

The impacts of anthropogenic ocean noise on cetaceans and implications for management

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Abstract: Ocean noise pollution is of special concern for cetaceans, as they are highly dependent on sound as their principal sense. Sound travels very efficiently underwater, so the potential area impacted can be thousands of square kilometres or more. The principal anthropogenic noise sources are underwater explosions (nuclear and otherwise), shipping, seismic exploration by mainly the oil and gas industries, and naval sonar operations. Strandings and mortalities of especially beaked whales (family Ziphiidae) have in many cases been conclusively linked to noise events such as naval maneuvers involving tactical sonars or seismic surveys, though other cetacean species may also be involved. The mechanisms behind this mortality are still unknown, but are most likely related to gas and fat emboli at least partially mediated by a behavioral response, such as a change in diving pattern. Estimated received sound levels in these events are typically not high enough to cause hearing damage, implying that the auditory system may not always be the best indicator for noise impacts. Beaked whales are found in small, possibly genetically isolated, local populations that are resident year-round. Thus, even transient and localized acoustic impacts can have prolonged and serious population consequences, as may have occurred following at least one stranding. Populations may also be threatened by noise through reactions such as increased stress levels, abandonment of important habitat, and "masking" or the obscuring of natural sounds. Documented changes in vocal behavior may lead to reductions in foraging efficiency or mating opportunities. Responses are highly variable between species, age classes, behavioral states, etc., making extrapolations problematic. Also, short-term responses may not be good proxies of long-term population-level impacts. There are many examples of apparent tolerance of noise by cetaceans, however. Noise can also affect cetaceans indirectly through their prey. Fish show permanent and temporary hearing loss, reduced catch rates, stress, and behavioral reactions to noise. Management implications of noise impacts include difficulties in establishing "safe" exposure levels, shortcomings of some mitigation tools, the need for precaution in the form of reducing noise levels and distancing noise from biologically important areas, and the role of marine protected areas and monitoring in safeguarding cetaceans especially from cumulative and synergistic effects.

Résumé : La pollution de l'océan par le bruit est d'importance particulière pour les cétacés parce qu'ils dépendent fortement de leur ouïe comme sens principal. Comme le son se transmet très efficacement sous l'eau, la zone potentielle d'impact peut représenter des milliers de kilomètres carrés ou plus. Les principales sources anthropiques de bruit sont les explosions sous-marines (nucléaires et autres), la navigation, l'exploration sismique par les industries pétrolière et gazière et les opérations navales avec sonar. Dans plusieurs cas, il a été possible de relier de manière probante des échouages et des mortalités, particulièrement de baleines à bec (la famille Ziphiidae) (bien que d'autres espèces puissent aussi être impliquées), à des événements de bruit, tels que des manoeuvres navales avec utilisation de sonars tactiques ou des inventaires sismiques. Les mécanismes responsables de cette mortalité restent encore inconnus, mais ils sont très vraisemblablement reliés à des embolies gazeuses ou lipidiques causées au moins en partie par une réaction comportementale, telle qu'un changement de patron de plongée. Les intensités estimées des sons perçus lors de ces événements ne sont normalement pas assez élevées pour causer un dommage à l'ouïe, ce qui fait que le système auditif peut ne pas toujours être le meilleur indicateur de l'impact du bruit. Les baleines à bec forment de petites populations locales, peut-être isolées génétiquement, qui restent sur place à l'année. Ainsi, même des impacts acoustiques passagers et localisés peuvent avoir des conséquences sérieuses et prolongées; un tel phénomène a pu survenir lors d'au moins un échouage. Le bruit peut aussi menacer les populations par l'intermédiaire de réactions telles qu'un accroissement des niveaux de stress, l'abandon d'un habitat important et le masquage ou la réduction des sons naturels. Les changements observés dans le comportement vocal peuvent entraîner une diminution de l'efficacité de la recherche de nourriture ou des occasions d'accouplement. Les réactions varient considérablement en fonction des espèces, des classes d'âge, des états comportementaux, etc., ce qui rend les extrapolations difficiles à faire. De plus, les réactions à court terme ne représentent peut-être pas bien les impacts à long terme à l'échelle de la population. Il y a, cependant, plusieurs exemples de tolérance apparente au bruit chez les cétacés. Le bruit peut aussi affecter les cétacés indirectement à travers leurs proies. En présence de bruit, les poissons souffrent

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de perte permanente ou temporaire de l'ouïe; ils ont des taux de capture réduits, du stress et des réactions comportementales. Les problèmes de gestion des impacts du bruit incluent la difficulté d'établir des niveaux « sécuritaires » d'exposition, les limites de certains outils de mitigation, les précautions nécessaires pour protéger les zones d'importance biologique en réduisant l'intensité du bruit et en éloignant les sources de bruit, ainsi que les rôles des zones de protection marine et du monitoring dans la protection des cétacés particulièrement des effets cumulatifs et synergiques du bruit.

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Introduction

Pollution can be defined as the release of a potentially harmful chemical, physical, or biological agent to the environment as a result of human activity (e.g., Johnston et al. 1996). Most people think of pollution as referring to chemical or biological contaminants. However, thermal sources from the generation of power, for instance, can be a form of pollution, as can man-made or anthropogenic noise. In fact, the 1982 United Nations Convention on the Law of the Sea includes the word “energy” to define “pollution of the marine environment,” as in “the introduction by man, directly or indirectly, of substances or energy into the marine environment . . . which results or is likely to result in such deleterious effects as harm to living resources and marine life . . .” (article 1.1.4). Energy in this context can include both thermal and acoustic or noise pollution (Dottinga and Oude Elferink 2000).

Acoustic pollution is of special concern for cetaceans (whales, dolphins, and porpoises), known to be a very vocal taxonomic group, as they are highly dependent on sound not only as their principal sense, but in critical areas of their social and sensory biology (Tyack and Miller 2002). Indeed, most marine species such as fish use sound for almost all aspects of their life, including reproduction, feeding, predator and hazard avoidance, communication, and navigation (Popper 2003). In the marine environment, vision is only useful over tens of metres, whereas sound can be heard for hundreds, even thousands, of kilometres.

The potential area impacted by even one noise source can be large. For instance, the US Navy's low-frequency active (LFA) sonar, used to detect submarines, has a potential area of impact (over which received levels of 120 dB¹ and above can be heard) on cetaceans estimated to be around 3.9 million km² (Johnson 2003²), though it is probably audible to cetaceans over a much larger area. Noise from a single seismic survey, used to discover oil and gas deposits under the sea floor, can cover a region of almost 300 000 km², raising noise levels two orders of magnitude (20 dB) higher than normal, continuously for days at a time (International Whaling Commission 2005). Seismic survey noise from eastern Canada measured 3000 km away in the middle of the Atlantic was the loudest part of the background noise heard underwater (Nieukirk et al. 2004). Ocean background noise levels have doubled every decade for the last several decades in some areas, probably as a result of increases in com-

mercial shipping (Ross 1993; Andrew et al. 2002; International Whaling Commission 2005; McDonald et al. 2006).

Ocean noise has been a very controversial issue since it first emerged in the early 1990s, when the wide media coverage of the ATOC (acoustic thermometry of ocean climate) project, since renamed North Pacific Acoustic Laboratory, brought anthropogenic noise to public attention. This basin-scale project sent loud sounds from underwater speakers off California and Hawai'i to receivers as far away as New Zealand (10 500 km away) to study ocean climate and thus global warming. After public opposition, the California sound source, first located in the Monterey Bay National Marine Sanctuary, was moved outside of the Sanctuary boundaries and finally removed after a few years of operation, but the Hawai'i source, off Kaua'i, continues to operate.

Since then, much louder sources of sound have further raised concern over the issue of undersea noise. A series of beaked whale (family Ziphiidae comprising 20 species) strandings that has occurred together with military sonar operations have recently come to light (e.g., Frantzis 1998; National Oceanographic and Atmospheric Administration and US Department of the Navy 2001; Jepson et al. 2003; Fernández et al. 2005), though the first published record that connected beaked whale strandings to military events dates back to 1991 (Simmonds and Lopez-Jurado 1991).

While such strandings can be acutely fatal, potential chronic effects also are cause for concern. Increased stress levels, abandonment of important habitat, and “masking” or the obscuring or interference of natural sounds are some of the ways populations may be threatened by noise. Such population-level effects are, however, particularly hard to detect in cetaceans, where only a handful of the approximately 84 species have population estimates that are more precise than $\pm 40\%$ (Whitehead et al. 2000). The percentage of serious population declines that would not be detected in cetaceans ranged from 72% to 90% with current monitoring effort (Taylor et al. 2007). This level of uncertainty and difficulty in conclusively documenting population-level effects has contributed to much of the controversy surrounding the impacts of noise on cetaceans. However, noise has been thought to at least contribute to some species' declines or lack of recovery (National Marine Fisheries Service 2002; Weller et al. 2006a, 2006b; International Whaling Commission 2007).

The lack of a definitive cause-and-effect relationship link-

¹ Decibel levels throughout the paper are given as re 1 μ Pa and source levels as re 1 μ Pa at 1 m. Mostly, these will be root-mean-square (rms) values unless otherwise stated. Received levels generally diminish with distance from the source and represent the sound level at the animal.

² J.S. Johnson. 2003. SURTASS LFA environmental compliance experience. Presentation at ECOUS (Environmental Consequences of Underwater Sound), San Antonio, Texas, 12–16 May 2003.

ing stressors to population-level effects is not restricted to the noise issue. Even environmental contaminants known to be harmful to cetaceans seldom produce incontrovertible population impacts, as such connections are difficult to establish in wild cetaceans (O'Hara and O'Shea 2005). As with beaked whale noise-induced strandings, acute, high-dose episodes of contamination demonstrate clearer links to environmental threats than more insidious, sublethal impacts such as deaths occurring over months or gradual reproductive dysfunction in the form of decreased neonatal survival over years or decades (O'Hara and O'Shea 2005). Yet, the latter impact may be more serious than the former.

This review will mainly attempt to synthesize current knowledge on ocean noise impacts on cetaceans and will critically evaluate some of the arguments put forth regarding this issue. Also, the potential population consequences of noise will be discussed, along with which management measures might be most successful in protecting cetaceans and their habitat. In this review, I will only briefly list the main sources of noise, both natural and anthropogenic, as other reviews cover this topic more than adequately (e.g., Hildebrand 2005). I will, however, contrast natural with anthropogenic noise sources, since such biologically important distinctions are often overlooked, which can cause much confusion and misleading conclusions. I will provide a brief overview of cetacean sound production and hearing, and then concentrate on the topic of the impacts of anthropogenic underwater noise on cetaceans. A significant section is devoted to noise-induced strandings and mortalities, with a focus on the beaked whale family, which seems particularly vulnerable to acoustic impacts. Here, I will discuss the history of such strandings, the possible extent of the problem, some proposed mechanisms of injury, and the possible consequences on populations. Other noise impacts are then reviewed, including hearing impairment, blast injury, masking, and some consideration of the possible effects noise might have on the auditory development of young animals. I will address the various behavioral reactions to noise, such as changes in vocal behavior, displacement from important habitat and avoidance, migration route deflections, and stress, and review the variability of such responses. Apparent tolerance of noise is also discussed, along with the critical issue of whether responses, if observed, are biologically significant. Here, I will review some of the literature on human disturbance of wildlife and consider the difficulty of using short-term reactions to ascertain long-term impacts. Also, there is a short overview of some indirect effects of noise on cetaceans, specifically, the reactions of prey species to noise. Finally, I will consider the management implications of noise impacts, including the difficulties in establishing "safe" exposure levels, the shortcomings of some mitigation tools, the need for precaution in the form of reducing noise levels and distancing noise from biologically important areas, and the role of marine protected areas and monitoring in safeguarding cetaceans from especially cumulative and synergistic effects.

This review is different from the recent review by Nowacek et al. (2007) in that I do not limit myself to research in which noise exposure levels at the animal are known or estimated. I do not agree with Nowacek et al. (2007) that "... [received levels] are critical to the interpretation of the

animal(s) responses or lack thereof." Certainly knowing the levels of noise at the animal is helpful, but many other, more important factors come into play, such as the animal's perception of the sound (including nonauditory effects), how well it can deal with the potential masking effects of the noise (by not only detecting signals of interest over the noise, but distinguishing important content in the signal), the context of the sound, the cumulative and synergistic effects of several noise sources and (or) other threats, and, critically, the possible long-term impact on the population. Nowacek et al. (2007) give the latter lip-service but no real treatment in their review. Nowacek et al. (2007) claim that management of noise cannot be undertaken without knowledge of sound exposure levels, stating that this would be like reporting responses of humans to drug trials without knowing the dosage received. Again, I agree that exposure information would be helpful, but many drug responses in humans are, in fact, uncovered by long-term epidemiological studies, rather than by research on acute reactions to particular dosages. Without knowledge of a patient's history, lifestyle, condition, etc., mere information on dosage will very much limit the validity of any conclusions drawn. Cetaceans are difficult enough to study, and the scientific literature is therefore sparse enough, without restricting oneself to an even narrower segment of it. Moreover, there are countless examples of individuals of even the same species receiving the same exposure levels of noise, yet reacting differently (e.g., Nowacek et al. 2004). In some circumstances, cetaceans also seem to react to the change in received level, rather than the received level per se, or whether a noise source is approaching the animal or not. Clearly, dosage is not the only, or possibly even the most important, factor to consider in noise impact studies.

As the ultimate objective of this review is to increase knowledge and understanding of the impacts of noise on cetaceans in the hopes of furthering their protection and management, I will be viewing anthropogenic sound from the point of view of the cetacean. Thus, unlike Nowacek et al. (2007), I will generally assume that human additions of sound into the marine environment are indeed perceived by cetaceans as noise, i.e., are unwanted, in the same way that a sonar operator legitimately views cetacean calls as "biological noise". Also, unlike Nowacek et al. (2007), who "... do not aim to assess the intentions of producers of anthropogenic sound ...", I will assume that noise producers do not intend to harass or harm cetaceans. I will assume that they simply want to get a job done.

Sources of ocean noise

There are many sources of natural and anthropogenic noise in the marine environment. They vary according to sound characteristics such as frequency (pitch), amplitude (loudness), duration, rise time (time required to reach maximum amplitude), directionality (the width of the broadcasted "beam"), duty cycle (percentage of time a sound is transmitted), and repetition rate. Natural noise sources include undersea earthquakes, volcanic eruptions, and lightning strikes on the water surface, in addition to biotic noise sources from snapping shrimp (family Alpheidae), fish, and marine mammals. High wind speed causing breaking waves

(Wilson et al. 1985) and precipitation (Nystuen and Farmer 1987) can contribute substantially to natural ocean noise. Anthropogenic ocean noise is mainly the result of underwater explosions (nuclear and otherwise), seismic exploration (undertaken by the oil and gas industries to find mineral deposits and by geophysicists to study the ocean floor), naval sonar operations, and shipping. When comparing the total energy output per year (in joules) of these various noise sources, 2.1×10^{15} J is the contribution from nuclear explosions and ship-shock trials (explosions used by the Navy to test the structural integrity of their ships), though these are very infrequent, especially nuclear underwater explosions, 3.9×10^{13} J is added from air-gun arrays (seismic exploration), 2.6×10^{13} J is from military sonars, and 3.8×10^{12} J is the contribution from supertankers, merchant vessels, and fishing vessels (Hildebrand 2005). Most commercial vessels or recreational boats use some sort of sonar such as a fish finder or depth sounder. These can be quite loud (150–235 dB; Hildebrand 2005), but most tend to use the higher frequencies (usually >70 kHz) that do not carry as far as low frequencies, and are generally directed in a narrowly focussed downward beam, further limiting their horizontal propagation. Side-scanning sonars are an exception, however. The total energy output of navigational and research sonars is 3.6×10^{10} J (Hildebrand 2005). Obviously, other factors beyond total energy contribution, such as the distribution of these noise sources and how sensitive cetaceans are to them, must also be considered when evaluating their impacts. Drilling, construction, ice breakers, oceanographic experiments, acoustic harassment devices (e.g., to repel marine mammals from aquaculture facilities or fishing nets from which they may steal fish), and recreational boating, among others, also contribute to man-made ocean noise levels (see Hildebrand 2005).

Cetacean sound production

Cetacean vocalizations cover a wide range of frequencies, from the infrasonic calls of the large mysticetes (baleen whales) to the ultrasonic clicks of the odontocetes (toothed whales). In general, the larger the body size, the lower the frequency of calls produced by the cetacean species. Mysticetes produce low-frequency sounds that are mostly around 10–2000 Hz, whereas odontocetes are more mid- and high-frequency specialists, using principally frequencies of 1–150 kHz (Richardson et al. 1995), though some biosonar or echolocation clicks can go as high as 250 kHz (Rasmussen et al. 2004). Whether animals actually use or even perceive these extremely high frequencies of their clicks (>150 kHz) is unclear. High-frequency clicks in general are used by odontocetes to sense their environment and find prey. Sperm whale (*Physeter macrocephalus* L., 1758) clicks can be detected over ranges of almost 10 km (Leaper et al. 1992). Mysticete calls, being lower in frequency, can travel over larger distances of around ≥ 100 km (Payne and Webb 1971). Mysticetes are not thought to use echolocation, though they may gain some general environmental information from their low-frequency calls. On migration, for instance, bowhead whales (*Balaena mysticetus* L., 1758) appear to take evasive action around ice floes well ahead of being able to detect them visually (Ellison et al. 1987; George et al. 1989).

Cetacean hearing

Cetaceans have highly sophisticated auditory systems. Just as cetacean calls span a broad range of frequencies, so too does their hearing. Most odontocetes hear well between 1 and 150 kHz (Dehnhardt 2002). Audiograms are available for only 11 species of odontocetes, out of a total of about 84 cetacean species (Dehnhardt 2002). Moreover, audiograms of those 11 species are usually only based on data from one or a few captive individuals. No audiograms for any mysticete exist, and the sperm whale audiogram is based on one newborn calf. Based on models incorporating call production and inner ear structure, mysticete hearing is thought to range from 5–20 Hz to 20–30 kHz. Uncertainty exists in the sound transmission pathways from the water to the inner ear in cetaceans, which has bearing on how vulnerable cetaceans might be to loud sounds.

Because of the dearth of cetacean audiograms, extrapolations between individuals, species, taxonomic suborders (odontocetes or mysticetes), age classes, captive vs. free-ranging animals, and marine vs. terrestrial animals are often made. Such extrapolations are controversial, especially when used in calculating “safe” exposure levels for cetaceans for the purposes of noise regulation and policy decision-making. When using auditory evoked potential to test the hearing of 62 free-ranging bottlenose dolphins (*Tursiops truncatus* (Montagu, 1821)) from Sarasota Bay, Florida, Cook (2006) found great individual variation in hearing abilities, i.e., up to 80 dB differences in auditory thresholds. She thus concluded that data from individual animals do not accurately represent the entire population and there was a “... need for larger sample sizes when making population-level assessments or management decisions.” (Cook 2006). However, in the past, management decisions regarding hearing damage have been based on hearing data from a few individuals of perhaps one or two cetacean species, and results have been extrapolated to characterize populations, and even species, to say nothing of whole taxonomic orders or suborders (e.g., National Marine Fisheries Service 2006). Interestingly, in the Sarasota Bay dolphins, no relationship was seen between hearing sensitivity and age (2–36 years), gender, and PCB load (Cook 2006). Electrophysiological measures of hearing such as auditory evoked potential or auditory brainstem response must be used with caution, however, as rigid stimulus control is required, masking thresholds are not taken into account, and these measures do not represent a “whole animal” response, including the totality of the animal’s sound pathways, perception, and processing abilities.

Auditory data from captive individuals cannot necessarily be extrapolated to free-ranging cetaceans, as captive animals must adjust to a radically different acoustical environment in the form of a tank, which could conceivably influence their hearing abilities over the long term, especially in younger animals. Au (1993) noted that “unnatural and suboptimal signals” may be used by captive dolphins (family Delphinidae) because the highly reverberant tank environment could discourage dolphins from emitting high-intensity sonar signals so as to prevent the signals’ high energy from being reflected back at them. Moreover, it is probable that there are considerable differences in how a captive cetacean in a tank

perceives a noise playback compared with an animal in the ocean environment, where, for instance, different propagation patterns (multipaths) exist, possibly making extrapolations between the two environments invalid.

In reviewing her research results along with other cited studies, Cook (2006) found that, in general, captive animals showed more hearing impairment than similar-aged free-ranging dolphins, even though the free-ranging dolphins lived in the very urban environment of Sarasota Bay, which is filled with large numbers of pleasure craft. The Sarasota dolphins showed no substantial hearing losses (with one possible exception), though dolphins <2 years or >36 years were not tested. One interpretation of these results, she noted, was that individuals with profound hearing losses may not survive because of their compromised echolocation abilities (Cook 2006).

Tests using a food reward could also alter the motivation of captive animals to show, for instance, more behavioral tolerance to playbacks of high noise levels. Background noise levels must be taken into account when testing the hearing of whales or dolphins. Captive animals tested in the higher background noise levels of San Diego Bay had much higher hearing thresholds (poorer hearing) than those tested in a pool, especially below 40 kHz (Finneran and Houser 2006). In this study, three out of the four captive bottlenose dolphins showed high-frequency hearing loss. Moreover, the hearing sensitivity of a stranded infant Risso's dolphin (*Grampus griseus* (G. Cuvier, 1812)) was much greater than a previously tested adult of the same species. Not only did the infant detect 100 kHz signals at nearly 60 dB lower than the adult, but it also could detect higher frequencies (Nachtigall et al. 2005). Thus, extrapolations between age classes may not be valid.

Differences between natural and anthropogenic noise

The argument is often made that because cetaceans themselves can produce very loud sounds, they should be able to cope with loud anthropogenic ocean noise. However, it is difficult to compare their sounds with man-made noise sources, since the two can vary in many characteristics (frequency, duration, directionality, etc.) even if their loudness is occasionally comparable. For instance, while a sperm whale click may be as loud as some naval sonars, it is very brief and extremely directional (Møhl et al. 2000; Møhl 2004). Imagine a pencil-thin flashlight beam, compared, in the case of naval mid-frequency sonar, with a floodlight radiating light in virtually all directions on a horizontal plane (National Oceanographic and Atmospheric Administration and US Department of the Navy 2001). The chances of being exposed to the full power of a sperm whale click are comparatively small. Similarly, a sound source, such as a porpoise (family Phocoenidae) click, may be very loud but ultrasonic or above the human hearing range. Such high frequencies do not carry over the large distances that low frequencies do, and more cetaceans are sensitive to the mid-frequency range than high frequencies. Moreover, it is probable that loudly vocalizing animals generally space themselves (e.g., as singing humpback (*Megaptera novaeangliae* (Borowski, 1781)) males do; Frankel et al. 1995), with the

result that they do not normally expose each other to the loud sounds of conspecifics. The human voice is also loud enough to cause hearing damage in other humans, if one were to yell or sing at close range to another's ear over hours, yet this is socially unacceptable. At the same time, it should not be assumed that sounds produced by cetaceans are always benign. It is very probable that cetaceans use their sounds to threaten or even injure one another on occasion, in competitive displays or fights (Tyack 1981; Connor and Smolker 1985).

Natural background noise levels in the ocean can be quite loud and variable. As such, it is possible that cetaceans have developed mechanisms that protect them from the more harmful effects of noise, such as hearing loss. There have even been suggestions that, as cetaceans must cope with pressure changes owing to diving, they may be more resilient to pressure changes from noise (e.g., in Ketten 1995), though there is little evidence to support this theory. It might be assumed that cetaceans have adapted over evolutionary time scales to at least some commonly encountered natural noise sources, but the same does not necessarily apply to the relatively recent addition of anthropogenic noise. Especially for long-lived species, such as whales, and in cases of rapidly increasing background noise levels, animals are highly unlikely to be able to genetically adapt at a pace similar to that of habitat change (Rabin and Greene 2002). Some natural and human-made sound sources share acoustic characteristics, but usually cetaceans are probably able to distinguish between them, especially considering factors such as the context in which they are produced. Moreover, there are probably biological constraints in the extent to which animals are able to overcome challenges to their perception and communication in the environment such that the capacity for adaptation to noise is not limitless.

Impacts of ocean noise on cetaceans

Cetacean strandings

The US National Marine Fisheries Service defines a stranding as a marine mammal found (i) dead on shore, (ii) alive on shore but unable to return to the water, or (iii) in a foreign habitat (river or shallow water) and unable to return to its own habitat (e.g., deeper water) without assistance. The reasons cetaceans strand are still largely unknown, but some strandings are due to biotoxins or disease. Although cetacean mass strandings (involving several animals) are uncommon, certain species, such as pilot whales (genus *Globicephala* Lesson, 1828) or false killer whales (*Pseudorca crassidens* (Owen, 1846)), are known to mass strand more frequently and were recorded doing so long before the industrial revolution. Strandings of single animals are more likely to occur because the animal is ill, diseased, or injured, whereas in many mass strandings, the majority of animals appear healthy.

History of noise-related beaked whale strandings

Recently, scientists have recognized a type of mass stranding involving beaked whales, a family of whales that do not typically mass strand (except for perhaps Gray's beaked whales, *Mesoplodon grayi* von Haast, 1876). Unusual aspects of these mass strandings have included the fol-

lowing: (i) the involvement of beaked whales; (ii) mixed species; (iii) animals spread out over several tens of kilometres of coastline, yet stranded within several hours of each other — a so-called “atypical” stranding pattern; (iv) animals apparently disease-free in good body condition, often with food in their stomachs; (v) the live stranding of some animals; (vi) strandings very closely linked in space and time to a noise event; (vii) evidence of acoustic trauma discovered upon examination of the carcasses; and (viii) no other explanations available for the stranding. Not all of these strandings showed all of these features, other than the involvement of beaked whales, the lack of disease, and the nearby noise event.

Noise was first implicated in these strandings because (i) no other threat could easily explain how, almost simultaneously, many whales could be affected over a large area and (ii) the locations and timing of individual whale strandings in a mass-stranding event would often closely coincide with the track of a noise-producing vessel. In the Bahamas stranding of 2000, the “smoking gun” of acoustic trauma was finally discovered. Hemorrhaging around the brain, in the inner ears, and in the acoustic fats (i.e., fats that are located in the head, including the jaw and “melon” or forehead of cetaceans, which are involved in sound transmission) showed up in stranded whales (National Oceanographic and Atmospheric Administration and US Department of the Navy 2001). This led the US Navy and the National Oceanic and Atmospheric Administration in their interim report (National Oceanographic and Atmospheric Administration and US Department of the Navy 2001) to conclude that “an acoustic or impulse injury ... caused the animals to strand ... and subsequently die as a result of cardiovascular collapse ...” and that “... tactical mid-range frequency sonars aboard U.S. Navy ships that were in use during the sonar exercise in question were the most plausible source of this acoustic or impulse trauma.”

Exposure to military sonar was determined to be the probable cause of a beaked whale stranding event in Greece in 1996, because of an “atypical” stranding pattern (Frantzis 1998). Similar stranding events occurred in the Bahamas in 2000 (see above), Madeira in 2000 (Freitas 2004), and the Canary Islands in 2002 (Fernández et al. 2005). Since 1960, more than 40 mass strandings, defined as two or more individuals, of Cuvier’s beaked whales (*Ziphius cavirostris* G. Cuvier, 1823) have been reported worldwide (see Table 1, as well as Hildebrand 2005; Brownell et al. 2004³). About 28 of these occurred at the same time and place as naval maneuvers or the use of active sonar or near naval bases (Frantzis 1998; National Oceanographic and Atmospheric Administration and US Department of the Navy 2001; Jepson et al. 2003; Brownell et al. 2004³) or co-occurred with other noise sources, such as seismic surveys (Hildebrand 2005; International Whaling Commission 2005).

While the co-occurrence of two events (noise and strandings) is not enough to prove causation, the probability that

the two are not related grows smaller as more linked incidents are observed. As both naval maneuvers and especially beaked whale mass strandings are comparatively rare events, the chance that these two rare events will repeatedly occur together by coincidence is vanishingly low. In addition, the historical record indicates that, aside from one exception, Cuvier’s beaked whale mass strandings first began to appear in the early 1960s (Table 1), when a different system of more powerful naval sonars began to be used (Friedman 1989). Some of this increase in strandings may be due to an enhanced effort to document strandings and the establishment of better stranding networks, but as stranding records for Cuvier’s beaked whales date back to around 1838 (Mead 2000⁴), there has been at least some effort present to document strandings since the 19th century. It is unlikely that reports of mass strandings in the 1960s are the result of a sudden jump in monitoring effort.

Possible underestimation of noise-induced strandings or mortalities

For a number of reasons, it is difficult to assess the magnitude of noise-induced strandings or mortalities, though there are several factors that would cause the true extent of strandings associated with noise to be underestimated. First, many strandings will go undocumented, as will the associated noise events. Second, if animals can die at sea owing to injuries sustained from a noise event and without any stranding taking place, as seems likely (Fernández et al. 2005; International Whaling Commission 2005), then detection is even more improbable. Whale carcasses are difficult to discover at sea, since, with few exceptions (e.g., right (genus *Eubalaena* Gray, 1864), bowhead, and sperm whales) (Whitehead and Reeves 2005), they usually immediately sink. Some carcasses may later float or strand, but even in well-studied inshore populations of cetaceans, only a small proportion of carcasses are recovered (a total of 14 killer whale, *Orcinus orca* (L., 1758), carcasses has been recovered out of 200 individuals known to have died along a well-populated coast — a 7% recovery rate; John K.B. Ford, personal communication). Third, only mass strandings of beaked whales are usually considered to be suspicious and thus linked with noise, because single strandings of beaked whales are more apt to be due to disease than mass strandings. Yet, it is possible that noise events may at least contribute to their stranding, though this has not been examined. Fourth, while acoustic trauma provides very convincing evidence to link a stranding with a noise event, the absence of such trauma cannot be used to rule out such an association. Whales may strand because they were near shore when they heard the noise and panicked, dying from the stranding alone without suffering additional acoustic trauma. Overall, the fact that it has taken observers 40 years, during which mid-frequency naval sonars have been widely used, to discover a link between this technology and beaked whale strandings underscores how easy it is to miss such impacts from human activities, even for such relatively obvious events as strandings.

³R.L. Brownell, Jr., T. Yamada, J. Mead, and A.L. van Helden. 2004. Mass strandings of Cuvier’s beaked whales in Japan: U.S. Naval acoustic link? Paper No. SC/56/E37 presented to the International Whaling Commission Scientific Committee, June 2004. Unpublished. Available from the International Whaling Commission Scientific Committee, Cambridge, UK.

⁴J.G. Mead. 2000. Historical mass mortalities of ziphiids. Unpublished paper. Available from Mead.James@nmnh.si.edu.

Table 1. Mass strandings of Cuvier's (*Ziphius cavirostris*; *Zc*), Gervais' (*Mesoplodon europaeus*; *Me*), and Blainville's (*Mesoplodon densirostris*; *Md*) beaked whales, in addition to species that stranded with them, namely the striped dolphin (*Stenella coeruleoalba*), northern bottlenose whale (*Hyperoodon ampullatus* (Forster, 1770)), pygmy sperm whale (*Kogia breviceps*), minke whale (*Balaenoptera acutorostrata*), and Atlantic spotted dolphin (*Stenella frontalis* (G. Cuvier, 1829)) (after Brownell et al. 2004³; Evans and Miller 2004; Hildebrand 2005; International Council for the Exploration of the Sea 2005; International Whaling Commission 2005).

Year	Location	Species (numbers)	Associated activity (when available)
1914	New York, USA	<i>Zc</i> (2)	
1960	Sagami Bay, Japan	<i>Zc</i> (2)	US fleet
1963	Gulf of Genoa, Italy	<i>Zc</i> (15+)	Naval maneuvers
1963	Sagami Bay, Japan	<i>Zc</i> (8–10)	US fleet
1964	Sagami Bay, Japan	<i>Zc</i> (2)	US fleet
1965	Puerto Rico	<i>Zc</i> (5)	
1966	Ligurian Sea, Italy	<i>Zc</i> (3)	Naval maneuvers
1967	Sagami Bay, Japan	<i>Zc</i> (2)	US fleet
1968	Bahamas	<i>Zc</i> (4)	
1974	Corsica	<i>Zc</i> (3), striped dolphin (1)	Naval patrol
1974	Lesser Antilles	<i>Zc</i> (4)	Naval explosion
1975	Lesser Antilles	<i>Zc</i> (3)	
1978	Sagami Bay, Japan	<i>Zc</i> (9)	US fleet
1978	Suruga Bay, Japan	<i>Zc</i> (4)	US fleet
1979	Sagami Bay, Japan	<i>Zc</i> (13)	US fleet
1980	Bahamas	<i>Zc</i> (3)	
1981	Bermuda	<i>Zc</i> (4)	
1981	Alaska, USA	<i>Zc</i> (2)	
1983	Galápagos	<i>Zc</i> (6)	
1985	Canary Islands	<i>Zc</i> (~10), <i>Me</i> (1)	Naval maneuvers
1986	Canary Islands	<i>Zc</i> (3), <i>Me</i> (1), beaked whale species (1)	
1987	Canary Islands	<i>Me</i> (3)	
1987	Italy	<i>Zc</i> (2)	
1987	Suruga Bay, Japan	<i>Zc</i> (2)	US fleet
1987	Canary Islands	<i>Zc</i> (2)	
1988	Canary Islands	<i>Zc</i> (3), bottlenose whale (a beaked whale) (1), pygmy sperm whale (2)	Naval maneuvers
1989	Sagami Bay, Japan	<i>Zc</i> (3)	US fleet
1989	Canary Islands	<i>Zc</i> (15+), <i>Me</i> (3), <i>Md</i> (2)	Naval maneuvers
1990	Suruga Bay, Japan	<i>Zc</i> (6)	US fleet
1991	Canary Islands	<i>Zc</i> (2)	Naval maneuvers
1991	Lesser Antilles	<i>Zc</i> (4)	
1993	Taiwan	<i>Zc</i> (2)	
1994	Taiwan	<i>Zc</i> (2)	
1996	Greece	<i>Zc</i> (12)	Naval low-frequency active sonar trials
1997	Greece	<i>Zc</i> (3)	
1997	Greece	<i>Zc</i> (9+)	Naval maneuvers
1998	Puerto Rico	<i>Zc</i> (5)	
1999	Virgin Islands	<i>Zc</i> (4)	Naval maneuvers
2000	Bahamas	<i>Zc</i> (9), <i>Md</i> (3), beaked whale species (2), minke whale (2), Atlantic spotted dolphin (1)	Naval mid-frequency sonar
2000	Galápagos	<i>Zc</i> (3)	Seismic research
2000	Madeira	<i>Zc</i> (3)	Naval mid-frequency sonar
2001	Solomon Islands	<i>Zc</i> (2)	
2002	Canary Islands	<i>Zc</i> (9), <i>Me</i> (1), <i>Md</i> (1), beaked whale species (3)	Naval mid-frequency sonar
2002	Mexico	<i>Zc</i> (2)	Seismic research
2004	Canary Islands and Morocco	<i>Zc</i> (4)	Naval maneuvers
2006	Spain	<i>Zc</i> (4)	NATO naval maneuvers

On the other hand, strandings that occur together with anthropogenic noise cannot immediately be assumed to be caused by it. If animals later are discovered to have died as a result of biotoxins, for instance, the noise event may be

truly coincidental to their stranding. Alternatively, several factors may act together in a cumulative or synergistic way to bring about a stranding. The relative contributions of each of these stressors will likely be difficult to determine.

Mechanism of injury

The mechanisms by which beaked whales are killed or injured by anthropogenic noise are still unknown (Cox et al. 2006). In contrast to the necropsies conducted in the Bahamas where principally only the heads of the carcasses were examined, pathologists in the 2002 Canary Islands stranding dissected the entire bodies of the whales. They found that "... whales had severe, diffuse congestion and hemorrhage, especially around the acoustic jaw fat, ears, brain, and kidneys." (Fernández et al. 2005). Additionally, they observed "gas bubble-associated lesions and fat embolism in the vessels and parenchyma of vital organs." This *in vivo* bubble formation, which can block blood vessels (an embolism), might have been the result of sonar exposure and may have been further exacerbated by abnormal surfacing behavior, such as too rapid ascents (Fernández et al. 2005). Alternatively, the sonar alone may interact with tissues that are supersaturated with nitrogen gas (as is possible in deep-diving whales), causing the expansion of *in vivo* bubble precursors or gas nuclei. The bubbles seen in the veins are consistent with, but not diagnostic of, decompression sickness (Fernández et al. 2005). Both gas and fat emboli should be present for proper diagnosis of this newly discovered syndrome, which seems related to noise exposure (Fernández et al. 2005). The time between estimated sonar exposure and death was short (around 4 h), and observations suggest that the animals were severely injured before stranding, at least in the 2002 Canary Islands event (Fernández et al. 2005).

Thus, the pathologies documented in the beaked whale stranding events in the Bahamas, Madeira, and Canary Islands may be the result of a physiological or behavioral response or some combination of the two. Beaked whales may be exhibiting the following: (i) a behavioral response to noise that leads directly to stranding, such as swimming away from the noise into shallow water; (ii) a behavioral response such as altering their dive pattern, e.g., staying too long at depth or near the surface, which leads indirectly to tissue damage (e.g., because of decompression sickness or lack of oxygen); or (iii) a direct physiological response to noise exposure that is unmediated by behavior through, for example, nonauditory effects such as gas bubble formation and growth, vertigo, or resonance (Cox et al. 2006). Gas bubble formation in at least partial combination with a behavioral response has been singled out as particularly plausible (Cox et al. 2006). If behavior is involved, responses will be more difficult to predict because of high interindividual variation.

By modeling the sound field (National Oceanic and Atmospheric Administration and US Department of the Navy 2001) and by knowing the distribution of Cuvier's beaked whales in the area of the Bahamas based on previous studies, whales were thought to be exposed to relatively moderate levels of noise, in the order of 150–160 dB re 1 μ Pa for 50–150 s (Hildebrand 2005). Such levels are too low to cause permanent or probably even temporary hearing loss (Hildebrand 2005), especially as beaked whales are likely most sensitive to higher frequencies, though there may be considerable interspecific variation. A juvenile Gervais' beaked whale (*Mesoplodon europaeus* (Gervais, 1855)) was tested, using auditory evoked potential, to show little sensi-

tivity at 5 kHz, around the frequency of the sonar (Cook et al. 2006). Bubble growth, in contrast, could theoretically be activated with exposure to sounds ≤ 150 dB under the right conditions, and bubbles could grow significantly as the animal rises to the surface (Houser et al. 2001; Crum et al. 2005).

Crum and Mao (1996) found, however, that bubble growth would be improbable from exposures < 190 dB unless tissues were extremely supersaturated. Supersaturation with nitrogen gas is considered a plausible condition for cetaceans, especially for deep-diving marine mammals (Ridgway and Howard 1979; Houser et al. 2001). Deep-diving whales, such as beaked whales and sperm whales, would then theoretically be most vulnerable to injury from bubble growth. Experiments involving bovine tissue placed under pressure (equivalent to 40–70 m in diving depth) and supersaturated with gas showed that extensive bubble production resulted when exposed to short pulses of low-frequency sound, supporting the possibility that sound sources could cause gas emboli syndrome in cetaceans under the right conditions (Crum et al. 2005). They note that the physics of bubble nucleation (formation) would not be expected to vary much with different frequencies of sound exposure. Recent anatomical studies of sperm whales and other species show that there may be unavoidable costs to chronic deep-diving (Moore and Early 2004; but see also Mitchell 2005, Moore and Early 2005, and Rothschild 2005) and that *in vivo* bubble formation is indeed possible in cetaceans other than beaked whales (Jepson et al. 2003; Jepson et al. 2005). Thus, cetaceans may not be as immune to decompression sickness and "the bends" as was previously thought.

Tyack et al. (2006), however, argue that, based on their calculations of diving physiology and observations of beaked whale diving behavior, these whales are neither chronically and highly supersaturated with nitrogen nor at risk for decompression sickness and embolism. They believe that the whales' pattern of diving is not an adaptation to prevent bubble formation and decompression sickness, since it does not fit with the diving behavior required for recompression. Instead, they suggest that an unusual behavioral response to noise could cause the observed emboli. Diving behavior most likely to cause decompression sickness, according to their calculations, would be repeated, long, shallow dives between 30 and 80 m with only short periods at the surface. Such a diving pattern could result in supersaturation levels of up to 400%–900% (Tyack et al. 2006).

Population-level impact

The population consequences of acoustically induced strandings and mortalities are unclear. The conservation status of most beaked whales is listed as "data deficient" (International Union for the Conservation of Nature and Natural Resources 2004), as this family of whales tends to be notoriously elusive and hard to study. However, the population structure of the few beaked whale populations that have been studied long term indicates that even transient and localized acoustic impacts could have prolonged and serious consequences. Beaked whales appear to be found in small local populations that are resident year-round (Balcomb and Claridge 2001; Wimmer and Whitehead 2004;

McSweeney et al. 2007). Additionally, Cuvier's beaked whales exhibit a high degree of genetic isolation among oceanic and, in some cases, regional populations (Dalebout et al. 2005). Such population characteristics make beaked whales particularly vulnerable to disturbance and population impacts.

In the case of the Bahamas March 2000 event, the only stranding for which baseline survey data are available, there were no sightings of Cuvier's beaked whales for a 20 month period (May 2000 to February 2002) following the stranding, despite increased effort in 2000 and 2001 (Claridge 2006). Sighting rates since February 2002 appear to be back to those from 1997 to 1999 or about 0.0006 sightings per km surveyed (Claridge 2006; D.E. Claridge, personal communication). Photographic data are limited for the genus *Ziphius* G. Cuvier, 1823 in this area, but of the 16 whales photographed before March 2000, there was one adult female that was resighted (Claridge 2006). This female has been photo-identified two more times since the stranding, suggesting residency of individual Cuvier's beaked whales to the area (D.E. Claridge, personal communication). Additionally, one of the whales that stranded in the March event had been photographed in the study area previous to the stranding (Claridge 2006). This seems to indicate that the affected local population of Cuvier's beaked whales was isolated from a larger population, implying that a population-level effect may have resulted from the brief transit of five naval vessels using sonar (Balcomb and Claridge 2001; International Whaling Commission 2005). It is unknown how many whales from the local population of the species were killed during the naval exercise, but at minimum they were displaced from their former habitat. For species such as beaked whales whose rates of increase are low, even seemingly minor effects may cause population declines (Whitehead et al. 2000).

Nonbeaked whale strandings

While beaked whales appear particularly vulnerable to the effects of noise, other cetaceans also have been involved in noise-induced strandings. Some species, such as minke whales (*Balaenoptera acutorostrata* Lacépède, 1804) (Bahamas 2000) and pygmy sperm whales (*Kogia breviceps* (Blainville, 1838)) (Canary Islands 1988), have stranded concurrently with beaked whales, while others, such as long-finned pilot whales (*Globicephala melas* (Traill, 1809)), minke whale, and dwarf sperm whales (*Kogia sima* (Owen, 1866)) (North Carolina 2005), melon-headed whales (*Peponocephala electra* (Gray, 1846)) (Hawai'i 2004), and harbor porpoises (*Phocoena phocoena* (L., 1758)) (Haro Strait 2003), have stranded in noise-related events that did not involve beaked whales (Table 2). In the Hawai'i stranding, Southall et al. (2006) concluded that active naval sonar transmissions likely contributed to the stranding of the melon-headed whales. Reports on the Haro Strait stranding (National Marine Fisheries Service 2005) and the North Carolina stranding (Hohn et al. 2006) were less conclusive in relating the strandings to naval sonar, though clear cetacean behavioral reactions to the sonar were reported in the Haro Strait event.

Which other species could be vulnerable to noise-induced strandings is unknown. As previously mentioned, certain

species of cetaceans, such as pilot whales, are known as frequent mass stranders. If these same species also occasionally strand because of noise events, it would be easy to miss such a connection and their susceptibility to noise-related injury and mortality may be underestimated. Jepson et al. (2005) found gas emboli, previously associated with sonar-related strandings, in the livers and other organs of four Risso's dolphins, three short-beaked common dolphins (*Delphinus delphis* L., 1758), and one harbour porpoise, in addition to one Blainville's beaked whale (*Mesoplodon densirostris* (Blainville, 1817)). While such lesions were more common in deep-diving species, they were also present in species inhabiting shallower waters, raising the possibility that sonar, or other noise, impacts may be more widespread than previously thought.

Other impacts of noise on marine mammals

Temporary or permanent hearing loss

Hearing loss can either be temporary (TTS or temporary threshold shift) or permanent (PTS or permanent threshold shift). Generally, with PTS, sensory hair cells in the inner ear are lost. The relationship between the onset of TTS and the onset of PTS is not well understood, but repeated TTS, especially if the animal receives another sound exposure before full recovery of the previous TTS, is thought to result in PTS. At which point TTS ceases to be recoverable is uncertain. PTS, however, can be incurred even without TTS, if the sound is intense enough. PTS has not purposely been induced in cetaceans for ethical and legal reasons.

Even in humans, predicting hearing loss is difficult. It is still unclear, for instance, how impulses add up over time and which pattern of delivery of impulses is most damaging to the human ear. Only recently have characteristics of noise such as kurtosis, or the "peakedness" of the amplitude distribution of a noise environment, been shown to help predict the magnitude of hearing loss from complex noise exposures (Hamernik et al. 2003).

In general, the chances of TTS occurring are increased the higher the sound level and the longer the duration. Using captive cetaceans, Schlundt et al. (2000) found that beluga whales (*Delphinapterus leucas* (Pallas, 1776)) and bottlenose dolphins showed masked TTS after being exposed to a single very high intensity sound of 192–201 dB re 1 μ Pa for 1 s per day, though one animal showed masked TTS at 182 dB at 75 kHz. In a different study using impulsive noise (seismic waterguns), 226 dB re 1 μ Pa (peak-to-peak) and 186 dB re 1 μ Pa²·s (total energy flux) produced masked TTS in the beluga whale but not in the bottlenose dolphin (Finneran et al. 2002). Another captive bottlenose dolphin incurred TTS after at most once-a-week exposures to a maximum of 179 dB re 1 μ Pa for 55 min, as determined by behavioral means. Recovery was complete within 45 min (Nachtigall et al. 2003). Using evoked auditory potentials (a way to test hearing by assessing the auditory brainstem response through passively measuring brainwave patterns from the skin surface), the same animal showed TTS after being exposed to 160 re 1 μ Pa (rms) for 30 min (Nachtigall et al. 2004). The authors warned that TTS is highly variable between individuals, as well as between species, and thus caution should be used when extrapolating results to other

Table 2. Associated mass strandings involving species other than solely Cuvier's (*Zc*), Gervais' (*Me*), or Blainville's (*Md*) beaked whales, namely pygmy sperm whale, northern bottlenose whale, minke whale, Atlantic spotted dolphin, harbor porpoise (*Phocoena phocoena*), Dall's porpoise (*Phocoenoides dalli* (True, 1885)), melon-headed whale (*Peponocephala electra*), long-finned pilot whale (*Globicephala melas*), and dwarf sperm whale (*Kogia sima*) (National Oceanographic and Atmospheric Administration and US Department of the Navy 2001; Martín et al. 2004; National Marine Fisheries Service 2005; Hohn et al. 2006; Southall et al. 2006).

Year	Location	Species (numbers)	Associated activity (when available)
1988	Canary Islands	Pygmy sperm whale (2), <i>Zc</i> (3), bottlenose whale (a beaked whale) (1)	Naval maneuvers
2000	Bahamas	Minke whale (2), Atlantic spotted dolphin (1), <i>Zc</i> . (9), <i>Md</i> (3), other beaked whale species (2)	Naval mid-frequency sonar
2003	Washington, USA	Harbor porpoise (14), Dall's porpoise (1)	Naval mid-frequency sonar
2004	Hawai'i, USA	Melon-headed whale (~200)	Naval mid-frequency sonar
2005	North Carolina, USA	Long-finned pilot whale (34), dwarf sperm whale (2), minke whale (1)	Naval maneuvers

bottlenose dolphins, let alone to other cetacean species (Nachtigall et al. 2004). Cetaceans must have internal mechanisms to protect themselves from their own vocalizations, as other species do, since the sounds they produce are often above the levels shown, in the previously mentioned experiments, to induce TTS.

Based on theoretical modelling, Erbe and Farmer (2000) predicted that belugas would experience TTS after only 20 min of ice breaker noise at distances of 1–4 km. The noise of fast whale-watching boats was modelled and predicted to cause TTS in killer whales after 30–50 min of exposure within distances of 450 m (Erbe 2002). The noise from several boats surrounding or following whales theoretically would reach critical levels considered high enough to cause permanent hearing loss with prolonged exposure (Erbe 2002).

There is currently a high degree of emphasis on TTS and PTS when assessing the impacts of noise on marine mammals. Certainly such impacts are of great concern. Even a temporary loss in hearing (TTS can last from minutes to days) can be fatal or injurious to animals in the wild, if the detection of a predator or other significant hazard is missed. A focus on TTS and PTS also has the advantage that these effects are more easily modeled and predicted than other impacts, in particular, behavioral ones. On the other hand, as was demonstrated with the Bahamas 2000 stranding, a narrow concentration on TTS and PTS will not provide a full picture of the potential harm to cetaceans. Exposures in this case were below those thought to be able to cause even TTS, yet beaked whales sustained damage to their inner ears and other tissues, probably as a result of indirect behavioral or nonauditory impacts. Thus, the most severe acoustic impacts on cetaceans recorded to date were due to exposures thought too low to induce TTS, according to current predictive models.

In fact, it is unclear at this point whether the vertebrate auditory system is indeed the most sensitive and vulnerable sensory system or structure in the body to all forms of noise exposure, though this is often assumed and appears logical on the surface. In certain circumstances, however, it may not be the best indicator for noise impacts. Depending on the frequency and other features of the noise source, it could be that nonauditory effects such as skin sensations, resonan-

ces in air sacs, vestibular responses such as vertigo, or gas or fat emboli, for instance, could cause more of an impact on a cetacean than any direct effect on its hearing. This means that cetaceans may even be impacted by noise frequencies outside of their range of hearing. Thus, I believe that it is too limiting to claim, as Nowacek et al. (2007) do, that “[i]t is in the shared frequency range that we are concerned about the effects that anthropogenic sound may have on cetaceans.” Though within human hearing range, human divers responded to underwater sounds of 160 dB (240 Hz center frequency) for 15 min in ways that did not affect their hearing, namely disorientation, light-headedness, sleepiness, shaking of the extremities, an inability to concentrate, and even a partial seizure, with some symptoms persisting for weeks (Steevens et al. 1999).

Blast injury

Explosions, as used for coastal construction, the removal of underwater structures (decommissioning oil rigs, for instance), in naval exercises, or for naval “ship-shock” trials to test the integrity of a ship's hull, compose a separate category of noise, as they contain a shock wave in addition to an acoustic wave. Blast waves cause a dramatic pressure drop over a very short duration (sharp rise time) and are relatively broadband in frequency, resulting in mechanical impact. Organ damage and the rupture of gas-filled cavities such as lungs, sinuses, and ears can occur (Richardson et al. 1995). A 5000 kg explosion apparently caused severe injury to the temporal bones of two humpback whales found dead near the explosion site (Ketten 1995).

Masking

Masking refers to the interfering or obscuring effects of noise, which limits animals from hearing signals important to them. In particular, masking may affect cetaceans that are thought to communicate over large distances of ocean. Certain low-frequency whale sounds such as blue (*Balaenoptera musculus* (L., 1758)) and fin (*Balaenoptera physalus* (L., 1758)) whale calls can be heard over hundreds or thousands of kilometres, and are thought to function in attracting widely spread-out mates (Croll et al. 2002). If such (presumably often faint) reproductive calls are masked, widely distributed mates may not be able to find each other and reproductive rates may fall as a consequence. The mere

fact that a call can be heard over large distances does not mean it is actually used to communicate with distant whales, however. Yet assuming there is some cost (energetic or risk in attracting predators) to loud sounds, animals would not be expected to make calls louder than is necessary to achieve their function (Stearns and Hoekstra 2000). In the case of loud, low-frequency whale calls, their function may not just be to increase their chances of being detected, but to advertise such features as quality and fitness to prospective mates (Croll et al. 2002). It is thus necessary to know the function of a call before one can evaluate the full significance of masking. In birds, for instance, there are indications that masking can make it more difficult for a receiver to discriminate between two signals (Leonard and Horn 2005).

Cetaceans may need to hear the sometimes very faint sounds of their prey or predators, mates, or navigation cues. Faint acoustic cues from distant sound sources may be important for navigation and orientation (e.g., Tyack and Clark 2000). Based on worst-case theoretical models, the ramming noise from ice breakers was predicted to mask beluga calls to ranges of 40 km and cause disturbance over ranges of 46 km (Erbe and Farmer 2000). The noise of fast whale-watching boats was modeled and predicted to mask killer whale calls over 14 km (Erbe 2002). The noise from a nearby ship was estimated to reduce a Cuvier's beaked whale's maximum range of echolocation by more than half and the maximum range of communication by more than a factor of five, assuming the whale auditory system is noise-limited (Aguilar Soto et al. 2006).

It is likely that cetaceans have evolved some resilience regarding masking from at least natural noise sources. Directional hearing, for instance, can help to overcome masking, as can shifting a call's frequency, amplitude, or other features to differentiate it from background noise. Indeed, captive beluga whales altered their vocal output in higher background noise conditions (Au et al. 1985). When moved to a high-noise environment, belugas shifted their sonar signals to higher frequencies (peak frequencies shifted from 50 kHz to over an octave higher at 110 kHz) and increased their amplitude (from a maximum peak-to-peak of 202 to 210 dB re 1 μ Pa; Au et al. 1985). However, there seemed to be an endpoint to some cetaceans' ability to adjust to masking. When captive bottlenose dolphins were experimentally subjected to masking noise, they did not increase their sonar signal level with increasing noise, perhaps because they were already producing high-intensity signals and had reached their limit (Au 1993). Increasing masking noise also caused the dolphins' accuracy in target detection to decrease monotonically. A 15–20 dB increase in the masking noise spectrum level resulted in a drop in successful target detection, from a 100% correct response rate to only 50%, where dolphins stopped emitting sonar clicks and appeared to start guessing whether the target was there or not (Au 1993).

Free-ranging belugas reduced their calling rate while vessels (a small motorboat and a ferry) were approaching, but at distances of <1 km, increased the repetition rate of specific calls. They also shifted the frequencies of their calls up when vessels were close by and changed the types of calls they used (Lesage et al. 1999). Comparing calls in the presence or absence of boats, killer whales increased their

call durations once critical levels of annual whale-watching boat traffic were reached, based on records of active boats per year (Foote et al. 2004). Bottlenose dolphins whistled more often when first approached by boats, perhaps to compensate for masking (Buckstaff 2004). Groups of Pacific humpback dolphins (*Sousa chinensis* (Osbeck, 1765)), which contained mother–calf pairs, increased their rate of whistling after a boat had transited the area (Van Parijs and Corkeron 2001). The authors postulated that the noise from vessels disrupted group cohesion, especially between mother–calf pairs, requiring the re-establishment of vocal contact after masking from boat noise. Humpback mating songs lengthened in response to LFA sonar, perhaps also in an effort to cope with the noise interference (Miller et al. 2000). Frstrup et al. (2003) additionally noted that higher source levels of the LFA sonar playbacks resulted in longer songs. Differences in song length lasted up to 2 h after the last broadcast (Frstrup et al. 2003). Such increases in signal duration or repetition rate can improve the likelihood that the signal will be heard over noise. The costs to the animals of such alterations in their calls, both energetically and functionally, are unknown.

Filtering and signal processing techniques may also enable cetaceans to cope with the effects of masking so that the signal of interest is distinguished from the surrounding noise. However, phenomena such as the “cocktail party effect” could also mean that cetaceans can “pick out” certain noise sources (ones they find alarming, for instance, based on past negative experiences) from background noise and thus be affected by them at levels below ambient noise. This could greatly extend a noise source's range of potential impact.

Noise does not need to be the same frequency as the signal of interest to mask it. Low-frequency noise can mask a much wider range of frequencies than can mid- or high-frequency noise (Richardson et al. 1995).

Auditory development

The long-term consequences of continuous exposure to increasing background noise levels in the ocean, especially on the development of hearing in the young, are unknown. Infant rats raised in even moderately elevated levels of background noise showed delays in brain and auditory developments (Chang and Merzenich 2003). These young rats retained a primitively organized auditory cortex that was similar to much younger infant control pups. As several cetacean species learn their vocalizations by listening to calls from conspecifics (Janik and Slater 1997) and as exposure to human-made sounds can change cetacean vocalizations (see above), such potential impacts of anthropogenic noise should be considered.

Effects of noise on cetacean behavior

Vocal behavior

Other than the vocal responses to masking already mentioned, the following changes in cetacean vocalizations to noise have been documented. These, in contrast, are not readily explainable in terms of techniques to overcome masking, as the response is generally one of cetaceans falling silent in the presence of noise. For example, reduced calling rates or a complete cessation of vocalizations have

been documented for fin whales in response to boat noise (Watkins 1986), for sperm whales in response to pingers (Watkins and Schevill 1975) and military sonar signals (Watkins et al. 1985), for pilot and sperm whales in response to low-frequency ATOC-like sounds (Bowles et al. 1994), and for sperm whales and perhaps pilot whales in response to a seismic survey (Bowles et al. 1994). Rendell and Gordon (1999), in contrast, found that significantly more pilot whale whistles occurred during and just after military sonar output. Based on a single individual Cuvier's beaked whale, significantly fewer creaks or buzzes (representative of prey-capture attempts) were heard during a dive that was exposed to ship noise (Aguilar Soto et al. 2006). This dive was also shorter than the non-noise-exposed dives, with less time spent in the echolocation (deep) phase of the dive. An estimated reduced foraging efficiency of >50% occurred during the noise-exposed dive compared with other dives of the same animal (Aguilar Soto et al. 2006), as less time was presumably spent attempting to capture prey by means of creaks. Sperm whales in the Gulf of Mexico exposed to a seismic survey also exhibited a change in their vocalizations. As with the above Cuvier's beaked whale, sperm whales reduced their rate of echolocation buzzes, an indication of prey-capture attempts, by an average of 19% (International Whaling Commission 2007). This result was not statistically significant, but probably a real effect according to a Bayesian analysis (International Whaling Commission 2007).

Seismic surveys can raise low-frequency noise levels over areas of >35 000 km² for more than a month, exposing large portions of a cetacean population to chronic noise. Around 250 male fin whales appeared to stop singing for several weeks to months during a seismic survey, yet resumed singing within hours or days after the seismic noise stopped (International Whaling Commission 2007). Assuming male fin whale songs have a reproductive function (Croll et al. 2002), it would be difficult to imagine that such an effect would not be biologically significant.

Displacement from important habitat and avoidance

Cetaceans have been shown to be displaced from important habitat when exposed to noise. Nowacek et al. (2007) note that a short-term or even long-term displacement may not be of concern, if the quality of habitat cetaceans were displaced from is poor. I think that it is more logical to assume that cetaceans are in a particular habitat for a reason. If they are present for some time, the habitat must provide them with something they need and, moreover, something they cannot easily find elsewhere (or they would be there). While Nowacek et al. (2007) emphasized that displacement may not be of significance to cetaceans, disturbingly, they did not address the opposite condition, where a lack of displacement should not mean that cetaceans are thriving. Animals may be forced to remain in an area of importance to them, despite having to endure "costs" such as stress, masking, or even hearing impairment that would be hard to detect.

Gray whales (*Eschrichtius robustus* (Lilljeborg, 1861)) were displaced for >5 years from one of their breeding lagoons in response to industrial sounds, returning only several years after the activities stopped (Jones et al. 1994).

Gray whales abandoned a breeding lagoon from the late 1950s to at least through 1970, during an increase in dredging and shipping (1957–1967) but returned once activities ceased (Bryant et al. 1984). Killer whales and harbor porpoises dramatically changed locations to avoid loud acoustic harassment devices (Morton and Symonds 2002; Olesiuk et al. 2002). Killer whales stayed away for about 6 years, only returning when devices were discontinued in the area (Morton and Symonds 2002). Critically endangered western gray whales off Sakhalin Island, Russia, were displaced by seismic surveys from their primary feeding area, returning only days after seismic activity ceased (International Whaling Commission 2005). This change in distribution closely corresponded to the timing of the seismic surveys (International Whaling Commission 2005, 2007; Weller et al. 2006a). Whales receiving seismic noise levels of about 153 dB re 1 μ Pa zero-to-peak and 159 dB peak-to-peak on their feeding grounds also swam faster and straighter over a larger area with faster respiration rates during seismic operations (Weller et al. 2006b; International Whaling Commission 2007). Two different research teams and data from several years showed that beluga whales typically avoided icebreakers at distances of 35–50 km, at the point where they could probably just detect them. They travelled up to 80 km from the ship track and usually remained away for 1–2 days (Finley et al. 1990; Cosens and Dueck 1993). Sperm whales that were approached most closely by an active seismic survey vessel did not make foraging dives. Whales significantly reduced their fluke stroke effort by 6% during exposure to seismic noise compared with after, and all seven sperm whales studied reduced their fluke strokes on foraging dives in the presence of seismic noise (International Whaling Commission 2007).

Stone and Tasker (2006) examined cetacean responses from 201 seismic surveys around UK waters, concluding that there was evidence of disturbance. All small odontocetes, killer whales, and all mysticetes were found farther from arrays that were active (shooting) than when they were not. Small odontocetes showed the greatest horizontal avoidance, which extended at least as far as the limit of visual observation (Stone and Tasker 2006). There was no decrease in sighting rates for mysticetes, sperm whales, pilot whales, or killer whales when air guns were shooting vs. not shooting. Instead, mysticetes and killer whales exhibited more localized avoidance (Stone and Tasker 2006). There were indications that fewer animals were feeding, that smaller odontocetes swam faster, and that mysticetes remained at the surface more where sound levels are thought to be lower. Larger volume arrays produced stronger reactions than did smaller ones. Stone and Tasker (2006) theorized that smaller odontocetes may adopt a strategy of moving out of the area entirely during seismic noise exposure, whereas slower moving mysticetes may simply be able to orient away from the seismic survey, increasing their distance from the noise, but not vacating the area completely.

While few studies on displacement have been undertaken, wind turbines have recently come under scrutiny for noise impacts on cetaceans. Wind farms produce the loudest noise from pile driving during their initial construction. Pile driving noise is probably audible to cetaceans over hundreds of

kilometres or more (Madsen et al. 2006; Thomsen et al. 2006), and behavioral responses of harbor porpoises may extend to distances of 20 km (Thomsen et al. 2006). However, operational noise from at least smaller turbines (of ~1.5 MW) is considered to have a minor impact on harbor porpoises, as their ability to detect the noise over larger ranges is probably low (Thomsen et al. 2006). Still, even high-frequency specialists such as harbor porpoises can detect the low-frequency noise generated by wind turbines, as evidenced by their reaction to it (Koschinski et al. 2003).

Migrating animals have exhibited avoidance of noise by detouring around sound sources. Two series of field studies (Malme et al. 1983, 1984; Richardson et al. 1985, 1990) demonstrated that gray and bowhead whales avoided continuous industrial noise at average received levels of around 120 dB. Gray whales avoided LFA sonar transmissions at similar received levels when the sound source was placed inshore but not offshore (Tyack and Clark 1998⁵).

Au and Green (2000) found that humpback whales in Hawai'i swam fastest in response to approaches by the loudest boat they studied. Humpbacks approached by boats showed abrupt course changes and remained submerged longer (Au and Green 2000). Playbacks of alarm signals (received levels of 133–148 dB, 18 min in duration) to North Atlantic right whales (*Eubalaena glacialis* (Müller, 1776)) caused whales to spend less time at the bottom during a foraging dive, ascent vigorously, and increase their surface and near-surface time (Nowacek et al. 2004). Two studies conducted on humpback whales in Hawai'i showed that both time and distance between successive surfacings increased with increasing estimated exposure level of ATOC noise (Frankel and Clark 1998, 2000).

Subtle responses

Reactions of cetaceans to noise can be quite subtle. Though summering bowheads showed no detectable avoidance of seismic surveys, no change in general activities or call types, and no obvious alteration of calling rate, they dove for shorter periods and their respiration rate was lower than bowheads not exposed to noise (Richardson et al. 1986). Such changes were observed up to 54–73 km from seismic surveys at received levels that could be as low as <125 dB re 1 μ Pa (Richardson et al. 1995). Similarly, humpback whales exposed to explosions showed little or no behavioral reaction to the noise. They were neither displaced nor changed their overall movements, yet subsequently displayed an unusual pattern of greater fatal entanglement in fishing gear, possibly because hearing impairment limited their ability to detect the nets through passive acoustics or some other compromise to their navigational or sensory systems (Todd et al. 1996). Entrapment rates increased during the time and in the area of blasting, even though there were fewer fishing nets in this area (Todd et al. 1996). Had these whales not blundered into nets in an unusual pattern (something that was discerned only because of a good previous baseline of whale entrapments in this area), this impact would not have been detected.

Stress

Noise is a known stressor and can affect the neuroendocrine system. Rats exposed to mild irregular white noise (~25 dB over background noise) for 9 h over 8 days exhibited a significant increase in basal prolactin, corticosterone, and noradrenaline levels, showing “subtle but significant changes in hormonal regulation” (van Raaij et al. 1997). Cardiovascular function in both animals and humans may be permanently impacted over the long term from prolonged exposure to noise (e.g., Altura et al. 1992). Stress effects or physiological changes, if chronic, can inhibit the immune system or otherwise compromise the health of animals. These can be very difficult to detect in cetaceans. Stress hormone levels increased with increasing noise-level exposure in a captive beluga whale (Romano et al. 2004). Norepinephrine, epinephrine, and dopamine levels were significantly higher under high-noise conditions compared with low-noise or control conditions. Dolphins also reacted to a dolphin threat sound by changes in heart rate (Miksis et al. 2001). For terrestrial animals at least, chronic stress can have repercussions for the health of populations, as it can affect fertility, mortality, and growth rates.

Variability of responses

Responses to noise can be highly variable, depending on species, individuals, age, sex, physical state, presence of offspring, prior experience, characteristics of the noise source, and other factors. Animals also react differently depending on their behavioral state or situation (e.g., whether at depth, resting, migrating, feeding, or breeding). Bowhead whales, for instance, showed avoidance of seismic air-gun noise at received levels of 120–130 dB (rms over pulse duration) during their fall migration, but they were much more tolerant when feeding in the summer, avoiding levels of 158–170 dB, which are roughly 10 000 times more intense (Richardson et al. 1995, 1999). Humpback cows and calves in key habitat demonstrated avoidance of seismic air guns at 140–143 dB re 1 μ Pa mean squared pressure, which was lower than the reaction of migrating humpbacks at 157–164 dB re 1 μ Pa mean squared pressure (McCauley et al. 2000). Species with similar hearing capabilities and audiograms showed markedly different responses to air-gun noise off British Columbia, with harbor porpoises appearing to be the most sensitive, responding to seismic noise at distances of >70 km, at received levels of <145 dB re 1 μ Pa rms (International Whaling Commission 2007). Similarly, a harbor porpoise showed a significant reaction to a pinger or acoustic deterrent device, though there was little response or change in behavior in a striped dolphin (*Stenella coeruleoalba* (Meyen, 1833)) (Kastelein et al. 2006). Thus, the reaction of one cetacean species to a noise source cannot necessarily be extrapolated to other cetacean species.

Apparent tolerance

Cetaceans also exhibit many examples of apparent tolerance to anthropogenic noise. Adult male sperm whales foraging in polar waters did not alter their acoustic output in response to seismic noise at received levels of up to 146 dB

⁵P.L. Tyack and C.W. Clark. 1998. Quick-look report: playback of low-frequency sound to gray whales migrating past the central California coast. Unpublished report. Available from the National Marine Mammal Laboratory, Seattle, Washington (e-mail: nmml.library@noaa.gov).

re 1 μ Pa peak-to-peak (Madsen et al. 2002). Avoidance was not observed with whales remaining in the area for at least 13 days of exposure. They also did not fall silent when artificial codas were presented to them (Madsen et al. 2002), in contrast to previous research using pingers (Watkins and Schevill 1975). The click rates and behavior of male sperm whales did not change during the discharge of detonators off Norway, exposing animals to received levels of around 180 dB re 1 μ Pa rms (Madsen and Møhl 2000). Croll et al. (2001) found no obvious responses of foraging blue and fin whales to LFA sonar transmissions at received levels of between 95 and 150 dB. Sperm whales in the Gulf of Mexico showed no significant change in their swim direction when exposed to seismic noise, and their horizontal movements were random in relation to an active seismic vessel (International Whaling Commission 2007).

There are also many cases of cetaceans remaining in, or repeatedly returning to, high-noise environments for prolonged periods. However, animals may be strongly motivated to stay in an area for the purposes of foraging or mating, even to the point of damaging their hearing. Sea lions (*Zalophus californianus* (Lesson, 1828)) will sometimes stay in a prime feeding area despite the presence of noise presumably loud enough to harm their hearing (National Marine Fisheries Service 1996). Moreover, the number of animals visible at the surface near a loud sound source may not be a reliable measure of their tolerance. Instead, they may be exhibiting vertical avoidance of the noise, since sound levels are lower at the surface than at depth (Würsig and Richardson 2002).

Short-term responses vs. long-term impacts

The biological significance (e.g., consequences for health, survival, or reproduction) of behavioral responses to noise in cetaceans is difficult to ascertain. For practical reasons, often only short-term reactions to noise are studied. How or whether short-term responses translate into long-term impacts is often beyond current scientific knowledge, however, especially for cetaceans. Short-term effects may indicate serious population consequences or they may be insignificant. Conversely, long-term population impacts may occur in the absence of dramatic or even observable short-term reactions, as has been demonstrated in bottlenose dolphins (Bejder 2005) and caribou (*Rangifer tarandus* (L., 1758)) (Harrington and Veitch 1992). Bejder (2005) found a reduction in bottlenose dolphin calf survival with whale-watching vessels, though short-term behavioral responses seemed very moderate. Harrington and Veitch (1992) found that caribou calf survival was reduced when females were exposed to low-level jet overflights during certain critical periods, despite exhibiting only an apparently minor short-term startle response. Thus, short-term research may be of very limited use in determining biologically significant effects of noise on cetaceans. Long-term studies, however, have more successfully related disturbance reactions to population impacts (Bejder 2005).

In the past, short-term impact studies have been conducted (e.g., the ATOC or LFA sonar research programs) but have resulted in outcomes that simply lead to more controversy about whether these responses are biologically significant or are deemed inconsequential to the health of the

cetacean population. As such, it may be advisable to only carry out short-term studies if there is prior agreement between researchers and regulators as to which short-term reactions would constitute a population-level effect. Ideally, particular effect sizes that would be considered “biologically significant” should be delineated prior to the study, e.g., a 1% reduction in indications of feeding may not be considered enough to impact a population, whereas a 5% reduction may be. If such a size of effect (or at least a range of effect sizes) cannot be agreed upon between researchers and regulators, the study will have little chance of contributing to management and, thus, may not be worth pursuing, especially in cases where the research poses some appreciable risk to cetaceans.

Controlled exposure experiments or CEEs (or behavioral response studies as they have been called more recently) are an example of research that can place animals at risk. CEEs purposely expose animals to an acoustic stimulus to assess behavioral responses. In contrast to what is implied by the name “controlled exposure experiment”, these studies cannot exactly control the exposure of noise (or dose) to the animal in the wild, since the animal is moving in three dimensions, not visible for most of the time, and the propagation of the noise is not usually precisely predictable. Rather, the experimenter controls the emission of the noise, at the source. As such, it is unknown what levels of noise the animal is actually receiving in real time. Even when a cetacean has been tagged with a device that measures received levels of sound (e.g., Dtag; Johnson and Tyack 2003), these levels can only be accessed once the tag has been recovered from the whale as the data are archived. Even then, received levels at the tag could be considerably underestimated because of body shading, if the cetacean’s body is between the sound source and the tag, causing greater attenuation (Madsen et al. 2006). Thus, Nowacek et al.’s (2007) contention that the interpretation of animal responses to noise is practically impossible without received levels is somewhat problematic, not to mention overly narrow.

While CEEs can be valuable in improving our understanding of the effects of noise exposure, they raise animal welfare concerns, especially as the exposure thresholds that may cause pain or stress are not well understood. For greatest validity, noise exposures must be realistic, with the same characteristics of the sound as will be used in practice. However, to reduce risk to the animals, CEEs often start at levels well below operational ones. This is safer but does not give much insight into responses at the levels of interest, namely under actual deployment conditions. While one can increase the sound level of the exposure gradually, whales may exhibit a threshold response that could occur without warning, especially as exposure levels are unknown by the experimenter at the time of the playback of sound. Exposures at the higher levels, on the other hand, place animals at risk, particularly in the case of naval sonars and beaked whales, where there may be fatal reactions that will be hard to predict. Thus, both scenarios (realistic but potentially hazardous vs. unrealistic but safer) yield results of limited usefulness, meaning that CEEs will remain problematic and controversial and must be considered with great care.

Additional concerns about CEEs are that there are cur-

rently insufficient baseline data to quantify the strength of various different responses from noise exposure. As noted above, to determine long-term effects, it is best to carry out long-term research, yet it is difficult and impractical to carry out a controlled experiment in the ocean over larger scales of space (tens of kilometres) and time (many months). It is also difficult to find controls that mimic the experimental setting in all respects, except for the addition of noise, and to eliminate confounding (spatio-temporal) factors such as location, season, and oceanographic conditions. Using realistic noise exposures and sources can be impractical and expensive, as some noise sources (e.g., military sonars) cannot easily be replicated and would require a specifically outfitted vessel. Alternatives to CEEs include systematic observations of populations in different noise conditions and regimes using ongoing sound-producing activities that do not require the artificial addition of noise. It must be recognized, however, that observational studies that require animals to be followed closely and obtrusively by boats with unpredictable patterns of movement are likely to cause harassment. This could be avoided in some situations by cliff-top observations or remote sensing, e.g., bottom-mounted acoustic sensors to detect changes in animal vocalizations with noise. On the other hand, if the observation vessel is maneuvered sensitively in ways that are predictable to the study species, there does not seem to be a statistically significant behavioral impact on cetaceans, at least in certain environments and conditions (Lusseau 2003, 2006), though masking effects from boat engine noise cannot be excluded.

The above is not meant to represent a blanket condemnation of CEEs, but rather to highlight the risks and limitations of this research method in certain situations. In cases where the addition of noise from a CEE only represents a small fraction of the same type of anthropogenic noise that the animals in the area are receiving anyway, the risk is probably inconsequential and much valuable knowledge can be gained from such experiments. Also, playbacks of commonly encountered natural sounds to cetaceans (e.g., prey sounds) are unlikely to be hazardous to them. However, while researchers conducting CEEs usually argue that the risk CEEs pose is counteracted by the potential conservation benefit to the animals (and indeed, this is one of the rationales behind the bona fide marine mammal research permit in the US), the few directly relevant CEEs on wild marine mammals have not clearly been translated into impact thresholds or conservation measures in the US. I am not aware of any CEE using LFA sonar, ATOC, or seismic noise that resulted in any more stringent or protective management measures, despite clear (but difficult to interpret) responses exhibited by the animals to the noise exposure. On the contrary, allowable noise exposure levels have steadily risen (become less protective) in recent years.

While Nowacek et al. (2007) argue strongly for the use of CEEs and also cite Bejder et al. (2006a, 2006b), they do not clarify sufficiently that the short-term CEE used in this research would have, in fact, resulted in conclusions that were contrary to what the long-term (non-CEE) study determined (Bejder et al. 2006a). From the CEE alone, the moderate behavioral responses of the impact-site dolphins seemed to show that long-term tourism vessel activity had no adverse effect on resident dolphins (Bejder et al. 2006a). Only be-

cause of the long-term study of photo-identified dolphins, however, were Bejder et al. (2006b) able to conclude that dolphin-watching tourism contributed to a long-term decline in abundance at the impact site. Adult females seem to stay in the impact site and suffer reduced reproductive success (Bejder 2005), though ecological contributing factors (e.g., prey abundance) could not be ruled out. Thus, CEEs lend themselves to being more easily incorrectly interpreted than long-term studies, further limiting the usefulness of CEEs.

Disturbance studies

Disturbance studies can be similarly difficult to interpret, as they may yield counterintuitive or paradoxical results. For instance, in some species and situations, the weaker the behavioral response, the more serious the impact on the population. Individuals with lower energy reserves or no alternative habitat cannot afford to flee repeatedly from disturbance but are forced to remain and continue feeding, apparently unresponsive to disruption (Gill et al. 2001; Stillman and GossCustard 2002). Yet these individuals are in fact more vulnerable to disturbance. Again, animals do not always react in an observable or obvious manner even if they are seriously impacted.

When repeatedly exposed to the same type of noise, animals may habituate or become accustomed to that particular noise over time. Alternatively, animals may show a heightened responsiveness to noise over time, especially if it is associated with a negative experience. Unfortunately, hearing impairment can be misinterpreted to represent habituation, as both would appear to the observer as a decrease in responsiveness to noise. In addition, what appears to be habituation may in fact be the most sensitive individuals permanently vacating the area, while the least sensitive stay (Bejder et al. 2006a). These two scenarios can only be distinguished if all individuals are known and tracked (Bejder et al. 2006b). This is another reason why indepth long-term studies are needed to clarify the full picture of impacts.

Cumulative and synergistic effects

The threats cetaceans are confronted with, such as fisheries bycatch, habitat degradation, chemical pollution, whaling, vessel strikes, and global warming, do not often occur in isolation. Such stressors may interact cumulatively or synergistically. For example, human impacts on marine ecosystems such as overfishing, eutrophication, climate change, and ultraviolet radiation interact to produce a larger effect than simply the sum of their parts (Lotze and Worm 2002; Worm et al. 2002). In the same way, anthropogenic noise could interact with marine mammal bycatch or ship collisions by preventing animals from sensing fishing gear or oncoming vessels (through either hearing damage or masking), making them more vulnerable to injury or death, as some evidence seems to indicate (Todd et al. 1996; Andre et al. 1997). Multiple sources of noise could also interact cumulatively or synergistically, such as when several seismic surveys take place in adjacent or even the same areas, or naval sonars from multiple ships produce confusing sound fields. Studies on fish have demonstrated that "... failure to properly account for interactions occurring between stressors can lead to substantial underestimation of stressor effects, particularly as stressor intensity rises" (Power 1997). Of course, synergistic interactions may also work in the opposite direc-

tion, in that stressors may at least partially cancel one another out. Regardless of the direction of the interaction, synergistic effects must be taken into account to properly evaluate the impacts of multiple stressors, though this will prove challenging when studying the consequences of noise on cetaceans.

Indirect impacts of noise on cetaceans

Although public attention has focussed on the effects of undersea noise on cetaceans, an increasing amount of research has established impacts on a broad range of species throughout the marine ecosystem, including fish and invertebrates. Cetaceans cannot be considered in isolation from other marine species, and acoustic impacts on prey species are of particular concern, as these may indirectly affect cetacean populations. Even apparent short-term responses of cetaceans to noise, such as fewer prey-capture attempts, may in reality represent reactions of the prey species to noise, with cetaceans responding to the prey rather than directly to the noise. Thus, a brief overview of selected studies on fish and invertebrates is warranted.

Fish are very acoustic animals, in general, using sound to perceive their environment, for mating, communication, and predator avoidance (Popper 2003). Settling reef fish larvae orient toward and select reefs based on sound (Simpson et al. 2005).

A wide range of acoustic impacts on fish has been observed. Seismic air guns extensively damaged fish ears at distances of 500 m to several kilometres from seismic surveys. No recovery was apparent 58 days after exposure (McCauley et al. 2003). TTS has been induced in several fish species, sometimes under fairly moderate levels of noise exposure and with fish occasionally requiring weeks to recover their hearing (Scholik and Yan 2002a; Amoser and Ladich 2003; Smith et al. 2004). In other species (e.g., bluegill sunfish, *Lepomis macrochirus* Rafinesque, 1819), no significant change in auditory sensitivity with noise was observed (Scholik and Yan 2002b). Noise has been shown to produce a stress response in some fish (Smith et al. 2004; Wysocki et al. 2006), but not in others (McCauley et al. 2000). Behavioral reactions to anthropogenic noise include dropping to deeper depths, milling in compact schools, "freezing", or becoming more active (Dalen and Knutsen 1987; Pearson et al. 1992; Skalski et al. 1992; Santulli et al. 1999; McCauley et al. 2000; Slotte et al. 2004). Reduced catch rates of 40%–80% and decreased abundance have been reported near seismic surveys in species such as Atlantic cod (*Gadus morhua* L., 1758), haddock (*Melanogrammus aeglefinus* (L., 1758)), rockfish (genus *Sebastes* G. Cuvier, 1829), herring (*Clupea harengus* L., 1758), sand eel (*Ammodytes marinus* Raitt, 1934), and blue whiting (*Micromesistius poutassou* (Risso, 1827)) (Dalen and Knutsen 1987; Løkkeborg 1991; Skalski et al. 1992; Engås et al. 1996; Hassel et al. 2004; Slotte et al. 2004). Other studies have shown no significant change in the hook-and-line catch rate (Pickett et al. 1994) and no migration out of the seismic survey area (Pickett et al. 1994; Wardle et al. 2001; Hassel et al. 2003). Popper et al. (2007) exposed rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)), a nonhearing specialist, to LFA sonar to a maximum received rms level of 193 dB re 1 μPa^2 for 324 or 648 s. They found a 20 dB hearing thresh-

old shift at 400 Hz, but there was within-species variation in different groups of trout obtained from the same supplier. As a freshwater species, this species would not be exposed to LFA sonar during operation.

There have also been indications that invertebrates are not immune from the effects of anthropogenic noise. Nine giant squid (*Architeuthis dux* Steenstrup in Harting, 1860) mass stranded, some of them live, together with geophysical surveys using air guns in 2001 and 2003 in Spain (Guerra et al. 2004). The squid all had internal injuries, some severe, with internal organs badly damaged. Bruised ovaries and injuries to the equilibrium receptor system or statocysts were also observed. Fisheries and Oceans Canada (formerly the Department of Fisheries and Oceans) held a scientific peer-review meeting in September 2004 of a study of snow crabs (*Chionoecetes opilio* (J.C. Fabricius, 1788)) under seismic noise conditions. Crabs showed bruised organs and abnormal ovaries, delayed embryo development, smaller larvae, sediments in their gills and statocysts, and changes consistent with a stress response compared with control animals (Department of Fisheries and Oceans 2004). Differences in environmental conditions between control and experimental sites may have accounted for some of the differences in response, but reviewing scientists largely felt these observations warranted concern. Brown shrimp (*Crangon crangon* (L., 1758)) reared in tanks showed an increase in metabolic rate with moderate increases in continuous background noise, leading to significant reduction in growth and reproduction over 3 months (Lagardère 1982; Régnault and Lagardère 1983).

Management implications

Safe exposure levels

Regulators have often sought to establish a particular noise level that would trigger management action, such as temporary shut-down of the noise source until the cetacean moves away. Such a noise level has been very difficult to determine, particularly as there is such a wide variety of responses between species, situations, and noise sources to name a few. Prior to 1994, the US National Marine Fisheries Service used the "120 dB criterion" as a received level above which potentially harmful noise effects may occur, and thus attempted to limit exposures to animals to below this level. The "120 dB criterion" was based on two series of field studies (Malme et al. 1983, 1984; Richardson et al. 1985, 1990) in which gray and bowhead whales showed a remarkable consistency in avoidance of continuous industrial noise at average received levels of 120 dB re 1 μPa (SPL, sound pressure level). Since then, allowable noise levels in the US have increased to 195 dB re 1 $\mu\text{Pa}^2\text{-s}$ received energy flux density for TTS and 215 dB re 1 $\mu\text{Pa}^2\text{-s}$ received energy flux density for PTS. Energy flux density (EL) is a measure that incorporates duration of exposure which seems appropriate, but is nevertheless based on very limited data from a few individuals of a few species. For a sound of 1 s duration, this level for only TTS (195 dB) is more than 10 000 000 times more intense than 120 dB (the decibel scale is logarithmic). EL is calculated as $\text{SPL} + 10 \log_{10} T$, where T is the sound duration (s). Thus, the allowable exposure level would be 185 dB re 1 $\mu\text{Pa}^2\text{-s}$ for a 10 s exposure

duration and 175 dB re 1 $\mu\text{Pa}^2\cdot\text{s}$ for a 100 s exposure duration. These exposure levels would only reach 120 dB re 1 $\mu\text{Pa}^2\cdot\text{s}$ after over 31 000 000 s or about 1 year (359 days).

Mitigation measures and their shortcomings

Mitigation measures are sometimes used to reduce the exposure of cetaceans to noise, though the effectiveness of many of these tools has not been established or even studied. Mitigation guidelines also vary considerably between countries and noise sources. Weir and Dolman (2007) compared marine mammal mitigation guidelines for seismic surveys between regions, making recommendations for a worldwide standard.

Safety zones are a common mitigation measure. Here, visual observers scan for cetaceans near the sound source and temporarily shut it down or reduce its power if animals are spotted within a prescribed distance. The size of a safety zone is determined based on a particular noise level above which cetaceans should not be exposed. Not only is this assumed “safe” noise level difficult to determine (see above), but ascertaining the safety zone distance corresponding to this level is not always straightforward. Sound levels drop with increasing distance from the source, but sometimes in complex ways. For example, US regulations prohibit exposing cetaceans to levels >180 dB rms re 1 μPa and establish a safety zone of 500 m. While this has become standard practice in some jurisdictions, not only is there little scientific justification for the 180 dB rms criterion, but several studies have demonstrated that for some noise sources in some environments exposures >180 dB rms can occur well beyond 500 m (International Whaling Commission 2007). Madsen et al. (2006) found that in the Gulf of Mexico received levels can be as high at a distance of 12 km from a seismic survey as they are at 2 km (in both cases >160 dB peak-to-peak). Received levels, as determined from tags on sperm whales, generally decreased at distances of 1.4 to 6–8 km from the seismic survey, but then at greater distances, levels increased again (Madsen et al. 2006). Moreover, Madsen (2005) pointed out that it is inappropriate to specify “safe” noise levels (such as the 180 dB rms criterion) by rms pressures for transients like seismic pulses. This measure depends on the window of time used to average squared pressures, resulting in differences of 2–12 dB in rms sound pressure for the same waveform. Thus, to more accurately characterize the energy of the pulse in the interest of preventing exposures to damaging high-peak pressures, safety levels for transients should be given by received peak-to-peak SPLs and energy flux density, rather than rms SPLs (Madsen 2005).

The frequency content and thus propagation of noise sources can also be different from what was originally thought, requiring constant verification in the field, rather than simply acoustic modelling. For instance, Goold and Fish (1998) and International Whaling Commission (2007) demonstrated that significant high-frequency noise and horizontal propagation is produced by seismic surveys, despite air guns generally being designed to produce mainly low-frequency sound directed vertically downward. Similarly, species can sometimes sense sounds that they would not be predicted to sense. Low-frequency noise generated by offshore wind turbines, for instance, is still audible to high-frequency special-

ists such as harbor porpoises, as evidenced by their reactions to it (Koschinski et al. 2003). As mentioned above, it is conceivable that animals may be able to detect other features of noise (e.g., its “envelope”) or may be sensing vibrations through their skin or through resonance or other nonauditory effects.

The effectiveness of visual safety zones in reducing the exposure of cetaceans to harmful noise is also questionable because visual detection rates for cryptic species such as beaked whales are very poor, especially under conditions of poor visibility (high winds, night, fog, etc.). For deep-diving beaked whales, average detection rates are only 1%–2% of all animals under typical survey conditions (Barlow and Gisiner 2006).

Similarly, use of the mitigation tool known as “ramp-up” or “soft start” assumes that animals will move away if the noise source is gradually increased in loudness. This has never been proven, however. In fact, “ramp up” may do more harm than good if animals approach the sound source initially out of curiosity when levels are still low and then become exposed to loud levels before they have a chance to retreat. In addition, as sound fields can be complex, “ramp ups” may not give the animal enough information to know in which direction to swim to minimize their noise exposure. Stone and Tasker (2006) found that the distance cetaceans were from the seismic survey vessel during “ramp up” was not significantly different from when the vessel was either shooting at full power or not shooting at all. However, cetaceans were generally seen heading away from the seismic vessel during “ramp up”, and some animals were seen to startle during the beginning of the “ramp up”, suggesting a full-powered start up would perhaps have elicited an even greater startle reaction.

Precaution

Because of the limited ability of scientific methods to detect the full impacts of noise on cetaceans and especially on the wider marine environment, and because of the potential for harm to occur before it is detected, the noise issue has been highlighted as a case where the application of precaution in management is particularly warranted (Mayer and Simmonds 1996). It is improbable that there will be conclusive evidence of causality for many, especially subtle, acoustically induced potential population-level impacts, particularly within the time frames where irreversible population and ecosystem-level effects may occur (Weilgart 2007). For instance, detecting precipitous declines in most marine mammal stocks, let alone population decreases linked with noise impacts, is all but impossible without substantially increased monitoring effort. Taylor et al. (2007) noted that 72% of large whale declines, 90% of beaked whale declines, and 78% of dolphin or porpoise declines would not be detected under current monitoring effort, even if the declines were so dramatic as to represent a 50% decrease in abundance in 15 years.

For such reasons, increasing numbers of international legislative fora have recognized that protective and preventative action should not be delayed until full scientific certainty is established, the so-called precautionary approach. For instance, as previously mentioned, the United Nations Convention on the Law of the Sea defines “pollution of the

marine environment” as “the introduction by man, directly or indirectly, of substances or energy into the marine environment . . . which results or is likely to result in such deleterious effects as harm to living resources and marine life . . .” (article 1.1.4). The reference to “is likely to result” in the definition indicates that “deleterious effects” do not need to be evident yet but would reasonably be expected to occur. Thus, precaution is inherent in the definition. This definition of marine pollution has been incorporated verbatim into several international conventions and treaties, e.g., the OSPAR and Helsinki Conventions, UNEP Regional Seas Program, etc. (Dotinga and Oude Elferink 2000). The precautionary approach increases the chances of being able to contain an environmental problem before irreversible damage is done. As such, reducing overall noise levels (the “acoustic footprint”) in the marine environment should be a priority. Secondly, distancing noise events from biologically important areas or concentrations of cetaceans should be pursued. These two mitigation measures will probably go furthest in protecting cetaceans from anthropogenic noise.

Source modification

Engineering modifications of the sound source and the use of alternative technologies can reduce overall noise levels. For instance, for seismic air guns, the International Whaling Commission’s Scientific Committee recommended additional research into other alternate signal sources or techniques (International Whaling Commission 2007). In addition to reducing overall noise levels, changes to certain characteristics of noise sources could make them less damaging to cetaceans. It is unknown exactly which characteristics are especially harmful, but some educated guesses can be made based on the characteristics of the animals’ own calls. For example, sound sources using mid-frequencies (1–20 kHz) or low frequencies above ~5 Hz, those with longer durations, rapid rise times, broad directionality (wide beams), higher duty cycles (percentage of time actually transmitting), and repetition rates would probably be most problematic for cetaceans (Møhl 2004). Consequently, noise producers could be developing alternatives that minimize these characteristics to the extent possible. The following are examples of ways in which overall noise levels could be reduced:

- Quieter ships can be constructed, as this is well within current technological knowledge and capability. Propellers can be designed to limit cavitation, the formation and collapse of tiny air bubbles, which is the source of most shipping noise. Noncavitating, surface-piercing drives are already available for smaller boats. Sound isolating and absorbing techniques such as resilient isolation mounts, flexible hoses, and pipe hangers can reduce radiated mechanical energy (Southall 2005). Much mechanical noise can be minimized by good engine maintenance. Such measures would tend to increase efficiency, decrease fuel usage, and reduce engine repairs, while providing quieter, more comfortable living conditions for humans onboard (Southall 2005). While retrofitting ships to make them quieter is usually a much more expensive proposition than building them new using quieting technologies, an exception is the use of large kites such as SkySails (<http://skysails.info/index.php?L=1> [accessed 23 Novem-

ber 2007]) that can be attached to the bow of practically any ship to dramatically increase fuel efficiency and decrease engine noise at the same time. Especially slower moving ships such as tankers could benefit from this technology. It is possible that some classes of ships, such as tankers, may contribute disproportionately to shipping noise, in which case such harnessing of wind power could make a considerable difference in reducing ocean noise. Altering shipping routes to distance them from biologically important cetacean habitats is another method for reducing sound levels in critical areas, and this mitigation would have the added benefit of reducing the risk of ship collisions with whales. Reducing ship speed also minimizes the chances of collisions with whales while reducing noise output. Laist et al. (2001) found that most serious or lethal injuries to whales from ship strikes occurred when ships were travelling at or in excess of 14 knots (~26 km/h).

- As an alternative to air guns used for seismic surveys, a quieter marine vibrator has been developed with substantially less energy above 100 Hz (Deffenbaugh 2002). A disadvantage of this technology is that, while quieter, the duration of noise is longer. Other alternatives include a mobile sea floor source with surface trawled receivers or even a fully autonomous sea floor seismic survey vehicle, as well as electromagnetic imaging or mapping. A highly sensitive optical fibre hydrophone (underwater microphone) developed in Australia may be a potential alternative to seismic air guns. This sensor could also be used for security and submarine surveillance, though it requires further testing. (<http://theage.com.au/news/National/New-sensor-to-boost-undersea-exploration/2005/08/18/1123958156896.html> [accessed 23 November 2007]). Geophysicists have found that they can process background acoustic noise to gain information about the earth’s crust, perhaps eventually obviating the need for seismic air guns. (<http://sciencedaily.com/releases/2006/12/061207161055.htm> [accessed 23 November 2007]). Increasing the number, configuration, and capacity of hydrophone receivers in general or improving signal-processing techniques could allow for reduced noise levels or a smaller area of impact (less horizontal propagation). The development of “suppressor” devices to reduce the high-frequency noise content from air guns, an unnecessary byproduct, has been recommended by the Joint Nature Conservation Committee (2004).
- The Dutch and Norwegian navies are experimenting with techniques to alter the characteristics of some of their sonars to reduce the risk to whales (Lok 2004). Levine et al. (2004) advised the US Navy to explore the use of complex waveforms that would retain Doppler sensitivity but would have lower peak amplitudes (Levine et al. 2004). A new sensor using optical fibres has been developed that can detect quiet underwater targets such as enemy submarines, while also providing unambiguous directional information without the addition of noise (<http://physorg.com/news89307791.html> [accessed 23 November 2007]).

Many of the abovementioned new technologies are still in development but are presented as possibilities or visions for the future.

Seasonal and geographic exclusions

Geographic areas or regions that are considered biologically important for cetaceans (breeding, feeding, and migratory areas) should be distanced from noise events or activities either seasonally, or year-round, depending on cetacean abundance. In November 2004, for example, because of the many past beaked whale strandings in the area, the Spanish government announced a moratorium on the military use of active sonar in waters around the Canary Islands of Lanzarote and Fuerteventura, out to a distance of 50 km (resolución 79/2004, 102 Boletín Oficial del Estado 16643-45, Statement of Bono Martínéz, Senior Defense Minister of Spain). Oil and gas explorations and, seasonally, vessel traffic are not allowed in the Marine Mammal Protection Zone in the Great Australian Bight (Anonymous 2005). The Brazilian government has prohibited seismic surveys off the Bahia and Espírito Santo coast during the humpback whale breeding season, a measure considered positive by the International Whaling Commission's Scientific Committee (International Whaling Commission 2007).

Marine protected areas

Marine protected areas (MPAs), if well-managed, offer one of the most effective means to protect cetaceans and their habitat. MPAs are also one of the only ways to safeguard cetaceans from the cumulative and synergistic impacts of noise, as well as from other anthropogenic stressors. Models of cetacean distribution could identify cetacean "hot spots" globally, which can be used to determine the location of suitable MPAs. Regulations surrounding MPAs should extend toward the entire ecosystem if they are to achieve their purpose. Noise buffer zones around existing and new MPAs may be required for adequate protection from noise sources.

Reduction in noise-producing activities

Different companies sometimes seismically survey the same areas for competitive reasons. Some of this duplication could be avoided by having companies share data or by employing a common surveyor. By maximizing the coverage of seismic survey lines to reduce the number of passes, by using simulators wherever possible in naval training exercises, and by attempting to fill every cargo ship to capacity for every journey to minimize the number of trips needed, overall noise output can be reduced.

Monitoring

Monitoring and reporting are essential parts of management since the effectiveness of management actions can thus be determined. To adequately monitor the impacts of noise-producing activities, the detection level of cetacean strandings and mortalities at sea needs to be improved. Passive acoustic monitoring (PAM) is also useful to detect the presence of vocalizing cetaceans (information which can be used to determine whether or when a noise event should proceed), to assess the sources and levels of anthropogenic noise present, especially in important habitats such as MPAs, and to ascertain how noise affects the distribution and vocalizations of cetaceans. PAM can be undertaken using either towed hydrophones or remote autonomous recording devices.

Research recommendations

While research on the effects of undersea noise on cetaceans is undoubtedly worthwhile, it will be difficult to gain enough insight into such impacts to protect cetaceans within the foreseeable future. As such, perhaps the emphasis for future research should instead be on how to make noise safer. Improving mitigation tools would thus be a worthwhile goal.

- (1) Research should be focussed on developing more effective mitigation tools, such as improving PAM, and engineering modifications, such as finding quieter or safer alternatives to noise sources (e.g., with shorter durations, narrower directionality, eliminating unnecessary frequencies, etc.).
- (2) To avoid exposing concentrations of cetaceans and other marine life to noise, baseline research needs to be undertaken to identify such "hot spots". Conversely, "cold spots" or deserts for marine life could be more suitable for noise-producing activities and should be identified.
- (3) Thorough and complete retrospective analyses of stranding data should be conducted, using suitable controls. For greatest validity, noise events worldwide, including naval maneuvers, should be disclosed and documented. Stranding networks should be expanded worldwide and data consolidated, while up-to-date protocols for stranding necropsies should be established and distributed, to better detect acoustic injuries.
- (4) To gain the most indepth information on population-level impacts, long-term, systematic observations of known individual cetaceans in the wild are necessary. Individuals should be studied in different noise conditions using ongoing noise-producing activities to avoid adding more noise to the environment.
- (5) The effects of noise on ecological processes and population dynamics should be studied, along with the cumulative and synergistic effects of noise together with other environmental stressors.
- (6) Stress hormones (e.g., in feces) should be examined from cetaceans in noisy and quiet areas.
- (7) Hearing in more easily studied free-ranging cetaceans or pinnipeds could be studied in high-noise areas compared with suitable controls.

Conclusions

Anthropogenic ocean noise is clearly a serious issue for cetaceans, though the full scale of the problem is difficult to determine. Large areas of ocean can be affected by even one noise source, and noise levels are steadily increasing, dramatically so in some areas. Some strandings, especially those involving beaked whales, are conclusively caused by noise events such as military maneuvers involving naval sonars, and these strandings or mortalities at sea are likely underestimated. Such strandings can and have produced at least local population-level impacts in beaked whales. Other ways cetacean populations can be impacted by noise are through chronic effects such as increased stress levels, abandonment of important habitat, and masking, as well as vocal responses that may reduce foraging efficiency or mating opportunities. While such reactions to noise have all been documented in cetaceans, it is unclear whether they translate

into population impacts, as such impacts are particularly difficult to prove for cetaceans. Much uncertainty still exists about cetacean hearing, and extrapolations across individuals, species, age classes, etc., remain controversial. The cetacean auditory system may also not be the most sensitive system in the body to noise exposure, and a narrow focus on hearing impairment may miss important nonauditory effects of noise such as skin sensations, resonance, and gas and fat emboli.

Variability (between individuals, species, age classes, etc.) in the behavioral response to noise makes the management objective of establishing "safe" noise exposure levels difficult, in addition to the problems with using short-term responses to noise as an indication of long-term population impacts. Noise impacts on other components of the ecosystem, such as prey species, must also be considered for management purposes, especially as fish seem quite vulnerable to noise. In addition, cumulative and synergistic impacts of noise should be taken into account, as interactions between environmental stressors may magnify their impacts on cetaceans. In light of the many data gaps and uncertainties, a precautionary approach to managing noise seems warranted. While many mitigation tools are questionable in their effectiveness, the two that will probably go furthest in protecting cetaceans from noise are reducing noise levels and distancing noise from biologically important areas. Marine protected areas may be especially important in safeguarding cetaceans from cumulative and synergistic effects. Monitoring noise levels and cetacean vocalizations in such critical areas will also be key to the success of any management effort. In any case, it is clear that ocean noise must be managed both nationally and internationally to protect cetaceans and the marine ecosystem before irreversible damage occurs.

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References

- Aguilar Soto, N., Johnson, M., Madsen, P.T., Tyack, P.T., Boccocelli, A., and Borsani, J.F. 2006. Does intense ship noise disrupt foraging in deep-diving Cuvier's beaked whales (*Ziphius cavirostris*)? *Mar. Mamm. Sci.* **22**: 690–699. doi:10.1111/j.1748-7692.2006.00044.x.
- Altura, B.M., Altura, B.T., Gebrewold, A., Ising, H., and Günther, T. 1992. Noise-induced hypertension and magnesium in rats: relationship to microcirculation and calcium. *J. Appl. Physiol.* **72**(1): 194–202. PMID:1537714.
- Amoser, S., and Ladich, F. 2003. Diversity in noise-induced temporary hearing loss in otophysine fishes. *J. Acoust. Soc. Am.* **113**: 2170–2179. doi:10.1121/1.1557212. PMID:12703727.
- Andre, M., Kamminga, C., and Ketten, D. 1997. Are low-frequency sounds a marine hazard: a case study in the Canary Islands. *In* Proceedings of the Underwater Bio-Sonar Systems and Bioacoustics Symposium, Loughborough University, Leicestershire, UK, 16–17 December 1997. Institute of Acoustics, Hertfordshire, UK.
- Andrew, R.K., Howe, B.M., Mercer, J.A., and Dzieciuch, M.A. 2002. Ocean ambient sound: comparing the 1960s with the 1990s for a receiver off the California coast. *ARLO*, **3**: 65–70. doi:10.1121/1.1461915.
- Anonymous. 2005. Great Australian Bight Marine Park (Commonwealth Waters) management plan 2005–2012. Commonwealth of Australia, Canberra. Available from <http://environment.gov.au/coasts/mpa/publications/gab-plan.html> [accessed 28 February 2007].
- Au, W.W.L. 1993. *The sonar of dolphins*. Springer-Verlag, New York.
- Au, W.W.L., and Green, M. 2000. Acoustic interaction of humpback whales and whale-watching boats. *Mar. Environ. Res.* **49**: 469–481. doi:10.1016/S0141-1136(99)00086-0. PMID:11285724.
- Au, W.W., Carder, D.A., Penner, R.H., and Scronce, B.L. 1985. Demonstration of adaptation in beluga whale echolocation signals. *J. Acoust. Soc. Am.* **77**: 726–730. doi:10.1121/1.392341. PMID:3973242.
- Balcomb, K.C., and Claridge, D.E. 2001. A mass stranding of cetaceans caused by naval sonar in the Bahamas. *Bahamas J. Sci.* **8**: 1–8.
- Barlow, J., and Gisiner, R. 2006. Mitigating, monitoring and assessing the effects of anthropogenic sound on beaked whales. *J. Cetacean Res. Manag.* **7**: 239–249.
- Bejder, L. 2005. Linking short and long-term effects of nature-based tourism on cetaceans. Ph.D. thesis, Department of Biology, Dalhousie University, Halifax, N.S.
- Bejder, L., Samuels, A., Whitehead, H., and Gales, N. 2006a. Interpreting short-term behavioural responses to disturbance within a longitudinal perspective. *Anim. Behav.* **72**: 1149–1158. doi:10.1016/j.anbehav.2006.04.003.
- Bejder, L., Samuels, A., Whitehead, H., Gales, N., Mann, J., Connor, R., Heithaus, M., Watson-Capps, J., and Flaherty, C. 2006b. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. *Conserv. Biol.* **20**: 1791–1798. doi:10.1111/j.1523-1739.2006.00540.x. PMID:17181814.
- Bryant, P.J., Lafferty, C.M., and Lafferty, S.K. 1984. Reoccupation of Guerrero Negro, Baja California, Mexico, by gray whales. *In* The gray whale, *Eschrichtius robustus*. Edited by M.L. Jones, S.L. Swartz, and S. Leatherwood. Academic Press, Orlando, Fla. pp. 375–387.
- Bowles, A.E., Smultea, M., Würsig, B., DeMaster, D.P., and Palka, D. 1994. Relative abundance and behavior of marine mammals exposed to transmissions from the Heard Island Feasibility Test. *J. Acoust. Soc. Am.* **96**: 2469–2484. doi:10.1121/1.410120. PMID:7963037.
- Buckstaff, K.C. 2004. Effects of watercraft noise on the acoustic behavior of bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Mar. Mamm. Sci.* **20**: 709–725. doi:10.1111/j.1748-7692.2004.tb01189.x.
- Chang, E.F., and Merzenich, M.M. 2003. Environmental noise retards auditory cortical development. *Science* (Washington, D.C.), **300**: 498–502. doi:10.1126/science.1082163. PMID:12702879.
- Claridge, D.E. 2006. Fine-scale distribution and habitat selection of

- beaked whales. M.Sc. thesis, Department of Zoology, University of Aberdeen, Aberdeen, Scotland, UK.
- Connor, R.C., and Smolker, R.A. 1985. "Pop" goes the dolphin: a vocalization male bottlenose dolphins produce during consortships. *Behaviour*, **133**: 643–662.
- Cook, M.L.H. 2006. Behavioral and auditory evoked potential (AEP) hearing measurements in odontocete cetaceans. Ph.D. thesis, College of Marine Science, University of South Florida, St. Petersburg.
- Cook, M.L.H., Varela, R.A., Goldstein, J.D., McCulloch, S.D., Bossart, G.D., Finneran, J.J., Houser, D., and Mann, D.A. 2006. Beaked whale auditory evoked potential hearing measurements. *J. Comp. Physiol. A*, **192**: 489–495. doi:10.1007/s00359-005-0086-1.
- Cosens, S.E., and Dueck, L.P. 1993. Ice breaker noise in Lancaster Sound, NWT, Canada: implications for marine mammal behavior. *Mar. Mamm. Sci.* **9**: 285–300. doi:10.1111/j.1748-7692.1993.tb00456.x.
- Cox, T.M., Ragen, T.J., Read, A.J., Vos, E., Baird, R.W., Balcomb, K., Barlow, J., Caldwell, J., Cranford, T., Crum, L., D'Amico, A., D'Spain, G., Fernández, A., Finneran, J., Gentry, R., Gerth, W., Gulland, F., Hildebrand, J., Houser, D., Hullar, T., Jepson, P.D., Ketten, D., MacLeod, C.D., Miller, P., Moore, S., Mountain, D., Palka, D., Ponganis, P., Rommel, S., Rowles, T., Taylor, B., Tyack, P., Wartzok, D., Gisiner, R., Mead, J., and Benner, L. 2006. Understanding the impacts of anthropogenic sound on beaked whales. *J. Cetacean Res. Manag.* **7**: 177–187.
- Croll, D.A., Clark, C.W., Calambokidis, J., Ellison, W.T., and Tershy, B.R. 2001. Effect of anthropogenic low-frequency noise on the foraging ecology of *Balaenoptera* whales. *Anim. Conserv.* **4**: 13–27. doi:10.1017/S1367943001001020.
- Croll, D.A., Clark, C.W., Acevedo, A., Tershy, B., Flores, S., Gerdamke, J., and Urban, J. 2002. Only male fin whales sing loud songs. *Nature (London)*, **417**: 809. doi:10.1038/417809a. PMID:12075339.
- Crum, L.A., and Mao, Y. 1996. Acoustically enhanced bubble growth at low frequencies and its implications for human diver and marine mammal safety. *J. Acoust. Soc. Am.* **99**: 2898–2907. doi:10.1121/1.414859. PMID:8642113.
- Crum, L.A., Bailey, M.R., Guan, J., Hilmo, P.R., Kargl, S.G., Matula, T.J., and Sapozhnikov, O.A. 2005. Monitoring bubble growth in supersaturated blood and tissue *ex vivo* and the relevance to marine mammal bioeffects. *ARLO*, **6**: 214–220. doi:10.1121/1.1930987.
- Dalebout, M.L., Robertson, K.M., Frantzis, A., Engelhaupt, D., Mignucci-Giannoni, A.A., Rosario-Delestre, R.J., and Baker, C.S. 2005. Worldwide structure of mtDNA diversity among Cuvier's beaked whales (*Ziphius cavirostris*): implications for threatened populations. *Mol. Ecol.* **14**: 3353–3371. doi:10.1111/j.1365-294X.2005.02676.x. PMID:16156808.
- Dalen, J., and Knutsen, G.M. 1987. Scaring effects on fish and harmful effects on eggs, larvae and fry by offshore seismic explorations. *In Progress in underwater acoustics. Edited by H.M. Merklinger.* Plenum Press, New York. pp. 93–102.
- Deffenbaugh, M. 2002. Mitigating seismic impact on marine life: current practice and future technology. *Bioacoustics*, **12**: 316–318.
- Dehnhardt, G. 2002. Sensory systems. *In Marine mammal biology. Edited by A.R. Hoelzel.* Blackwell Science Ltd., Oxford, UK. pp. 116–141.
- Department of Fisheries and Oceans. 2004. Potential impacts of seismic energy on snow crab. DFO Can. Sci. Advis. Sec. Habitat Status report No. 2004/003.
- Dotinga, H.M., and Elferink, A.G.O. 2000. Acoustic pollution in the oceans: the search for legal standards. *Ocean Dev. Int. Law*, **31**: 151–182. doi:10.1080/009083200276102.
- Ellison, W.T., Clark, C.W., and Bishop, G.C. 1987. Potential use of surface reverberation by bowhead whales, *Balaena mysticetus*, in under-ice navigation: preliminary considerations. *Rep. Int. Whal. Comm.* **37**: 329–332.
- Engås, A., Løkkeborg, S., Ona, E., and Soldal, A.V. 1996. Effects of seismic shooting on local abundance and catch rates of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). *Can. J. Fish. Aquat. Sci.* **53**: 2238–2249. doi:10.1139/cjfas-53-10-2238.
- Erbe, C. 2002. Underwater noise of whale-watching boats and potential effects on killer whales (*Orcinus orca*), based on an acoustic impact model. *Mar. Mamm. Sci.* **18**: 394–418. doi:10.1111/j.1748-7692.2002.tb01045.x.
- Erbe, C., and Farmer, D.M. 2000. Zones of impact around ice-breakers affecting beluga whales in the Beaufort Sea. *J. Acoust. Soc. Am.* **108**: 1332–1340. doi:10.1121/1.1288938. PMID:11008834.
- Evans, P.G.H., and Miller, L.A. (Editors). 2004. Proceedings of the Workshop on Active Sonar and Cetaceans, Las Palmas, Gran Canaria, 8 March 2003. European Cetacean Society Newsletter No. 42, Special Issue.
- Fernández, A., Edwards, J.F., Rodríguez, F., Espinosa de los Monteros, A., Herráez, P., Castro, P., Jaber, J.R., Martín, V., and Arbelo, M. 2005. "Gas and fat embolic syndrome" involving a mass stranding of beaked whales (family Ziphiidae) exposed to anthropogenic sonar signals. *Vet. Pathol.* **42**: 446–457. doi:10.1354/vp.42-4-446. PMID:16006604.
- Finley, K.J., Miller, G.W., Davis, R.A., and Greene, C.R. 1990. Reactions of belugas, *Delphinapterus leucas*, and narwhals, *Monodon monoceros*, to ice-breaking ships in the Canadian high arctic. *Can. Bull. Fish. Aquat. Sci.* **224**: 97–117.
- Finneran, J.J., and Houser, D.S. 2006. Comparison of in-air evoked potential and underwater behavioral hearing thresholds in four bottlenose dolphins (*Tursiops truncatus*). *J. Acoust. Soc. Am.* **119**: 3181–3192. doi:10.1121/1.2180208. PMID:16708973.
- Finneran, J.J., Schlundt, C.E., Dear, R., Carder, D.A., and Ridgway, S.H. 2002. Temporary shift in masked hearing thresholds (MTTS) in odontocetes after exposure to single underwater impulses from a seismic watergun. *J. Acoust. Soc. Am.* **111**: 2929–2940. doi:10.1121/1.1479150. PMID:12083226.
- Foot, A.D., Osborne, R.W., and Hoelzel, A.R. 2004. Whale-call response to masking boat noise. *Nature (London)*, **428**: 910. doi:10.1038/428910a. PMID:15118717.
- Frankel, A.S., and Clark, C.W. 1998. Results of low-frequency playback of M-sequence noise to humpback whales, *Megaptera novaeangliae*, in Hawai'i. *Can. J. Zool.* **76**: 521–535. doi:10.1139/cjz-76-3-521.
- Frankel, A.S., and Clark, C.W. 2000. Behavioral responses of humpback whales (*Megaptera novaeangliae*) to full-scale ATOC signals. *J. Acoust. Soc. Am.* **108**: 1930–1937. doi:10.1121/1.1289668. PMID:11051519.
- Frankel, A.S., Clark, C.W., Herman, L.M., and Gabriele, C.M. 1995. Spatial distribution, habitat utilization, and social interactions of humpback whales, *Megaptera novaeangliae*, off Hawai'i, determined using acoustic and visual techniques. *Can. J. Zool.* **73**: 1134–1146.
- Frantzis, A. 1998. Does acoustic testing strand whales? *Nature (London)*, **392**: 29. doi:10.1038/32068. PMID:9510243.
- Freitas, L. 2004. The stranding of three Cuvier's beaked whales *Ziphius cavirostris* in Madeira archipelago. *In Proceedings of the Workshop on Active Sonar and Cetaceans, Las Palmas, Gran Canaria, 8 March 2003. Edited by P.G.H. Evans and L.A.*

- Miller. European Cetacean Society Newsletter No. 42, Special Issue. pp. 28–32.
- Friedman, N. 1989. The Naval Institute guide to world naval weapons systems. Naval Institute Press, Annapolis, Md.
- Fristrup, K.M., Hatch, L.T., and Clark, C.W. 2003. Variation in humpback whale (*Megaptera novaeangliae*) song length in relation to low-frequency sound broadcasts. *J. Acoust. Soc. Am.* **113**: 3411–3424. doi:10.1121/1.1573637. PMID:12822811.
- George, J.C., Clark, C., Carroll, G.M., and Ellison, W.T. 1989. Observations on the ice-breaking and ice navigation behavior of migrating bowhead whales (*Balaena mysticetus*) near Point Barrow, Alaska, Spring 1985. *Arctic*, **42**: 24–30.
- Gill, J.A., Norris, K., and Sutherland, W.J. 2001. Why behavioural responses may not reflect the population consequences of human disturbance. *Biol. Conserv.* **97**: 265–268. doi:10.1016/S0006-3207(00)00002-1.
- Goold, J.C., and Fish, P.J. 1998. Broadband spectra of seismic survey air-gun emissions, with reference to dolphin auditory thresholds. *J. Acoust. Soc. Am.* **103**: 2177–2184. doi:10.1121/1.421363. PMID:9566337.
- Guerra, A., González, A.F., Rocha, F., Gracia, J., and Verrhione, M. 2004. Calamares gigantes varados: victimas de exploraciones acústicas. *Investig. Cienc.* 2004(July): 35–37. [Spanish edition of Scientific American.]
- Hamernik, R.P., Qui, W., and Davis, B. 2003. The effects of the amplitude distribution of equal energy exposures on noise-induced hearing loss: the kurtosis metric. *J. Acoust. Soc. Am.* **114**: 386–395. doi:10.1121/1.1582446. PMID:12880050.
- Harrington, F.H., and Veitch, A.M. 1992. Calving success of woodland caribou exposed to low-level jet fighter overflights. *Arctic*, **45**: 213–218.
- Hassel, A., Knutsen, T., Dalen, J., Løkkeborg, S., Skaar, K., Østensen, Ø., Haugland, E.K., Fonn, M., Høines, Å., and Misund, O.A. 2003. Reaction of sandeel to seismic shooting: field experiment and fishery statistics study. *Inst. Mar. Res. Fiskeri og Havet, Rep. No. 4*. Available from http://imr.no/Dokumenter/Rapporter/Fisken_havet_4_2003.pdf [accessed 28 February 2007].
- Hassel, A., Knutsen, T., Dalen, J., Skaar, K., Løkkeborg, S., Misund, O.A., Østensen, Ø., Fonn, M., and Haugland, E.K. 2004. Influence of seismic shooting on the lesser sandeel (*Ammodytes marinus*). *ICES J. Mar. Sci.* **61**: 1165–1173. doi:10.1016/j.icesjms.2004.07.008.
- Hildebrand, J.A. 2005. Impacts of anthropogenic sound. *In* Marine mammal research: conservation beyond crisis. *Edited by* J.E. Reynolds III, W.F. Perrin, R.R. Reeves, S. Montgomery, and T.J. Ragen. Johns Hopkins University Press, Baltimore, Md. pp. 101–124.
- Hohn, A.A., Rotstein, D.S., Harms, C.A., and Southall, B.L. 2006. Report on marine mammal unusual mortality event UME-SE0505Sp: multi-species mass stranding of pilot whales (*Globicephala macrorhynchus*), minke whale (*Balaenoptera acutorostrata*), and dwarf sperm whales (*Kogia sima*) in North Carolina on 15–16 January 2005. NOAA Tech. Mem. NMFS SEFSC-537. Available from: <http://nmfs.noaa.gov/pr/pdfs/health/umese0501sp.pdf> [accessed 28 February 2007].
- Houser, D.S., Howard, R., and Ridgway, S. 2001. Can diving-induced tissue nitrogen supersaturation increase the chance of acoustically driven bubble growth in marine mammals? *J. Theor. Biol.* **213**: 183–195. doi:10.1006/jtbi.2001.2415. PMID:11894990.
- International Council for the Exploration of the Sea. 2005. Report of the ad-hoc group on the impact of sonar on cetaceans and fish (AGISC). *ICES C.M.* 2005/ACE:01.
- International Union for the Conservation of Nature and Natural Resources. 2004. IUCN red list of threatened species: a global species assessment. IUCN, Gland, Switzerland.
- International Whaling Commission. 2005. Report of the scientific committee. Annex K. Report of the Standing Working Group on environmental concerns. *J. Cetacean Res. Manag.* **7**(Suppl.): 267–305.
- International Whaling Commission. 2007. Report of the scientific committee. Annex K. Report of the Standing Working Group on environmental concerns. *J. Cetacean Res. Manag.* **9**(Suppl.): 227–296.
- Janik, V.M., and Slater, P.J.B. 1997. Vocal learning in mammals. *Adv. Stud. Behav.* **26**: 59–99.
- Jepson, P.D., Arbelo, M., Deaville, R., Patterson, I.A.P., Castro, P., Baker, J.R., Degollada, E., Ross, H.M., Herraes, P., Pocknell, A.M., Rodriguez, F., Howie, F.E., Espinosa, A., Reid, R.J., Jaber, J.R., Martin, V., Cunningham, A.A., and Fernandez, A. 2003. Gas-bubble lesions in stranded cetaceans. *Nature (London)*, **425**: 575–576. doi:10.1038/425575a. PMID:14534575.
- Jepson, P.D., Deaville, R., Patterson, I.A.P., Pocknell, A.M., Ross, H.M., Baker, J.R., Howie, F.E., Reid, R.J., Colloff, A., and Cunningham, A.A. 2005. Acute and chronic gas bubble lesions in cetaceans stranded in the United Kingdom. *Vet. Pathol.* **42**: 291–305. doi:10.1354/vp.42-3-291. PMID: 15872375.
- Johnson, M.P., and Tyack, P.L. 2003. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE J. Ocean Eng.* **28**: 3–12. doi:10.1109/JOE.2002.808212.
- Johnston, P.A., Stringer, R.L., and Santillo, D. 1996. Cetaceans and environmental pollution: the global concerns. *In* The conservation of whales and dolphins. *Edited by* M.P. Simmonds and J.D. Hutchinson. John Wiley and Sons, New York. pp. 219–261.
- Jones, M.L., Swartz, S.L., and Dahlheim, M.E. 1994. Census of gray whale abundance in San Ignacio Lagoon: a follow-up study in response to low whale counts recorded during an acoustic playback study of noise effects on gray whales. *Rep. No. NTIS PB94195062 to the US Marine Mammal Commission, Washington, D.C.*
- Joint Nature Conservation Committee. 2004. Guidelines for minimizing acoustic disturbance to marine mammals from seismic surveys. Joint Nature Conservation Committee, Aberdeen, Scotland, UK.
- Kastelein, R.A., Jennings, N., Verboom, W.C., de Haan, D., and Schooneman, N.M. 2006. Differences in the response of a striped dolphin (*Stenella coeruleoalba*) and a harbour porpoise (*Phocoena phocoena*) to an acoustic alarm. *Mar. Environ. Res.* **61**: 363–378. doi:10.1016/j.marenvres.2005.11.005. PMID: 16439011.
- Ketten, D.R. 1995. Estimates of blast injury and acoustic trauma zones for marine mammals from underwater explosions. *In* Sensory systems of aquatic mammals. *Edited by* R.A. Kastelein, J.A. Thomas, and P.E. Nachtigall. De Spil Publishers, Woerden, the Netherlands. pp. 391–407.
- Koschinski, S., Culik, B.M., Henriksen, O.D., Tregenza, N., Ellis, G., Jansen, C., and Kathe, G. 2003. Behavioural reactions of free-ranging porpoises and seals to the noise of a simulated 2 MW windpower generator. *Mar. Ecol. Prog. Ser.* **265**: 263–273. doi:10.3354/meps265263.
- Lagardère, J.-P. 1982. Effects of noise on growth and reproduction of *Crangon crangon* in rearing tanks. *Mar. Biol. (Berl.)*, **71**: 177–185. doi:10.1007/BF00394627.
- Laist, D.W., Knowlton, A.R., Mead, J.G., Collet, A.S., and Podesta, M. 2001. Collisions between ships and whales. *Mar. Mamm. Sci.* **17**: 35–75. doi:10.1111/j.1748-7692.2001.tb00980.x.

- Leeper, R., Chappell, O., and Gordon, J. 1992. The development of practical techniques for surveying sperm whale populations acoustically. *Rep. Int. Whal. Comm.* **42**: 549–560.
- Leonard, M.L., and Horn, A.G. 2005. Ambient noise and the design of begging signals. *Proc. R. Soc. Lond. B Biol. Sci.* **272**: 651–656. doi:10.1098/rspb.2004.3021.
- Lesage, V., Barrette, C., Kingsley, M.C.S., and Sjare, B. 1999. The effect of vessel noise on the vocal behavior of belugas in the St. Lawrence River Estuary, Canada. *Mar. Mamm. Sci.* **15**: 65–84. doi:10.1111/j.1748-7692.1999.tb00782.x.
- Levine, H., Bildsten, L., Brenner, M., Callan, C., Flatté, S., Goodman, J., Gregg, M., Katz, J., Munk, W., and Weinberger, P. 2004. Active sonar waveform. Report from MITRE Corporation, JASON program, JSR-03-200, to the Office of Naval Research, Arlington, Va.
- Lok, J.-J. 2004. Green issues loom larger in future blue-water active sonar operations. *Jane's International Defense Review*, 2004(Aug.): 44–47.
- Løkkeborg, S. 1991. Effects of a geophysical survey on catching success in longline fishing. *ICES C.M. B*: 40.
- Lotze, H.K., and Worm, B. 2002. Complex interactions of climatic and ecological controls on macroalgal recruitment. *Limnol. Oceanogr.* **47**: 1734–1741.
- Lusseau, D. 2003. Male and female bottlenose dolphins *Tursiops* spp. have different strategies to avoid interactions with tour boats in Doubtful Sound, New Zealand. *Mar. Ecol. Prog. Ser.* **257**: 267–274. doi:10.3354/meps257267.
- Lusseau, D. 2006. The short-term behavioral reactions of bottlenose dolphins to interactions with boats in Doubtful Sound, New Zealand. *Mar. Mamm. Sci.* **22**: 802–818. doi:10.1111/j.1748-7692.2006.00052.x.
- Madsen, P.T. 2005. Marine mammals and noise: problems with root mean square sound pressure levels for transients. *J. Acoust. Soc. Am.* **117**: 3952–3957. doi:10.1121/1.1921508. PMID:16018497.
- Madsen, P.T., and Møhl, B. 2000. Sperm whales (*Physeter catodon* L. 1758) do not react to sounds from detonators. *J. Acoust. Soc. Am.* **107**: 668–671. doi:10.1121/1.428568. PMID:10641677.
- Madsen, P.T., Møhl, B., Nielsen, B.K., and Wahlberg, M. 2002. Male sperm whale behaviour during exposures to distant seismic survey pulses. *Aquat. Mamm.* **28**: 231–240.
- Madsen, P.T., Johnson, M., Miller, P.J.O., Aguilar Soto, N., Lynch, J., and Tyack, P. 2006. Quantitative measures of air-gun pulses recorded on sperm whales (*Physeter macrocephalus*) using acoustic tags during controlled exposure experiments. *J. Acoust. Soc. Am.* **120**: 2366–2379. doi:10.1121/1.2229287. PMID:17069331.
- Madsen, P.T., Wahlberg, M., Tougaard, J., Lucke, K., and Tyack, P. 2006. Wind turbine underwater noise and marine mammals: implications of current knowledge and data needs. *Mar. Ecol. Prog. Ser.* **309**: 279–295. doi:10.3354/meps309279.
- Malme, C.I., Miles, P.R., Clark, C.W., Tyack, P., and Bird, J.E. 1983. Investigations of the potential effects of underwater noise from petroleum industry activities on migrating gray whale behavior. Rep. No. NTIS PB86-174174 of Bolt Beranek & Newman, Inc., Cambridge, Mass., to U.S. Minerals Management Service, Anchorage, Alaska.
- Malme, C.I., Miles, P.R., Clark, C.W., Tyack, P., and Bird, J.E. 1984. Investigations of the potential effects of underwater noise from petroleum industry activities on migrating gray whale behavior. Phase II: January 1984 migration. Rep. No. NTIS PB86-218377 of Bolt Beranek & Newman, Inc., Cambridge, Mass., to U.S. Minerals Management Service, Anchorage, Alaska.
- Martín, V., Servidio, A., and García, S. 2004. Mass strandings of beaked whales in the Canary Islands. *In* Proceedings of the Workshop on Active Sonar and Cetaceans, Las Palmas, Gran Canaria, 8 March 2003. *Edited by* P.G.H. Evans and L.A. Miller. European Cetacean Society Newsletter No. 42, Special Issue. pp. 33–36.
- Mayer, S., and Simmonds, M.P. 1996. Science and precaution in cetacean conservation. *In* The conservation of whales and dolphins. *Edited by* M.P. Simmonds and J.D. Hutchinson. Wiley and Sons, New York. pp. 391–406.
- McCauley, R.D., Fewtrell, J., Duncan, A.J., Jenner, C., Jenner, M.N., Penrose, J., Prince, R.I.T., Adhitya, A., Murdoch, J., and McCabe, K. 2000. Marine seismic surveys — a study of environmental implications. *Australian Petroleum Production and Exploration Association Journal*, **40**: 692–708.
- McCauley, R.D., Fewtrell, J., and Popper, A.N. 2003. High intensity anthropogenic sound damages fish ears. *J. Acoust. Soc. Am.* **113**: 638–642. doi:10.1121/1.1527962. PMID:12558299.
- McDonald, M.A., Hildebrand, J.A., and Wiggins, S.M. 2006. Increases in deep ocean ambient noise in the Northeast Pacific west of San Nicolas Island, California. *J. Acoust. Soc. Am.* **120**: 711–718. doi:10.1121/1.2216565. PMID:16938959.
- McSweeney, D.J., Baird, R.W., and Mahaffy, S.D. 2007. Site fidelity, associations, and movements of Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales off the island of Hawai'i. *Mar. Mamm. Sci.* **23**: 666–687. doi:10.1111/j.1748-7692.2007.00135.x.
- Miksis, J.L., Grund, M.D., Nowacek, D.P., Solow, A.R., Connor, R.C., and Tyack, P.L. 2001. Cardiac responses to acoustic playback experiments in the captive bottlenose dolphin (*Tursiops truncatus*). *J. Comp. Psychol.* **115**: 227–232. doi:10.1037/0735-7036.115.3.227. PMID:11594491.
- Miller, P.J.O., Biasson, N., Samuels, A., and Tyack, P.L. 2000. Whale songs lengthen in response to sonar. *Nature (London)*, **405**: 903. doi:10.1038/35016148. PMID:10879521.
- Mitchell, E.D. 2005. What causes lesions in sperm whale bones? *Science (Washington, D.C.)*, **308**: 631–632. doi:10.1126/science.1109805. PMID:15864831.
- Moore, M.J., and Early, G.A. 2004. Cumulative sperm whale bone damage and the bends. *Science (Washington, D.C.)*, **306**: 2215. doi:10.1126/science.1105452. PMID:15618509.
- Moore, M.J., and Early, G.A. 2005. Response: What causes lesions in sperm whale bones? *Science (Washington, D.C.)*, **308**: 631–632.
- Morton, A.B., and Symonds, H.K. 2002. Displacement of *Orcinus orca* (L.) by high amplitude sound in British Columbia. *ICES J. Mar. Sci.* **59**: 71–80. doi:10.1006/jmsc.2001.1136.
- Møhl, B. 2004. Sperm whale sonar rivals tactical sonar with source levels at 235 dB. *In* Proceedings of the Workshop on Active Sonar and Cetaceans, Las Palmas, Gran Canaria, 8 March 2003. *Edited by* P.G.H. Evans and L.A. Miller. European Cetacean Society Newsletter No. 42, Special Issue. pp. 41–42.
- Møhl, B., Wahlberg, M., Madsen, P.T., Miller, L.A., and Surlykke, A. 2000. Sperm whale clicks: directionality and source level revisited. *J. Acoust. Soc. Am.* **107**: 638–648. doi:10.1121/1.428329. PMID:10641672.
- Nachtigall, P.E., Pawlowski, J.L., and Au, W.W.L. 2003. Temporary threshold shifts and recovery following noise exposure in the Atlantic bottlenose dolphin (*Tursiops truncatus*). *J. Acoust. Soc. Am.* **113**: 3425–3429. doi:10.1121/1.1570438. PMID:12822812.
- Nachtigall, P.E., Supin, A.Y., Pawlowski, J.L., and Au, W.W.L. 2004. Temporary threshold shifts after noise exposure in a bottlenose dolphin (*Tursiops truncatus*) measured using evoked auditory potentials. *Mar. Mamm. Sci.* **20**: 673–687. doi:10.1111/j.1748-7692.2004.tb01187.x.

- Nachtigall, P.E., Yuen, M.M.L., Mooney, T.A., and Taylor, K.A. 2005. Hearing measurements from a stranded infant Risso's dolphin, *Grampus griseus*. *J. Exp. Biol.* **208**: 4181–4188. doi:10.1242/jeb.01876. PMID:16244176.
- National Marine Fisheries Service. 1996. Environmental assessment on conditions for lethal removal of California sea lions at the Ballard Locks to protect winter steelhead. NMFS Environmental Assessment Report. Available from Northwest Regional Office, NMFS, NOAA, 7600 Sand Point Way NE, Seattle, WA 98115, USA.
- National Marine Fisheries Service. 2002. Status review under the Endangered Species Act: southern resident killer whales (*Orcinus orca*). NOAA Tech. Mem. NMFS NWFSC-54. Available from <http://nwfsc.noaa.gov> [accessed 28 February 2007] or by e-mail at orders@ntis.fedworld.gov.
- National Marine Fisheries Service. 2005. Assessment of acoustic exposures on marine mammals in conjunction with USS Shoup active sonar transmissions in the eastern Strait of Juan de Fuca and Haro Strait, Washington, 5 May 2003. Available from NMFS, 1315 East-West Highway, Silver Spring, MD 20910, USA.
- National Marine Fisheries Service. 2006. Small takes of marine mammals incidental to specified activities; Rim of the Pacific antisubmarine warfare exercise training events within the Hawaiian Islands Operating Area. *Fed. Regist.* **71**: 38710–38738.
- National Oceanographic and Atmospheric Administration and US Department of the Navy. 2001. Joint interim report: Bahamas marine mammal stranding event of 15–16 March 2000. US Department of Commerce, Washington, D.C.
- Nieukirk, S.L., Stafford, K.M., Mellinger, D.K., Dziak, R.P., and Fox, C.G. 2004. Low-frequency whale and seismic airgun sounds recorded in the mid-Atlantic Ocean. *J. Acoust. Soc. Am.* **115**: 1832–1843. doi:10.1121/1.1675816. PMID:15101661.
- Nowacek, D.P., Johnson, M.P., and Tyack, P.L. 2004. North Atlantic right whales (*Eubalaena glacialis*) ignore ships but respond to alerting stimuli. *Proc. R. Soc. Lond. B Biol. Sci.* **271**: 227–231. doi:10.1098/rspb.2003.2570.
- Nowacek, D.P., Thorne, L.H., Johnston, D.W., and Tyack, P.L. 2007. Responses of cetaceans to anthropogenic noise. *Mammal Rev.* **37**: 81–115. doi:10.1111/j.1365-2907.2007.00104.x.
- Nystuen, J.A., and Farmer, D.M. 1987. The influence of wind on the underwater sound generated by light rain. *J. Acoust. Soc. Am.* **82**: 270–274. doi:10.1121/1.395563.
- O'Hara, T.M., and O'Shea, T.J. 2005. Assessing impacts of environmental contaminants. In *Marine mammal research: conservation beyond crisis*. Edited by J.E. Reynolds III, W.F. Perrin, R.R. Reeves, S. Montgomery, and T.J. Ragen. Johns Hopkins University Press, Baltimore, Md. pp. 62–83.
- Olesiuk, P.F., Nichol, L.M., Sowden, M.J., and Ford, J.K.B. 2002. Effect of the sound generated by an acoustic harassment device on the relative abundance and distribution of harbor porpoises (*Phocoena phocoena*) in Retreat Passage, British Columbia. *Mar. Mamm. Sci.* **18**: 843–862. doi:10.1111/j.1748-7692.2002.tb01077.x.
- Payne, R., and Webb, D. 1971. Orientation by means of long range acoustic signaling in baleen whales. *Ann. N.Y. Acad. Sci.* **188**: 110–141. doi:10.1111/j.1749-6632.1971.tb13093.x. PMID:5288850.
- Pearson, W.H., Skalski, J.R., and Malme, C.I. 1992. Effects of sounds from a geophysical survey device on behavior of captive rockfish (*Sebastes* spp.). *Can. J. Fish. Aquat. Sci.* **49**: 1343–1356.
- Pickett, G.D., Eaton, D.R., Seaby, R.M.H., and Arnold, G.P. 1994. Results of bass tagging in Poole Bay during 1992. Laboratory Leaflet No. 74, Ministry of Agriculture, Fisheries and Food, Directorate of Fisheries Research, Lowestoft, UK.
- Popper, A.N. 2003. The effects of anthropogenic sounds on fishes. *Fisheries* (Bethesda), **28**: 24–31. doi:10.1577/1548-8446(2003)28[24:EOASOF]2.0.CO;2.
- Popper, A.N., Halvorsen, M.B., Kane, A., Miller, D.L., Smith, M.E., Song, J., Stein, P., and Wysocki, L.E. 2007. The effects of high-intensity, low-frequency active sonar on rainbow trout. *J. Acoust. Soc. Am.* **122**: 623–635. doi:10.1121/1.2735115. PMID:17614519.
- Power, M. 1997. Assessing the effects of environmental stressors on fish populations. *Aquat. Toxicol.* **39**: 151–169. doi:10.1016/S0166-445X(97)00020-9.
- Rabin, L.A., and Greene, C.M. 2002. Changes in acoustic communication systems in human-altered environments. *J. Comp. Psychol.* **116**: 137–141. doi:10.1037/0735-7036.116.2.137. PMID:12083606.
- Rasmussen, M.H., Wahlberg, M., and Miller, L.A. 2004. Estimated transmission beam pattern of clicks recorded from free-ranging white-beaked dolphins (*Lagenorhynchus albirostris*). *J. Acoust. Soc. Am.* **116**: 1826–1831. doi:10.1121/1.1775274. PMID:15478450.
- Régnault, M.R., and Lagardère, J.-P. 1983. Effects of ambient noise on the metabolic level of *Crangon crangon* (Decapoda, Nanantia). *Mar. Ecol. Prog. Ser.* **11**: 71–78. doi:10.3354/meps011071.
- Rendell, L.E., and Gordon, J.C.D. 1999. Vocal response of long-finned pilot whales (*Globicephala melas*) to military sonar in the Ligurian Sea. *Mar. Mamm. Sci.* **15**: 198–204. doi:10.1111/j.1748-7692.1999.tb00790.x.
- Richardson, W.J., Fraker, M.A., Würsig, B., and Wells, R.S. 1985. Behavior of bowhead whales *Balaena mysticetus* summering in the Beaufort Sea: reactions to industrial activities. *Biol. Conserv.* **32**: 195–230. doi:10.1016/0006-3207(85)90111-9.
- Richardson, W.J., Würsig, B., and Greene, C.R., Jr. 1986. Reactions of bowhead whales, *Balaena mysticetus*, to seismic exploration in the Canadian Beaufort Sea. *J. Acoust. Soc. Am.* **79**: 1117–1128. doi:10.1121/1.393384. PMID:3700867.
- Richardson, W.J., Würsig, B., and Greene, C.R., Jr. 1990. Reactions of bowhead whales, *Balaena mysticetus*, to drilling and dredging noise in the Canadian Beaufort Sea. *Mar. Environ. Res.* **29**: 135–160. doi:10.1016/0141-1136(90)90032-J.
- Richardson, W.J., Greene, C.R., Jr., Malme, C.I., and Thomson, D.H. 1995. *Marine mammals and noise*. Academic Press, New York.
- Richardson, W.J., Miller, G.W., and Greene, C.R. 1999. Displacement of migrating bowhead whales by sounds from seismic surveys in shallow waters of the Beaufort Sea. *J. Acoust. Soc. Am.* **106**: 2281. [Abstract only.] doi:10.1121/1.427801.
- Ridgway, S.H., and Howard, R. 1979. Dolphin lung collapse and intramuscular circulation during deep diving: evidence from nitrogen washout. *Science* (Washington, D.C.), **206**: 1182–1183. doi:10.1126/science.505001. PMID:505001.
- Romano, T.A., Keogh, M.J., Kelly, C., Feng, P., Berk, L., Schlundt, C.E., Carder, D.A., and Finneran, J.J. 2004. Anthropogenic sound and marine mammal health: measures of the nervous and immune systems before and after intense sound exposure. *Can. J. Fish. Aquat. Sci.* **61**: 1124–1134. doi:10.1139/f04-055.
- Ross, D.G. 1993. On ocean underwater ambient noise. *Acoustics Bull.* 1993(January/February): 5–8.
- Rothschild, B.M. 2005. What causes lesions in sperm whale bones? *Science* (Washington, D.C.), **308**: 631–632. doi:10.1126/science.308.5722.631c. PMID:15864830.
- Santulli, A., Modica, A., Messina, C., Ceffa, L., Curatolo, A., Rivas, G., Fabi, G., and D'amelio, V. 1999. Biochemical re-

- sponses of European sea bass (*Dicentrarchus labrax* L.) to the stress induced by off shore experimental seismic prospecting. *Mar. Pollut. Bull.* **38**: 1105–1114. doi:10.1016/S0025-326X(99)00136-8.
- Scholik, A.R., and Yan, H.Y. 2002a. Effects of boat engine noise on the auditory sensitivity of the fathead minnow, *Pimephales promelas*. *Environ. Biol. Fishes*, **63**: 203–209. doi:10.1023/A:1014266531390.
- Scholik, A.R., and Yan, H.Y. 2002b. The effects of noise on the auditory sensitivity of the bluegill sunfish, *Lepomis macrochirus*. *Comp. Biochem. Physiol. A*, **133**: 43–52. doi:10.1016/S1095-6433(02)00108-3.
- Schlundt, C.E., Finneran, J.J., Carder, D.A., and Ridgway, S.H. 2000. Temporary shift in masked hearing thresholds (MTTS) of bottlenose dolphins and white whales after exposure to intense tones. *J. Acoust. Soc. Am.* **107**: 3496–3508. doi:10.1121/1.429420. PMID:10875394.
- Simmonds, M.P., and Lopez-Jurado, L.F. 1991. Whales and the military. *Nature (London)*, **351**: 448. doi:10.1038/351448a0.
- Simpson, S.D., Meekan, M., Montgomery, J., McCauley, R., and Jeffs, A. 2005. Homeward sound. *Science (Washington, D.C.)*, **308**: 221. doi:10.1126/science.1107406. PMID:15821083.
- Skalski, J.R., Pearson, W.H., and Malme, C.I. 1992. Effects of sounds from a geophysical survey device on catch-per-unit-effort in a hook-and-line fishery for rockfish (*Sebastes* spp.). *Can. J. Fish. Aquat. Sci.* **49**: 1357–1365.
- Slotte, A., Hansen, K., Dalen, J., and One, E. 2004. Acoustic mapping of pelagic fish distribution and abundance in relation to a seismic shooting area off the Norwegian west coast. *Fish. Res.* **67**: 143–150. doi:10.1016/j.fishres.2003.09.046.
- Smith, M.E., Kane, A.S., and Popper, A.N. 2004. Noise-induced stress response and hearing loss in goldfish *Carassius auratus*. *J. Exp. Biol.* **207**: 427–435. doi:10.1242/jeb.00755. PMID:14691090.
- Southall, B.L. 2005. Shipping noise and marine mammals: a forum for science, management, and technology. Final report of the National Oceanic and Atmospheric Administration International Symposium. Available from http://nmfs.noaa.gov/pr/pdfs/acoustics/shipping_noise.pdf [accessed 28 February 2007].
- Southall, B.L., Braun, R., Gulland, F.M.D., Heard, A.D., Baird, R.W., Wilkin, S.M., and Rowles, T.K. 2006. Hawaiian melon-headed whale (*Peponocephala electra*) mass stranding event of 3–4 July, 2004. NOAA Tech. Mem. NMFS OPR-31. Available from http://nmfs.noaa.gov/pr/pdfs/health/stranding_melonheadedwhales_final_report.pdf [accessed 28 February 2007].
- Stearns, S.C., and Hoekstra, R. 2000. *Evolution: an introduction*. Oxford University Press, London.
- Steevens, C.C., Russell, K.L., Knafelc, M.E., Smith, P.F., Hopkins, E.W., and Clark, J.B. 1999. Noise-induced neurologic disturbances in divers exposed to intense water-borne sound: two case reports. *Undersea Hyper. Med.* **26**: 261–265. PMID:10642074.
- Stillman, R.A., and Goss-Custard, J.D. 2002. Seasonal changes in the response of oystercatchers *Haematopus ostralegus* to human disturbance. *J. Avian Biol.* **33**: 358–365. doi:10.1034/j.1600-048X.2002.02925.x.
- Stone, C.J., and Tasker, M.L. 2006. The effect of seismic airguns on cetaceans in UK waters. *J. Cetacean Res. Manag.* **8**: 255–263.
- Taylor, B.L., Martinez, M., Gerrodette, T., Barlow, J., and Hrovat, Y.N. 2007. Lessons from monitoring trends in abundance of marine mammals. *Mar. Mamm. Sci.* **23**: 157–175. doi:10.1111/j.1748-7692.2006.00092.x.
- Thomsen, F., Lüdemann, K., Kafemann, R., and Piper, W. 2006. Effects of offshore wind farm noise on marine mammals and fish. biola, Hamburg, Germany on behalf of COWRIE Ltd. Available from: <http://offshorewind.co.uk/Downloads/BIOLAREport06072006FINAL.pdf> [accessed 28 February 2007].
- Todd, S., Stevick, P., Lien, J., Marques, F., and Ketten, D. 1996. Behavioural effects to underwater explosions in humpback whales (*Megaptera novaeangliae*). *Can. J. Zool.* **74**: 1661–1672.
- Tyack, P.L. 1981. Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behav. Ecol. Sociobiol.* **8**: 105–116. doi:10.1007/BF00300822.
- Tyack, P.L., and Clark, C.W. 2000. Communication and acoustic behavior of dolphins and whales. *In Hearing by whales and dolphins. Edited by W. Au, A.N. Popper, and R. Fay. Springer Handbook of Auditory Research Series. Springer-Verlag, New York.* pp. 156–224.
- Tyack, P.L., and Miller, E.H. 2002. Vocal anatomy, acoustic communication and echolocation. *In Marine mammal biology. Edited by A.R. Hoelzel. Blackwell Science Ltd., Oxford, UK.* pp. 142–184.
- Tyack, P.L., Johnson, M., Aguilar Soto, N., Sturlese, A., and Madsen, P.T. 2006. Extreme diving of beaked whales. *J. Exp. Biol.* **209**: 4238–4253. doi:10.1242/jeb.02505. PMID:17050839.
- Van Parijs, S.M., and Corkeron, P.J. 2001. Boat traffic affects the acoustic behaviour of Pacific humpback dolphins, *Sousa chinensis*. *J. Mar. Biol. Assoc. U.K.*, **81**: 533–538. doi:10.1017/S0025315401004180.
- van Raaij, M.T., Dobbe, C.J., Elvers, B., Timmerman, A., Schenk, E., Oortgiesen, M., and Wiegant, V.M. 1997. Hormonal status and the neuroendocrine response to a novel heterotypic stressor involving subchronic noise exposure. *Neuroendocrinology*, **65**: 200–209. PMID:9088001.
- Wardle, C.S., Carter, T.J., Urquhart, G.G., and Johnstone, A.D.F. 2001. Effects of seismic air guns on marine fish. *Cont. Shelf Res.* **21**: 1005–1027. doi:10.1016/S0278-4343(00)00122-9.
- Watkins, W.A. 1986. Whale reactions to human activities in Cape Cod waters. *Mar. Mamm. Sci.* **2**: 251–262. doi:10.1111/j.1748-7692.1986.tb00134.x.
- Watkins, W.A., and Schevill, W.E. 1975. Sperm whales (*Physeter catodon*) react to pingers. *Deep-Sea Res.* **22**: 123–129.
- Watkins, W.A., Moore, K.E., and Tyack, P. 1985. Sperm whale acoustic behaviors in the southeast Caribbean. *Cetology*, **49**: 1–15.
- Weilgart, L.S. 2007. The need for precaution in the regulation and management of undersea noise. *J. Int. Wildl. Law Policy*, **10**(3–4).
- Weir, C.R., and Dolman, S.J. 2007. Comparative review of the regional marine mammal mitigation guidelines implemented during industrial seismic surveys, and guidance towards a worldwide standard. *J. Int. Wildl. Law Policy*, **10**: 1–27. doi:10.1080/13880290701229838.
- Weller, D.W., Rickards, S.H., Bradford, A.L., Burdin, A.M., and Brownell, R.L., Jr. 2006a. The influence of 1997 seismic surveys on the behavior of western gray whales off Sakhalin Island, Russia. Paper No. SC/58/E4 presented to the International Whaling Commission Scientific Committee, Cambridge, UK. Available from the Office of the Journal of Cetacean Research and Management, Cambridge, UK.
- Weller, D.W., Tsidulko, G.A., Ivashchenko, Y.V., Burdin, A.M., and Brownell, R.L., Jr. 2006b. A re-evaluation of the influence of 2001 seismic surveys on western gray whales off Sakhalin Island, Russia. Paper No. SC/58/E5 presented to the International Whaling Commission Scientific Committee, Cambridge, UK.

- Available from the Office of the Journal of Cetacean Research and Management, Cambridge, UK.
- Whitehead, H., and Reeves, R.R. 2005. Killer whales and whaling: the scavenging hypothesis. *Biol. Lett.* **1**: 415–418. doi:10.1098/rsbl.2005.0348. PMID:17148221.
- Whitehead, H., Reeves, R.R., and Tyack, P.L. 2000. Science and the conservation, protection, and management of wild cetaceans. *In* *Cetacean societies*. Edited by J. Mann, R.C. Connor, P.L. Tyack, and H. Whitehead. University of Chicago Press. Chicago. pp. 308–332.
- Wilson, O.B.J., Wolf, S.N., and Ingenito, F. 1985. Measurements of acoustic ambient noise in shallow water due to breaking surf. *J. Acoust. Soc. Am.* **78**: 190–195. doi:10.1121/1.392557.
- Wimmer, T., and Whitehead, H. 2004. Movements and distribution of northern bottlenose whales, *Hyperoodon ampullatus*, on the Scotian Slope and in adjacent waters. *Can. J. Zool.* **82**: 1782–1794. doi:10.1139/z04-168.
- Worm, B., Lotze, H.K., Hillebrand, H., and Sommer, U. 2002. Consumer versus resource control of species diversity and ecosystem functioning. *Nature (London)*, **417**: 848–851. doi:10.1038/nature00830. PMID:12075351.
- Würsig, B., and Richardson, W.J. 2002. Effects of noise. *In* *Encyclopedia of marine mammals*. Edited by W.F. Perrin, B. Würsig, and J.G.M. Thewissen. Academic Press, San Diego, Calif. pp. 794–802.
- Wysocki, L.E., Dittami, J.P., and Ladich, F. 2006. Ship noise and cortisol secretion in European freshwater fishes. *Biol. Conserv.* **128**: 501–508. doi:10.1016/j.biocon.2005.10.020.

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