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IMPLICATIONS FOR MARINE MAMMALS OF LARGE-SCALE CHANGES IN THE MARINE ACOUSTIC ENVIRONMENT

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The amount of underwater sound from ship traffic, commercial, research, and military sound sources has increased significantly over the past century. Marine mammals and many other marine animals rely on sound for short- and long-range communication, for orientation, and for locating prey. This reliance has raised concern that elevated sound levels from human sources may interfere with the behavior and physiology of marine animals. The dominant source of human sound in the sea stems from propulsion of ships. Shipping noise centers in the 20- to 200-Hz band. Frequencies this low propagate efficiently in the sea, and shipping has elevated the global deepwater ambient noise 10- to 100-fold in this frequency band. Baleen whales use the same frequency band for some of their communication signals, and concern has been raised that elevated ambient noise may reduce the range over which they can communicate. Marine mammals have a variety of mechanisms to compensate for increased noise, but little is known about the maximum range at which they may need to communicate. Some of the most intense human sources of sound include air guns used for seismic exploration and sonar for military and commercial use. Human sources of sound in the ocean can disturb marine mammals, evoking behavioral responses that can productively be viewed as similar to predation risk, and they can trigger allostatic physiological responses to adapt to the stressor. Marine mammals have been shown to avoid some human sound sources at ranges of kilometers, raising concern about displacement from important habitats. There are few studies to guide predictions of when such changes start to lower the fitness of individuals or have negative consequences for the population. Although acute responses to intense sounds have generated considerable interest, the more significant risk to populations of marine mammals is likely to stem from less visible effects of chronic exposure.

Key words: ambient ocean noise, effects of noise, marine mammal

There are a variety of ways that anthropogenic sound can affect animals. If detection of a signal is noise-limited, then elevation of noise can reduce the probability of detecting a signal, effectively reducing the range of communication. Within limits, animals may be able to compensate for noise by increasing the level of their own calls, by shifting their signals out of the noise band, by making their signals longer or more redundant, or by waiting to signal until noise is reduced. However, these changes may be costly and may not completely compensate for the noise. If an anthropogenic signal stimulates a disturbance response, then this response may cost the animal in terms of energy and lost opportunities. Sound also may trigger stress responses, which involve other physiological costs. Some sound exposures may be loud enough to make it more difficult for an animal to perform its regular functions. At high exposure levels, sound may even decrease hearing sensitivity, ultimately leading to hearing loss if the exposure is intense enough or long enough.

Most receivers designed to detect distant signals are sensitive enough that they are limited by noise rather than the sensitivity of the receiver. Many sensory systems have evolved remarkable sensitivity for detecting signals in noise. Although the importance of noise for signal detection theory has been recognized in psychophysics since the work of Green and Swets (1966), effects of noise have not been a central topic for behavioral ecology and ethology. This topic is not only an important area for basic research, but as researchers recognize how humans have elevated the ambient noise in many environments, it is becoming an important issue for conservation biology.

Those with a primary interest in animal welfare may focus on the boundaries where brief minor effects may transition to chronic ones, where annoyance turns into suffering, where

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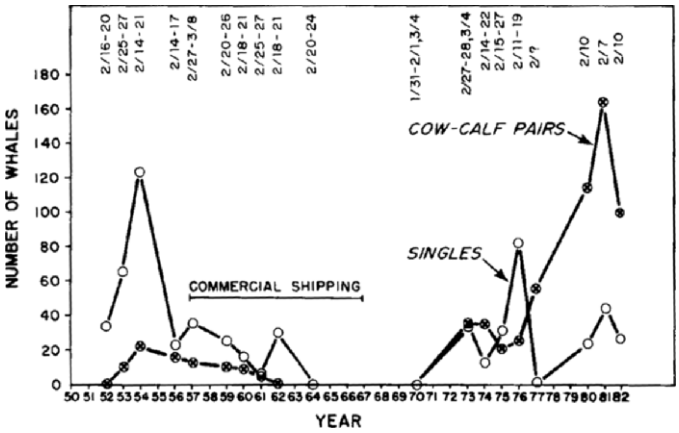

Fig. 1.—Censuses of single gray whales (*Eschrichtius robustus*) and mother–calf pairs in Laguna Guerrero Negro, Baja California, Mexico, from 1952 to 1982, showing numbers of whales before, during, and after commercial shipping and dredging was present in the lagoon. From Bryant et al. (1984).

disturbance prevents an animal from engaging in its normal behavior (Dawkins 2006). But from a conservation perspective, the most important changes are those that affect populations, changes which can be thought of in terms of changes in growth, reproduction, and survival of individuals. Wartzok et al. (2005) argue that science has not advanced to the point where we can predict population consequences of the effects of sound listed in the 1st paragraph. However, acoustic stimuli from human disturbance can pose clear risks when they cause animals to abandon important habitat, or when they reduce the ability of animals to use the habitat. Bryant et al. (1984) combined results from a series of censuses of gray whales (*Eschrichtius robustus*) in one of their primary breeding lagoons in Baja California, Mexico. Fig. 1 shows that large numbers of single whales and moderate numbers of mother–calf pairs were sighted during the early 1950s in this lagoon. From 1957 to 1967 barges were used to transport salt from the lagoon, and the mouth of the lagoon was dredged. Although it is possible that visual or chemical stimuli from this industrial activity could be sensed by the whales, the dominant stimulus likely was the sounds of shipping and dredging. Censuses from 1957 to 1964 show a steady decrease in the number of whales with the exception of a jump in singles in 1 year. By 1964, no whales were reported in the census. For economic reasons, the saltworks closed in 1967. No whales were sighted in 1970 but by 1973 whales began to be counted in censuses, and by the early 1980s the lagoon was used by more than 100 mother–calf pairs. This review suggests that the sound of shipping and dredging caused gray whales to abandon the lagoon for years after the industrial activity stopped. Gray whales have several major breeding lagoons in Baja California, and the loss of 1 lagoon did not have an obvious impact on the recovery of this population. However, sounds from industrial activity seem to have caused the abandonment of critical habitat from the early 1960s to the early 1970s by a species listed as endangered by the United States from 1970 to 1994. This kind of abandonment of habitat clearly should be avoided, especially for endangered species.

Long-term studies of wild animals can be used to evaluate the long-term effects of human activities, even when the exact factors causing the effect are unknown. Bejder et al. (2006) took advantage of a long-term study of individually identified bottlenose dolphins (*Tursiops*) in Shark Bay, Western Australia, to examine the impact of being followed by vessels used for commercial dolphin watching and research. This study started in 1984 in part to take advantage of provisioned dolphins that since the 1960s have been coming to the shore to be fed. Bejder et al. (2006) divided the study into 3 periods, 1 before the 1st commercial dolphin-watch vessel (T0), 1 with 1 dolphin-watch vessel (T1), and 1 with 2 dolphin-watch vessels (T2). The study itself involved following dolphins in small research vessels, so the influence of the research vessels had to be accounted for as well. Tour vessels operated primarily in 1 site, and it was possible to identify a control site nearby with no commercial dolphin watching and little activity by research vessels. Based upon research records and monitoring of dolphin watches, commercial vessels were estimated to have spent 0, 0.8, and 1.8 h/day in the whale-watching sites during periods T0, T1, and T2, respectively. The values for research vessels were 0.5, 0.4, and 0.8 h/day for the same site and periods. In the adjacent control site, there was no commercial dolphin watching and research vessels spent 0.006, 0.04, and 0.1 h/day during periods T0, T1, and T2. There was no change in dolphin abundance from T0 to T1, but the abundance of dolphins showed a significant decline from T1 to T2 of 15%/km^2, whereas there was a slight (9%/km^2) increase in abundance in the control site. Allen and Read (2000) showed that dolphins will move away from foraging habitats when vessel traffic is heavy. Bejder et al. (2006) suggest that their results represent a long-term shift in habitat use because of vessel traffic. Their paper demonstrates that even ''benign'' human activities supported by environmentalists as economic alternatives to whaling (Hoyt 1993) may harm cetacean populations by disrupting behavior and causing abandonment of local habitats.

There has been growing appreciation that anthropogenic noise may affect terrestrial animals, but because of the physics of sound propagation underwater, effects of noise are likely more important in aquatic environments. Sound propagates so much better than light in water that many aquatic animals have evolved ways to use sound to communicate and orient. Toothed whales have evolved a sophisticated biosonar that they use to find and select prey (Au 1993; Johnson et al. 2004; Madsen et al. 2005). For sound to reflect energy efficiently from a rigid target, the wavelength of the sound must be less than or equal to the circumference of the target (Tyack 1998). Sound travels in the water at nearly 1,500 m/s, which means that the wavelength to match a roughly 0.15-m circumference would have a corresponding frequency of 10 kHz or higher, and that for a 0.015-m circumference would be 100 kHz or higher. Toothed whales evolved high-frequency echolocation systems that can detect prey sized less than 1 m at ranges of tens to hundreds of meters (Madsen et al. 2007). Echoes from larger targets such as the sea surface and seafloor can be detected at round-trip ranges of kilometers with some of the most intense and low-frequency echolocation signals of toothed whales,

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such as those of the sperm whale (Tyack 1997; Zimmer et al. 2005). The size of toothed whales is consistent with their demonstrated capabilities to produce directional sounds and to hear with good directionality at their echolocation frequencies.

In contrast with toothed whales (Odontoceti), baleen whales (Mysticeti) have evolved communication signals that emphasize low frequencies. Baleen whales are the largest of animals, so have the capacity for large enough sound production systems to generate sounds with long wavelengths and low frequencies. Baleen whales need low-frequency calls for long distance communication because they are both social and highly mobile. Many baleen whales have annual migrations of thousands of kilometers, and some species may disperse into low-latitude oceans during the breeding season. It is common for a migrating baleen whale to swim more than 100 km in a day (Mate et al. 1998). This puts a premium on the capability for long-distance communication in these social oceanic animals, where sound is the only way to communicate at ranges greater than tens of meters.

Baleen whales can use low-frequency sound for long-distance communication because of a specific feature of how sound propagates in the ocean. As sound passes through seawater some of the acoustic energy is absorbed, and the higher the frequency, the more sound energy is lost through absorption (Urick 1983). A 20-Hz sound would have to travel more than 10,000 km before half of the sound energy was absorbed, whereas a 40-kHz sound would only have to travel about 300 m before the same halving of energy. This means that if a whale was communicating with another whale hundreds of kilometers away, the lower the frequency, the less sound energy it would take to deliver the same signal at the receiver.

The lowest frequency whale calls come from whales that disperse into low-latitude oceans during their winter breeding seasons (Tyack 1986). Blue whales (*Balaenoptera musculus*) produce calls with fundamental frequencies from 8 to 25 Hz that can last more than 10 s (Stafford et al. 1998), and finback whales (*B. physalus*) produce calls with fundamental frequencies near 15–30 Hz and durations of near 1 s (Watkins et al. 1987). In a path-breaking paper, Payne and Webb (1971) used the standard theory of how sound propagates underwater (e.g., described by Urick 1983) to argue that these 20-Hz calls would have been audible at ranges of 1,000 km or more, and in some propagation conditions, audible across whole ocean basins. Although Northrop et al. (1968) used a bottom-mounted array of hydrophones to detect 20-Hz calls at ranges reported to be >160 km, there was some skepticism in the 1960s and 1970s about the ability of whales to communicate over such huge ranges. More recently, use of the United States Navy's sound surveillance system has routinely demonstrated detection of blue and finback calls at ranges of hundreds of kilometers (Stafford et al. 1998; Watkins et al. 2000).

Does Shipping Noise Interfere with Communication by Marine Mammals?

An important point raised by Payne and Webb (1971) was that changes in the ambient noise in the ocean could have a significant effect on the range at which low-frequency whale calls could be detected. As humans introduced motorized shipping over the past century, the machinery and propulsion noise of ships has caused a remarkable change in the global ambient noise of the deep ocean. Fig. 2 shows a set of typical levels for deep-ocean ambient noise measured during the 1960s (Urick 1983). Above about 200 Hz, the ambient noise is affected mainly by sea state, which is driven by wind speed. For normal variations in wind speed, the ambient noise from 200 to 10,000 Hz can vary by at least 20 dB or a factor of 100 in terms of energy level. This natural variation was part of the acoustic environment in which marine animals evolved their hearing capacity. However, between 20 and 200 Hz, the ambient noise in the modern ocean is driven by the propulsion sound of ships, and this level is increasing (Ross 2005). The various curves in this frequency region of Fig. 2 represent parts of the ocean with differing intensities of shipping. Pause a moment to reflect that ships put enough acoustic energy into this frequency band to raise the global ambient sound level in all of the oceans on our planet. To me it is surprising that an unintentional by-product of shipping could have such a global impact. As in the case of gases we introduce unintentionally into the atmosphere, it would be prudent to consider how we are changing our planet and to manage the negative consequences.

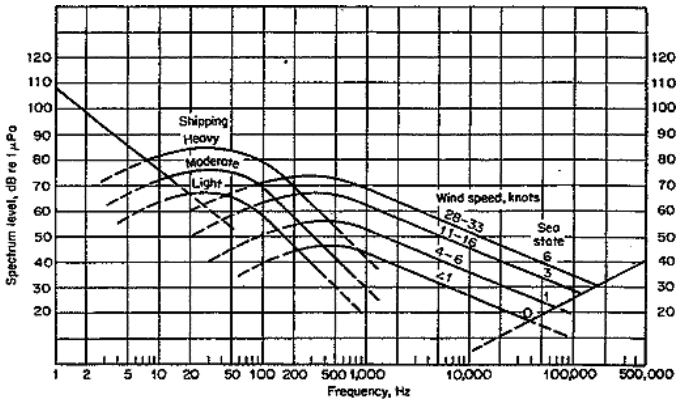

Fig. 2.—Average deep-sea noise levels as measured during the 1960s. The noise below about 20 Hz has natural causes. Shipping noise dominates the ambient noise from about 20 to 200 Hz. From 200 Hz to about 100 kHz, noise stems primarily from wind and waves. From Urick (1983).

Payne and Webb (1971) suggested that the introduction of shipping noise could reduce the range over which finback whales could communicate with their 20-Hz signals. They calculated a minimum detection range assuming poor sound-propagation conditions of 90 km for finback calls at 20 Hz, with a noise level corresponding to moderate shipping in Fig. 2, and a range of about 280 km for a noise value corresponding to a preshipping ocean consistent with light shipping in Fig. 2, which is a relatively high value for natural ambient noise at 20 Hz judging by the figure. Low-frequency sound can travel very efficiently when it refracts in a deep-ocean sound channel. With this kind of propagation, Payne and Webb (1971) calculated a detection range of 1,000 km for finback sounds in moderate shipping and 7,000 km in the ocean before motorized shipping.

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More modern acoustic models confirm reliable propagation of 20-Hz calls of finback whales well beyond 400 km (Spiesberger and Fristrup 1990).

The noise estimates of Payne and Webb (1971) derive from the 1960s. Since then, 2 papers have described how noise levels have increased off the California coast since the 1960s. Andrew et al. (2002) measured ambient sound from 1994 to 2001 using an acoustic receiver mounted on the seafloor off Point Sur, California. They compared these sound levels to those measured from the same receiver from 1963 to 1965, and found that noise levels near 20 Hz were elevated by about 10 dB. A similar increase of 10–12 dB was found by McDonald et al. (2006), who compared 2 sets of measurements from the same site: one made in 1964–1966 and the other made in 2003–2004. This elevation in ambient noise would reduce the minimum detection range estimated by Payne and Webb (1971) from 90 km in the 1960s to about 32 km now.

The minimum and maximum detection ranges calculated by Payne and Webb (1971) are generic, and the actual detection range can be calculated with more accuracy for any specific set of propagation conditions (Spiesberger and Fristrup 1990). The general point is that the increase in ambient noise from shipping seems to have reduced the detectable range of low-frequency whale calls from many hundreds of kilometers in the prepropeller ocean down to tens of kilometers in many settings today. This decrease in detection range of whale calls has coincided with the modern period of commercial whaling, when populations of humpback whales in the North Atlantic are estimated to have dropped from as high as 240,000 down to current estimates of 9,300–12,100, and populations of fin whales decreased from 360,000 down to 56,000. (Note that the values for prewhaling population sizes used here are drawn from the population genetic analyses of Roman and Palumbi [2003]. Baker and Clapham [2004] point out that these values are considerably higher than those derived from analysis of whaling records.) The 20-Hz calls of fin whales are reported to be produced by males (Croll et al. 2002; Watkins et al. 1987); the calls are produced primarily during the breeding season (Watkins et al. 1987) and are thought to function as reproductive advertisement displays. If the reduction in these populations of whales increased the typical separation of whales during the breeding season, then this could combine with the reduced range of communication to pose a risk of disrupting breeding behavior, with potential adverse impacts on the recovery of these endangered species (Frisk et al. 2003).

The primary uncertainty about the effect of this reduction in range lies in our ignorance of the typical distance between a signaling whale and important receivers. Watkins and Schevill (1979) used an airplane to follow fin whales, and reported whales swimming 7–10 km to join a foraging group. Tyack and Whitehead (1983) reported a humpback whale to stop singing and swim directly to a surface-active group of whales 9 km away. It is possible, but was not demonstrated, that the approaching whales were responding to calls produced by the whales in these distant groups. Although whales are likely to be able to detect calls at much greater ranges, I am not aware of any studies showing that whales communicate over ranges greater than this. Indeed, short of using acoustic recording tags (Johnson and Tyack 2003) on the receiving whale to record calls of distant whales and response of the receiving whale coupled with long-range acoustic localization of calling whales, it is difficult to imagine how to test whether whales respond to signals at ranges of tens or hundreds of kilometers away.

The costs associated with producing loud calls include the energy required for sound production and the risk that competitors, predators, or parasites may detect the call. These costs suggest that animals should be selected to produce sounds with source levels no higher than required for reliable communication over the ranges typical for important receivers. On the other hand, sexual selection may select for extreme values of advertisement displays. For acoustic displays, theory would suggest the possibility of selection for source levels much higher than required to detect the signal at typical distances of females monitoring song (Brackenbury 1979; Gil and Gahr 2002). These observations create problems for the argument that the required effective range for a signal must be the same as the actual range at which it can be detected by human acoustic sensors.

Do Marine Mammals Alter Their Vocal Behavior to Compensate for Noise?

It is very difficult to test whether elevated ambient noise is preventing an animal from hearing and reacting to a communication signal. The cost of this kind of lost opportunity is not normally included in studies of behavioral disruption, and it is difficult to design ecologically valid studies of this problem. An alternative approach to get at this issue is to ask whether and when animals modify their vocal signals to compensate for changes in noise. Potential mechanisms for increasing the detectability of signals include waiting to call until noise decreases, increasing the rate of calling, increasing signal intensity, increasing signal duration, and shifting signal frequency outside of the noise band. These changes increase costs for signaling, so if animals show systematic use of compensation mechanisms, this would suggest that the noise is compromising effective communication sufficiently to incur the cost of compensation.

There is enough variation in natural sources of ambient noise that it is safe to assume that all animal communication systems evolved under conditions requiring adaptation to noise. For an aquatic example, Fig. 2 shows that wave noise varies as a function of wind speed, with nearly 30-dB difference in the noise level at 1,000 Hz from calm seas to seas associated with 30-knot winds. Sounds of conspecifics or other animals also can dominate the ambient noise in areas where animals are likely to congregate. For another marine example, tiny snapping shrimp (e.g., *Alpheus heterochaelis*) can make a sound by closing a specialized claw. As the claw closes, it causes a bubble to form by cavitation (Versluis et al. 2000). Collapse of this bubble can produce source levels near 220 dB re 1 μPa at 1 m. Other species of snapping shrimp, such as *Synalpheus parneomeris*, can produce an impulse with a source level of about 185 dB re 1 μPa at 1 m and a power of about 3 W (Au and Banks 1998; Ferguson and Cleary 2001). The combined

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effect of large numbers of these tiny animals producing very short signals can elevate the ambient noise in coastal environments by 30 dB in the 25- to 50-kHz frequency band (Widener 1967). Fish and marine mammals can produce similar elevations in ambient noise in different frequency bands (Cato and McCauley 2001). Conspecifics pose a particularly tough source of interference, because their signals usually overlap in frequency and some conspecifics may be intentionally competing with a signaler, attempting to reduce the salience of its calls or songs (Greenfield 1994).

The problem of communicating in a noisy channel is ubiquitous and important enough that it is likely to have created selection pressures for compensation mechanisms in most taxa that rely heavily upon sound for communication or echolocation. One of the simplest mechanisms involves simply waiting to signal until the noise level reduces, or timing vocalizations to minimize overlap with competing transient sounds. These mechanisms for timing calls with respect to interfering noise are well developed in insects (Cade and Otte 1982), anurans (Zelick and Narins 1983), birds (Brumm 2006; Ficken et al. 1974), and mammals (Egnor et al. 2007). Mechanisms for timing signals seem particularly sophisticated when the signalers are competing for attention and the ''noise'' comprises competing signals from conspecifics (Greenfield 1994; Hall et al. 2006). However, this effect has not been well documented for marine mammals. Whether marine mammals can time calls to minimize interference from intermittent noise is of practical importance for interpreting the potential effects of intermittent anthropogenic sound sources.

If the noise level is not changing rapidly enough, and if the animal cannot wait to get a signal through, then it can modify the acoustic structure of calls to compensate for the noise. One of the 1st such compensation mechanisms to be described is an increase in the source level of a vocalization as the noise level increases. This was described by Etienne Lombard in 1911 (Lombard 1911) and is known in psychophysics as the Lombard effect (Lane and Tranel 1971; Pick et al. 1989). Several Old World nonhuman primates (*Macaca nemestrina* and *M. fascicularis*—Sinnott et al. 1975) and New World primates (*Callithrix jacchus*—Brumm et al. 2004; *Saguinus oedipus*—Egnor and Hauser 2006; Egnor et al. 2006) have been demonstrated to increase their source level during exposure to increased levels of noise. The Lombard effect has also been shown for several different bird species, including budgerigars (*Melopsittacus undulatus*—Manabe et al. 1998), Japanese quail (*Coturnix japonica*—Potash 1972), nightingales (*Luscinia megarhynchos*—Brumm and Todt 2002), and zebra finches (*Taeniopygia guttata*—Cynx et al. 1998). More recently several studies have demonstrated that several species of marine mammal in the wild, including beluga whales (*Delphinapterus leucas*—Scheifele et al. 2005) and manatees (*Trichechus manatus*—Miksis-Olds 2006), increase the source level of their calls when in the presence of elevated levels of shipping noise. Manatees are more likely to increase source level in noise when calves are present and animals are dispersed, suggesting context-specific use of this compensation mechanism.

The observation that the Lombard effect in humans and several animal species is strongest for noise in the same frequency band as the vocalization frequency (e.g., Manabe et al. 1998) means that these species sense whether the interfering noise is in-band or not. Some animals respond to band-limited noise by changing the frequencies of their vocalizations to shift away from the noise. Just as some animals can wait to call until after a conspecific calls, avoiding interference in the time domain, so some animals can shift their call away from the frequency of a conspecific call, avoiding interference in the frequency domain. Some bats shift their echolocation calls away from the frequencies of conspecifics nearby; this is called a jamming-avoidance response (Ulanovsky et al. 2004). Serrano and Terhune (2002) have shown that when harp seals (*Pagophilus groenlandicus*) are calling at high rates during the breeding season, calls of different seals often overlap, and during these overlaps seals tend to produce calls that differ in frequency by more than one-third octave, the typical filter bandwidth of mammalian hearing. Terhune (1999) also proposes that Weddell seals (*Leptonychotes weddellii*) separate the pitch of their calls to avoid jamming. Slabbekoorn and Peet (2003) have shown that great tits (*Parus major*) increase the frequency of their songs when in urban noise, which emphasizes low frequencies. Lesage et al. (1999) report a similar increase in the frequency of calls of beluga whales in the presence of low-frequency vessel noise. Parks et al. (2007) document a remarkable long-term change in the frequency band of contact calls of North Atlantic right whales (*Eubalaena glacialis*) and South Atlantic right whales (*Eubalaena australis*), comparing low-noise (1950s or South Atlantic) to high-noise (present or North Atlantic) conditions (Fig. 3a). The average frequencies of these contact calls changed from 70–171 Hz in 1956 to 101–195 Hz in the North Atlantic and from 69–137 Hz in 1977 to 78–156 Hz in 2000 in the South Atlantic. There is no significant difference between the North Atlantic in 1956 and the South Atlantic in 1977, but all other comparisons are highly significant (Fig. 3b). These results suggest that right whales have made long-term changes in the frequencies of their contact calls, apparently to compensate for increasing low-frequency shipping noise. Marine mammals have thus been demonstrated to have the capability to respond immediately to band-limited interference by shifting the frequency of their call and also to gradually shift the frequency of a basic call type in the face of long-term changes in the spectrum of ambient noise.

Several animal taxa have been shown to increase the length of their calls in the presence of prolonged noise. Brumm et al. (2004) showed that the New World monkey the common marmoset (*C. jacchus*) lengthens its calls when exposed to white noise. Foote et al. (2004) have shown that killer whales (*Orcinus orca*) increase the length of their calls when more vessels are present, but they did not measure noise levels directly.

One of the predictions of communication theory (Shannon and Weaver 1949) is that the redundancy of signaling should increase as the channel becomes more noisy. Japanese quail (Potash 1972) and king penguins (*Aptenodytes patagonicus*—Lengagne et al. 1999) increase the number of syllables in their calls with increasing noise. Although nonhuman primates have

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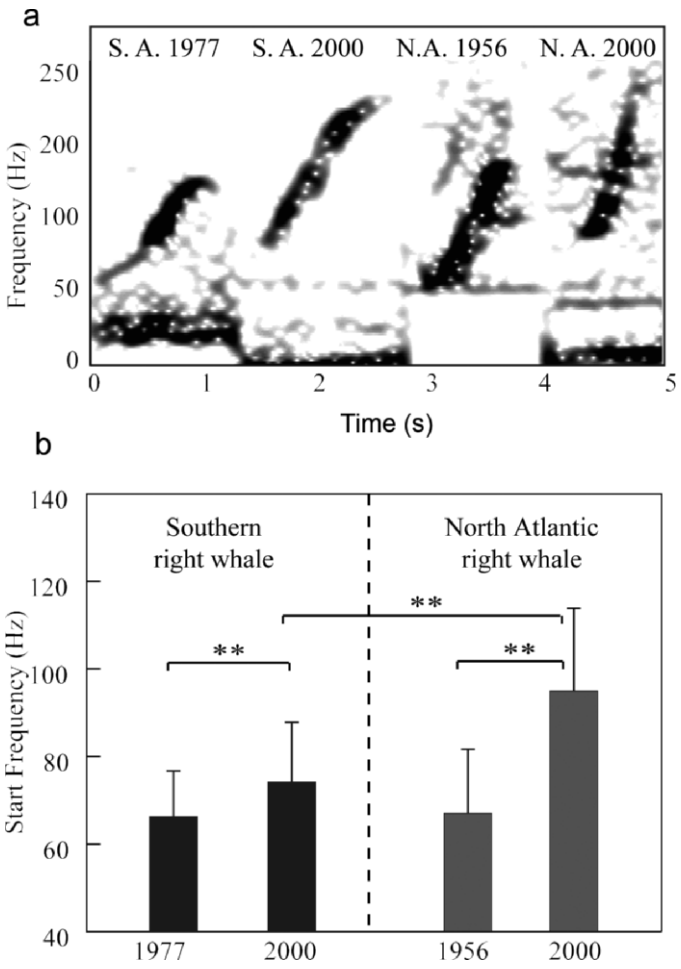

Fig. 3.—a) Spectrograms of representative right whale contact calls from the South Atlantic (S. A.; *Eubalaena australis*) in 1977 and the North Atlantic (N. A.; *Eubalaena glacialis*) in 1956 and 2000. Notice the upward shift in frequency in 2000 that represents almost a full octave change in start frequency. b) Summary of start-frequency differences between species and frequency differences over time for both species. Two asterisks (**) indicate $P < 0.001$; 2-way analysis of variance. From Parks et al. (2007).

not demonstrated such vocal flexibility (Brumm et al. 2004), humpback whales (*Megaptera novaeangliae*) increased the repetitions of phrases in their songs when they were exposed to a low-frequency sonar (Miller et al. 2000). These responses have been interpreted as compensation to increase the ability of receivers to detect and classify signals in a noisy channel. Turnbull and Terhune (1993) have shown that a harbor seal (*Phoca vitulina*) can detect a regular series of calls at a lower signal to noise ratio than a single call alone, providing support on the receiver side for this interpretation.

The preceding review demonstrates that the underwater noise from vessels causes marine mammals to alter the loudness, frequency, duration, and redundancy of their signals. This suggests that vessel noise clearly does interfere with communication in marine mammals. However, there are several important questions that have not been answered: What are the costs of these compensation mechanisms? What are the limits of noise exposure beyond which animals cannot compensate? When does noise so degrade the usefulness of a habitat that animals leave? Can this level be predicted by the compensation behavior? What nonacoustic factors are important in predicting adverse effects of noise—for example, what is the cost of missing a signal, and are animals forced to change their distribution patterns in noise to maintain contact?

Disturbance Responses

As humans have learned to use sound in the ocean, there are increasing sources of noise from depth-sounders, sonars used to find fish or manmade objects, and air guns used to explore geological strata below the seafloor. Most of these sounds are intermittent with low duty cycle, so unlike vessel noise, which is continuous, they provide opportunities for signaling or listening during quiet intersignal gaps. However, many of these intentional sound sources have higher source levels than most vessel-propulsion systems. There have been studies of the impact of some long-term deployments of such sound sources on marine mammals. For example, a low-frequency sound source used for research (the Acoustic Thermometry of Ocean Climate or ATOC source) was placed for years off the California coast to study properties of the ocean over sound paths to other parts of the Pacific (The ATOC Consortium 1998). Costa et al. (2003) studied the effects of this sound source on the diving behavior of juvenile northern elephant seals (*Mirounga angustirostris*), which were tagged with acoustic recording tags. Seals did not cease diving near the sound source, but there was a significant correlation between sound-pressure level measured at the seal and the descent rates of the diving seals.

Many other observational studies such as that described above have demonstrated statistically significant changes in behavior during exposure to anthropogenic sounds, but it has proved difficult to interpret the long-term effects of such changes with purely descriptive studies that lack a theoretical framework for disturbance behavior. As an example of such a framework, avoidance responses can be evaluated in terms of loss of habitat. For example, Morton and Symonds (2002) surveyed killer whales in British Columbia, Canada, to evaluate avoidance of acoustic harassment devices that were placed for many years near fish farms in an attempt to keep marine mammals from depredating the fish. They used preexposure data from 1985 to 1992, exposure data from 1993 to 1998, and postexposure data from 1999 to 2000. The estimated avoidance ranges were approximately 4 km. Olesiuk et al. (2002) conducted a similar but shorter-term study in which they shut down acoustic harassment devices for 3 weeks and then activated them for three 3-week intervals over a period of 18 weeks. Comparing the number of sightings when the acoustic harassment devices were active versus silent, only 8.1% of the expected number of sightings was observed at distances ranging from 2.5 to 3.5 km. Even fewer porpoises were sighted closer to the active device. The avoidance must have extended well beyond the maximum sighting range of 3.5 km. The effect of such a habitat reduction can be estimated by comparing

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the quality and area of habitat lost versus the quality and area of habitat still available, but ultimately the effect must be measured directly in the population.

What are the Consequences to Individuals and Populations of Disturbance Responses?

Many descriptive studies assume that the intensity of response is a good predictor of the population consequences of disturbance. Gill et al. (2001) caution that there are problems with this assumption. For example, if many habitats are available to a population when their habitat is disturbed, then more animals may move than if no other habitats are available. But the decrease in fitness from moving in the 1st case may be lower than the cost of not being able to move in the 2nd. Similarly, if an animal is in bad enough condition that the risk of altering behavior is high, then it may be less likely to show a disturbance response. For example, a starving animal might not move out of a prime feeding area as disturbance increased, well after the exposure that might cause a well-fed animal to move. In this case, the least-vulnerable animals may be the 1st to respond.

Frid and Dill (2002) suggest that behavioral ecological theories about how animals should balance the benefits of antipredator behavior against the costs of responding may be a useful way to view responses to anthropogenic disturbance. They point out that many sources of human disturbance involve stimuli that are approaching the animal, often with increasing and ultimately high stimulus values. Such stimuli are likely to trigger a general antipredator response. Viewing disturbance in terms of antipredator behavior is likely to be particularly useful for intense sources of sound that move in a way that might trigger responses similar to antipredator behavior. Zimmer and Tyack (2007) point out that 1 explanation for mass strandings of beaked whales that coincide with sonar exercises is that the sonars have fundamental frequencies well outside of the frequency band of the whales' own signals, but that are quite similar to the calls of killer whales. In this case it may literally be more appropriate to call the response an antipredator response rather than simple disturbance.

Research on responses of prey to predators suggests that antipredator responses such as vigilance, escaping capture, and avoiding habitats not only impose costs in terms of time and energy, but also costs in terms of lost opportunities. These costs may reduce immediate risk of predation, but may influence the fitness of individuals and the dynamics of populations. For example, during the spring, pink-footed geese (*Anser brachyrhynchus*) feed before nesting. When undisturbed, geese increased their body mass and had a 46% breeding success, whereas in nearby areas where farmers scared them off their fields, they did not gain mass and had a breeding success of only 17% (Madsen 1995). Goss-Custard et al. (2006) used behavioral modeling to predict how much disturbance it would take to reduce the fitness of oystercatchers (*Haematopus ostralegus*) wintering on tidal flats where they feed. The model assessed the energy required for a bird to fly up when a shellfishing human arrived, time lost before resumption of feeding, and the cost of exclusion from the disturbed area. These results suggest that during bad times, a lower level of disturbance may be required to decrease fitness than during good times.

McEwen and Wingfield (2003) point out that all organisms must gather energy for growth and reproduction throughout their life cycle, and that organisms must retain reserves for predictable changes such as seasons, and challenges that are less predictable such as disturbance, predation pressure, or social conflict. McEwen and Wingfield (2003) use the balance between energy intake and demand to define the accumulated cost, called the allostatic load, of physiological and behavioral mechanisms that enable allostasis or adaptation to these changes. The word ''allostasis'' is meant to signify mechanisms that allow an organism to regain equilibrium in the face of external challenges, in analogy to the use of ''homeostasis,'' which represents mechanisms to maintain internal equilibrium in the face of internal changes. When energy demand outpaces the intake, animals may activate a survival mode that may increase energy available, reduce energy demand, or both, to regain energy balance. McEwen and Wingfield (2003:5) discuss how human disturbance can activate the glucocorticosteroid hormone system to stimulate a suite of changes that can help the animal deal with the challenge:

> Free-living animals responding to storms, change in social status, or human disturbance that result in reduced access to resources such as food and shelter increase glucocorticosteroid secretion to facilitate foraging and promote gluconeogenesis (especially from muscle). There is also an inhibition of processes not essential for survival (e.g., reproduction), an increase in activity associated with moving away from the perturbation or finding shelter, and promotion of night restfulness with a savings in energy (e.g., Wingfield 1994; Wingfield and Ramenofsky 1999; Wingfield et al. 1998).

McEwen and Wingfield (2003) make 2 critical points about allostasis with regard to disturbance. First, although these mechanisms help an animal deal with a transient stressor, they can cause problems in the case of exposure to a chronic stressor. Romano et al. (2004) showed that the level of catecholamines in trained dolphins exposed to loud sounds increased the louder the sound was, and that the levels of aldosterone (a corticoid hormone important in marine mammals) increased after exposure to noise. This study only looked at exposures to a single pulsed sound per day. It is not known whether chronic exposure to continuous noise, such as that from ships, causes chronic allostatic stress. However, long-term changes in relevant physiological parameters were measured over the 25-week experimental period of the study of Romano et al. (2004). Second, there are some seasons or phases of the life cycle when animals have less of a reserve and are more vulnerable to the impact of a stressor. For example, if a baleen whale is stressed at the end of the feeding season when it is just about to migrate, it may have plenty of energy reserves to deal with the stress. But if the same whale is confronted with the same stress after migrating and fasting for 9 months, it may not have sufficient reserves to deal with the stress. Similarly if a female baleen whale is stressed after several years of building

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up energy reserves for reproduction, she may be better able to deal with a stressor than after giving birth and lactating for half a year while fasting during migration. These observations suggest a logic for selecting the most vulnerable animals as subjects for a studies designed to understand the effects of disturbance.

Wartzok et al. (2005) argue that a major scientific effort is required to be able to predict long-term effects on marine mammal populations from behavioral and physiological effects of anthropogenic noise on individual marine mammals. The least certain element of the science required to solve this problem involves estimating the consequences of changes in behavior on survival, growth, and reproduction of individuals. This review of how noise may influence communication suggests the importance of some areas of research that have received less attention than observation of disturbance. The theories of predator risk and allostasis may help to provide a framework for progress in understanding the consequences to individuals and populations of disturbance caused by anthropogenic sound.

Resumen

El ruido emitido por el tráfico de embarcaciones comerciales, de investigación y militares se incrementó de manera significativa en el siglo pasado. Los mamíferos y otros animales marinos dependen del sonido para comunicarse a corta-larga distancia y para localizar a sus presas. Esto ha provocado preocupación ante los niveles de ruido emanados de fuentes humanas que pueden estar interfiriendo con la conducta y fisiología de los mamíferos marinos. La principal fuente emisora de ruido humano son las propelas que impulsan a las embarcaciones, este ruido se encuentra dentro de la banda de los 20–200 Hz. Estas bajas frecuencias se propagan eficientemente en el mar y la actual navegación tan intensa ha elevado el ruido ambiental global en una magnitud de 10 a 100 veces en este espectro. Las ballenas usan la misma banda de frecuencia para comunicarse por lo que la preocupación actual se centra en si los elevados niveles de ruido pueden reducir el campo de alcance de sus señales e interferir en su comunicación. Los mamíferos marinos cuentan con una variedad de mecanismos que compensan este incremento en los niveles de ruido, pero poco se conoce acerca de la distancia necesaria para establecer comunicación. Algunas de las fuentes humanas emisoras de ruido marino incluyen las pistolas de aire usadas en las exploraciones sísmicas y los sonares empleados tanto por la milicia como comercialmente. Estas fuentes intermitentes también pueden alterar la mastofauna marina y evocar respuestas conductuales que pueden derivar en riesgo de depredación y que pueden desencadenar respuestas fisiológicas alostáticas para adaptarse al estrés. Se ha observado que los mamíferos marinos evaden las fuentes emisoras de sonidos por varios kilómetros, lo cual eleva las preocupaciones acerca del desplazamiento de la fauna de hábitats importantes. Existen estudios para guiar las predicciones de cuándo estos cambios comienzan a mermar la adecuación de los individuos o a tener consecuencias negativas en la población. Aunque respuestas agudas y contundentes ante los sonidos intensos han generado un interés considerable, el mayor riesgo para las poblaciones de mamíferos marinos puede recaer en los efectos menos visibles como la exposición crónica.

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