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Do Marine Mammals Experience Stress Related to Anthropogenic Noise?

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Sound travels much further than light in the marine environment. As a result, marine mammals, especially cetaceans, rely heavily on sound for many important life functions, including breeding and foraging. This reliance on sound means it is quite likely that exposure to noise will have some detrimental effects on these life functions. However, there has been little application to marine mammals of the knowledge available in other species of stress responses to noise and other stressors. In this paper we begin to integrate what is known about marine mammals with the current knowledge gained in terrestrial mammals about stress physiology, specifically considering physiological and psychological context and thus also cumulative and synergistic impacts. We determined that it is reasonable to extrapolate information regarding stress responses in other species to marine mammals, because these responses are highly conserved among all species in which they have been examined to date. As a result, we determined that noise acts as a stressor to marine mammals. Furthermore, given that marine mammals will likely respond in a manner consistent with other species studied, repeated and prolonged exposures to stressors (including or induced by noise) will be problematic for marine mammals of all ages. A range of issues may arise from the extended stress response including, but not limited to, suppression of reproduction (physiologically and behaviorally), accelerated aging and sickness-like symptoms. We also determined that interpretation of a reduction in behavioral responses to noise as acclimation will be a mistake in many situations, as alternative reasons for the observed results are much more likely. We recommend that research be conducted on both stress responses and life-history consequences of noise exposure in marine mammals, while emphasizing that very careful study designs will be required. We also recommend that managers incorporate the findings presented here in decisions regarding activities that expose marine mammals to noise. In particular, the effects of cumulative and synergistic responses to stressors can be very important and should not be dismissed lightly.

As sound travels much better than light in the ocean (Urick, 1983) many marine animals, including marine mammals, use sound instead of light to gain information about their environment (Popper, 2003; Richardson, Greene, Malme & Thomson, 1995; Tyack & Miller, 2002). Cetaceans (whales, dolphins and porpoises) in particular are heavily dependent on sound to find food, communicate (including for reproduction), detect predators and navigate. Increasing mechanized use of the sea, such as for shipping, military activities, oil and gas exploration, and recreation (including cruises and pleasure boating), is increasing the amount of noise that humans introduce into the oceans, sometimes over very large distances (for details and discussion, see Hatch & Wright, this issue).

As cetaceans (as well as other marine mammals) are primarily acoustic animals, it appears likely that they will suffer more from exposure to noise than other species, including rats and humans - both species for which there is some information available about the consequences of noise exposure. It is reasonable to assume that marine mammals' reliance on sound has led to the evolution of a number of adaptive mechanisms to deal with natural noise, but whether those mechanisms are sufficient to compensate for the comparatively recent advent of anthropogenic ocean noise is uncertain (see Bateson, this issue; Weilgart, this issue). For example, cetaceans may have developed various strategies that are better than those employed by terrestrial species at averting or handling the problems created by masking (i.e., the drowning out of a signal of interest by noise). Regardless, their ability to cope with noise will still have limits. Indeed, anthropogenic underwater noise is a novel environmental element for marine mammals and some species have been exposed to it for only one generation (e.g., bowhead whale, *Balaena mysticetus*). This is a very short period in terms of evolutionary time, making it very unlikely that any marine mammals have developed appropriate coping mechanisms (Rabin & Greene, 2002).

Here we attempt to increase our understanding of the effects of sound on marine mammals through the application of the current state of knowledge about noise, physiological stress and the influence of context, as outlined in Wright et al. (this issue, a) and detailed further in the other papers in this issue. Wright et al. (this issue, a) and the references therein should thus be considered the source for information included in this document unless other sources are cited. Working definitions for the terminology related to 'stress' are provided by Wright & Kuczaj (this issue).

Review of known effects of noise in marine mammals

Marine mammals have demonstrated various responses to specific noise exposures ranging from changes in their vocalizations (shifts in frequency, becoming silent, etc.) and displacement or avoidance (including shifting their migration paths) through alterations in their diving, swim speed, respiration or foraging behavior, to hearing damage and strandings (see Appendix 1). Weilgart (this issue) provides a summary of the known effects and the references therein offer additional details.

Hearing damage is not discussed here, as this is not a result of a noise-induced stress response. However, it should be noted that ear damage and other physical injuries would, if not immediately fatal, act as a variety of stimuli/stressors in their own right, each with the potential for producing a stress response. Thus, sound may generate both auditorily-mediated (i.e., heard) stimuli/stressors and non-auditory (i.e., those not directly resulting from sound perception through the ear) stimuli/stressors.

Noise and Stress in Marine Mammals

Two studies to date have investigated the physiological stress response to noise in captive marine mammals. Thomas, Kastelein & Awbrey (1990) exposed four captive beluga whales (*Delphinapterus leucas*) to playbacks of drilling noise but found no changes in blood adrenaline and norarenaline ("stress hormones", also known as epinephrine and norepinephrine) levels measured immediately after playbacks. Romano et al. (2004) exposed captive bottlenose dolphins (*Tursiops truncatus*) and a beluga whale to sounds from a seismic water gun and (for the bottlenose dolphins only) 1 s, 3 kHz pure tones and observed detrimental changes in some of the various hormones in the blood (for more details, also see Weilgart, this issue). However, the small sample sizes of these studies, their use of captive animals and other technical limitations mean that extrapolation of their results to wild animals should be done with caution (as recommended by Thomas, Kastelein & Awbrey, 1990). Additionally, there may have been some level of response to background noise levels that were not accounted for in the baseline measurements (see Baldwin, this issue).

It should also be noted that the epidemiological studies undertaken in humans examining physiological effects such as hypertension and coronary heart disease have been more consistent and conclusive than those considering the various stress hormones (see Clark & Stansfeld, this issue). Accordingly, it appears to be possible for noise to cause effects consistent with prolonged exposure to a stressor, such as hypertension and coronary heart disease, without necessarily displaying a consistent increase in stress hormones, such as glucocorticoids (GCs), and other metrics.

Three specific examples of the effects of sound on marine mammals are considered here in greater detail: the stranding of beaked whales (*Ziphiidae*) in association with military sonar exercises; the effects of shipping noise on beaked whale foraging and communication; and the various effects on the energy budget of odontocetes (toothed cetaceans) from disturbance due to whalewatching activities. Disruptions caused by whalewatching are likely to result from a combination of the actual presence of the whalewatching vessels as well as their noise. However, the effects of whalewatching and those of noise from moderately distant shipping are similar in many respects (see Lusseau & Bejder, this issue; Weilgart, this issue), suggesting that noise is probably the predominant source of impact of whalewatching. Furthermore, playback experiments have demonstrated that vessel noise alone can elicit responses in at least some species (e.g., manatees, *Trichechus manatus*: Miksis-Olds, Donaghay, Miller, Tyack & Reynolds, 2007).

Beaked whale strandings

Beaked whales have repeatedly mass-stranded a few hours to days after naval maneuvers during which military ships used midrange frequency sonar (Fernandez et al., 2005; Hildebrand, 2005)[1]. These whales were consistently affected by a new syndrome, never described in marine mammals prior to these events, consisting of extensive fat and gas bubble emboli: an ensemble of lesions most similar to decompression sickness in human divers (Fernández et al., 2005; Jepson et al., 2003). It is clear that the severity of emboli is the direct cause of death and that the constant temporal and spatial coincidence with naval exercises involving sonar designates these exercises as the cause of this new syndrome (Fernandez et al., 2005; Hildebrand, 2005). Recent studies have qualified beaked whales as the deepest diving mammals (down to 1.8 km: Tyack, Johnson, Aguilar Soto, Sturlese & Madsen, 2006) and have shown that these animals typically

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[1] With regards to the debate over the frequency of strandings coincident with such activities, it should be noted that the discovery of just one dead body from a wild population is widely accepted in terrestrial biology to be always indicative of a wider problem, as it is easy to miss carcasses (p14-15 in Wobeser, 1994). This is likely to be even more true with marine mammals, where dead animals can be quickly scavenged upon, carried away by strong currents, or sink beneath the waves if they float at all. Deep diving marine mammals, such as beaked whales, that die at depth may be prevented from rising to the surface at all due to inhibition of decay-induced floating by the increased hydrostatic pressure (Allison, Smith, Kukert, Deming & Bennett, 1991). There are also fewer potential observers that are much more widely scattered than in terrestrial environments.

(although not always) follow a highly stereotyped diving pattern. This pattern consists of a deep dive followed by progressively shallower dives, apparently similar to the decompression stops used by human divers to avoid decompression sickness, although this is not necessarily their function (Tyack et al., 2006). Tyack et al. (2006) instead argued that the collapse of the whales' lungs at depth alleviates the need for such decompression dives.

In either case, behavioral disturbances, such as a startle or flight response, that disturb this highly stereotyped diving pattern, may overwhelm or circumvent the normal nitrogen buffering physiology of beaked whales and trigger the formation of nitrogen bubbles (i.e., 'the bends'), with the ultimate outcome being death from gas embolism and/or hemorrhage (see Cox et al., 2006; Tyack et al., 2006). While this remains the predominant theory, the physiological processes by which it occurs are still unknown (Cox et al., 2006) and other causes of death have also been suggested (see review by Rommel et al., 2006). For example, it has been hypothesized that instead of or in addition to indirect action via behavior disturbance, the navy maneuvers may directly induce the formation of nitrogen bubbles through a process termed "rectified diffusion" (Crum & Mao, 1996; Houser, Howard & Ridgway, 2001).

Additional support for the flight hypothesis is found in the similar response to novel sounds observed in other cetacean species. For example, Nowacek, Johnson & Tyack (2004) exposed foraging North Atlantic right whales (*Eubalaena glacialis*) tagged with a Digital Acoustic Recording Tag (DTag: Johnson & Tyack, 2003) to vessel noise, whale social sounds, silence, and a synthetic signal designed to alert the whales to the presence of vessels and thus reduce ship-strikes. Five out of six whales exposed to the alert signal responded by abandoning their foraging dive prematurely and executing a shallow-angled, high power (i.e., significantly increased fluke stroke rate) ascent and continued to swim at shallow depths, surfacing only to breathe, for the duration of the exposure: an abnormally long surface interval. This response was elicited by alarm sounds at received levels as low as 133 to 148 dB re 1 μPa at 1000 Hz. None of the whales exposed to ship noise playbacks responded at all.

There is also some indication that a stress response may be at least partly involved in reactions of beaked whales to military exercises involving sonar. Intracellular globules composed of acute phase protein have been found in the cells of six out of eight livers examined from beaked whales stranded in association with such exercises (tissue decay prevented detailed examination in nine others; Godinho/Fernandez, unpublished data). The globules are also found in the cytoplasm of hepatocytes in a range of examined cetacean species that stranded for many different reasons, including animals that are known to have died in 'very stressing' circumstances (e.g., anthropogenic interactions, such as bycatch; pathologies; or heat shock; Godinho et al., 2005). For example, globules have been seen in 26 of the 27 livers examined from bycaught harbor porpoises (*Phocoena phocoena*) in one study, with the only negative result being a neonate, possibly because of its immature metabolism (Godinho et al., 2006). Furthermore, only 7 of the other 11 examined porpoises that stranded for other or unknown reasons were positive (Godinho et al., 2007; Godinho, unpublished data). It is acknowledged that live stranding itself is also likely to be an intense stressor.

The mechanism for the accumulation of acute phase proteins and the function that they have in the organism are not clear and there are various theories. For example, one hypothesis is that the vascular compromise (e.g., resulting from live-stranding) leads to acute liver congestion, which has been observed in 17 different cetacean species, that could in turn prevent the proteins from leaving the cell, where they thus accumulate and the globules are formed (Godinho et al., 2005; Godinho/Fernandez, unpublished data). However, for reasons not yet known, the globules in the above study vary both within and between species, as shown by electron microscopy and inmumohistochemistry (Godinho et al., 2007).

Hypoxia may also become a compounding issue for any marine mammal exposed to a stressor at depth, because oxygen consumption increases dramatically with increased heart rate as a result of release of catecholamines (adrenalin/epinephrine and noradrenalin/norepinephrine) through activation of the sympathetic nervous system (SNS: see Deak, this issue, Romero & Butler, this issue). The increase in heart rate is usually associated with a corresponding increase in respiration; however this is not possible at depth. This additional oxygen demand during pronounced SNS activation could therefore be particularly problematic for deep divers that are already living right on the physiological edge. Beaked whales are thought to be diving beyond their aerobic limits (Tyack et al., 2006; Aguilar Soto et al., 2006) so additional oxygen demands could force them to cut their dives short. Regardless, the combination of a psychological stressor (extreme noise that is perceived as threatening) with a more direct physiological stressor (fat and gas emboli or hypoxia) may have some potentially deleterious consequences (see Deak, this issue). Such a combination may have contributed to beaked whale deaths recorded in the mass strandings or unobserved at sea, as well as negatively affecting the health and fecundity of survivors of the events.

Although it is possible that a stress response contributed directly in some way to the lethal consequences resulting from exposure of beaked whales to military exercises involving sonar, it remains most likely that the fatalities resulted from the whales' flight response. In understanding this subtle difference, it is useful to consider the three successive stages of adaptation to insult (i.e., a stressor) presented by Selye (1946): alarm reaction; stage of resistance; and stage of exhaustion. An animal may respond at the very initial stages of a stress response (alarm) by fleeing (i.e., flight arising from the SNS response). If this action removes the animal from exposure to the stimulus then it may only lead to a short GC response (resistance), if any at all (see Deak this issue, Romero & Butler, this issue). However, if the flight response is lethally mal-adaptive, as appears to be the case with beaked whales and military sonar exercises, the exposure may still result in death, just not as a consequence of 'stress' *per se* (as in 'chronic stress' – exhaustion). It might also be possible that flight responses are increased if a stimulus is not only psychological, but also noxious (i.e., painful) by the direct effect of the noise pressure on the tissues and/or ear.

Shipping and masking of signals of importance for cetaceans

Shipping is most likely the main overall source of man-made noise in the marine environment (NRC, 1994, 2003) and masking has been identified as the primary auditory effect of vessel noise on marine animals (Southall, 2005). Most concern on this subject has traditionally focused on mysticetes (baleen whales), which communicate at the low frequencies typically associated with shipping noise (e.g., Payne & Webb, 1971). Consequently, it is noteworthy that ambient noise levels in the deep ocean at low frequencies have increased by 10-15 dB over the past 50 years due to motorized shipping (see Hatch & Wright, this issue, a and references therein). However, there is increasing evidence that modern ship noise can reach higher frequencies (e.g., up to 30 kHz: Arveson & Venditis, 2000; up to 44.8 kHz: Aguilar Soto et al., 2006) at distances of at least 700 m (Aguilar Soto et al., 2006). For example, there is a recording of a passing vessel on a DTag attached by suction cups to a Cuvier's beaked whale (*Ziphius cavirostris*) that demonstrates clearly that ship noise can mask ultrasonic vocalizations of odontocetes (Aguilar Soto et al., 2006). The high-frequency components of shipping noise may also be increasing due to the trend toward faster ships (Southall, 2005), because broadband cavitation noise (including the higher frequencies) generally increases with vessel speed (Arveson & Venditis, 2000).

Masking predominantly results from noise at similar frequencies to the signals of interest, although there may be some masking effects from "out-of-band" frequencies. Considering only in-band masking, the measured increase of up to 15 dB in low frequency noise due to shipping will greatly reduce the maximum functional range for signals in that band (Au, 1993). Similarly, calculations made be Aguilar Soto et al. (2006) demonstrated that the maximum communication range at frequencies used by Cuvier's beaked whales would be reduced by 82% (to 18% of its normal value) when exposed to a 15 dB increase in ambient noise at these frequencies, as was observed in the above-mentioned recording of a passing vessel. They also determined that the effective detection distance of echolocation clicks would also be reduced by 58% (to 42% of their normal range). Furthermore, if the current trend observed at low frequencies were applied to the higher frequencies component of ship noise, leading to a further increase of 15 dB by 2050, beaked whale communication at those frequencies would be reduced by 97% (to only 3 % of their 1950 maximum range) with each passing vessel (Aguilar Soto et al., 2006).

It is important to note that these calculations are based on observed increases in noise at high frequencies from a single passing vessel, that noise profiles from ships are highly variable and that high frequency noise attenuates much more rapidly than low frequency noise (see Hatch & Wright, this issue), limiting the area over which Cuvier's beaked whales would be affected. However, the trend towards faster boats, producing more cavitation and thus noise at higher frequencies, should also be considered. Furthermore, marine mammals that predominantly use low frequencies (e.g., baleen whales) may suffer similar reductions in the effective range of communication and other signals over much larger areas with additional reductions nearer a passing vessel. At the very low frequencies used by many mysticetes (e.g., under 200 Hz), masking may occur in the majority of the oceans, especially in the northern hemisphere (see Hatch & Wright, this issue). Consequently, it would not be possible for these species to employ an avoidance strategy (see Bateson, this issue; Wright et al, this issue, a) because of the omnipresence of increased background noise from ships.

This reduction in effective distances for communication will almost certainly be associated with an increase in the ambiguity of information received. The reception of ambiguous signals can act as a stressor and/or potentially lead to consequences such as missed mating opportunities and unidentified predators (see Bateson, this issue). These consequences can be especially problematic for animals that are already compromised in some way (see Wright et al., this issue, a). For example, a whale that is already in a state of chronic stress is more likely to interpret ambiguous information pessimistically and act accordingly, such as not chasing as many possible prey items or wasting energy avoiding more possible predators.

Whalewatching and energy budgets

Interactions between boats and cetaceans are known to have a number of effects on marine mammals, although they may not even be consistent among different groups within the same species (see Lusseau & Bejder, this issue). For example, in Doubtful Sound, New Zealand, female bottlenose dolphins (*Tursiops* spp.) responded linearly to increased disturbance intensity (increased intrusiveness of boat interactions) by increasing dive duration (Lusseau 2003). Conversely, the males almost immediately adopted an avoidance strategy by substantially increasing their dive duration, but then did not increase it further with increasing interaction intrusiveness. There are a number of possible reasons for this difference between males and females, including the fact that energetic demands and consequences differ between the sexes (e.g., reproduction). Whatever the reason, it may be that the males' avoidance strategy spares them from higher noise exposure and disturbance rates, limiting their physiological stress response. Alternatively, the males may be falling into an ecological trap and the females may be better off if the physiological stress response is actually quite limited and they can still continue to forage effectively.

Although difficult, it is possible to estimate the energetic consequences of behavioral alterations and other avoidance strategies (see Lusseau and Bejder, this issue). For example, increases in time spent traveling and decreases in time foraging in northern resident killer whales (*Orcinus orca*) in response to disturbance by whalewatching traffic led not only to a relatively small (although not necessarily inconsequential) estimated increase in energetic demands of 3%, but also to a estimated reduction in energetic intake of 18% (Williams, Lusseau & Hammond, 2006). It should be noted that these are minimum estimates, as any costs associated with a stress response (physiological or psychological) or as a consequence of masking would be in addition to these figures.

Dolphins have been observed apparently shifting from short-term avoidance (local behavioral) to long-term avoidance (habitat displacement) strategies in response to passing a threshold of disturbance from tourist boats (see Lusseau & Bejder, this issue). Presumably, at the point where this behavioral switch occurred, the dolphins determined in some way that the various costs associated with remaining in the disturbed habitat had become larger than the potential benefits. Consequently, when either habitat value is very high or habitat displacement is not an option (e.g., because boat interactions occur throughout the home range of the population), the costs of short-term avoidance strategies can accumulate and have serious implications for the population's viability. Alternatively, habitat displacement can also be very costly, as new habitats may have to be found or fought for, and knowledge of the area (e.g., prey locations) may have to be learned anew, the reduced habitat awareness potentially acting as a stressor in the meantime.

In either case, the various changes in the energy budget of an animal can, in turn, have a number of additional consequences. If the animal is still consuming more energy than it is using, it can continue to survive and grow, although unquestionably it will be less able to deal with anything that places additional energetic demands upon it, such as disease, migration and reproduction. As any remaining energetic surplus diminishes, a number of significant effects may begin to appear. For example, if the energy and resources available to a parent limits natal and/or parental investment, there will be various consequences for the health of the offspring (see Wright et al., this issue, a). Ultimately, if the animal is not able to consume enough energy to meet the increased demands, then it will begin to metabolize its lipid stores before it slowly starves to death or is forced to leave the area. In marine mammals the largest lipid store is the blubber layer, the mobilization of which will concurrently lead to an increase in contaminant levels in the blood (see Cumulative and Synergistic Effects). It should also be noted that hypoglycemia is a very powerful threat to homeostasis (i.e., a large stressor) that leads to rapid activation of stress responsive systems.

Something akin to the above may be occurring in both Shark Bay, Australia and Doubtful Sound, New Zealand. In Shark Bay a significant 15% decline in the relative abundance of dolphins was observed in an area where dolphin-watching activities occur, while a similar decline was not observed in an adjacent control site free from whalewatching activity (Bejder et al., 2006). In Doubtful Sound, the rate and frequency of perinatal deaths have significantly increased and the population abundance has decreased concurrently with a significant and substantial increase in the number of boats as well as the number of trips per boat (Lusseau, Slooten & Currey, 2006). The costs associated with boat interactions are such that females have to maintain homeostasis by reducing energetic investment in the only extrinsic factor they can manipulate: reproduction. It is not known how the males are faring in comparison.

Cumulative and Synergistic Effects

If context is important in controlling how noise induces stress responses in marine mammals and the various potential consequences thereof, it is crucial to consider the other potential stressors and anthropogenic activities that may be influencing marine mammals at any given time. We will not go into detail about the various possible additional anthropogenic stressors here, as the U.S. Marine Mammal Commission (Reeves & Ragen, 2004) provided an effective summary of the majority of other threats to marine mammals. Its annual reports also provide more information (MMC, 2007 and previous).

The following threats will almost certainly contribute in one way or another to a reduction in the condition of individuals (i.e., an increase in the "allostatic load"), which might, among other things, make them more susceptible to other potential stressors, including noise. As mentioned above, a reduction in the overall condition can also influence the psychological outlook of an animal (see Bateson, this issue). Although acting primarily on individuals, the impacts of these stressors may filter up to the population level if they affect an individual's survival or fecundity. These threats include:

- climate change and other ecosystem-wide change;
- habitat loss or degradation through coastal and offshore development, fishery activity (including due to a reduction in available prey), inland development (that results in material washing downriver either immediately or over an extended period as a consequence of a change in land-use, such as clearing forests), etc.;
- disease;
- toxic algal blooms ; and
- contaminants (especially adrenocorticotoxic contaminants: see Martineau, this issue).

Several other threats may also induce stress responses in individual marine mammals. However, they generally result in removal of an individual from the wild (either through mortality or permanent capture). Consequently, these other threats do not usually contribute to any existing stress response an animal may be experiencing prior to an exposure to noise, but are more likely to act cumulatively with noise-related stress effects at the population level. These include:

- fisheries bycatch;
- ship strikes;
- whaling; and
- dolphin drives.

It is also possible for exposure to noise (through a stress response or other means) to make individuals more susceptible to any of the above additional threats, including the generally lethal ones. For example, Nowacek et al. (2004) concluded that the alarm stimuli mentioned previously were poor options in attempts to mitigate vessel collisions with North Atlantic right whales, since the reaction of most animals in the study likely placed them at greater risk of vessel collision. Consequently, it is very important for managers to consider this conclusion when making decisions regarding the introduction of other novel sounds into the habitat of this highly endangered and declining species (Carretta et al., 2007), especially as the entire range for the species (the coasts of southern Canada to northern Florida) is an area that has a high concentration of shipping traffic.

Additionally, marine mammals, especially deep divers, are often thought to be pushing their physiological and anatomical limits as part of their normal behavior. They often subject themselves to considerable pressures as well as large changes in pressure on a regular basis, all while holding their breath for prolonged periods. The hypothesized anaerobic diving in beaked whales discussed above is one example of this. Another would be the bone damage seen in sperm whales (*Physeter macrocephalus*), which is thought to be a manifestation of the "bends" (Moore & Early, 2004). Such extreme conditions and related injuries could potentially be acting as additional injury stressors in their own right and might thus make marine mammals more susceptible to cumulative effects with other stressors, especially those thought to be mainly psychological in nature (see Deak, this issue).

Although information is generally lacking about how exposure to noise may ultimately affect marine mammals, it is possible to draw from the available information on how they respond to exposure to other stressors. Consequently, the following discussions examine the various effects of two of the most common threats to marine mammals: contaminant loads, with examples from pinnipeds and belugas; and interactions with fisheries, with an example from tuna-dolphin sets. These examples also provide some insight into the possible physiological and psychological condition that marine mammals might be in when exposed to noise (i.e., context), thus indicating potential pathways for cumulative interactions with noise exposure.

Contaminants

Marine mammals are especially susceptible to the effects of contaminants due to their high trophic level in the food web, long-life span, relatively late maturity and low reproductive potential. Many contaminants (or their metabolic products) bioaccumulate, meaning that they are found at increasing concentrations in the tissues of animals that occupy higher trophic positions. This process can lead to very high concentrations in long-lived adults or in newborns, when lipophilic contaminants are transferred from the mother through milk (see Martineau, this issue). This is because much of the contaminant load is stored in the blubber layer, which is partially metabolized for milk production (see Martineau, this issue). In many marine mammals, the first offspring stands to receive the highest dosage as the mother might have been bioaccumulating for many years before the first offspring is born, while only accumulating contaminant loads for a year or two in between pregnancies (Beckmen, Blake, Ylitalo, Stott & O'Hara, 2003). The blubber layer is also metabolized during periods of fasting or starvation (including times of migration, such as in mysticetes, or reproduction, such as in many pinnipeds), delivering the contaminant load to the fasting animal.

While contaminant loads compromise animals and are often associated with increased occurrences of various pathological conditions, different contaminants can have very different effects. For example, some organochlorine compounds (OCs), such as dioxin-like polychlorinated biphenyls (PCBs), can cause apoptosis (i.e., self-destruction) of T-cells in the same way that a GC stress response does. Dioxin-like PCBs (and their metabolites) are also known to interfere with the size and effectiveness of the GC response (see Martineau, this issue). Other OCs metabolites, such as DDT's, are known to damage the adrenal cortex (see Martineau, this issue), which is also involved in the stress response.

Many substances (or groups of substances) may have a range of effects (see Kakuschke & Prange, this issue). For example, studies have linked high metal burdens with a large variety of impacts in marine mammals ranging from lower resistance to diseases, through harmful influences on the liver, kidney, central nervous system and reproductive system, to stillbirths. Metals also impair immune cell function through a number of mechanisms. Depending on the particular metal, its chemical bond, concentration, bioavailability and a host of other factors (including the age of the animal), the result can either be immunosuppression or immunoenhancement leading to hypersensitivity and autoimmunity (see Kakuschke & Prange, this issue). Studies on marine mammals from the North Sea have demonstrated a relationship between pollutant exposure and infectious disease mortality (Jepson et al., 2005). Higher levels of contaminants were also found in seals that died during the Phocine distemper virus epizootic that interrupted the increase of the harbor seal (*Phoca vitulina*) population in the Wadden Sea (Hall et al., 1992).

One population that may be particularly at risk from cumulative effects of noise and contaminants is the beluga whale population of the St Lawrence estuary. These beluga may already be quite compromised as they live in a historically highly polluted area (Fox, 2001; Lebeuf & Nunes, 2005; Lebeuf, Noëla, Trottier & Measures, 2007; Martineau, Béland, Desjardins & Lagacé, 1987; Muir et al., 1996; Muir, Koczanski, Rosenberg & Béland, 1996). For example, immunosuppressive contaminants most likely led to a high susceptibility to infections by opportunistic bacteria (i.e., bacteria that are part of the usual bacterial load in many animals and are not usually pathogenic) reported in the population (Martineau et al., 1988). High levels of shipping activity in the area is also exposing the whales to noise, with the imminent construction of a liquefied natural gas (LNG) terminal and planned natural gas exploration in the estuary set to raise noise levels further. As stressors related to contaminant loads are predominantly physiological and those related to noise are likely to be mostly psychological, increasing exposure to either also increases the risk of sickness-like conditions developing in the whales (e.g., neuroinflammation: Deak, this issue).

Tuna-dolphin fishery

The yellowfin tuna (*Thunnus albacares*) purse-seine fishery targets dolphins in the eastern tropical Pacific Ocean (ETP), as the tuna schools are associated with the dolphins. It should be noted that this makes it a somewhat unusual example of fisheries interactions, as marine mammals are not often targeted directly. However, there are a relatively large number of studies into the effects of the ETP tuna fishery upon the dolphins, which is why it was selected as an example here.

Edwards (this issue) describes the process of chase, capture and release that the ETP dolphins are subjected to by the fishery. High mortality rates in the early days of the fishery (see Edwards, this issue) substantially reduced abundance in the two dolphin species most often involved (northeastern offshore spotted, *Stenella attenuata*, and eastern spinner, *S. longirostris*) to 20% - 30% of pre-fishery (1960) levels (Wade, Reilly & Gerrodette, 2002). Despite the substantial reduction of mortality rates to sustainable levels in 1990 due to the implementation of new fishing procedures, the populations do not appear to be recovering (Edwards, this issue; Gerrodette & Forcada, 2005).

Fishery-related stress responses (e.g., acute stress responses, “heat stress”, etc.) became a suspected limiting factor in both of the most commonly targeted species, as the number of sets (i.e., the number of times dolphins are disturbed, chased and potentially captured) has not decreased (see Edwards, this issue). The role of capture myopathy (a disease complex involving muscle damage that is associated with the combination of intense physical exertion and physiological stress effects of capture or handling, and which can in some cases have immediate or delayed fatal consequences: Spraker, 1993) in the lack of recovery is yet to be fully determined for a number of reasons (see Reilly et al., 2005). However, it seems possible that detrimental sub-lethal consequences arising from each individual’s stress response are playing an important role at the population level, at least through the more sensitive animals (see Edwards, this issue).

Great concern also surrounds the separation of calves from their mothers during fishery evasion, as the subsequent potential for unobserved calf mortality if not reunited promptly with their mother is quite high (Noren & Edwards, 2007). Even if calves are reunited, or do not suffer separation in the first place, there may still be serious consequences resulting from the experience. Neonates and young calves will be particularly sensitive to GCs because their brains are still developing, like all young mammals with immature nervous systems (see Romero & Butler, this issue). The purse-seine set experience, which appears to represent a severe but intermittent stressor to the ETP dolphins, may therefore have quite significant non-lethal effects on young calves. These would result from the double dose of GCs arising from the massive influx transmitted to them via the mother’s milk as a consequence of her physiological stress response, combined with those produce by their own stress responses. These excessive stress-chemical loads have the potential for generating both acute neurological damage and long-lasting neurological re-programming in any nursing calves involved in evasion of a tuna purse-seine set in the ETP (see Sapolsky, 1992).

The various studies investigating fishery-related stress effects in ETP dolphins (e.g., changes in blood and muscle chemistry; damage to various organ systems, etc.: Reilly et al., 2005) illustrate the wide variety of impacts that can accompany an escape response (possibly acoustically-initiated) to an impending threat. At the present time, it is impossible to determine whether physiological effects of the whole chase/capture/escape experience are either short- or long-lived.

In general, physiological effects related to the stress response are likely to be reasonably short-lived for otherwise healthy adults in situations where even fairly intense natural stressors (e.g., predation attempts) occur only once every few weeks (see Dallman & Bhatnagar, 2001). Although the rate of occurrence may be similar in the ETP dolphins (see Edwards, this issue), surviving calves and fetuses in utero may still suffer a range of long-term impacts as they are exposed to maternal cortisol (if not also their own) each time their mother has been stressed during the chase-hunt, as discussed above. Some of these impacts may persist until the animals are adults and can include the development of an abnormal stress response system (e.g., Kapoor, Dunn, Kostaki, Andrews & Matthews, 2006). However, adults could also be affected as the chase process is characterized by an intensity and duration never encountered in nature (e.g., predators get tired and remain silent in contrast to motor vehicles). The set attempts likely involve both physiological and psychological stressors, such as noise and intense exercise, which may lead to sickness-like conditions in the exposed individuals (see Deak, this issue). Furthermore, the extent to which the stress response is involved in the initiation of capture myopathy has not yet been identified (see Reilly et al., 2005). The potential also exists for some serious cumulative impacts in dolphins of any age if they are in any way compromised prior to attempted purse-seine sets.

Acclimation in Marine Mammals

There is very little (if any) evidence of acclimation (as defined in Wright & Kuczaj, this issue) in marine mammals in the wild, although this does not mean that it does not occur. Many references to “habituation” have not demonstrated that the observed reduction in behavioral response is associated with a reduction in the physiological stress response and processes other than acclimation may explain the results (see Wright et al., this issue, a). For example, the observed reduction in behavioral responses of ETP dolphins when in the purse-seine net (i.e., originally they appeared to panic, but now seem to wait relatively passively until released), could indicate acclimation, but more likely indicates learning, and/or natural selection instead. It is important to recognize that these processes can change behavior in adaptive ways that nevertheless continue to be accompanied by a full internal physiological stress response.

Thus, apparent behavioral tolerance of noise in marine mammals cannot be automatically interpreted as acclimation (see Beale, this issue). However, there has been little opportunity for adaptation to noise to occur through natural selection in many marine mammals because of their long lifespans (except if there are lethal consequences of exposure to the stimulus: see below). This is especially true in large whales, as the increases in noise in the oceans may have occurred in a single lifetime. Consequently, an observed reduction in behavioral responses in marine mammals may often reflect a learning process, whereby repeated exposures to a stressor leads to reduced or altered behavioral responses, but not necessarily reduced physiological responses. The animals learn either how to behave to reduce any negative effects or that the stressor is not as noxious as it first appeared. However, the stimulus is still perceived as a stressor. It is then possible that this information and any associated behaviors are conveyed to the next generation through cultural transmission.

With regards to the apparent acclimation in ETP dolphins to capture by the purse-seine the tuna-dolphin fishery, it is important to separately consider the capture by itself, as well as the whole purse-seine set experience collectively. It is unlikely that physiological acclimation to the whole purse-seine set activity occurs for several reasons. First, most ETP dolphins are only chased about once per month (and captured less often still; see Edwards, this issue) which is probably not often enough to lead to acclimation given the probable size of the stressor involved (although these catch frequency estimates are merely averages: some dolphins will evade sets more often, some will evade less often). Second, the dolphins still respond to capture efforts by fleeing immediately upon perception of an impending set (which, as an aside, is the cause of capture myopathy in free-ranging ruminants: Spraker, 1993). Third, they still engage in prolonged escape behavior after getting out of the net (also involved in capture myopathy: Spraker, 1993). Fourth, ETP dolphins in the more heavily fished areas exhibit escape reactions in response to all approaching big boats while responding less to vessels not approaching them directly (Au & Perryman, 1982; Hewitt, 1985), even though the combination of sounds that signal an approach are unlikely to be identical due to vessel and engine variety. Fifth, the number of ETP dolphins has been severely reduced. Finally, the social structure of the dolphins appears to have changed since the onset of the fishery as the average school size has decreased. Although the last two pieces of evidence do not necessarily reduce the likelihood that acclimation is at work, they suggest that other explanations for any tolerance displayed may be more likely, such as half a century of selective pressure (approximately four generations in these species: Myrick, Hohn, Barlow & Sloan, 1986).

It may be that the dolphins have acclimated somewhat to their temporary capture in the purse-seine nets, although the frequency of exposure remains a major issue (i.e., it may not occur frequently enough for acclimation to take place). Consequently, it appears more likely that the dolphins' relatively calm behavior reflects learning or selection, rather than acclimation. Furthermore, the dolphin's prolonged escape response after release from the net also implies that the animals have not acclimated to either capture or the full set experience. For example, it may be that, having experienced enough sets to realize that there is nothing they can do until the backdown maneuver (see Edwards, this issue), the dolphins may have learned to behave more calmly in the net, although they are very likely not internally calm at all. In comparison, learning to ignore the chase is unlikely as the result is uncertain: there is the possibility of either escape or capture.

As mentioned above, selective pressures may also be involved, fuelled by variation in individual susceptibilities to in-net mortality, the stressors of chase and capture, and possibly also capture myopathy. These factors, in combination with the fact that fishermen actively target larger schools, may have very quickly selected for dolphins that aggregated in smaller groups and behaved most appropriately to the sets. Consequently the reduction in apparent agitation in the net could be a result of the massive and efficient loss of the more sensitive individuals (potentially through unobserved capture myopathy in addition to direct mortality in the net). Given the dramatic reduction in abundance, it appears reasonable that the remaining dolphins are those best ‘suited’ to surviving purse-seine sets.

Similar processes are also at work in modern fisheries. Observed effects include a reduction in the average size of collected fish, due to slower growth rates (within any given species), because only larger fish are big enough to be legally captured (see Conover & Munch, 2002). Under those conditions, fish that mature at a smaller size (either by growing slower or maturing earlier) have a selective advantage. However, smaller breeding animals may also have less resources and energy available to invest in reproduction, which could explain the associated reduction in egg size (Conover & Munch, 2002).

North Atlantic right whales

There are several possible explanations for the reactions of North Atlantic right whales to shipping noise and alarm sounds as discussed above (Nowacek et al., 2004). Two of the most likely are: 1) the whales have not learned to react to ship noise sounds appropriately (i.e., by swimming away), while they do not distinguish alarm sounds from those emitted by possible predators, such as killer whales; and 2) the whales have acclimated, wrongly, to continuous ship noise so that they do not react even at levels likely indicating danger of collision, while they do react to novel noise sources such as alarm sounds.

It is therefore no surprise that the following statements (which we demonstrate below are likely incorrect), with their associated management ramifications, are common in attempts to further understand why right whales do not appear to use sound to avoid ship strikes: 1) North Atlantic right whales appear to have “habituated” to ship noise, thus increasing the numbers and/or types of vessels in their coastal habitat does not constitute a potential threat to this endangered species; and/or 2) North Atlantic right whales have “habituated” to ship noise thus introduction of other industrial sounds to their coastal habitat does not constitute a potential threat to this endangered species.

If indeed right whales have actually acclimated to the constellation of low-frequency dominant sources in their environment, then the probability of a stress response occurring as a direct result of repeated exposure to industrial and vessel noise may be decreased. However, masking and signal discrimination would continue to create problems for right whale communication efficiency (and thus may indirectly lead to a stress response). In fact, the occurrence of ship strikes and entanglements in right whales may indicate that there is so much noise (or the noise has caused enough hearing damage) that the whales are unable to hear or locate anything except the loudest of sounds.

If acclimation is not occurring and a repeated and/or continuous stress response is being maintained by right whales due to a high incidence of exposure to acoustic and other stressors, then the observed lack of behavioral response in right whales may be due to various other factors. First, their physiological response to vessel noise exposure may not result in changes in behavior. Second, the animals may be less likely to respond if they are in poor overall health, perhaps as chronically stressed individuals (see Beale & Monaghan, 2004). Third, any changes in behavior that do occur may be too subtle to have been detected, or have not been correctly identified (and thus recorded) by researchers due to a lack of understanding regarding the context for those changes. Finally and perhaps most likely, the whales just can't afford to react to ship noise as it happens all the time in the area they have to be in, so they carry on regardless (e.g., they have learned not to respond to the noise).

Given the lack of evidence for acclimation in this situation and in studies of other animals, as well as the discussion of acclimation above and in Wright et al. (this issue, a), it seems quite unlikely that North Atlantic right whales have acclimated, as defined, to loud sources of low frequency sound in their environments,. Consequently, the likelihood that the apparent tolerance is due to one or more of the other possible reasons needs to be considered in efforts to manage anthropogenic impacts on the species.

Conclusions

It is clear that noise can act as a stressor to marine mammals. If marine mammals react in a similar manner to other animals (including mammals) that have been studied in controlled circumstances, repeated and prolonged exposures to stressors (including or induced by noise) will be problematic for marine mammals of all ages. The resulting extended stress response may then lead to a range of issues including, but not limited to, suppression of reproduction (physiologically and behaviorally), accelerated aging, and sickness-like symptoms. Acclimation to such exposures seems unlikely for a number of reasons, including differences in the perceived stimuli, changing context, time-scales, etc. Examples of apparent "habituation" may instead indicate selection, or learning without acclimation. Learned responses, like acclimation, are highly dependent on the predictability of stimuli. However, learned responses, like other possible mechanisms of adaptation but unlike acclimation, may or may not reduce the magnitude of the physiological stress response.

Regardless, acclimation or some other apparent tolerance of a noise may have various pernicious effects, such as limiting the ability of the animals to react to actual threats. These may, in some cases, have lethal consequences (e.g. right whales' lack of reaction to ship noise, possibly resulting in collisions), but the majority of knock-on outcomes are likely to be physiological (e.g. dolphins approaching acoustic pingers, risking receiving noise levels with the potential to cause temporary hearing impairment, also known as a temporary threshold shift – TTS) or psychological (e.g., annoyance) effects that are not immediately lethal. However, physical injuries and other consequences of noise exposure may then act as additional stressors upon marine mammals. For example, if masking leads to increases in information ambiguity, or group or mother-calf separation, animals may suffer from anxiety as a result. Masking by increasing noise levels would be roughly analogous to a human trying to see through increasingly dirty glasses. Eventually, the lack of reliable acoustic information prevents marine mammals, especially cetaceans, from 'seeing' their environment, essentially leaving animals blind. Confounding the issue further, maladaptive efforts to avoid a noise can also indirectly lead to detrimental outcomes for marine mammals.

In addition to the myriad possible affects from noise exposure that can all interact together, it is important to consider the potential cumulative effects of multiple anthropogenic stressors. For example, should the energy balance of a marine mammal become negative (due to disturbance or disease, etc.) lipids and the lipophilic contaminants stored within them are mobilized from the blubber. The release of these contaminants into the circulation not only constitutes *de facto* a second exposure to the individual concerned during a period of nutritional challenge, but mothers also expose newborns through transfer in milk (Martineau, Béland, Desjardins & Lagacé, 1987; Tornero et al., 2005; Wells et al., 2005). Affected animals would then be less able to respond sufficiently or appropriately to any additional stressors.

Further contextual complications may be involved in beaked whales and other deep diving marine mammal species, as their normal behavior may put them already at the limits of their physiological capabilities. Cumulative and synergistic effects can be assessed in different ways, but any such assessment should be undertaken very cautiously as synergistic effects can be very unpredictable. The following hypothetical chain of events illustrates the complexities of cumulative and synergistic effects in which noise-related stress may have deleterious consequences for a marine mammal.

A young male sperm whale in the Gulf of Mexico is exposed to nearby shipping noise and experiences a stress response. This response is more extreme than it would otherwise be as the young animal was exposed in utero and immediately after birth to high GC levels transferred through the placenta and milk from its mother, when she was undergoing a stress response. Despite a flight response sending the whale to the surface, the animal is lucky and avoids a potentially lethal ship strike. After repeated non-lethal exposures to that (or similar) sounds, the whale learns that the noise is not followed by any serious immediate consequences and so it stops responding behaviorally. Despite this, the animals GC levels remain high, because it has not acclimated to the passing ships and also because of its altered HPA axis. The resulting GC levels cause slow growth. If a ship passes nearby, the whale might experience TTS and/or the disruption of sleep, as well as interference in communication and foraging resulting from the masking. From time to time these problems annoy or agitate the whale and produce their own stress responses, depending on the exact situation.

As it ages, the sperm whale builds up a contaminant load over and above the dose it received as a calf from its mother. It also begins to suffer from bone damage related to diving. Frequent exposure to a variety of anthropogenic noise sources continues to disrupt foraging efforts and begins to directly affect its body condition and psychological outlook. A compromised immune system allows an infection to take hold and the whale begins to lose weight. Blubber is metabolized and the whale is exposed to the mobilization of its contaminant load. A seismic survey begins in the area and the resulting total exposure over the next several days exhausts the supply of components for GC production and pushes the combination of psychological and physiological stressors beyond a certain threshold, resulting in neuroinflammation and other sickness-like conditions. In the face of this worsening condition, the sperm whale beaches itself and dies with no particular cause of death apparent.

Many of the effects discussed in this paper can be incorporated into population viability assessments and other models used by managers in their decision making process. There are a small number of studies in marine mammals where controls have been appropriately established that are beginning to provide some of the information required for this. However, for the majority of marine mammals, accounting for these effects will require some assumptions about the implications of the various stress responses on fecundity and survivorship, as the data that concern these parameters are not available. Fortunately, extrapolation from data in other species (and possibly even from other animal groups) appears reasonable, because the physiological stress response is highly conserved across the many different species that have been studied to date.

In addition to the more general conclusions and findings offered by Wright et al. (this issue, a) pertaining to stress responses to noise, we suggest that the following findings and recommendations (presented in no particular order) are especially important with regards to marine mammals. We propose that marine mammal managers and scientists consider these findings and specific recommendations when planning research or management actions (e.g., in assessments of environmental impact).

Findings

1. "Stress" is a very important concept to consider in managing the impacts of anthropogenic activities on marine mammals, yet definitions vary greatly among specialists as well as laymen. There is also much confusion over the use of the related term "habituation" (see also Wright et al., this issue, a).

2. Given the physiological, psychological, behavioral and ecological information presented, considered and discussed in this issue, the conclusions that have been drawn from them, and the other findings presented here, it is reasonable to assume that anthropogenic noise, either by itself and/or in combination with other stressors, can reduce the fitness of individual marine mammals and decrease the viability of some marine mammals populations.

3. The physiological stress response is highly conserved among those animal species in which it has been studied (including a few marine mammal species: e.g., Martineau, this issue) and thus extrapolation to marine mammals is reasonable.

4. Very young individuals (and fetuses) are particularly sensitive to the neurological consequences of the stress response and can suffer permanent neurological alterations as a result. Similarly, deep diving marine mammals may be particularly sensitive to noise as a stressor given that many marine mammal species are thought to live close to their physiological limits.

5. Acoustic masking may act in several ways to induce stress responses in marine mammals. These may include but are not limited to: reducing the range of signals important for communication and finding of prey; reducing the clarity of received signals; and inducing anxiety and annoyance. These combine with potential effects on foraging efficiency and social cohesion, with possible subsequent effects on reproductive success and survivorship.

6. Scientists need to study stress responses in marine mammals and their epidemiological and psychological consequences. Most immediately, classical stress measures will be needed to marry the extrapolations from studies in other animals with observed behavioral responses. Such studies will be complex and require defining concepts such as "need" and "risk" in terms of the decision making process in the often highly developed brains of marine mammals. Adequate techniques to obtain physiological data (e.g., heart rates, cortisol levels, adrenal morphology and other information) are also required. Implicitly, these various techniques should be the least invasive as possible to minimize additional stressors. It is also very important to include a comparison or control group (i.e., mammals not exposed) or baseline data (i.e., data from animals before they became exposed). However it is acknowledged that non-exposed populations of marine mammals are likely to be quite rare.

Research Recommendations

1. Efforts should be made to collect information on the dynamics of stress-related chemicals (particularly cortisol) in cetaceans and other marine mammals. Collection from blood plasma may not currently be practical for assessing the effects of most stressors, given that animals would generally need to be captured, which is a complex task when handling large marine mammals. Currently available methodologies that do not require capture involve the collection of feces from free-ranging animals (either after visual detection or through the use of the canine sense of smell: Hunt, Rolland, Kraus & Wasser, 2006), or the collection of mucus expelled during exhalation (Hogg, Vickers, & Rogers, 2005). The time between exposure to a stressor and the increase in cortisol levels in the various samples need to be considered. The period from stressor exposure to increased cortisol levels is very short in blood samples. In contrast, cortisol levels in samples from feces will be averaged between bowel movements, and those from samples of respiratory mucus exhaled with a breath are likely to take 10-15 minutes or more to reflect the impact of a stressor. Cortisol levels in fecal and mucosal samples are likely to be more variable than in blood samples, but the less invasive collection methods are less likely to trigger a stress response of their own, allowing the techniques to be used to study the effects of other stressors, such as noise. Such investigations would need to be carefully constructed, with well-designed controls. Efforts should acknowledge that is not possible to distinguish between acute and chronic stress responses in blood, fecal and mucosal

samples without a time-series. It should also be noted that animals often expel fecal matter as part of a sympathetic response when they become stressed. In addition, GC levels are fairly variable from one individual to another, so baselines will be needed for each individual against which to measure relative stress levels.

2. Opportunistic collection of information about the level of stress-related chemicals from various tissues and stores in stranded and bycaught animals should also be undertaken. Investigations should also be made to see if it is possible to obtain these chemicals from skin and/or blubber. If so, the amounts in the blubber may be long-term average levels, providing indication of cumulative stress responses for marine mammals over the long-term. However, there is some active exchange between the blubber and the blood, so levels of stress-related chemicals in the different layers of the blubber may reflect shorter-term averages, although there may also be high variability both between and within species. Post mortem examinations of stranded marine mammals should also record other pathologic effects related to exposure to stressors. For example, the size and weight of, as well as the presence of any lesions on, the adrenal glands should be noted. Chronic stress leads to chronic stimulation of the adrenal cortex by adrenocorticotrophic hormone (ACTH). In turn, ACTH chronic stimulation results in adrenocortical hyperplasia (increased number of cells) or hypertrophy (increased size of cells) necessary to allow for sustained overproduction of GC and possibly catecholamines. These morphological changes are seen grossly as increased size and weight of the adrenal glands (Clark, Cowan & Pfeiffer, 2006; Dorovini-Zis & Zis, 1987; Lair, Beland, De Guise & Martineau, 1997; Nemeroff et al., 1992; Ulrich-Lai, Figueiredo, Ostrander, Choi, Engeland & Herman, 2006). Furthermore, the presence of acute phase proteins in different organs, such as the liver or skin, could indicate recent exposure to an intense stressor. This could also provide important information on “normal” background levels of the proteins in different species, which would be very useful in developing further studies on the evaluation of stress response in marine mammals.

3. Skin biopsies, sampled from live cetaceans with minimal disturbance, have yielded unique information about genetics and contaminants (Fossi et al., 2004; Hobbs et al., 1998). Not only is skin a major target organ for cortisol (and thus cortisol is present in the skin) but skin is also a site of cortisol synthesis (Slominski, Wortsman, Tuckey & Pau, 2007). Measurement of cortisol levels in skin biopsies carried out on free-ranging cetaceans should be explored, although the possible effects of any chase and handling required to obtain the samples needs to be considered. It may also be possible to obtain this information through collection of sloughed skin from the water in the wake of a whale, which could largely circumvent this problem.

4. Given that studies on cortisol in humans have generated mixed results, efforts should also be made to study epidemiological effects in marine mammals, especially in the wild.

A Strategy for Managing the Impacts of Noise on Cetaceans in the Face of Uncertainty

Based on the available evidence, a non-trivial negative impact of noise-related stress responses on vital rates is expected for many marine mammals, especially cetacean species, although there is still substantial research needed to determine the magnitude of impacts. The Bayesian approach outlined by Wintle (this issue) is likely to be viable, logical and coherent in quantifiably extrapolating noise-related impacts from other mammals to cetaceans, given the highly conserved nature of stress physiology.

There are clearly grounds to justify initiating an adaptive noise mitigation strategy based on the available evidence and theory concerning the impacts of both acute and chronic noise on humans and terrestrial mammals, as well as the sparse data available on cetacean noise impacts. Potential noise exclusion zones should be identified as a matter of urgency. However, in order to commence the learning cycle, it is essential to measure vital rates under both noisy and noise-excluded management conditions so that the specific benefits of noise exclusion/mitigation can be better understood. Until an adequately stratified study of cetacean vital rates under various levels of noise impacts can be established, the value of noise mitigation efforts will be clouded by uncertainty. It is acknowledged that this will be a difficult and lengthy task.

A detailed description of a suitable management and monitoring strategy to assess the impacts of noise and noise mitigation on cetacean vital rates is beyond the scope of this issue. However, some general recommendations to those managing the impacts of noise on marine mammals can be made. We recommend that:

1. An expert working group should be convened with the specific goal of identifying noise impacts on cetacean (or other marine mammal) vital rates, using all available data and systematically integrating knowledge of impacts from other species.

2. Areas suitable for broad-scale noise exclusion/reduction should be identified.

3. Where possible, environmentally similar areas that cannot have noise exclusions/reductions should also be identified.

4. Based on the results of expert working groups, models should be developed to predict likely population responses to noise mitigation strategies.

5. Levels of noise should be closely monitored and measurement of cetacean vital rates initiated in all locations.

6. The relationship between noise level and cetacean vital rates may then be updated and predictions about future gains modified to reflect the new information.

7. Monitoring of vital rates should be maintained to enable better decisions about future allocation of mitigation efforts.

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Appendix 1

The following table compares some of the scientific evidence for physiological, psychological and behavioral responses to various stressors with some of the known behavioral effects of noise in marine mammals and other species. It should not be considered an exhaustive list. It should also be noted that authors contributed predominantly to the rows in which they had expertise. This has given rise to different application of the columns “mechanisms’, ‘observations’ and ‘consequences’. For example, in some cases a physiological stress response is listed as a consequence, while in others the whole response is, or elements of it are, listed as either a mechanism and/or an observation. These inconsistencies highlight the diverse approaches in the various disciplines and may arise from the different methodologies available to the scientists in the various fields and from one species to another. They should therefore not necessarily be interpreted as inconsistencies in the actual results. Finally, some of the potential impacts resulting from noise exposure discussed in this and other papers in this issue have been added to many of the marine mammal entries as possible consequences. Items in italics are uncertain and those marked ‘*???*’ are unknown.

Animal	Stimulus	Mechanisms	Observations	Consequences	Sources
General	Chronic/cumulating acute non-specific (e.g., contaminants, predators, etc.)	Chronic GC response.	Increased GC levels prior to eventual fall-off.	Chronic: Disregulation of glucose and metabolism; Stress-induced dwarfism; Behavioral changes (context dependant); Reproductive disruption (psychological and physiological); Immune-suppression.	McEwen & Goodman, 2001; Sapolsky, Romero & Munck, 2000
Guinea pigs	Maternal separation	*Probable increase cytokine expression?*	See consequences.	Initial anxiety followed by ‘sickness’.	Hennessy et al., 2007
Lab rat	Footshock	Increase cytokine expression and microglial activation and CNS.	See consequences.	‘Sickness’ behavior, Neurodegeneration.	Deak, Bellamy & D'Agostino, 2003; Nguyen et al., 1998; Plata-Salaman et al., 2000; Shintani et al., 1995
Lab rat	White noise (experimental)	Release of corticosterone; Intestinal inflammation; Microvasular damage; Transient increase in blood pressure.	Redness around eyes and on back of neck. Also see mechanisms.	Non-selective molecular exchange intestine-blood stream leading to septicemia.	Baldwin, Primeau & Johnson, 2006; Baldwin & Bell, 2007; Burwell & Baldwin, 2006; Windle et al., 1998

Animal	Stimulus	Mechanisms	Observations	Consequences	Sources
Humans	Aircraft noise, road traffic noise, community/ambient noise and occupational noise	Physiological responses: Hypertension; Coronary heart disease (CHD).	Increased systolic BP or hypertension diagnosis; Increased rates of CHD.	Problems with hypertension leading to heart disease; CHD; Annoyance.	Babisch, 2006; van Kempen et al., 2002; Babisch, 2000
Humans	Aircraft noise, road traffic noise, community/ambient noise and occupational noise	Physiological responses in adults and children: Stress hormones in the endocrine system (cortisol, adrenaline, noradrenaline).	Increased levels of these hormones being measured in urine and saliva.	Evidence linking stress hormone levels to health impairment is lacking but raised levels may impact of peripheral vascular system; Annoyance.	Babisch, 2003 (meta-analysis)
Humans	Aircraft noise, road traffic noise, community/ambient noise and occupational noise	Sleep disturbance.	Increased awakenings due to noise exposure; Taking longer to fall asleep; Evidence that habituation (as defined by Clark & Stansfeld, this issue) to exposure occurs.	Performance effects; Mood effects; Health effects associated with sleep disturbance; Noise during sleep may also stimulate heart rate; Annoyance.	Basner & Samel, 2005; HCN 2004; Miedema & Vos, 2007
Humans	Aircraft noise, road traffic noise, community/ambient noise	Psychological health.	Dose-response relationships between aircraft noise and depressiveness in adults; Some child studies have found increase reports of poor psychological health but others haven't.	Poor psychological functioning, wellbeing, quality of life.	Haines et al., 2001; Haines et al., 2001; Hiramatsu et al., 2000; Lercher et al., 2002; Stansfeld et al., 2005
Humans	Aircraft noise, road traffic noise, community/ambient noise	Children's cognition.	Impaired reading and short-term and long-term memory.	Impact on children’s learning and schooling.	Clark et al., 2006; Haines et al., 2001; Haines et al., 2001; Hygge, Evans & Bullinger, 2002; Stansfeld et al., 2005
Wedge-tailed eagle	Forestry operations *(chainsaw noise??)*	Fleeing.	Nest abandonment.	Breeding failure (for that year).	Mooney & Holdsworth, 1991; Mooney & Taylor, 1996

Animal	Stimulus	Mechanisms	Observations	Consequences	Sources
Robin	Ambient Noise	*Masking?*	Nocturnal Singing.	Increased risk of predation; Sleep deprivation.	Fuller, Warren & Gaston, 2007
Starlings	Barren cages	Anxiety.	Risk averse foraging.	Reduced intake of food.	Bateson & Matheson, 2007; Matheson, Asher & Bateson, 2007
Turnstones	Human presence	'Decision' based on context.	Variable alert and evasive depending on context.	Probably minimal (in this case).	Beale & Monaghan, 2004a
Kittiwake	Human presence	*Sympathetic responses?*	Variable: Elevated heart rate; Sleep/Awake proportion.	Variable: Increase nest failure (debatable long-term impact).	Beale & Monaghan, 2004a, 2004b
Wood lark	Human presence	'Decision' based on context.	Variable: nest selection; Disturbance avoidance.	Complicated: Potentially population level effects.	Mallord et al., 2007
Seals	Pollutants	Immunmodulation by metal (pollutants); Activation and/or suppression of lymphocyte reactions; Influence on cytokine expression.	See consequences.	Immunological dysfunction like hypersensitivity or immunosuppression; Changes in susceptibility to infection diseases.	Bennett et al., 2001; De Swart et al., 1996; Kakuschke et al., 2005; Kakuschke et al., 2006; Lalancette et al., 2003; Pillet et al., 2000; Ross, 2002; Siebert, et al., 1999
Cetaceans (15 different species)	Live stranding	*Vascular compromise?*	Accumulation of acute-phase proteins in hepatocytes; Acute liver congestion.	Unclear.	Godinho et al., 2005
Beluga	(Mutagenic) Pollutants	Activation and/or suppression of lymphocyte reactions; Consistent with GC and/or toxic effects of contaminants; Effects of mutagenic pollutants; PCB toxicology.	See consequences.	Immunological dysfunction in vitro & in vivo; Increase opportunistic bacterial infection; Adrenal cortex degeneration/proliferation; Cancer; CYP induction.	Buckingham, 2006; De Kloet et al., 1998; Escriva et al., 1997; Hahn, 2002; Herold, McPherson & Reichardt, 2006; Matsumara, 1995; McMillan et al., 2007; Remillard & Bunce, 2002; Wang et al., 2003; Williamson, Gasiewicz & Opanashuk, 2005

Animal	Stimulus	Mechanisms	Observations	Consequences	Sources
Eastern Tropical Pacific (ETP) dolphins	Purse-seine fishery (Acoustic cues associated with imminent capture attempt)	Set evasion.	Increased swim speed (2-3 m/sec); Leaping out of the water to breathe; Evasive maneuvering; Likely separation of mothers and young calves.	Energetic cost; Physiological stress response; School (social) disruption; Foraging disruption, Calf separation, Calf mortality, Capture myopathy.	Edwards, 2002, 2006; Myrick & Perkins, 1995; Noren & Edwards, 2007; Noren, Biedenbach & Edwards, 2006; NRC, 1992; Reilly et al., 2005; Weihs, 2004
ETP dolphins	Fishery capture	Wait for release.	Relatively calm milling and schooling in section of net far from vessel and close to section of net section where backdown channel will form.	Reduced net entanglement – therefore reduced in-net mortality; Interrupted social and foraging activities.	Edwards, 2002, 2006; Myrick & Perkins, 1995; Noren & Edwards, 2007; Noren, Biedenbach & Edwards, 2006; NRC, 1992; Reilly et al., 2005; Weihs, 2004
ETP dolphins	Release from purse-seine	Escape.	Prolonged (90 minutes) high speed (3-4 m/sec) escape swimming.	Energetic cost; Physiological stress response; School (social) disruption; Foraging disruption, Calf separation; calf mortality; Capture myopathy.	Edwards, 2002, 2006; Myrick & Perkins, 1995; Noren & Edwards, 2007; Noren, Biedenbach & Edwards, 2006; NRC, 1992; Reilly et al., 2005; Weihs, 2004
Harbor porpoise	Bycatch	*Suffocation?*	Accumulation of acute-phase proteins in hepatocytes; Death.	Death by suffocation.	Godinho et al., 2006
Marine mammals	Tonal/impulsive noise	Temporary Threshold Shift (TTS) in hearing.	TTS.	Compromised food-finding, navigation, and communication; Increased risk of predation	Finneran et al., 2002; Kastak et al., 1999; Schlundt et al., 2000
Cetaceans	Seismic surveys	*???*	Lower sighting rates; Avoidance of seismic array; Less feeding.	Energetic consequences.	Stone & Tasker, 2006
Coastal odontocetes	Chronic intermittent boat interactions	Flight response.	Behavioral budget alteration.	Reduced reproductive success; Decreased population viability; Habitat displacement.	Bejder, 2005; Bejder et al., 2006; Lusseau, 2004; Lusseau, Slooten & Currey, 2006

Animal	Stimulus	Mechanisms	Observations	Consequences	Sources
Coastal odontocetes	Boat interactions	Masking.	Reduce foraging time.	*Decreased survival rates?*	Erbe, 2002; Lusseau et al., submitted; Williams, Lusseau & Hammond, 2006
Small odontocetes	Seismic surveys	*???*	Faster swimming.	*Energetic consequences?*	Stone & Tasker, 2006
Bottlenose dolphins	Boat approach	*Masking of signals of interest for social communication and foraging?*	Higher whistling rate.	*Time/energy costs?* *Information ambiguity?*	Buckstaff, 2004
Beaked whales	Shipping noise	Masking of signals of interest for social communication and foraging.	High noise levels.	*Energetic consequences?* *Information ambiguity?*	Aguilar Soto et al., 2006
Beaked whales	Military exercises	Gas and fat embolism (hypothesis).	Atypical mass stranding (land and/or sea); Gas and fat embolic pathology.	Individual deaths; Possibly local population displacement or death.	Fernández et al., 2005; Jepson et al., 2003
Beaked whales	Shipping noise	*???*	*Activation of evasion mechanisms??*	Possible change in diving behaviour leading to reduction in foraging efficiency; Reduction in communication range.	Aguilar Soto et al., 2006
Killer whale	High boat traffic	*Masking of signals of interest for social communication and foraging?*	Increased call length.	*Time/energy costs?* *Information ambiguity?*	Foote, Osborne & Hoelzel, 2004
Killer whale	Acoustic Harassment Devicess	*???*	Long-term avoidance of area.	*Time/energy costs? Loss of opportunity for foraging, social interaction, mating?*	Morton & Symonds, 2002
Beluga	Boat noise	*Masking?*	Shifted frequencies; Used different call types.	Energetic/time/predator/prey costs; *Information ambiguity?*	Lesage et al., 1999
Beluga	Seismic like noise	*???*	Increased stress hormone levels.	*Immunity/illness consequences?*	Romano et al., 2004

Animal	Stimulus	Mechanisms	Observations	Consequences	Sources
Beluga	Icebreaker noise	*???*	Avoidance and flight at long ranges.	*Time/energy costs? Loss of opportunity for foraging, social interaction, mating?*	Cosens & Dueck, 1993; Finley et al., 1990
Pilot whales	MF sonar	*Masking?*	Increases in whistles.	*Time/energy costs?*	Rendell & Gordon, 1999
Sperm whales	Pingers	*???*	Fell silent.	*Compromised foraging or communication?*	Watkins & Schevill, 1975
Sperm whales	MF Sonar	*???*	Fell silent.	*Compromised foraging or communication?*	Watkins, Moore & Tyack, 1985
Sperm whales	Seismic surveys	*???*	Fewer creaks; No foraging dives near seismic vessel; Reduced fluke strokes and effort.	*Compromised foraging?*	IWC, 2007
Pilot, sperm whales	Low frequency pulses (similar to Acoustic Thermometry of Ocean Climate – ATOC – signals)	*???*	Decrease in vocalizations.	*Compromised foraging or communication?*	Bowles et al., 1994
Pilot, sperm whales	Seismic surveys	*???*	Decrease in vocalizations.	*Compromised foraging or communication?*	Bowles et al., 1994
Mysticetes	Seismic surveys	*???*	Avoidance; More time at surface; Fewer animals feeding.	*Time/energy costs?* *Reduced foraging?*	Stone & Tasker, 2006
Blue whales	Long range shipping noise	Masking.	Shifting frequency of call; May be some amplitude increase.	*Reduced mating opportunity?*	Croll et al., 2001; Payne & Webb, 1971
Fin whales	Seismic surveys	*???*	Suspension of vocalizations for weeks/months.	*Reduced mating opportunity?*	IWC, 2007
Fin whales	Boat noise	*???*	Decrease in vocalizations.	*Reduced mating opportunity?*	Watkins, 1986
Gray whales	Industrial noise, dredging and shipping	*???*	Long-term displacement of breeding area.	*Reduced mating opportunity?*	Bryant, Lafferty & Lafferty, 1984; Jones et al. 1994

Animal	Stimulus	Mechanisms	Observations	Consequences	Sources
Gray whales	Low frequency active (LFA) sonar (inshore)	*???*	Shift in migration path.	*Increased predation?* *Greater mother-calf/group separation??* *Anxiety?*	Tyack & Clark, 1988
Gray whales	Seismic surveys	*???*	Displacement out of primary feeding area; Faster respiration; Faster, straighter movement over larger areas.	*Reduced foraging?* *Time/energy costs?*	IWC, 2005, 2007
Gray whales and bowheads	Industrial noise	*???*	Shift in migration path.	*Increased predation?* *Greater mother-calf/group separation??* *Anxiety?*	Malme et al., 1983, 1984; Richardson et al., 1985; Richardson, Würsig & Greene, 1990
Bowheads	Seismic surveys	*???*	Shorter dives and lower respiration rates at as much as 50-70 km away.	*Widespread reduction in foraging?*	Richardson, Würsig & Greene, 1986
Humpbacks	LFA sonar	*???*	Mating songs lengthened.	*Long-term mating/energetic/time consequences?*	Fristrup, Hatch & Clark, 2003; Miller et al., 2000
Humpbacks	Seismic surveys	*???*	Avoidance; Occasional attraction prior to swimming away.	*Compromised foraging or breeding?*	McCauley et al., 2000
Humpbacks	Explosions	*???*	Greater entrapment in fishing gear	Often death.	Todd et al., 1996
Northern elephant seals	ATOC	*???*	Increased descent and decreased ascent rate in dives; Escape response.	*Reduced foraging?* *Time/energy costs?*	Costa et al., 2003

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