The effects of aircraft on cetaceans: implications for aerial whalewatching

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Abstract
The effects of anthropogenic noise on marine mammals are a rich subject for study and have attracted considerable attention in the past two decades. Aircraft noise may not only affect the biology of cetaceans but may also skew aerial survey data. Since 1995 few studies have been published, but these have documented behavioral responses of cetaceans to aircraft in much greater detail.. This paper reviews and discusses progress in the study of aircraft noise effects on marine mammals since the landmark review of Richardson et al. (1995). In each of the studies reviewed here, cetaceans responded to aircraft to some extent, in most cases by diving. Several major gaps in knowledge on the effects of noise on marine mammals also apply to aircraft noise, e.g. quantification of received sound level, the role of vision, knowledge of baseline behavior, the effect on vocalizations. The possible implications for whalewatching by aircraft are discussed.

INTRODUCTION

Cetaceans are highly dependent on sound for communication, navigation and detection of potential predators and prey (Würsig & Richardson 2002). Anthropogenic noise may therefore affect various aspects of cetacean biology. The impact of anthropogenic noise on cetaceans is a rich subject for study and has attracted considerable attention during the past decade and a half (e.g., Richardson et al. 1995, Perry 1998, Hildebrand 2005, Nowacek et al. 2007, Johnson et al. 2007). Most studies of the effects of anthropogenic noise on cetaceans have focused on underwater noise, caused by sources such as motorized boats, sonar, and seismic airguns. The effects of aerial sources of noise pollution have received far less attention.

Aircraft, including helicopters and fixed-wing airplanes, are used in various human activities, including transportation, military training exercises, the off-shore oil and gas industry, recreational flights, cetacean research and whale-watching tours (Patenaude et al. 2002, Richter et al. 2006, Smultea et al. 2008). Aircraft produce noise at frequencies that are well within the frequency range of cetacean calls and also produce visual signals such as the aircraft itself and its shadow (Richardson et al. 1995, Richardson & Würsig 1997). A major difference between aircraft noise and noise caused by other anthropogenic sources is that the sound is generated in the air, transmitted through the water surface and then propagates underwater to the receiver. As a result, analysis of the effects of aircraft noise on marine mammals is complicated (Richardson et al. 1995, Nowacek et al. 2007). A detailed review of the air-to-water transmission of aircraft noise was provided by Richardson et al. (1995). Aircraft noise also differs from boat noise in that it is typically present for shorter periods, and moves at a greater speed due to the higher travel speed of aircraft. The sound pressure levels produced by even small-sized aircraft may be extremely high (exceeding 120 dB re 20 μPa at 1m) and thus could have profound effects on cetacean populations near e.g. airports and along busy flight trajectories.

The last comprehensive review of the effects of aircraft noise on marine mammals was Richardson et al. (1995). This review was based largely on anecdotal evidence scattered in a large number of papers, mostly involving population surveys using aircraft. Evidence available at the time indicated that the responses of cetaceans to aircraft were highly variable among individuals and species, ranging from no apparent reaction to active avoidance (Richardson et al. 1995). Some responses (e.g. changes in respiration frequency) were subtle and became apparent only after statistical analysis (Richardson et al. 1995). Nonetheless, several factors affecting the responsiveness of cetaceans to aircraft noise were identified. A stronger response was observed in small groups or single individuals than in large groups (e.g. Herman et al. 1980, Payne et al. 1983, Richardson et al. 1985a, Richardson et al. 1985b, Fairfield 1990), in mothers with calves (e.g. Ljungblad et al. 1983, Clarke et al. 1989), in shallow waters (e.g. Richardson et al. 1985a, Richardson et al. 1985b) and in situations where the initial observed behavior was resting (Richardson & Malme 1993). A stronger response was also seen when the aircraft flew at low altitudes (e.g. Walker 1949, Bel'kovich 1960, Kleinenberg et al. 1964, Best 1981, Seargeant & Hoek 1988). However, it remains unclear to what extent these factors, identified in studies of a limited number of species, apply generally to cetaceans.

The purpose of this paper is to review and discuss progress in the study of the effects of aircraft noise on cetaceans since the landmark review of Richardson et al. (1995) and to identify critical aspects that require detailed additional study. This paper was prepared in response to a request for information on the possible impacts of aerial whalewatching (for a definition see Parsons et al. 2006a) on cetaceans at the 60th Meeting of the International Whaling Commission (International Whaling Commission 2009).

RECENT STUDIES (1995-2008)

Würsig et al. (1998) assessed the responses of cetaceans to aerial surveys in the north-central and western Gulf of Mexico using a DeHavilland Twin Otter fixed-wing airplane. Species of cetaceans were grouped in 6 categories according to their morphology and behavior. Observations were made aboard the plane. The altitude of the plane was 229 m at a speed of 204 km/hr over waters from 100–1000 m deep. A minimum of 305 m straight line distance from the cetaceans was maintained. Upon sighting of a pod, the plane approached the animals after an assessment of their behavior. Pods were usually circled for a period of time (approximately 10–50 min) and in some cases fly-bys were carried out at less than 229 m altitude.

'Cryptic' species, such as beaked whales (*Ziphiidae*), pygmy sperm whale (*Feresa attenuata*) and dwarf sperm whale (*Kogia simus*), showed a stronger response to the airplane than other species. Forty percent (12/30) of the observed *Kogia* spp. and 89% (8/9) of the observed ziiphids changed their behavior in response to the airplane. Of the smaller delphinids, pantropical spotted (*Stenella attenuata*) (43%, 18/42), Clymene (*S. clymene*) (71%, 5/7), striped (*S. coeruleoalba*) (75%, 6/8) and spinner dolphins (*S. longirostris*) (100%, 4/4) changed their behavior in response to aircraft. Sperm whales (*Physeter macrocephalus*) reacted in 28% of the observations (7/25). The other cetacean species (e.g. the larger delphinids: short-finned pilot whale (*Globicephala macrorhynchus*), Risso's dolphin (*Grampus griseus*), false killer whale (*Pseudorca crassidens*), Atlantic spotted dolphin (*S. frontalis*), and bottlenose dolphin (*Tursiops truncatus*)) responded in less than 29% of the sightings. The authors noted that the species responding to the NOAA survey ships also responded to the aircraft.

The authors noted the observed behavior prior to disturbance by aircraft. Their results suggest that when the initial behaviors are 'milling' (43%) and 'resting,' (39%), the animals are most sensitive to disturbance by aircraft. Some species, especially the smaller delphinids, were sensitive to disturbance while traveling (31%). They changed their behavior 100% of the time. However, the sample sizes for the initial behavioral categories and observed behavioral reactions were small, ranging from 1 to 14 observations.

The type of reaction to the aircraft differed among species. Most of the *Kogia* spp. (100%) and ziiphids (87%) responded to the aircraft by diving. In the small delphinid species, diving occurred in 50% of the cases. Bottlenose dolphins most commonly responded by diving (48%), while 14% responded by moving away. Most of the sperm whales (86%) also responded to the aircraft by diving. Würsig et al. (1998) demonstrates that different species vary in their sensitivity to aircraft disturbance, and that the initial behavior of the animal affects the response to aircraft noise.

Patenaude et al. (2002) assessed the short-term behavioral responses of migrating bowhead whales (*Balaena mysticetus*) and beluga whales (*Delphinapterus leucas*) to aircraft in the western Beaufort Sea. Two types of aircraft, a Bell 212 helicopter and a Twin Otter fixed-wing airplane, were compared. The reactions of bowhead and beluga whales were observed via brief sightings made by biologists aboard the aircraft and on the ice (only when the aircraft was at 0 m altitude). Most observations were made of whales in open-water corridors. Reactions to the aircraft were noted at 3 altitude levels. The altitude of the helicopter ranged from 150-460 m (over-flight), 30-300 m (within 2 min. after landing/take-off), and 0 m (stationary on the ice with engine running); the altitude of the fixed wing airplane ranged from 150-460 m, ~145 m, and circling at 460 m.

With the Bell 212 helicopter present, 14% of bowhead whales (singletons or groups) (n=63 observations) responded. These responses consisted of abrupt dives, breaching, tail slapping, and brief surfacing. The most common responses were abrupt dives and breaching. Most responses occurred when the helicopter was at altitudes of ≤ 150 m and at lateral distance ≤ 250 m. The sample sizes for the higher altitude (n=8) and when the helicopter was stationary on the ice (n=8) were small. Only one whale (a sub-adult) out of 8 observations reacted to a helicopter stationary on the ice. This animal made an unusually brief surfacing at a lateral distance of 230 m from the helicopter. A mother-calf bowhead whale pair was observed during four passes by a helicopter over 2.8 hours. Of those four passes, three passes were at 50-150 m lateral range and low altitudes of 15-30 m and one pass was at 500 m lateral distance. The mother dove during the two times she was at the surface, while the calf dove once during the four times it was at the surface. Although this study confirms that brief single straight-line helicopter over-flights can affect the behavior of some bowhead whales, the behavioral effects may not be biologically significant (Patenaude et al. 2002). In 38% of the beluga whale observations (n=40 observations) a response to the helicopter was noted, which included immediate dives, changes in heading, changes in behavioral state, and apparent displacement. Forty-seven percent of the responses were observed when the helicopter was stationary on the ice and 33% of the responses were observed when the helicopter was at low altitudes (≤ 150 m). Most observed responses by beluga occurred when the helicopter was at a lateral distance ≤ 250 m. The biological significance of these reactions is uncertain. It is also uncertain if the small-scale reactions were caused by the noise of the helicopter, visual cues, or both (Patenaude et al. 2002).

For the Twin Otter airplane, in 2.2% of the 507 observations of bowhead whales a response was noted, with the majority of reactions occurring when the plane was at altitudes ≤ 182 m and at a lateral distance ≤ 250 m. The most common reaction was an unusually short surfacing, but abrupt dives and turning or heading away from the plane were also observed. Two of the 11 groups reacting to the plane were mother-calf pairs. No conspicuous startle reaction to a circling plane at 460 m altitude was observed, but when the responses were analyzed statistically, subtle effects on blow intervals, number of blows per surfacing and duration of dives were found (Patenaude et al. 2002). However, the changes in blow intervals were very small and were felt to be unlikely to seriously diminish the fitness of the bowhead whales (Patenaude et al. 2002). A small proportion (3.2%; n = 24/760) of the beluga whales responded to the fixed-winged plane with immediate dives with a tail thrash (n=10), unusual turns or changes in heading (n=6), twisting to look upwards (n=5), changes in behavioral state (n=2) or some other unrecorded reaction (n=1). Most of the responses of beluga whales occurred when the plane was at altitudes ≤ 182 m and at a lateral distance ≤ 250 m. Direct

over-flights generated the most conspicuous reactions, such as vigorous swimming, abrupt dives or tail thrashing.

Both bowhead and beluga whales responded more frequently to the helicopter than to the fixed-wing plane. These reactions may correspond to higher levels, greater complexity, and variability of sounds from a passing helicopter as compared to a fixed-wing plane. Beluga whales showed more detectable responses to the helicopter than bowhead whales (38% vs. 14% of observations).

The characteristics of the aircraft sounds underwater, at 3 m and 18 m depth when the aircraft flew directly overhead, were measured. The helicopter sounds were generally stronger that the plane. The authors concluded that the dominant low-frequency components of aircraft sound are audible to bowhead whales, but may be inaudible to beluga whales. Beluga whales might barely detect the mid-frequency sound components from either aircraft flying at 300 m altitude overhead. However, these sounds should be readily audible during an over-flight at 150 m altitude. For beluga whales mid-frequency sound components, visual cues, or both may elicit a reaction.

The study by Patenaude et al. (2002) was reviewed by Nowacek et al. (2007). Nowacek et al. (2007) argued that although Patenaude et al. (2002) did report the received level of sound at 3 m depth and 18 m depth, these measurements were taken directly under the aircraft and the authors did not model the received level of sound away from this track. Nowacek et al. (2007) also noted that Patenaude et al. (2002) did not elaborate on the choice of the range categories; that is, ≤ 250 m versus > 250 m lateral distance.

Richter et al. (2003, 2006) studied the reactions of male sperm whales off Kaikoura, New Zealand, to airplanes and whale-watching boats using a 6.6 m boat (1998-2001) and land-based observations (in years 2000-2001) between November 1998 and February 2001. Kaikoura is one of the few places worldwide where aerial whale watching is carried out on a regular basis. In this region both resident and transient male sperm whales are present. In New Zealand there are two companies that use fixed-wing planes (Cessna 172, Piper Cherokee, Pilatus Britten Norman Islander) or helicopter (Bell Model 206 JetRanger) for 'on demand' whale-watching trips. The whale-watching flights last between 30 and 50 minutes. It is unclear how often these whale-watching flights go out.

Behaviors quantified in this study included blow duration (ventilation), time until first click production after a fluking up (vocalization patterns), and surface time (spatial behavior at the surface). A total of 145 observations with an aircraft present were recorded, 116 observations from the research boat and 29 observations from the shore. A total of 996 observations with no aircraft or other boats present were recorded, of which 244 observations were made from shore. Richter et al. (2003, 2006) made visual observations of sperm whale reactions when the aircraft made a circular flying pattern at a distance within at least 150 m.

Overall, they found that transient sperm whales responded more strongly to aircraft than residents. In both resident and transient sperm whales there was little change in the blow duration (ventilation) when exposed to aerial whale watching (0 and 0.8 sec. shorter duration with aircraft present). Surface times were also similar for resident whales, with a slightly longer surface duration when exposed to aircraft. For the transient whales a substantially shorter surface duration time of 2.7 minutes was recorded. This could indicate that resident whales show signs of habituation to aircraft (Richter et al. 2006). The time to first click after 'fluke-up' dive showed a stronger reaction to aircraft. Resident sperm whales tended to delay their first click after a 'fluke-up' dive by less than 5 s, whereas transient sperm whales tended to delay their first click after fluke-up by almost 20 s when an aircraft was present. Both transient and resident male sperm whales showed no reaction by altering the frequency of the heading changes. This could be the result of less noise entering the water and thus less disturbance or, alternatively, the inability of whales to pinpoint the position of the aircraft (Richter et al. 2006).

The study showed a very high degree of variation in responses among individuals. The effects of whale-watching activities could be more severe on specific animals. Especially, transient whales are less tolerant of aerial whale-watching activities and may not cope as well with aircraft exposure. Resident whales may cope better with these activities due to

habituation, but the downside could be that they are less likely to avoid ships, increasing the chance of ship strikes (Richter et al. 2006).

This study did not report the altitude of the whale-watching aircraft over the sperm whales or the received sound levels under the aircraft. Information on these factors is important for the interpretation of the observed responses by cetaceans. Also, no distinction was made between the fixed-wing airplane and the helicopter. It is known that helicopters elicit more responses from cetaceans than fixed-wing planes (Richardson et al. 1995).

Smultea et al. (2008) also observed reactions of sperm whales from an airplane within 45 km from the shore of the main Hawaiian Islands. For the surveys, small fixed-winged planes (Cessna 172, Skymaster 1994 and 1995, and a Partenavia) were used over water less than 2000 m deep. Visual observations of sperm whale reactions were made to initial straight-line fly-bys with an average altitude of 233–269 m, a speed of 185 km/h and a lateral distance ranging from 103 to 3,427 m.

Three of the 24 sperm whales observed reacted to the plane. All reactions consisted of a sudden dive. These reactions occurred when the plane was at a lateral distance of < 360m. Of the 24 observations of sperm whales, 8 groups were observed at lateral distances of < 360 m (38% reacted to the plane) and the remaining 16 groups were observed at lateral distances of > 360 m. Interestingly, no reaction was observed during the two closest initial passes, 103 m and 208 m lateral distance respectively. The authors interpreted these abrupt dive behaviors as a mild fright response to the plane. The authors noted that although perceived sound levels from the plane were not calculated, the expected frequency range and dominant tones produced by the plane overlap with the known low-end frequency range of sperm whale vocalizations.

Smultea et al. (2008) had the opportunity to observe a unique behavioral reaction, perhaps indicative of stress, by a group of 11 sperm whales (including an adult male and a calf) to a fixed-wing plane (Skymaster) circling for nine minutes. When, after an initial pass at 103 m lateral distance and 235 m altitude, the plane circled (0–500 m lateral distance, 245–335 m altitude) the sperm whales. The whales ceased their forward movement and positioned themselves closer to each other, first in a parallel flank-to-flank formation and later in a semi-circle “fan” formation. This behavior may have represented agitation, distress and/or a defense reaction to the plane and was similar to behavior seen in another study in the Bahamas when a Cessna 172 passed and circled 6 sperm whales. The group was directly under the plane where there is transmission of sound from the air into the water (see discussion on Snell’s law sound cone -a 26° arc under an aircraft where sound transmission is greatest- in Richardson et al. 1995). One sperm whale was observed on its side with its mouth agape. The authors considered this to be a distress response elicited by the plane and speculated that the animal was swimming on its side possibly to look up at the plane.

No explanation was given for the choice of the lateral distance categories, and no details were presented on the specific lateral distance for each observation. Although the results indicate that airplanes at close range have an increasingly disruptive effect on cetaceans, it remains difficult to interpret the precise influence of an aircraft’s lateral distance without more detailed study.

DISCUSSION

Our review of the literature indicates that there is a trend towards a more systematic approach to the study of the effects of aircraft on cetaceans since 1995. Whereas most studies reviewed by Richardson et al. (1995) documented opportunistically observed behavioral changes, subsequent studies have examined behavioral responses of cetaceans to aircraft in a more detailed and hypothesis-driven manner.

In each of the studies reviewed here, cetaceans responded to aircraft in some manner to varying degrees, in many cases by diving. However, behavioral changes were sometimes subtle and became apparent only after statistical analysis (Patenaude et al. 2002). Furthermore, the lack of a pronounced behavioral reaction to an aircraft did not necessarily

mean that there were no other effects (Richardson & Würsig 1997). For example, there was a 6.5% increase (resident sperm whales) and a 28% decrease (transient sperm whales) in surface time and a 26% increase (resident and transient sperm whales) in the time to first click after a 'fluke-up' dive after a fly-by from an aircraft (Richter et al. 2006).

Various factors have been identified that affect the response of cetaceans to aircraft noise. The sensitivity of whales and dolphins to aircraft noise may depend on the animals' behavioral state at the time of exposure (e.g. resting, socializing, foraging or travelling). Resting individuals appear to be most sensitive to disturbance (Würsig et al. 1998). Also, the altitude and lateral distance of the aircraft to the animals have been identified as important factors affecting the response. Thus, aircraft flying at low altitude, at close lateral distances and above shallow water elicit stronger responses than aircraft flying higher, at greater lateral distances and over deep water (Patenaude et al. 2002, Smultea et al. 2008). The sensitivity to disturbance by aircraft may also differ among species (Würsig et al. 1998). In the Alaskan Beaufort Sea, beluga whales responded more often to all noise than bowhead whales (Patenaude et al. 2002).

Although some research progress has been made, the number of studies on the impacts of aircraft on cetaceans since 1995 is meager compared to the number of studies published between 1980 and 1995 (Richardson et al. 1995), and the great number of studies on the impacts of other sources of potential disturbance, such as whalewatching or Acoustic Deterrent Devices (aka 'pingers') (Parsons et al. 2006a, Nowacek et al. 2007). In addition, recent studies on aircraft and cetaceans are limited to sperm whales, bowhead whales and beluga whales. This bias in species representation is not specific to studies involving aircraft, but seems to be an overall gap in information on how cetaceans respond to anthropogenic noise (Nowacek et al. 2007).

Previous authors have indicated several major gaps in knowledge on the effects of noise on marine mammals (e.g. Richardson et al. 1995, Richardson & Würsig 1997, Nowacek et al. 2007). Their conclusions also apply to aircraft noise. First, both the observed behavioral change and the received sound level from the aircraft should be quantified (Richardson et al. 1995, Nowacek et al. 2007). Data on received sound levels are needed to assess whether there is a relationship between noise exposure levels and the type and degree of response of the animals (Richardson et al. 1995, Nowacek et al. 2007). Only one recent study included an analysis of received levels of sound from the aircraft at 3 m and 18 m depth (Patenaude et al. 2002).

Second, the role of vision in the observed responses of cetaceans to aircraft remains unclear (Richardson et al. 1995, Richardson & Würsig 1997). Although in most cases noise is probably the dominant stimulus, there is anecdotal evidence indicating that visual cues affect cetacean behavior. Bottlenose dolphins have been observed to react when an aircraft's shadow passed over them (Mullin et al. 1991). Some species (e.g. beluga whales and Dall's porpoise, *Phocoenoides dalli*) have been observed looking up at the aircraft (Withrow et al. 1985, Richardson et al. 1995, Richardson & Würsig 1997). As noted earlier, a sperm whale was also observed apparently looking up (Smultea et al. 2008). Thus, the aircraft and/or its shadow may represent a disturbing factor in addition to noise. This issue has not been discussed by any of the studies reviewed here and should be considered in future studies.

Third, as noted above, an animal's initial behavioral state is known to have an effect on its responsiveness to aircraft (Richardson et al. 1995). Unfortunately, most studies did not document initial behavioral states. Thus, future assessments of the effects of aircraft should document initial behavioral states.

Finally, the possibility that aircraft noise affects cetacean vocalizations has rarely been investigated. Only one recent study documented a delay in the production of the first click after 'fluke-up' dives in sperm whales (Richter et al. 2006). During the last decade, several studies have demonstrated that some whales and dolphins are able to change their acoustic signals in response to anthropogenic noise. These studies have further demonstrated that whales and dolphins may modify their calls in various ways, e.g. by changing the source level (Holt et al. 2009), frequency (Lesage et al. 1999), duration (Miller et al. 2000; Foote et al. 2004), number

of frequency modulations (Morisaka et al. 2005) and call rate (Van Parijs & Corckeron 2001b; Buckstaff 2004). Repeated and prolonged exposure to aircraft may affect the vocalizations of (particularly resident) cetacean populations. Such exposure might be most common near coastal airports, such as Anchorage International Airport and Elmendorf Air Force Base in Alaska (Blackwell et al. 2002), but also in areas with intensive whale-watching flights, and in areas with daily flights for oil and gas drilling and production.

All studies in this review, except that of Richter et al. (2006), were conducted from aircraft. A well known problem of such studies is that the observer is on board the source of potential disturbance (Richardson & Würsig 1997, Patenaude et al. 2002, Smultea et al. 2008). This has important implications. First, such studies typically do not include a control group (i.e. a group of whales not exposed to the aircraft). Second, because the observer is moving, the opportunity to observe the behavior before, during and after the disturbance is very limited (Richardson & Würsig 1997, Smultea et al. 2008). Third, there is an inverse relationship between the distance to the animal and the duration of the observation time, two factors that may lead to an underestimation of the number of responses (Richardson & Würsig 1995, Patenaude et al. 2002, Smultea et al. 2008).

Aircraft noise may not only affect the biology of cetaceans but also cause a bias in aerial survey data, including the numbers of individuals and their distribution (Smultea et al. 2008, Richardson & Malme 1993). The sightability of cetaceans might change as a response to aircraft, which could lead to an underestimation of the population density (Würsig et al. 1998). The use of aerial surveys seems particularly problematic for assessments of the behavioral responses of cetaceans to other anthropogenic noise sources, such as seismic airguns. In these studies, the aircraft noise may exacerbate the effects of the other noise sources. If the effects of the aircraft are not understood this could create biases in the behavioral data, since it is unknown if the response is triggered by the aircraft, the other source of noise, or both. Therefore, great care should be taken with the interpretation of the results of such studies.

The study of the effects of aircraft on cetaceans has applications for the whale-watching industry. Whale watching is a significant and growing industry worldwide (Parsons et al. 2006, Hoyt 2007). As a result, the number of companies that offer aerial whale-watching trips is likely to increase. Whale watching via aircraft has the potential to have long-term (negative) effects on cetaceans for several reasons. First, for practical and economic reasons aerial whale watching often occurs not far from shore in relatively shallow waters. Shallow water and close proximity to shore are known to increase the sensitivity of whales to disturbances (Richardson et al. 1985a, Richardson et al. 1985b). Second, to give a better view of the whales and dolphins, whale-watching aircraft often fly at low altitudes, another factor known to increase the impact of aircraft noise on cetaceans. This is especially the case when an aircraft is at low altitude above shallow water (Richardson et al. 1985a, Richardson et al. 1985b). Third, aerial whale watching often involves repeated circling above a group or an individual animal. Circling for a longer period could increase the sensitivity of the particular animal, group or population to disturbance (Smultea et al. 2008). Finally, aerial whale watching increases the chance that the same resident individuals will be viewed multiple times (Richter et al. 2006). If these individuals and populations are unable to habituate to the presence of the aircraft, this could affect the reproductive success and survival of the population. Cetaceans often use coastal waters for breeding and resting (Karczmarski et al. 2005), behaviors that are more sensitive to disturbance than other behaviors such as travelling (Würsig et al. 1998). It is therefore important that the effects of aircraft on cetaceans are fully understood so that guidelines may be developed to mitigate these effects.

CONCLUSIONS

The response of cetaceans to noise is known to be influenced by several factors, although much remains to be learned. There is still a complete lack of information on noise impacts at the population level, including impacts on reproductive success, survival, communication and

migratory patterns. Future studies may benefit from considering the biological and methodological factors reviewed in this paper. The effect of aircraft noise on marine mammals is an important but neglected field in marine mammal acoustics research and thus offers an area for further study.

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