivity index (DI) is a measure of the effectiveness of an acoustic receiver in reduc-

ing the effects of omni-directional noise. The directivity index indicates the number of dB by which an omni-directional noise source has to exceed a noise source on the same axis as the signal in order to produce the same masking effect. Au and Moore (1984) investigated the DI of a bottlenose dolphin for a signal arriving from ahead and found that it ranged from 10.4 dB at 30 kHz to 20.6 dB at 120 kHz. At these frequencies, sounds arriving from ahead, such as echolocation return echoes, will be substantially protected from masking. Directional hearing is less acute in pinnipeds (Moore and Au, 1975) and has not been measured formally in any of the baleen whales.

Masking of Representative Signals by Realistic Noise

Most studies of masking with captive animals have explored the effects on detection of a very simple signal, typically a pure tone, by broadband noise of constant spectral density (i.e., white noise). In the real world, both signals and masking noise are more complex spectrally and temporally, and only a few studies have explored these more realistic scenarios.

Bain and Dalheim (1994) investigated the effects of a real masking noise—that of oil-spill cleanup vessels—on killer whale detection of simple tones and playbacks of killer whale vocalizations. Intensities of boat noise that raised the detection levels of pure tones at 16 kHz and 20 kHz by 21 dB and 41 dB, respectively, had no effect on the detection of either killer whale clicks or killer whale calls.

Concern about interference with beluga whales' communication by icebreaking activity led Erbe and coworkers to explore masking of a beluga call by three different types of icebreaker noise (Erbe, 1997, 2000; Erbe and Farmer, 1998; Erbe et al., 1999). The noise types were ice ramming (primarily propeller cavitation), natural ice cracking, and an icebreaker's bubbler system (high-pressure air blown into the water to push floating ice away from the ship). Bubbler noise was the most effective masker of beluga calls with a critical noise-to-signal ratio (CNSR) of 15.4 dB, followed by ramming noise (CNSR of 18 dB), with natural ice-

cracking noise being least effective (CNSR 29 dB). Human performance in masking tests was very similar to that of the beluga whale (Erbe et al., 1999).

Strategies to Reduce the Probability of Masking

Marine mammals evolved in an environment containing a wide variety of naturally occurring sounds, and thus they show a variety of strategies to reduce masking. Vocal signals may be designed to be not easily impeded by masking sounds. Vocal signals can be more easily detected in noise if they are stereotyped and occur in a distinctive pattern (Jouventin et al., 1999). Such signals may also show a high level of redundancy; they may be repeated many times to increase the probability that at least some will be detected. However, these characteristics all minimize the amount of information that a signal can convey. Animals can adapt their behaviors to minimize masking and it is reasonable to interpret such behavioral changes as an indication that masking has occurred. For example, vocal output of a beluga whale changed when it was moved to a location with higher levels of continuous background noise (Au et al., 1985). In the noisier environment, the animal increased both the average level and frequency of its vocalizations, as though it were trying to compensate for and avoid the masking effects of the increased, predominantly low-frequency background noise levels. Penner et al. (1986) conducted trials in which a beluga whale was required to echolocate on an object placed in front of a source of noise. The animal reduced masking by reflecting its sonar signals off the water surface to ensonify the object. The strongest echoes from the object returned along a path that was different from that of the noise. This animal's ready application of such complex behavior suggests the existence of many sophisticated strategies to reduce masking effects.

Beluga whales increased call repetition and shifted to higher peak frequencies in response to boat traffic (Lesage et al., 1999). Gray whales increased the amplitude of their vocalizations, changed the timing of vocalizations, and used more frequency-modulated signals in noisy environments (Dahlheim,

1987). Humpback whales exposed to low-frequency active sonar increased the duration of their songs by 29 percent (Miller et al., 2000).

The physiological costs to ameliorate masking effects—such as using more energy to increase the level of vocalizations—have not been determined. Although these examples all appear to show animals adapting their vocal behavior to reduce the impact of masking, this does not imply that there were no costs resulting from increased levels of noise. Masking may have been reduced but not eliminated when animals use these strategies.

Critical Research Needs to Understand the Effects of Masking

Attempts to assess the masking effects of a particular type of noise in marine mammals are hindered by our poor understanding of how animals make use of the many acoustic cues in their environment. Though it is assumed that animals attend to, and make use of, each other's communication vocalizations, it is unclear what received levels are necessary to elicit recognition and response to social calls.

The biological implications of signal masking will depend greatly on the function of the signal and the context. In an animal population in which males compete with each other vocally to attract a female, the introduction of masking noise might have little effect if the numbers in the population are near environmental carrying capacity. Even if the females' ability to make a mating choice were diminished they would still be likely to find a mate. In the case of a severely depleted population, if additional noise reduced acoustic range by masking and reproduction were compromised, the consequences for individuals and populations could be very significant (Payne and Webb, 1971; Myrberg, 1980).

How marine mammals make use of the myriad acoustic cues in the marine environment, or the "acoustic scene," is even more poorly understood than masking of communication. Many of these acoustic cues, such as waves breaking on distant shores, rain patterns, or noises produced by schools of fish prey, may be fairly faint and are thus susceptible to masking by even low levels of noise. While a vocalizing animal may adapt its vo-

cal behavior to compensate for increased levels of masking noise by vocalizing more intensely, changing the emphasized frequency, or increasing redundancy, masking of these other acoustic cues cannot be mitigated. A better understanding of the role of passive listening—investigation of the environment through listening without active generation of echolocation pulses—in the lives of marine mammals may well be the most fundamental research need for assessing masking impacts. Detailed field research involving fine-scale behavioral observations linked to sensitive real-time acoustic monitoring will be required to gain any appreciation of how marine mammals utilize these low-level noises.

To investigate the occurrence of masking in the real world, field projects could be designed to study behavioral changes thought to be indicative of masking (such as the strategies to avoid masking outlined earlier), and behavioral performance in situations with different levels of background noise could be monitored (see also recommendations in NRC, 2000; Appendix D). Measures of feeding rates and hunting success, mate-searching behavior, and predator avoidance would be necessary to elucidate whether masking effects were likely to affect the survival or reproduction of the individual and ultimately impact populations.

Habituation, Sensitization, and Tolerance of Marine Mammals to Marine Noise

Habituation to repeated presentations of a signal that is not associated with physical discomfort or overt social stress is a common adaptive feature of sensory systems that predates the evolution of mammals. It is not surprising that marine mammals show habituation to many signals that initially cause an overt reaction. To demonstrate habituation, the same signal needs to be presented to the same individual repeatedly and the response of that individual charted over the sequential presentations. Such a demonstration for marine mammals is rare. Instead, habituation is inferred by the changes in the response of animals of the same species in the same area over time. This assumes that

although the individuals are unidentified in the group, there is consistency in group composition over the course of the study. A second-order inference of habituation can also be made by comparing the reactions of individuals of the same species from two different areas to the same stimulus, the stimulus being one to which animals in one area have been exposed previously, whereas animals in the other area are assumed naive with respect to this particular stimulus.

Some of the clearest evidence of habituation comes from attempts to use sound sources to keep marine mammals away from an area or a resource (Jefferson and Curry, 1996). Acoustical Harassment Devices (AHDs) have been used in an attempt to keep pinnipeds away from aquaculture facilities or fishing equipment. AHDs emit tone pulses or pulsed frequency sweeps in the 5–30 kHz range at source levels up to 200 dB re 1 µPa at 1 m. Although initially effective, over time some of the devices became less able to deter harbor seals, presumably because of habituation (Mate and Harvey, 1987) but also because of a change in seal behavior in which the animals spend more time swimming with their heads out of the water when they are in intense sound fields. Seals and California sea lions even habituate to "seal bombs" that can have peak sound pressure levels of 220 dB re 1 µPa at 1 m (Mate and Harvey, 1987; Myrick et al., 1990). Harbor porpoises (*Phocoena phocoena*) habituate to pingers placed on gillnets in an attempt to reduce the incidental catch of porpoise in these nets. The probability of porpoises being within 125 m of a pinger decreased when the pinger was first activated, but within 10-11 days had increased to equal the control (Cox et al., 2001).

Watkins (1986) summarized 25 years of observations of whale responses to whale-watching boats and other vessels near Cape Cod. Minke whales (*Balaenoptera acutorostrata*) changed from frequent positive interest in the boats to generally uninterested reactions. Fin whales changed from mostly negative to uninterested reactions. Humpbacks changed dramatically from mixed responses that were often negative, to often strongly positive reactions, and right whales continued the same variety of responses with little change. In Baja California, gray whales

wintering in San Ignacio Lagoon are less likely to flee from whale-watching boats later in the season than they are shortly after arriving in the lagoon (Jones and Swartz, 1984). In all these examples, factors in addition to habituation could also have contributed to the observed changes and habituation could have been to stimuli other than acoustic.

In contrast to habituation, which results from repeated presentations of an apparently innocuous stimulus, sensitization is the result of prior presentation of a stimulus that either by itself, or in conjunction with another action results in a negative experience for the animal. In sensitization, responses at subsequent presentations are more marked than are the responses at the initial presentation. Northern fur seals (*Callorhinus ursinus*) showed little initial reaction to a ship, but if that ship were subsequently used in seal hunting, the seals avoided it at distances up to a mile (H. Kajimura, in Johnson et al., 1989). Walruses hauled out on land are more tolerant of outboard motorboats in years when they are not hunted from such craft than they are in years when these boats are used in walrus hunts (Malme et al., 1989). Bottlenose dolphins that had previously been captured and released from a 7.3-m boat would flee when that boat was as far away as 400 m, whereas bottlenose dolphins that had not been captured by the boat often swam quite close to it (Irvine et al., 1981). All the reported cases of sensitization are the result of conditioning: the pairing of a given stimulus with a significantly negative experience. The stimulus in these examples was not necessarily exclusively auditory.

Animals will tolerate a stimulus they might otherwise avoid if the benefits in terms of feeding, mating, migrating to traditional habitat, or other factors outweigh the negative aspects of the stimulus. Already noted is the case of the bowhead whales on spring migration that passed through a sound field with projected drilling ship sounds at levels of 131 dB re 1 µPa when they needed to use the one available lead in the ice cover to continue on their eastward migration (Richardson et al., 1991). Bowheads also return to the same areas of the Canadian Beaufort Sea year after year even though seismic

surveys occurring at the same time are an annual feature of these areas (Richardson et al., 1987). It is not evident that the prey consumed in these areas make a significant contribution to the annual energy budget of the whales and thus the driving features for migrating into this area of high seismic activity remain unknown.

In at least one case, a source that did not elicit a fleeing response turned out to be capable of causing damage. Humpback whales in Newfoundland remained in a feeding area near where seafloor blasting was occurring. The humpbacks showed no behavioral reaction in terms of general behavior, movements, or residency time. In fact, residency time was greater in the bay closest to the blast site than it was in other bays of equivalent size and productivity nearby. Estimated peak received levels during blasting were approximately 153 dB re 1 μPa with most of the sound energy below 1,000 Hz (Todd et al., 1996). Two humpback whales found dead in fishing nets in the area had experienced significant blast trauma to the temporal bones, although the seafloor blasting could not be determined to be causal (Ketten et al., 1993).

Variability of Marine Mammal Responses

The range of variability of responses of marine mammals to anthropogenic noise and other disturbance can be summarized in the responses of beluga whales to ships. One of the most dramatic responses in any species of marine mammal has been observed over several years in beluga whales in the Canadian high Arctic during the spring. At distances of up to 50 km from icebreakers, or other ships operating in deep channels, beluga whales respond with a suite of behavioral reactions (LGL and Greeneridge, 1986; Cosens and Dueck, 1988; Finley et al., 1990). The reactions include rapid swimming away from the ship for distances up to 80 km; changes in surfacing, breathing, and diving patterns; changes in group composition; and changes in vocalizations. The initial response occurs when the higher frequency components of the ship sounds, those to which the beluga whale are most sensitive, are just au-

dible to the whales. Possible explanations for this unique sensitivity to ship sounds are partial confinement of whales by heavy ice, good sound propagation conditions in the arctic deep channels in the spring, and lack of prior exposure to ship noise in that year (LGL and Greeneridge, 1986). Supporting the annual novelty of the ship noise is the observation that beluga whales that fled icebreaker noise at received levels between 94 and 105 dB re 1 μPa returned in one to two days to the area where received icebreaker noise was 120 dB re 1 μPa (Finley et al., 1990).

Beluga whales in the St. Lawrence River appeared more tolerant of larger vessels moving in consistent directions than they were of small boats, fast-moving boats, or two boats approaching from different directions. Older animals were more likely to react than younger ones, and beluga whales feeding or traveling were less likely to react than animals engaged in other activities, but when the feeding or traveling whales did react, they reacted more strongly (Blane and Jaakson, 1994). In contrast to the lower rate of observed reactions of these beluga whales to larger vessels, a study of the response of beluga whale vocalizations to ferries and small boats in the St. Lawrence River showed more persistent reactions to the ferries. The calling rate was reduced from 3.4 — 10.5 calls per whale per minute to one or fewer calls per whale per minute while vessels were approaching. Repetition of specific calls increased when vessels were within 1 km, and the mean frequency of vocalizations shifted from 3.6 kHz prior to noise exposure to frequencies of 5.2-8.8 kHz when vessels were close to the whales (Lesage et al., 1999).

In Alaska, beluga whale response to small boats varied depending on the location. Beluga whales feeding on salmon in a river stopped feeding and moved downstream in response to the noise from outboard motorboats, whereas they were less responsive to the noise from fishing boats to which they may have habituated (Stewart et al., 1982). On the other hand, beluga whales in Bristol Bay continued to feed when surrounded by fishing vessels and resisted dispersal even when purposely harassed by motorboats (Fish and Vania, 1971).

Thus, depending on habitat, demography, prior experience, activity, resource availability, sound transmission characteristics, behavioral state, and individual variability, the response of beluga whales can range from the most sensitive reported for any species, to ignoring of intentional harassment. Beluga whales also show the full range of types of behavioral response, including altered headings, fast swimming, changes in dive, surfacing, and respiration patterns, and changes in vocalizations.

Responses of Marine Mammals to Noise Over Extended Time Periods

Almost all the studies conducted so far have looked at only short-term effects of anthropogenic noise on marine mammals. In most cases the observed responses have been over periods of minutes to hours. Even the dramatic response of beluga whales to icebreakers in the high arctic, in which the whales moved up to 80 km and were out of the area for one to two days, falls into the category of a transient response over the annual activity budget of the animals. The whales had reduced responses to subsequent icebreakers and ships in a given season.

Multiyear abandonment of a portion of the habitat because of human activity has been reported for Guerrero Negro Lagoon in Baja California, where shipping and dredging associated with an evaporative salt works project appeared to cause the whales to abandon the lagoon through most of the 1960s. When the boat traffic declined, the lagoon was reoccupied, first by single whales and subsequently by cow–calf pairs. By the early 1980s the number of cow–calf pairs using the lagoon far exceeded the number prior to the commencement of the commercial shipping (Bryant et al., 1984). Killer whales significantly reduced their use of Broughton Archipelago in British Columbia when high-amplitude acoustic harassment devices (AHDs) were installed to deter harbor seal predation at salmon farms. The AHDs operated between 1993 and 1999, and almost no whales were observed in the archipelago throughout most of this period. However, when the de-

vices were removed in 1999, killer whales repopulated Broughton Archipelago within six months (Morton and Symonds, 2002).

Clearly there are costs associated with even the transient behavioral changes in response to noise. The movements require energy that might otherwise have been spent in acquiring food or mates or enhancing reproduction. Repetitive transient behavioral changes have the potential of causing cumulative stress. Even transient behavioral changes have the potential to separate mother–offspring pairs and lead to death of the young, although it has been difficult to confirm cases of this. On the other hand, pups can be injured or killed when trampled by adults rapidly leaving the land for the sea in a transitory response to a disturbance.

New Research Tools to Understand Marine Mammal Behavior

Any real understanding of long-term and cumulative effects of noise on marine mammals will require the development and refinement of a number of new research instruments. Ideally, sound pressure level should be recorded as it is received by the animal, and it also would be valuable to record the vocalizations of the animal in real time along with as many movement parameters and physiological parameters as possible. Recently several new recording devices that can be attached to marine mammals have been developed that incorporate some of these features. Researchers working on northern elephant seals, *Mirounga angustirostris*, have developed acoustic recording packages that include a hydrophone and temperature and depth sensors (Burgess et al., 1998) or a digital audio recorder with a time-depth recorder and a time-depth-velocity recorder (Fletcher et al., 1996) in a package that can be placed on juvenile seals. The devices record received sound, seal swim strokes, and during quiet intervals at the surface, both respiration and heartbeats. Cetacean researchers further developed these concepts into digital sound recording tags that record onto solid-state memory received signal levels, animal vocalizations, pitch roll and orientation, and

depth (Burgess, 2001; Johnson et al., 2001; Madsen et al., 2002). Three-dimensional tracks of the whale's movements can be reconstructed from the recorded data. These tags are typically applied with suction cups so they are only on the animal for a short period of time. Still, they provide a good deal of data while they are in place. Another suction cup tag places a hydrophone on a dolphin to record heartbeats. This has been tested so far on captive animals where the dolphin showed significant heart rate accelerations in response to playbacks of conspecific vocalizations compared to baseline rates or to playbacks of tank noise (Miksis et al., 2001). Finally, radio tags need to be developed that overcome foreign body rejection and remain attached for several years and transmit only on a programmed cycle, or in response to a query signal in order to conserve battery life. For most marine mammal species, the difficulty in identifying individual animals rapidly and reliably makes it very difficult to follow animals for long periods of time to determine cumulative effects. Borggaard et al. (1999) were able to follow individually identified minke whales over four years and noted that this provided a more sensitive means of assessing impacts of industrial activity than did abundance and distribution measures. At a minimum, animals must be identified and observed pre-exposure, during exposure, and post-exposure for a sufficient number of repetitions and for a sufficient period of time to be able to make any reasonable statements on the effect of the exposure on a given animal and potentially on the population. Without these data, we will simply continue to collect disparate observations of transient behavioral changes, which tell us little about the impact of anthropogenic noise on marine mammals.

Conclusions

Observations concerning the effects of ocean noise on marine mammals are limited. Both short- and long-term effects on marine mammals of ambient and identifiable components of ocean noise are poorly understood. There is no documented evidence of ocean noise being the direct physiological agent of

marine mammal death under any circumstances, although there is a clear causal connection between mid-range tactical sonar and stranding of beaked whales (Evans and England, 2001; Jepson et al., 2003). Marine mammals have been shown to change their vocalization patterns in the presence of background and anthropogenic noise. Furthermore, the long-term effects of ambient noise on marine organisms are even less well understood. Potential effects include changes in hearing sensitivity and behavioral patterns, as well as acoustically induced stress. Because these effects may occur in many species ranging from invertebrates to marine mammals, there is the potential for impacts on marine ecosystems at many levels.

Although it is difficult to obtain evidence of direct impacts of human activity on marine mammals, it is even more difficult to determine long-term impacts on individual animals or on populations. Although the few documented cases of direct impact on individuals have raised awareness of potential population impacts, no evidence exists of marine mammal population effects from ocean noise. Research on marine mammal response to noise should be conducted in a way that would allow the findings to be related to possible population-level effects.

Impacts resulting from increases in background ambient noise have not been documented. Research to determine subtle changes in marine mammal behavior, as well as failure to detect calls from other animals or echoes from their own echolocation, that might result from masking of biologically important acoustic information by anthropogenic sounds is ripe for investigation.

Marine mammal tagging studies are providing exciting new access to the behavior patterns of marine mammals. When used in conjunction with acoustic recording devices the data should vastly improve our understanding of marine mammal responses to ocean noise. Two technological improvements of current tags are needed: (1) increase the duration of long-term data gathering tags from months to multiple years to observe annual behavior cycles and migration patterns, and (2) extend the duration of high-resolution tags from hours to days to gather

more data on daily behavior and environmental cues and to insure that the observed data are uncontaminated by any residual effect of the tagging operation.

Potentially, anthropogenic sounds can have effects on marine life at a number of different levels, from short-term effects on individuals to long-term effects on populations and even species. Effects that can be dramatic, even potentially lethal, at the level of the individual may have negligible consequences at the population level if, for example, small numbers of a large healthy population are affected. Conversely, effects that may seem insignificant for the well-being of individuals could have important conservation consequences for populations that are depleted and under stress. For example, a decrease in feeding rate which might equate to a year's delay in attaining sexual maturity, a small increase in infant mortality, or a slightly shorter lifespan, may not be overly significant to an individual animal, but could mark the difference between extinction and recovery for a critically endangered species. It is important to emphasize that whether or not a particular impact could be of conservation significance will depend on the status of the population; thus the conservation significance of particular impacts must be assessed on a case-by-case basis. While much legislation and scientific work focuses on conservation goals, it is important to recognize that the well-being and welfare of individual wild animals is also a concern for many members of the public and harassment of any individual marine mammal is prohibited by the Marine Mammal Protection Act.

Acknowledgements

References

Au, W.W.L. and P.W.B. Moore. 1984. Receiving beam patterns and directivity incidents of the Atlantic bottlenose dolphin. J Acoust Soc Am. 75:255-262.

Au, W.W.L., D.A. Carder, R.H. Penner, and B.L. Scronce. 1985. Demonstration of adaptation in beluga whale echolocation signals. J Acoust Soc Am. 77:726-730.

Bain, D.E. and M.E. Dahlheim. 1994. Effects of masking noise on detection thresholds of killer whales. In: Marine Mammals and the Exxon Valdez. ed. T.R. Loughlin, pp. 243-256. San Diego, CA: Academic Press.

Bauer, G.B., J.R. Mobley, and L.M. Herman. 1993. Responses of wintering humpback whales to vessel traffic. J Acoust Soc Am. 94:1848.

Blane, J.M. and R. Jaakson. 1994. The impact of ecotourism boats on the St. Lawrence beluga whales. Environ Conserv. 21:267-269.

Borggaard, D., J. Lien, and P. Stevick. 1999. Assessing the effects of industrial activity on large cetaceans in Trinity Bay, Newfoundland. Aquatic Mammals. 25:149-161.

Bowles, A.E., M. Smultea, B. Würsig, D.P. DeMaster, and D. Palka. 1994. Relative abundance and behavior of marine mammals exposed to transmissions from the Heard Island Feasibility Test. J Acoust Soc Am. 96:2469-2484.

Bregman, A.S. 1990. Auditory Scene Analysis. Cambridge, MA: MIT Press. 773 pp.

Bryant, P.J., C.M. Lafferty, and S.K. Lafferty. 1984. Reoccupation of Laguna Guerrero Negro, Baja California, Mexico, by gray whales. In: The Gray Whale *Eschrichtius robustus,* eds. M. L. Jones et al. pp. 375-386. Orlando, FL: Academic.

Burgess, W.C. 2001. The bioacoustic probe: A miniature acoustic recording tag. Abstract. Presented to 14th Biennial Conference on the Biology of Marine Mammals, November/December 2001. Vancouver, BC, Canada.

Burgess, W.C., P.L. Tyack, B.J. Le Boeuf, and D.P. Costa. 1998. A programmable acoustic recording tag and first results from free-ranging northern elephant seals. Deep-Sea Research Part II 45:1327-1351.

Burns, J.J. and G.A. Seaman. 1985. Investigations of beluga whales in coastal waters of western and northern Alaska II - Biology and ecology. U.S. National Oceanic and Atmospheric Administration, 129 pp.

Calkins, D.G. 1979. Marine mammals of Lower Cook Inlet and the potential for impact from outer continental shelf oil and gas exploration, development, and transport. In: Environmental Assessment of the Alaskan Continental Shelf: Final Reports of Principal Investigators, Volume 20. pp. 171-263. U.S. National Oceanic and Atmospheric Administration, Juneau, AK.

Cosens, S.E. and L.P. Dueck. 1988. Responses of migrating narwhal and beluga to icebreaker traffic at the Admiralty Inlet ice-edge, N.W.T. in 1986. In: Port and Ocean Engineering Under Arctic Conditions, Volume II, eds. W.M. Sackinger et al., pp. 39-54. Fairbanks: Geophysics Institute, University of Alaska.

Cox, T.M., A.J. Reed, A. Solow, and N. Tregenza. 2001. Will harbour porpoises (*Phocoena phocoena)* habituate to pingers? Journal of Cetacean Research Management 3:81-86.

Dahlheim, M.E. 1987. Bio-acoustics of the gray whale (*Eschrichtius robustus*). Ph.D. thesis, University of British Columbia, Vancouver, 315 pp.

Edds, P.L. 1988. Characteristics of finback (*Balaenoptera physalus*) vocalizations in the St. Lawrence Estuary Canada. Bioacoustics. 1:131-150.

Erbe, C. 1997. The masking of beluga whale (*Delphinapterus leucas*) vocalizations by icebreaker noise. Vancouver: University of British Columbia. 164 pp.

Erbe, C. 2000. Detection of whale calls in noise: Performance comparison between a beluga whale, human listeners, and a neural network. J Acoust Soc Am. 108:297-303.

Erbe, C. and D.M. Farmer. 1998. Masked hearing thresholds of a beluga whale (*Delphinapterus leucas*) in icebreaker noise. Deep-Sea Research Part II-Topical Studies in Oceanography. 45:1373-1388.

Erbe, C., A.R. King, M. Yedlin, and D. Farmer. 1999. Computer models for masked hearing experiments with beluga whales (*Delphinapterus leucas*). J Acoust Soc Am. 105:2967-2978.

Evans, D.I. and G.R. England. 2001. Joint interim report Bahamas marine mammal stranding event of 15-16 March 2000. National Oceanic and Atmospheric Administration. Available at: http://www.nmfs.noaa.gov/prot_res/PR2/Health_and_Stranding_Response_Program/Interim_Bahamas_Report.pdf

Fay, R.R. and A.N. Popper. 2000. Evolution of hearing in vertebrates: The inner ears and processing. Hear Res. 149:1-10.

Fay, F.H., B.P. Kelly, P.H. Gehnrigh, J.L. Sease, and A.A. Hoover. 1984. Modern populations, migrations, demography, tropics, and historical status of the Pacific walrus. In: Environmental Assessment of the Alaskan Continental Shelf: Final Reports of Principal Investigators, Volume 37. pp. 231-376. U.S. National Oceanic and Atmospheric Administration, Anchorage, AK.

Finley, K.J., G.W. Miller, R.A. Davis, and C.R. Greene. 1990. Reactions of belugas, (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) to ice-breaking ships in the Canadian high arctic. Can J Fish Aquat Sci. 224:97-117.

Fish, J.F. and J.S. Vania. 1971. Killer whale (*Orcinus orca*) sounds repel white whales (*Delphinapterus leucas*). Fish Bull. 69:531-535.

Fletcher, S., B.J. Le Boeuf, D.P. Costa, P.L. Tyack, and S.B. Blackwell. 1996. Onboard acoustic recording from diving northern elephant seals. J Acoust Soc Am. 100:2531-2539

Irvine, A.B., M.D. Scott, R.S. Wells, and H.J. Kaufmann. 1981. Movements and activities of the Atlantic bottlenose dolphin (*Tursiops truncates*) near Sarasota, Florida. Fish Bull. 79:671-688.

Jefferson, T.A. and B.E. Curry. 1996. Acoustic methods of reducing or eliminating marine mammal—fishery interactions: Do they work? Ocean & Coastal Management. 31:41-70.

Jepson, P.D., M. Arbelo, R. Deaville, I.A.P. Patterson, P. Castro, J.R. Baker, E. Degollada, H.M. Ross, P. Herráez, A.M. Pocknell, F. Rodríguez, F.E. Howie, A. Espinosa, R.J. Reid, J.R. Jaber, V. Martin, A.A. Cunningham, and A. Fernández. 2003. Was sonar responsible for a spate of whale deaths after an Atlantic military exercise? Nature. 425:575–576.

Johnson, M.P., P.L. Tyack, W.M.X. Zimmer, P.J.O. Miller, and A. D'Amico. 2001. Acoustic vocalizations and movement patterns of a tagged sperm whale (*Physeter macrocephalus*) during foraging dives. Abstract. Presented at the 14th Biennial Conference on the Biology of Marine Mammals, Vancouver, BC, Canada.

Johnson, S.R., J.J. Burns, C.I. Malme, and R.A. Davis. 1989. Synthesis of information on the effects of noise and disturbance on major haulout concentrations of Bering sea pinnipeds. OCS Study MMS 88-0092. Report from LGL Alaska Research Associates, Inc. for U.S. Minerals Management Service, Anchorage, AK NTIS PB89-191373.

Jones, M.L. and S.L. Swartz. 1984. Demography and phenology of gray whales and evaluation of whale-watching activities in Laguna San Ignacio, Baja California Sur, Mexico. In: The Gray Whale (*Eschrichtius robustus*), eds. M.L. Jones, et al., pp. 309-374. Orlando, FL: Academic.

Jouventin, P., T. Aubin, and T. Lengagne. 1999. Finding a parent in a king penguin colony: The acoustic system of individual recognition. Anim Behav 57:1175–1183.

Ketten, D.R., J. Lien, and S. Todd. 1993. Blast injury in humpback whale ears: evidence and implications. J Acoust Soc Am. 94:1849-1850.

Lesage, V., C. Barrette, M.C.S. Kingsley, and B. Sjare. 1999. The effect of vessel noise on the vocal behavior of belugas in the St. Lawrence River Estuary, Canada. Mar Mam Sci. 15:65-84.

LGL and Greeneridge. 1986. Reactions of beluga whales and narwhals to ship traffic and ice-breaking along ice edges in the eastern Canadian High Arctic 1982-1984. Environmental Studies 37. Ottawa, Ontario: Indian and Northern Affairs Canada. 301 pp.

Loughrey, A.G. 1959. Preliminary investigations of the Atlantic walrus [*Odobenus rosmarus rosmarus* (*Linnaeus*)]. Canadian Wildlife Service Wildlife Management Bulletin Series 1, Number 14, 123 pp.

Madsen, P.T. and B. Møhl. 2000. Sperm whales (*Physeter catodon* L. 1758) do not react to sounds from detonators. J Acoust Soc Am. 107:668-671

Madsen, P.T., R. Payne, N.U. Kristiansen, M. Wahlberg, I. Kerr, and B. Møhl. 2002. Sperm whale clicks: bimodal, pneumatic sound production at depth. J Exp Biol. 205:1899-1906.

Malme, C.I., P.R. Miles, P. Tyack, C.W. Clark, and J.E. Bird. 1985. Investigation of the potential effects of underwater noise from petroleum industry activities on feeding humpback whale behavior. BBN Report 5851, OCS Study MMS 85-0019. Report from BBN Laboratories Inc., Cambridge, MA for U.S. Minerals Management Service, NTIS PB86-218385. Bolt, Beranek, and Newman, Anchorage, AK.

Malme, C.I., P.R. Miles, G.W. Miller, W.J. Richardson, D.G. Roseneau, D.H. Thompson, and C.R. Greene, Jr. 1989. Analysis and ranking of the acoustic disturbance potential of petroleum industry activities and other sources of noise in the environment of marine mammals in Alaska. BBN Report 6945, OCS Study MMS 89-0006. Report from BBN Systems and Technological Corporation, Cambridge, MA for U.S. Minerals Management Service, NTIS PB90-188673. Bolt, Beranek, and Newman, Anchorage, AK.

Mate, B.R., and J.T. Harvey, eds. 1987. Acoustical deterrents in marine mammal conflicts with fisheries. Oregon State University Sea Grant College Program, ORESU-W-86-001. Corvallis, OR. 116 pp.

Maybaum, H.L. 1993. Responses of humpback whales to sonar sounds. J Acoust Soc Am. 94:1848-1849.

Miller, P.J.O., N. Biasson, A. Samuels, and P.L. Tyack. 2000. Whale songs lengthen in response to sonar. Nature. 405:903.

Miksis, J.L., M.D. Grund, D.P. Nowacek, A.R. Solow, R.C. Connor, and P.L. Tyack. 2001. Cardiac responses to acoustic playback experiments in the captive bottlenose dolphin (*Tursiops truncatus*). J Comp Psychol A 115:227-232.

Moore, P.W.B., and W.W.L. Au. 1975. Underwater localization of pulsed pure tones by the California sea lion *Zalophus californianus*. J Acoust Soc Am. 58:721-727.

Morton, A.B., and H.K. Symonds. 2002. Displacement of *Orcinus orca* (L.) by high amplitude sound in British Columbia. ICES Journal of Marine Science. 59:71-80.

Myrberg, A.A. 1980. Hearing in damsel fishes: an analysis of signal detection among closely related species. J Comp Physiol A 140:135-144.

Myrick, A.C. Jr., E.R. Cassano, and C.W. Oliver. 1990. Potential for physical injury, other than hearing damage, to dolphins from seal bombs used in the yellowfin tuna purse-seine fishery: results from open-water tests. Admin. Rep. LJ-90-08. U.S. National Marine Fisheries Service. La Jolla, CA. 28 pp.

National Research Council (**NRC**). 2000. Marine Mammals and Low-Frequency Sound. Washington, DC: National Academy Press. 146 pp.

National Research Council (**NRC**). 2003. Ocean Noise and Marine Mammals. National Washington, DC: Academy Press. 192 pp.

Payne, R. and D. Webb. 1971. Orientation by means of long range acoustic signaling in baleen whales. Annals of the New York Academy of Sciences. 188:110-141.

Penner, R.H., C.W. Turl, and W.W. Au. 1986. Target detection by the beluga using a surface-reflected path. J Acoust Soc Am. 80:1842-1843.

Renaud, D.L. and A.N. Popper. 1975. Sound localization by the bottlenose porpoise (*Tursiops truncatus*). Journal of Exp Biol. 63:569-585.

Richardson, W.J. and C.I. Malme. 1993. Man-made noise and behavioral responses. In: The Bowhead Whale, eds. J.J. Burns, et al., pp. 631-700. Special Publication No. 2. Lawrence, KS: Society for Marine Mammalogy.

Richardson, W.J., R.A. Davis, C.R. Evans, D.K. Ljungblad, and P. Norton. 1987. Summer distribution of bowhead whales, *Balaena mysticetus*, relative to oil industry activities in the Canadian Beaufort Sea, 1980-1984. Arctic 40:93-104.

Richardson, W.J., C.R. Greene, Jr., W.R. Koski, and M.A. Smultea, with G. Cameron, C. Holdsworth, G. Miller, T. Woodley, and B. Würsig. 1991. Acoustic effects of oil production activities on bowhead and white whales visible during spring migration near Pt. Barrow, Alaska–1990 phase. OCS Study MMS 91-0037. Report from LGL Ltd., King City, Ontario, for U.S. Minerals Management Service, NTIS PB92-170430, Herndon, VA.

Richardson, W.J., C.R. Greene, C.I. Malme, and D.H. Thomson. 1995. Marine Mammals and Noise. San Diego, CA: Academic. 576 pp.

Scharf, B. 1970. Critical bands. In: Foundations of Modern Auditory Theory, ed. J. Tobias, pp. 159-202. New York: Academic Press.

Stewart, B.S., W.E. Evans, and F.T. Awbrey. 1982. Effects of man-made waterborne noise on behavior of beluga whales (*Delphinapterus leucas*) in Bristol Bay, Alaska. HSWRI Technical Report 82-145. Report from Hubbs/Sea World Research Institute, San Diego, CA for the U.S. National Oceanic and Atmospheric Administration, Juneau, AK, 29 pp.

Tilt, W.C. 1985. Whales and whalewatching in North America with special emphasis on the issue of harassment. Yale School of Forestry and Environmental Studies. New Haven, CT, 122 pp. Unpublished.

Todd, S., P. Stevick, J. Lien, F. Marques, and D. Ketten. 1996. Behavioural effects of exposure to underwater explosions in humpback whales (*Megaptera novaeangliae*). Can J Zool. 74:1661-1672.

Tyack, P.L. and C.W. Clark. 1998. Quick-look report: playback of low-frequency sound to gray whales migrating past the central California coast. Unpublished.

Wartzok, D., W.A. Watkins, B. Würsig, and C.I. Malme. 1989. Movements and behaviors of bowhead whales in response to repeated exposures to noises associated with industrial activities in the Beaufort Sea. Report from Purdue University for Amoco Production Company, Anchorage, AK, 228 pp.

Watkins, W.A. 1977. Acoustic behavior of sperm whales. Oceanus 20(2):50-58.

Watkins, W.A. 1986. Whale reactions to human activities in Cape Cod waters. Mar Mam Sci. 2:251-262.

Watkins, W.A. and W.E. Schevill. 1975. Sperm whales (*Physeter catodon*) react to pingers. Deep-Sea Research. 22:123-129.

Watkins, W.A., K.E. Moore, and P. Tyack. 1985. Sperm whale acoustic behaviors in the southeast Caribbean. Cetology. 49:1-15.