

# Protecting Wild Dolphins and Whales: Current Crises, Strategies, and Future Projections

Guest Editors: Lori Marino, Frances Gulland, and E. C. M. Parsons





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Journal of Marine Biology

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## Editorial

# Protecting Wild Dolphins and Whales: Current Crises, Strategies, and Future Projections

Lori Marino,<sup>1</sup> Frances Gulland,<sup>2</sup> and E. C. M. Parsons<sup>3</sup>

<sup>1</sup>Neuroscience and Behavioral Biology and Center for Ethics, Emory University and The Kimmela Center for Animal Advocacy, Atlanta, GA 30322, USA

<sup>2</sup>The Marine Mammal Center, Sausalito, CA 95965-2619, USA

<sup>3</sup>Environmental Science & Policy, George Mason University, Fairfax, VA 203-4444, USA

Correspondence should be addressed to Lori Marino, lmarino@emory.edu

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In the past few years, we witnessed the first anthropogenic-caused extinction of a dolphin species in our lifetimes: the Baiji (*Lipotes vexillifer*). There are currently several other cetacean species on the brink of extinction or endangered. Moreover, many cetacean subpopulations are under siege from various stressors. This year alone, we have witnessed a number of unusual high mortality events in the Gulf of Mexico, and off the coasts of Peru and New England. As all of these stressors, that is, climate change, chemical, pathogen and noise pollution, ship traffic, and fisheries bycatch increase, we are likely to see more of these tragic events in the near future. At a time when the problems cetaceans face are converging with a myriad of other issues, the possible approaches to be employed to mitigate these problems require unprecedented flexibility and sophistication.

Adding to the complexity of these issues is the knowledge that cetaceans are not only intelligent, highly social, and self-aware mammals [1], but they possess cultural traditions [2]. These characteristics necessitate a move from the traditional “numbers-based” approach of conservation to a more progressive protection-based strategy that takes into account cumulative impacts of multiple stressors on their health, their psychology as unique individuals, their social complexity, and their cultural identities. No longer will traditional population studies provide the totality of the picture for wild cetaceans. The approach towards this group of mammals must be expanded to accommodate our new view of them as socially complex and cultural individuals who are each an important component of their group, and arguably, ecosystem. Sustainability is not the only criterion

for making conservation decisions. Now health and animal welfare must be considered if we are to accept the current scientific understanding of who cetaceans are.

In this special issue, we will explore the topic of protecting wild dolphins and whales from several angles. The papers in this volume reach across previously separated domains and also reflect the new approach of moving beyond the numbers and incorporating individual welfare into conservation analyses. New stressors and threats of concern are highlighted, such as marine debris and the growth of whale watching. Whale watching is currently the most globally important economic activity involving cetaceans that have been put forward by many as a sustainable practice, that is, obviously more ethically acceptable than whaling. But even so, without proper management, even this activity can be a stressor to cetacean populations. The papers also reflect the urgency that is felt as we strive to protect and conserve wild cetaceans. We hope that the papers in this volume engender further thinking about new and even further “out of the box” ideas about how to ensure that wild cetaceans move into the future in their own natural habitats.

Lori Marino  
Frances Gulland  
E. C. M. Parsons

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## Review Article

# The Negative Impacts of Whale-Watching

**E. C. M. Parsons<sup>1,2</sup>**

<sup>1</sup>Department of Environmental Science and Policy, George Mason University, Fairfax, VA 22030, USA

<sup>2</sup>University Marine Biological Station Millport, Great Cumbrae, Scotland KA28 0EG, UK

Correspondence should be addressed to E. C. M. Parsons, ecm-parsons@earthlink.net

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Whale watching is an international industry worth more than US\$2 billion globally and is currently the greatest economic activity reliant upon cetaceans. However, there is concern that whale watching is detrimental to the target species. Numerous studies have shown that cetaceans exhibit behavioral changes in response to whale-watching boat traffic. Some of these behavioral changes involve inhibiting biologically important behaviors such as feeding and resting. There is convincing evidence for some species that these can translate into population-level effects such as reduced reproductive rates. Whale watching can also cause direct mortality through collisions between vessels and animals. The introduction of guidelines or regulations for whale watching has been the most common method of trying to mitigate the impacts of boat-based whale watching. However, there is great variety in the comprehensiveness of guidelines, and even if operators have guidelines, compliance with them can be poor. Compliance might be improved if guidelines have legal under-pinnings, with monitoring and enforcement or via pressure to comply by other operators and whale-watching tourists. Simple guidelines may be more easily complied with than ones requiring specialist knowledge. Likewise undertaking simple measures, such as establishing temporal or spatial “refuges” protecting biologically important areas (e.g., feeding grounds) where whale-watching activity is prohibited, could be an appropriate mitigation strategy.

## 1. Introduction

In 2009, it was estimated that 13 million tourists took trips to see whales, dolphins, and porpoises (cetaceans) in their natural habitat, as part of an industry that generated US\$2.1 billion dollars (1.7 billion Euros) and employed 13,000 people in 119 countries [1, 2]. As a class of tourism, it is particularly desirable as it can specifically draw tourists to a region, with many whale-watching tourists only visiting locations because of the presence of cetaceans [3–5]. It has been estimated that potentially the industry would be worth an additional US\$400 million and an additional 5,700 jobs, if maritime countries with cetacean populations, currently without whale-watching industries, were to develop them [2]. Whale watching is currently the greatest economic activity reliant upon cetaceans.

Many environmental and animal welfare groups have promoted whale watching as a tourism activity, as an alternative to the consumptive use of whales, that is, commercial whaling. Indeed, whale watching in countries that are still actively hunting whales is arguably more lucrative than whaling [5–7]. Statements from politicians in whaling

countries claim that whaling and whale-watching can coexist without impacting each other (e.g., [8–12]), but data suggest that whaling can inhibit whale-watching development or potentially reduce whale watching tourism revenues within a country [6, 7, 13–15]. Whaling may even reduce tourism revenues in general, because of ethical boycotts of whaling locations by tourists [16].

Some of the fastest growing whale-watching industries are in developing countries, such as China, Cambodia, Laos, Nicaragua and Panama [1], and there is potential for considerable growth in whale-watching operations in other developing nations [2]. Seeing cetaceans as an important economic resource in developing countries may aid their conservation, with losses from directed takes (such as hunts or culling) or indirect takes (such as fisheries entanglements or boat strikes) possibly seen as removing a valuable tourism resource. In addition, it has been argued that whale-watching can provide other intangible benefits, such as being educationally beneficial, or promoting a conservation ethic in whale-watching tourists [17–19]. At present some studies suggest that these benefits are minimal [20], whilst others are more positive about the educational and public

conservation-promoting benefits of whale watching [21–24]. It has been found that provision of education on-board whale-watching vessels increased customer satisfaction with trips [25] or was considered to be an important part of a whale-watching trip [21, 26, 27] in several locations and this does suggest that on-board education is providing some benefits to customers.

In contrast, there is also concern that promotion of whale watching could be detrimental to the target species [28, 29], and that adverse impacts of whale watching on target species could be not only detrimental to threatened species, but also potentially “killing the goose that laid the golden egg” as far as tourism is concerned.

## 2. Defining Whale Watching

The International Whaling Commission (the recognized intergovernmental authority on the management of whales as a resource) defined whale watching as “*any commercial enterprise which provides for the public to see cetaceans in their natural habitat*” (page. 33 in [30]). Although the term “whale” is used, the activity refers to all cetacean species, whether they are baleen whales, or dolphins or porpoises [31]. Whale watching does not, however, include tourism activities where animals are captive in pools or sea pens [31]. In 2005, the International Whaling Commission Whale Watching Sub-committee defined various types of whale-watching activity, noting that it might not necessarily be commercial, but could include members of the public taking their personal boats out to see whales, or research trips where there are paying customers on board (which they termed “whalewatching-aided research”).

It should be emphasized that although the majority of whale-watching activities are boat-based, whale watching could potentially include aerial activities (e.g., from a dirigible/airship or aircraft) or land-based whale-watching platforms. Whale-watching from land-based platforms or aerial craft such as hot air balloons is unlikely to have major impacts on cetaceans. However, powered aircraft and helicopters could produce substantial amounts of noise that could impact cetaceans, and although there has been little research into this area, it is a cause of concern (e.g., [32, 33]).

A subset of whale-watching activities involves trips where humans enter the water with wild cetaceans (i.e., “swim-with-cetacean tourism” [31]). Such activities can be “passive” where cetaceans are allowed to approach human swimmers of their own volition or “active” where the swimmers are placed in the path of oncoming cetaceans, or the cetaceans are pursued [31]. Both types of activity are more invasive than regular boat-based whale watching, especially the “active” form. Again, this is an area of particular concern of the International whaling Commission due to the potential risk to both humans and cetaceans involved in the activity [75]. Another type of tourism involving marine mammals is “provisioning” or feeding wild cetaceans—which most famously occurs in Monkey Mia in Australia. There are many concerns about the impact of this activity on the target species [76–80] as well as the risk to humans [81, 82]. However, for purposes of this paper, land-based and

aerial whale watching and the impacts of wild cetacean feeding programs and swim-with-cetacean tourism are not discussed.

## 3. Negative Impacts of Whale Watching

Several studies have recorded changes in cetacean behaviour in response to whale watching. These have included changes in surfacing, acoustic, and swimming behaviour and changes in direction, group size, and coordination (Table 1).

However, it is difficult to determine the long-term negative effects (if any) of these short-term behavioural changes. Possibly they can increase an animal’s energy expenditure or result in chronic levels of stress, which might have a negative effect on health [83], and it has been suggested in at least one study on bottlenose dolphins that long-term behavioural disruption may eventually lead to reduced reproductive rates [55]. Studies have shown an alteration or cessation of essential behaviours, such as feeding or resting (Table 1), and this would obviously be detrimental and could reduce fitness in the long-term, especially in situations where there is prolonged or repeated exposure. Research has also shown that boat-related sound can be drowned out or “mask” cetacean vocalizations [84]. This could result in animals either being unable to communicate (which could include prevention of biologically important communication related to mating or danger) or the animals having to increase the volume of their vocalizations, which may entail an additional energetic cost [52]. The effect of noise from whale-watching traffic and its population-level impacts are issues that require more quantification and attention [85, 86].

Disturbance has also been linked to cetaceans temporarily or permanently abandoning areas [68, 87, 88]. In addition to the energetic costs of moving to a new location and potentially establishing a new territory, animals may be displaced to less than optimal habitats—perhaps areas with higher predation, lower quality, or more difficulty in accessing prey species. All of these would have a cost.

However, absence of an observable reaction to whale-watching should not be interpreted as absence of an effect on cetaceans. In noncetaceans, researchers have noted that sometimes the most vulnerable animals do not react or move away from a disturbance, possibly because they lack the energy surplus to do so [89, 90]. There are a number of reasons why cetaceans may remain within an area or continue certain behaviours despite disturbance [91]. The location may be an important source of prey or outside the area may have a high rate of predation. Animals may also lack the foraging skills to feed on different species outside of the area. These are factors that might cause animals to “tolerate” disturbance, but as noted above, the lack of an obvious reaction does not mean that the animals is not being stressed or impacted [85].

The cumulative effect of changing behaviours, displacement, or the chronic stress induced by exposure to whale-watching activity may translate into declines in health and vital rates [85]. Bejder et al. [55, 88] linked the cumulative cost of short-term behavioural changes to a decline in female reproduction, and it was this and similar studies

TABLE 1: Examples of behavioral changes observed in cetacean species in response to whale-watching traffic.

Behaviour change	Species	Reference
Surfacing/diving	Common bottlenose dolphin, <i>Tursiops truncatus</i>	[34–38]
	Indo-Pacific bottlenose dolphin, <i>Tursiops aduncus</i>	[39, 40]
	Indo-Pacific humpback dolphin, <i>Sousa chinensis</i>	[41]
	Costero, <i>Sotalia guianensis</i>	[42]
	Killer whale, <i>Orcinus orca</i>	[43]
	Humpback whale, <i>Megaptera novaeangliae</i>	[44]
	Fin whale, <i>Balaenoptera physalus</i>	[45]
“Active” behavior (e.g., tail slapping and beaching)	Sperm whale, <i>Physeter macrocephalus</i>	[46]
	Common bottlenose dolphin, <i>Tursiops truncatus</i>	[37]
	Commerson’s dolphin, <i>Cephalorhynchus commersonii</i>	[47]
	Killer whale, <i>Orcinus orca</i>	[48]
Acoustic	Humpback whale, <i>Megaptera novaeangliae</i>	[49]
	Common bottlenose dolphin, <i>Tursiops truncatus</i>	[50, 51]
	Killer whale, <i>Orcinus orca</i>	[52]
	Humpback whale, <i>Megaptera novaeangliae</i>	[53]
Group size or cohesion	Sperm whale, <i>Physeter macrocephalus</i>	[54]
	Common bottlenose dolphin, <i>Tursiops truncatus</i>	[55, 56]
Swimming speed	Costero, <i>Sotalia guianensis</i>	[42]
	Indo-Pacific bottlenose dolphin, <i>Tursiops aduncus</i>	[40]
	Spinner dolphin, <i>Stenella longirostris</i>	[57]
	Killer whale	[43, 58]
Swimming direction	Humpback whale, <i>Megaptera novaeangliae</i>	[59]
	Common bottlenose dolphin, <i>Tursiops truncatus</i>	[55, 56]
	Indo-Pacific bottlenose dolphin, <i>Tursiops aduncus</i>	[39]
	Indo-Pacific humpback dolphin, <i>Sousa chinensis</i>	[41]
	Spinner dolphin, <i>Stenella longirostris</i>	[57]
	Costero, <i>Sotalia guianensis</i>	[60]
	Killer whale, <i>Orcinus orca</i>	[43, 58, 61]
Altered feeding or resting	Humpback whale, <i>Megaptera novaeangliae</i>	[49, 59]
	Common bottlenose dolphin, <i>Tursiops truncatus</i>	[62–65]
	Indo-Pacific bottlenose dolphin, <i>Tursiops aduncus</i>	[66]
	Short-beaked common dolphin, <i>Delphinus delphis</i>	[67]
	Costero, <i>Sotalia guianensis</i>	[68]
	Dusky dolphin, <i>Lagenorhynchus obscurus</i>	[47, 69]
	Commerson’s dolphin, <i>Cephalorhynchus comersonii</i>	[47]
	Risso’s dolphin, <i>Grampus griseus</i>	[70]
	Killer whale, <i>Orcinus orca</i>	[71, 72]
Humpback whale, <i>Megaptera novaeangliae</i>	[73]	

that persuaded the whalewatching subcommittee of the International whaling Commission to state in 2006 that

“... there is new compelling evidence that the fitness of individual odontocetes repeatedly exposed to whale-watching vessel traffic can be compromised and that this can lead to population-level effects” (page. 54 in [92]).

In addition to altering behaviour, masking communication, or displacing animals, whale-watching tourism can also have more direct impacts. Whales have been injured or killed as a result of collisions with whale-watching vessels, especially in areas where there is a high intensity of whale-watching traffic, such as off the coast of Massachusetts or

Hawaii [92–94]. An increasing number of large, high-speed whale-watching vessels are of particular concern [75]: the speed of these vessels limits their ability, as well as that of the whales, to avoid collisions. In addition, a higher speed means greater force when collisions occur and a higher likelihood of a lethal outcome [93]. From an analysis of vessel-cetacean collisions, it was suggested that the likelihood of lethal collisions decreased when vessel speeds were below 11 knots [93]. Thus, speed restrictions may be an effective way to mitigate this problem. However, reducing speeds may impact whale-watching business profits, as a faster speed means accessing cetacean habitat more quickly, more trips being taken throughout a day, and thus more customers and revenue.

#### 4. Mitigating Whale-Watching Impacts

The introduction of guidelines or regulations has been the most common method of trying to mitigate the impacts of boat-based whale-watching. In 2004, a review and comparison of international whale watching guidelines and codes of conduct from around the world found that one-third were regulatory, that is, legal requirements and non-voluntary, but two-thirds were entirely voluntary [95]. Most codes of conduct had regulations for minimum approach distances (e.g., 50–100 m or more), but most did not curtail especially invasive activities, for example, two-thirds had no proscriptions on feeding cetaceans and three-quarters did not prohibit touching cetaceans [95].

A study in Scotland conducted in 2000 found relatively high levels of acceptance of codes of conduct amongst operators, although it should be noted that this study found that there was a preference for operator organization or local NGO-produced guidelines, rather than guidelines produced by the national government [96]. Indeed there seemed to be resistance towards government intervention and a top-down approach in whale-watching management [96]. However, it should also be noted that a subsequent change in Scottish law led to the production of a new, government-mandated set of marine wildlife-watching guidelines. These governmental guidelines had greater acceptance because whale-watching operators and tourism organizations were consulted extensively during the drafting of the guidelines, that is, there was a top-down remit for the production of new guidelines, but there was bottom-up involvement in their construction [97].

The existence of guidelines, regulations, or laws in an area is no guarantee of compliance with these guidelines. In Doubtful Sound in New Zealand, two-thirds of tour boat encounters with common bottlenose dolphins violated the New Zealand Marine Mammal Protection Act, with one-third of encounters involving more than one violation [98]. In Victoria, Australia, swim-with-dolphin trip operators complied with only one out of the four regulations (i.e., the number of swimmers allowed in the water with dolphins), with regulations governing time spent with animals and boat approaches frequently disregarded [99]. After this research was presented to the government and a tour operator education/awareness program was introduced, the rates of noncompliance actually increased [100]. This may have been because operators realized that despite high levels of regulatory infractions, there was little enforcement or punishment. This is arguably the crux of the matter—guidelines are often poorly monitored and there is chronic lack of enforcement.

A study in New South Wales, Australia, found good levels of compliance with whale-watching guidelines [101]. Despite this, however, there were still probably impacts to cetaceans, as follows:

*“The code’s aim in reducing exposure of dolphins to boats was not achieved as dolphin schools were subject to consecutive approaches by numerous boats and interactions also involved boats to which the code did not apply.” (page. 159 in [101]).*

Therefore, although there was good compliance, a lack of broader management of whale-watching activities in the area, such as limiting vessel numbers and addressing the potential whale-watching “carrying capacity” for the region, ultimately led to a likely unsustainable situation. In several locations numbers of operators are limited by requiring licenses in order to operate, and the number of these licenses is restricted.

A factor in assessing whale-watching guideline effectiveness is that sometimes infractions are difficult to judge, especially by nonexperts. For example, it is frequently difficult to judge distances accurately at sea, especially during rough weather. If a regulation relies on an absolute approach distance, enforcement may be difficult. In addition, guidelines that mention specific behaviours (such as “feeding” or “distress” behaviours) may not be effective, as nonscientist operators could misinterpret, or simply miss, exhibited behaviours (e.g., [102]). Likewise, guidelines that have subjective values, such as “noisy activities,” could be misconstrued. Guidelines with approach distances can be problematic if cetaceans actively approach a vessel—should the operator undertake avoidance manoeuvres, which could possibly be noisy and stressful for the animals? Or should the operator continue current activities despite the approaching cetaceans, as this could cause less actual disturbance to the animals?

Scarpaci et al. [100] suggested that guidelines should be simple and easily understood, be realistic/feasible in the field (considering operator expertise and local conditions), and be easily enforceable. Whilst being practical, however, simple guidelines do not necessarily cover every eventuality and unexpected problem situations may arise. Thus an ability to change and alter guidelines quickly (i.e., adaptive management) may be crucial.

Very often authorities with the responsibility to monitor whale watching lack the will, resources, or logistical support to do so (e.g., the whale-watching location might be especially remote and difficult to access). Therefore monitoring of compliance may be very poor. In some regions, enforcement may effectively come down to operator peer-pressure; that is, responsible operators may report or otherwise criticize or pressure operators who are not adhering to codes of conduct or who are not behaving responsibly (pers. obs.). Moreover, whale watching tourists may be a possible enforcement tool. A study in Scotland found that many whale-watchers engaged in environmental activities, one-half were members of environmental groups, and an astonishing one-quarter stated that they conducted voluntary work for such organisations [103]. Few other studies have looked at environmental attitudes in this tourism sector, but the high level of involvement in environmental activities suggests that whale-watching tourists could be educated as to how a sustainable whale-watching operation should be run through articles in environmental organizations’ magazines and newsletters or via websites such as Planet Whale (<http://www.planetwhale.com/>). The environmental attitudes of the tourists could also be used to persuade operators that it is in their interest to be as environmentally-friendly and conservation-conscious as possible or they may risk alienating their customers.

TABLE 2: A checklist of questions to ascertain whether whale watching is sustainable in a region (after [74]).

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Is the marine mammal population growing?
Are marine mammals moving out of an area?
Are the marine mammals exhibiting changes in behavior?
What are the levels of biological and chemical pollutants in coastal waters?
Are marine mammal tourism operators knowledgeable about marine mammals and local culture?
Are they good education providers?
Are marine mammal operators concerned about the safety and welfare of their customers?
Does the marine mammal tourism activity aid or benefit the local community?

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After reviewing many studies on the effectiveness, or lack thereof, of whale-watching guidelines, the International Whaling Commission recommended

*“... that, in general, codes of conduct should be supported by appropriate legal regulations and modified if necessary as new biological information emerges” (page. 59 [32]).*

One simple method for reducing the impacts of whale watching is to establish “refuges” that is, “no-go” or “sanctuary” areas. Ideally such areas would allow animals to engage in biologically important behaviours (e.g., feeding, resting, or nursing) without being disturbed by whale-watching vessels. Refuges could be spatial (e.g., a marine protected area limiting whale-watching traffic), or they could be temporal (e.g., prohibitions on whale-watching activity in a location at certain times of day, days, or seasons [104]). A clearly defined (and less subjective) spatial or temporal refuge should allow monitoring or compliance and therefore make enforcement easier for managers.

## 5. Conclusions

Whale watching can provide many socioeconomic benefits, and it also could potentially aid conservation and/or allow the public to view cetaceans as being an economically important resource alive rather than dead. However, there are many direct and indirect impacts on the target species. To be sustainable environmentally and economically, these impacts need to be minimized. In an attempt to assess whether whale watching is sustainable in an area, Hoyt [74] suggested a check list of questions to gauge the sustainability of a whale-watching industry in an area (Table 2). Many regions have accreditation schemes, where operators receive training and have to abide by certain strictures (e.g., adhering to a code of conduct or whale-watching guidelines, providing certain levels of education, using environmentally-friendly practices), and such schemes can be beneficial if the standards for accreditation are high and the scheme is monitored, policed appropriately, and widely recognized. Along these lines, the International Whaling Commission developed a definition of “whale ecotourism,” which could potentially be used as benchmark criteria for an accreditation

scheme or standard for sustainable whale watching. A whale ecotourism operation is one that has taken major steps to

- (i) “actively assist with the conservation of cetaceans (for example, assisting local scientists or promoting conservation initiatives),
- (ii) provide accurate educational materials and/or activities about cetaceans and their associated habitats for tourists,
- (iii) ...minimize their environmental impact (whether by reducing their carbon footprint, reducing the amount of waste produced by their operation or introducing other environmentally beneficial practices),
- (iv) abide by a set of whale-watching regulations or an appropriate set of guidelines if no specific regulations are available for the area,
- (v) provide benefits to the local host community within which the company operates. Examples of such benefits might include a company policy of preferential employment of local people, selling local handicrafts, or supporting conservation, educational, or social and cultural projects or activities in the local community.” (page. 250-251 in [31]).

It is possible for whale-watching operations to minimize their impacts on cetaceans, perhaps enough so that there are no lasting or unduly negative effects. However, arguably the majority operations around the world are not doing so, to the detriment of cetacean populations internationally.

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## Review Article

# Social and Behavioural Factors in Cetacean Responses to Overexploitation: Are Odontocetes Less “Resilient” Than Mysticetes?

Paul R. Wade,<sup>1</sup> Randall R. Reeves,<sup>2</sup> and Sarah L. Mesnick<sup>3</sup>

<sup>1</sup> National Marine Mammal Laboratory, Alaska Fisheries Science Center, National Oceanic and Atmospheric Administration, Seattle, WA 98115, USA

<sup>2</sup> Okapi Wildlife Associates, 27 Chandler Lane, Hudson, QC, Canada J0P 1H0

<sup>3</sup> Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 3333 North Torrey Pines Court, La Jolla, CA 92037, USA

Correspondence should be addressed to Paul R. Wade, paul.wade@noaa.gov

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Many severely depleted populations of baleen whales (Mysticeti) have exhibited clear signs of recovery whereas there are few examples in toothed whales (Odontoceti). We hypothesize that this difference is due, at least in part, to social and behavioural factors. Clearly, a part of the lack of resilience to exploitation is explained by odontocete life history. However, an additional factor may be the highly social nature of many odontocetes in which survival and reproductive success may depend on: (a) social cohesion and organization, (b) mutual defence against predators and possible alloparental care, (c) inter-generational transfer of “knowledge”, and (d) leadership by older individuals. We found little evidence of strong recovery in any of the depleted populations examined. Their relatively low potential rates of increase mean that odontocete populations can be over-exploited with take rates of only a few percent per year. Exploitation can have effects beyond the dynamics of individual removals. Four species showed evidence of a decrease in birth rates following exploitation; potential mechanisms include a deficit of adult females, a deficit of adult males, and disruption of mating systems. The evidence for a lack of strong recovery in heavily exploited odontocete populations indicates that management should be more precautionary.

## 1. Introduction

In a 1993 paper, Best [1] examined increase rates in severely depleted stocks of baleen whales (Mysticeti). Of 44 that had been depleted to less than 10% of their original abundance, 12 were being adequately monitored to determine trends, and of those, ten exhibited significant positive rates of increase. In effect, Best concluded that there was no clear evidence for a “lag” in the response to protection (e.g., due to depensation or so-called “Allee effects”) and that apparent delays in recovery by some stocks were more likely due to the inadequacy of monitoring effort than to impaired reproduction or recruitment failure. Further, he offered the hypothesis that in many stocks “a combination of range retraction and underestimation of the extent of depletion

has hindered detection of a recovery.” In the nearly 20 years since Best’s analysis, a number of the 32 severely depleted stocks that he judged to have been inadequately monitored have now shown clear signs of increase. For example, there is evidence for increases in blue whale (*Balaenoptera musculus*) abundance [2] in the Antarctic and fin whale (*Balaenoptera physalus*) abundance in central California [3]. Bowhead whales (*Balaena mysticetus*) in eastern Canada and West Greenland are now known to be much more numerous than previously supposed and have shown clear signs of increase since 1981 off West Greenland [4].

No analysis similar to Best’s for mysticetes has been carried out to examine whether severely depleted populations of toothed cetaceans, or odontocetes (Odontoceti), have shown evidence of recovery. The hypothesis developed

in the present paper is that odontocetes are less resilient to intensive exploitation than mysticetes (whether deliberate by hunting or nondeliberate, e.g., by incidental killing in fishing gear) and that this difference is due, at least in part, to social and behavioural factors. The concept of resilience is in some respects the obverse of extinction proneness, which has become a subject of mainstream discussion in conservation biology. In general, resilience, or lack of it, is an ecological concept, whereas extinction proneness is very much a species concept. Our approach here is to consider species, or population, resilience as something that can be measured in terms of ability to recover from extreme depletion.

Clearly, a part of the lack of resilience to exploitation stems from the life history of odontocetes. Their relatively old age of first reproduction and low calving rate lead to relatively low maximum rates of increase [5–7]. Some species of baleen whales have been observed or estimated to increase at rates of 6% per year and higher (e.g., humpback whales (*Megaptera novaeangliae*) and gray whales (*Eschrichtius robustus*)), and this has obviously contributed to the strong recovery seen in some of these species [1]. In contrast, though data are admittedly scarce, there is still no evidence to show that any odontocete population can increase at a rate greater than 4% per year, and for some species it is questionable if they are capable of even that. A related factor is that the life history of long-lived animals with relatively old ages of first reproduction can create delays in recovery if exploitation has been selective for reproductive-aged animals.

However, an additional factor that may contribute to the lack of resilience seen in odontocetes is related to their social and behavioural traits. Consistent with their long evolutionary history, global dispersal and habitat specializations, odontocetes exhibit a diverse array of social systems, ranging from the relatively hierarchical and relatively stable pattern of killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*), to the classic fission-fusion pattern of many dolphins (Delphinidae), to the seemingly unstructured societies of porpoises (Phocoenidae) [8]. Group sizes vary from the small social units (perhaps only 3 to 10 individuals) of transient killer whales and some beaked whales (Ziphiidae), to the intermediate-sized pods (ten to a few tens) of resident killer whales, sperm whales, and white-beaked dolphins (*Lagenorhynchus albirostris*), to the large aggregations composed of hundreds or thousands of individuals characteristic of pantropical spotted (*Stenella attenuata*), striped (*Stenella coeruleoalba*), spinner (*Stenella longirostris*), and short-beaked common dolphins (*Delphinus delphis*). In at least some odontocetes, survival and reproductive success may depend on such things as (a) social cohesion and social organization, (b) mutual aid in defence against predators and possible alloparental care such as “babysitting” and communal nursing, (c) sufficient opportunities for transfer of “knowledge” (learned behaviour) from one generation to the next, and (d) leadership by older individuals that know where and when to find scarce prey resources and how to avoid high-risk circumstances (e.g., ice-entrapment, stranding, and predation). Group living has numerous potential benefits for marine mammals generally [9]. Therefore, the

effects of exploitation on these social animals—for example, social disruption, fragmentation of social units, and loss of key individuals—could be nonlinear and unpredictable, with severity contingent upon various features of the exploitation regime such as age and sex selectivity, methods of capture, seasonality, and habitat quality or integrity.

The role of social and behavioural traits in determining the cumulative effect of hunting has been shown in many terrestrial species. The removal of both matriarchs and trophy males from elephant (*Loxodonta africana*) populations has been shown to cause social disruption [10, 11], and lower fecundity has been correlated with heavy hunting in two populations, apparently because older males with large tusks are responsible for most mating in undisturbed populations [10]. In elephants, the selective killing of matriarchs for their large tusks is also thought to reduce the availability of “social knowledge” to a group or herd [11]. Similar concerns have arisen in relation to trophy hunting of ungulates, where the selective removal of alpha adult males leads to the loss of valuable genetic as well as cultural capital [12]. There are numerous terrestrial examples, where the deliberate selection by hunters for phenotypic traits has led to a loss of genetic fitness in the wildlife population [13, 14]. Examples include the lower reproductive success of bighorn sheep (*Ovis canadensis*) when rams with larger horns are removed [15] and the increased occurrence of tusk-less female elephants as a result of hunting for ivory [16]. Darimont et al. [14] found average phenotypic changes in 40 populations subject to hunting to be much more rapid than changes reported in studies of naturally perturbed populations and wild populations subject to other human perturbations, outpacing them by >300% and 50%, respectively. They concluded that hunted populations show some of the most abrupt trait changes ever observed in wild populations, which include average declines of almost 20% in size-related traits and shifts in life history traits of nearly 25%. Additionally, they found the most rapid changes occurred in commercially exploited populations, and they cautioned that such alterations to phenotypes might also generate large and rapid changes in population and ecological dynamics including those that affect population persistence.

Trophy hunting of male ungulates and subsequently skewed sex ratios have been shown to reduce fecundity, at sex ratios ranging from 1:2 (in Soay sheep (*Ovis aries*) and in moose (*Alces alces*) to 1:12 (in caribou (*Rangifer tarandus*)) [12]. Species with highly synchronous breeding can be particularly susceptible to this if females are widely dispersed, and even in some species where females do not disperse widely, sperm production may be limiting [12]. Also, sex-biased hunting can cause social disruption through mechanisms such as increased competition for females between remaining males, or an inadequate number of large dominant males to fertilize receptive females [12]. In the sable antelope (*Hippotragus niger*), an increase in calf mortality was linked to a decrease in calving synchrony, and thus less effective “predator swamping”; the lack of synchrony was caused by too few adult male antelopes [17]. A study of wolves (*Canis lupus*) showed that heavy hunting pressure decreased the average size of social groups,

caused mating to be less selective, increased variability in territories and home ranges, and led to higher natural mortality rates (excluding the kills from hunting by humans) [18]. One mechanism identified for the higher mortality was disruption of social groups, leading to the formation of new groups and dispersal of individuals that usually died.

Here, we review exploitation of populations of highly social odontocetes and attempt to assess whether they were depleted and, if so, whether they have shown evidence of recovery after exploitation ceased, or instead not recovered as expected. Additionally, we look for evidence of social and behavioural factors that may have hindered recovery. Finding examples of well-studied populations of odontocetes, where resilience to exploitation has been “tested” and measured in some manner is not easy. Even “precipitous declines” in marine mammal populations can be hard to detect using presently available methods [19]. In the case of cetaceans, small, accessible populations are the most easily monitored. This creates the potential for a serious bias because such populations may not be representative and may even be anomalous. Nonetheless, we attempt to review all known cases of exploitation of highly social odontocetes where data are available and discuss aspects of their social structure and behaviour that may affect their resilience to exploitation. Importantly, this means that we do not focus on porpoises, whose lack of resilience to exploitation, evident in multiple regions, appears to be explained primarily by their life history.

We reemphasize that the life history of odontocetes, which prevents their populations from growing quickly, is likely the primary reason for their apparent lack of resilience to heavy exploitation. What we consider here is whether social and behavioural traits of odontocetes (not seen in mysticetes) contribute further to this observed lack of resilience. After our review of these traits, we also consider alternative contributing factors, primarily the higher levels of contaminants in odontocetes relative to mysticetes, the higher levels of bycatch often seen in populations of small odontocetes, and the competition often inferred between odontocete populations and commercial fisheries for the same prey (something not usually seen in mysticetes, which generally feed at lower trophic levels that are not commercially exploited). It is likely that multiple factors often act in concert to inhibit recovery of odontocete populations, and our objective here is to increase awareness and consideration of the possible role of social and behavioural traits.

## 2. Sperm Whale, *Physeter macrocephalus*

Sperm whales have been likened to elephants in their social organization, life history, and vulnerability to exploitation. It has been suggested that large size, wide range, and temporally extensive communal memory help both sperm whales and elephants “ride out considerable temporal fluctuations in their food supply” [20, p. 169]. Furthermore, female reproductive output declines with age in both sperm whales and elephants, and in elephants, and perhaps also in sperm whales, old females (“matriarchs”) function as herd leaders

and as “reservoirs of ecological knowledge” [21, p. 279]. As mentioned previously, the selective killing of elephant matriarchs for their large tusks may reduce the “social knowledge” available to a group or herd [11]. Although it is difficult to quantify, or even to prove the existence of, this function in sperm whale society, there is some circumstantial evidence for it. In warm El Niño years when foraging conditions deteriorate around the Galápagos Islands (Ecuador), groups of females and young sperm whales move “fast and straight” to areas as much as 1000 km away, presumably “where an older female remembers fair feeding during previous Niños” [21, p. 285]. The downside is that the loss of old individuals due to hunting or “cropping,” on the assumption that they are surplus or expendable, could mean the loss of valuable cultural capital in the sperm whale group. A recent study showed that different sperm whale social groups have different foraging success under different climatic conditions, with some doing better during El Niño events [22]. Thus, social groups may differ in their ability to adapt to changing environmental conditions. The implications of lost wisdom are hard to discern and may vary greatly, depending on chance events and circumstances—if all goes well, the group may persist long enough to regain or replace the lost knowledge, it may merge with another group that still has plenty of cultural capital, veterans may join it, and so forth.

Sperm whale social groups appear to be formed by temporary associations between smaller, more stable social units, therefore creating a mix of clusters of closely related individuals and others with no close relations [23]. Calf protection is thought to be an important function of sociality among female sperm whales because adults make long feeding dives to depths where calves cannot follow; non-synchronous diving patterns ensure that adult females are often at the surface with calves and perform a “babysitting” role to protect calves from predation by killer whales or other predators [24]. In general, allomaternal care makes individuals dependent on one another for communal care of young, which promotes sociality [23]. Whaling could disrupt the social relations and social structure of sperm whale groups and, in turn, affect survival of sperm whale calves and juveniles.

Using the population of sperm whales around the Galápagos Islands as a case study, Whitehead et al. [25] argued that exploitation can continue to have substantial negative effects on the size and recruitment rate of a population for at least a decade after the exploitation has ended. In a long-term photoidentification study, they documented a decrease in sperm whale abundance around the Galápagos of about 20% per year (95% CI: 7 to 32%) between 1985–1995. In the absence of any evidence of substantial mortality or health problems, and given some direct evidence of emigration by individual female sperm whales to mainland Ecuador, northern Peru, and the Gulf of Panama, those authors concluded that the marked decline in the Galápagos was principally due to emigration. However, they also found a remarkably low reproductive rate in the Galápagos whales, about 0.05 calves/female/year. With so little recruitment, the population would be, at best, barely sustainable even if there

were no emigration. To explain their results, Whitehead et al. pointed to an intense period of modern whaling in Peru from 1958–1981, when virtually the entire local population of large male sperm whales (>13.5 m) had been wiped out [26]. This whaling, they reasoned, was affecting the sperm whales in their Galápagos study area in two main ways. Firstly, it reduced the density of sperm whales in the productive Peru Current system, “leaving both good feeding for animals entering these waters and providing little incentive to leave, effectively resulting in one-way migrations” [25, p. 1394]. Secondly, by drastically depleting large males in the region, it led to very low pregnancy rates, which persisted “for many years.” The point here is that if there were a strong female preference for large males, a lack of “suitable” males would lead to lower pregnancy rates even though younger and smaller males still exist in the population (see above regarding examples in terrestrial mammals). Mate selection by females is generally ignored or discounted in most population models, where it is assumed that any number of reproductive-aged males will successfully impregnate all reproductive-aged females that are ovulating. Ginsberg and Milner-Gulland [12] describe scenarios in ungulates, where a sex-biased hunt leading to decreased fecundity can lead to population collapse.

Determining whether sperm whales have recovered from exploitation is difficult. In a worldwide review, no evidence was found to suggest that any population of sperm whales had increased significantly [27], but few areas with trend data were available. In California, one of those few areas, the sperm whale population was relatively stable from 1979 to 1991 [28]. On a global scale, Whitehead [29] used three methods for scaling up available abundance estimates to produce a worldwide estimate, and these resulted in a consistent total of about 360,000 ( $CV = 0.36$ ) sperm whales. A back-calculation model using catch records suggested that pre-whaling numbers were about 1,110,000 (95% CI: 672,000 to 1,512,000), and that the population was about 71% (95% CI: 52 to 100%) of its original level in 1880 as open-boat whaling drew to a close and about 32% (95% CI: 19 to 62%) of its original level in 1999, 10 years after the end of large-scale industrial whaling [29]. Recent estimates of sperm whale density have been much higher in the western North Atlantic than in other parts of the world [29], suggesting there may have been recovery in this region. This could be due to the fact that although the North Atlantic population was subject to open-boat (nonmechanised) whaling throughout most of the 18th and 19th centuries and, at least locally (e.g., the Azores and Madeira; see [30]), during much of the 20th century, it was largely spared from large-scale, modern, factory-ship whaling which was concentrated in the southern oceans and North Pacific throughout the first three-quarters of the 20th century. Maximum potential rates of increase are thought to be quite low in sperm whales. A value of 0.9% has been suggested by the Scientific Committee of the International Whaling Commission [31] for a population with a stable age distribution. Whitehead [29] used a mortality schedule from killer whales combined with pregnancy rate data from sperm whales to estimate a maximum rate of increase of 1.1%, with

a “reasonable range” of 0.7 to 1.5%, suggesting that sperm whale populations would be vulnerable (i.e., nonresilient) to relatively modest exploitation rates.

### 3. Beluga or White Whale, *Delphinapterus leucas*

Belugas are highly social odontocetes that are commonly found in groups of 2–10 and often aggregate in assemblages of up to hundreds or possibly thousands [32]. There is limited evidence that the basic social units of groups are matrilineal, consisting of adult nursing females accompanied by older female offspring [33]. These “triads” may sometimes join to form large nursery groups [32]. Separate pods of adult males are sometimes observed. There is also some evidence that males migrate separately from or feed apart from females, calves, and immatures. It is not clear whether belugas form stable social groups beyond those of the immediate matrilineal. However, their substantial vocal repertoire and observed behaviour (e.g., closely spaced grouping and susceptibility to “driving” by hunters) indicate a high degree of sociality in this species, even though their social system is not completely understood or described. Many populations of belugas make large seasonal movements in relation to prey availability and ice conditions, suggesting that cultural retention of knowledge of movement patterns could be important. Avoidance of ice entrapment, for example, is a risk that may be lessened by experience and knowledge of older individuals in groups.

Through the 1970s, it was generally believed that belugas could be exploited sustainably by removing on the order of 0.05 to 0.10 of a given population annually [34]. With larger samples of biological material and better analytical techniques, it came to be widely accepted that  $r_{max}$  for belugas (and, incidentally, narwhals, *Monodon monoceros*) is well below 0.10. Sergeant [35] reasoned that an offtake rate of 0.05 was “probably sustainable” for monodontids as long as the hunting was selective for males and especially adult males. Kingsley [36], using a simple model of population dynamics, suggested that 0.03–0.04 was a more realistic range of “permissible exploitation rates” for these species. Such rates are generally used to assist in the management of hunts that can be highly stochastic. In their formulation, they do not explicitly incorporate consideration of social, behavioural, or cultural factors.

Belugas have been heavily exploited in much of their range, often over timescales of hundreds of years. In at least two areas, southwestern Greenland and southern Ungava Bay (eastern Canada), they were essentially extirpated by commercial whaling [37, 38]. In both of those cases, the mode of capture extended beyond the single hunter in a kayak or canoe armed with a harpoon or rifle, to include drive and net hunts in which tens or hundreds of whales could be taken at a time. Although similar hunting techniques were practiced in many other areas (e.g., Svalbard, eastern Hudson Bay, Cumberland Sound, Prince Regent Inlet, central-western Greenland, and the Okhotsk, Kara, White and Barents seas

[39]) at least relict numbers of belugas survived so that the populations in those areas are still extant.

Trends in beluga populations have been monitored intensively in two areas: the St. Lawrence River in Canada and Cook Inlet in Alaska. In both areas, hunting (along with weir trapping in the St. Lawrence) reduced the populations to less than a third of pre-hunting levels [40–43]. In the St. Lawrence, belugas have been completely protected from direct exploitation since the late 1970s, but the question of whether any recovery has occurred is unresolved despite careful population monitoring since then [43]. Similarly, the closure of hunting for Cook Inlet belugas in the early 2000s has not resulted in any measurable recovery by that population [44]. Several other areas where large beluga populations were greatly depleted by hunting, for example, central-western Greenland, eastern Hudson Bay and Cumberland Sound, have been monitored periodically, and there is no clear evidence of sustained recovery by any of those populations. Importantly, none of the once-large beluga populations in northern Russia has been monitored rigorously for trends following decades of intensive exploitation under the Soviet regime.

We are aware of only one example where there is direct evidence for a beluga population increase. The results of aerial surveys of inner Bristol Bay (Alaska) between 1993 and 2005 have been interpreted as suggesting that the local population of belugas increased during that period at a rate of nearly 5% per year [45]. In this instance, however, there was no history of intensive exploitation, no tradition of using drive or net techniques leading to mass removals, and no reason to believe the population had been seriously depleted prior to 1993.

Social systems of belugas are not well understood, partly due to the lack of individual-based studies, such as the long-term photoidentification studies of sperm whales, killer whales, and bottlenose dolphins (*Tursiops* spp). Therefore, we have little direct evidence that exploitation has caused disruption of beluga societies in ways that would lead to population consequences. However, there are at least five and perhaps as many as seven areas where belugas have failed to show any sign of recovery following exploitation: southwestern Greenland, southern Ungava Bay, Cook Inlet, the St. Lawrence River, and eastern Hudson Bay, possibly also Cumberland Sound and central-western Greenland. Although there is a good reason to believe that continued direct removals by hunting are partly responsible for the lack of recovery in some of those areas, we suggest that the disruption of beluga behaviour and social systems is a contributing factor.

#### 4. Narwhal, *Monodon monoceros*

Even less is known about the social system of the narwhal, a close relative of the beluga. The pronounced sexual dimorphism of narwhals, most obvious in that usually only males have tusks, along with observations of “sparring” by males and heavy scarring on the melons of adult males, together implies a mating system where males physically

compete for dominance or access to mating opportunities [46]. This suggests a mating system where relatively few males mate successfully.

Narwhals have been hunted intensively by northern people in Canada and Greenland for centuries. In Greenland, the hunt became subject to annual catch limits only as recently as 2005, and in Canada narwhal hunting has been managed in recent decades largely at the community level and through federal land-claims agreements [47]. The number of narwhals in northwestern Greenland was estimated to have declined between 1985–86 and 2001–02 at a rate of 6% per year [48], and Heide-Jørgensen and Acquarone [49] expressed concern that narwhal abundance had also declined off western Greenland. In both cases, overexploitation was suspected as the cause, or at least as a contributing causal factor. More recent surveys of narwhals in Greenland waters resulted in higher abundance estimates and therefore called into question the earlier indications of declines [50].

It is likely that in areas of heavy exploitation, not only the numbers but also the social structure of narwhals have been affected by the hunting. Hunters in some areas and at some times select individuals with large, commercially valuable tusks [51]. As was mentioned above, this type of trophy hunting, with selective removal of alpha adult males, has been shown in bighorn sheep to lead to decreased reproductive success [15]. Besides the potentially disruptive effects on reproduction, removals of older individuals may have some of the same insidious effects on narwhal populations that we suspect they have on belugas. For example, although warming trends in the Arctic have generally caused sea ice to shrink in extent and thickness, ice coverage has been increasing over the last several decades in Baffin Bay, one of the narwhal’s main wintering areas, increasing the risk of ice entrapment [52]. Laidre et al. [53] suggest a recent increasing trend in large entrapments of narwhals in summer. As was suggested for belugas, this risk may be lessened by availability of the experience and knowledge of older individuals in groups.

#### 5. Killer Whales cf. *Orcinus orca*

Killer whales have a life history that is similar to that of humans, as they reach sexual maturity in their teens, females reach reproductive senescence in their 40s, and some individuals are thought to live to 80 years or older [54]. Various types of killer whales have been described, differing in their morphology, genetics, and foraging specialization (e.g., [55, 56]), but all killer whales that have been studied appear to live in relatively stable social units. In many or most populations, these stable social units are matrilineal, and often exist over long periods of time. The extreme is seen in North Pacific “resident-type” (fish-eating) whales, where matrilineal social groups appear to be permanent, meaning offspring never or very rarely disperse from their mother’s group [56, 57]. For most or all populations, these stable social units have long-term associations with other such units. In resident-type killer whales in the eastern North Pacific, lineages of vocally and matrilineally related social groups

appear to form acoustic “clans,” which are maintained by vocal traditions [58], giving a social hierarchy of matriline, pods (collections of matrilines that frequently associate), and clans (collections of pods that are genetically related and acoustically similar).

It has been suggested that some killer whales exhibit evidence of culture, such as foraging specializations between sympatric fish-eating and mammal-eating populations as well as group-specific call dialects that are used by matrilines to stay in contact [59]. Killer whales in different parts of the world have unique foraging techniques that are apparently learned, including hunting of pinnipeds on beaches by intentional stranding [60] and “carousel feeding” techniques used by whales in Norway to herd and prey on herring (*Clupea harengus*) schools [59]. In many populations there are examples of substantial seasonal movements in search of prey, such as movements following herring out of fjords in Norway into the Atlantic Ocean. These characteristics make killer whales, like the other species described above, potentially vulnerable to social disruption and the loss of cultural and ecological knowledge through removal of older individuals.

Two populations of resident-type killer whales in the northeastern Pacific were exploited in the 1960s and early 1970s by live-capture removals for the aquarium industry, and by intentional shooting by fishermen who perceived them as competitors [61]. As mentioned earlier, resident-type killer whales live in a social structure of long-term associations of matrilines. This suggests that the cultural capital retained by older individuals (both female and male) in the matriline is of considerable importance, and therefore the removal of such individuals would have a disproportionately large effect on the population’s ability to adapt and flourish.

The southern resident population is estimated to have declined from a population size of ~140 or greater when live-captures began, to only 71 in the mid 1970s when such removals stopped following passage of the US Marine Mammal Protection Act [62]. The population has shown some signs of recovery but has fluctuated over the last few decades between ~80–100. This variability has been driven by fluctuations in survival rates that are correlated with Chinook salmon (*Oncorhynchus tshawytscha*) at-sea abundance indices [63]. The direct removals may have caused substantial disruption to the social structure of the population, so this is a plausible hypothesis to explain, at least partially, the lack of recovery. However, there are other competing hypotheses, particularly that recovery has been hampered by human-caused declines of Chinook and other species of salmon, or by the high levels of persistent organic pollutants (POPs) in their fat stores [64–66]. There could be an interaction between these two factors, where a lack of prey in some years leads to utilization of fat stores that remobilize sequestered POPs into the bloodstream, perhaps to levels capable of causing reproductive problems and immune suppression [62]. Southern resident killer whales make substantial seasonal movements: one group (J pod) moves into southern Puget Sound in autumn in pursuit of chum salmon (*Oncorhynchus keta*) runs, while two other

groups (K and L pods) move from Washington to Oregon and California in winter, apparently in pursuit of Chinook salmon, and these whales also move as far north as the Queen Charlotte Islands [67]. According to contaminant ratios, L and K pods have a partially “California signature,” whereas J pod does not [65, 66]. Given that these whales apparently undertake long-range movements intended to intercept specific salmon runs at specific times and places, and that salmon runs themselves undergo substantial interannual fluctuations tied to oceanic regime shifts, killer whales must adapt their movement patterns to existing conditions in different years. Therefore, the population may benefit greatly from knowledge of older individuals that have experienced a broad range of ocean conditions. Different matrilines may have different cultural knowledge that could be more or less helpful as ocean conditions change, as mentioned above for sperm whales.

The northern resident population was also exploited by live-capture removals and intentional shooting, but was likely not depleted to the same degree as the southern resident population. The northern resident population increased at a rate of 2.6% in the 1970s, 1980s, and early 1990s [68] and has been roughly stable since then. The southern-most pods of the northern resident population have experienced fluctuations similar in scale to those of the southern resident population, which is interesting as these are the pods that live in closest proximity to the southern resident population and may share its food supply [63]. Survival rates in the northern resident population have also been correlated with salmon abundance [63], and northern residents also have high levels of POPs, so the same confounding factors apply to this population when it comes to explaining the lack of sustained recovery.

Individuals from both resident and “transient”-type (mammal-eating) populations of killer whales in Alaska apparently died from exposure to oil in the Exxon Valdez spill and suffered losses of 33% and 41%, respectively, in the year following the event [69]. Additionally, resident-type whales were shot by commercial fishermen defending their catches prior to regulations outlawing such shooting in 1986. Sixteen years after the spill, the AB pod from the resident-type population had not recovered to pre-spill numbers, and its rate of increase was significantly lower than other pods that did not decline after the spill (1.6% per year versus 3.2% per year). The slowness of the AB pod’s recovery is attributed largely to the loss of juvenile and young adult females, which resulted in a significantly lower birth rate than observed in other pods [69]. Also, an apparent change in social structure was observed after the spill as one subpod changed its pattern of association with other subpods, the only such change documented in more than 20 years of monitoring [69]. A potential mechanism for this type of change can be seen in the study by Lusseau and Newman [70], who inferred from association data that a few key individuals provide the connections among subgroups to maintain social cohesion within a small population of bottlenose dolphins, and in a similar simulation study of northern resident killer whales [71]. The transient-type AT1 population of killer whales was already heavily skewed towards adult males prior to

the Exxon Valdez spill and apparently had a low reproductive rate, but the deaths of nine whales (seven of juvenile or reproductive age) immediately after the spill likely did not help. The population has not produced a calf in over 20 years and is likely to go extinct within the next several decades. Additional causes of its failure to recover, besides the demographic problems, may include high POP levels [72] and a sharp regional decline in harbour seals (*Phoca vitulina*) [73], the primary prey of AT1 killer whales.

These examples suggest that killer whale populations are not very resilient to exploitation. This may be solely or primarily due to their life history, as was suggested for the AB pod by Matkin et al. [69], who cited a low birth rate caused by a shortage of reproductive-age females due to removals as the main hindrance to recovery in that case. On the other hand, the lack of sustained recovery of southern resident killer whales could be partially due to social disruption and the loss of cultural capital. Specifically, the whales may find it harder to find alternative prey when their primary salmon prey are at low availability, for example, in winter months when certain types of prey are not as highly concentrated as they are at other times [63]. However, depletion of many of their prey fish populations by overfishing or habitat degradation confounds any interpretation of the root cause of this population's failure to recover.

Williams and Lusseau [71] showed from data on northern resident killer whales that particular individuals were more important than others to maintaining the social network throughout the population. When those authors simulated the removal of individuals of the same age and sex, as the live-capture industry had done, there was a greater probability of fragmentation of the social network connecting the entire population. They interpreted their results as suggesting that anthropogenic removals targeting particular matriline implicitly and particular age or sex classes explicitly could have different population-level effects than random culling.

## 6. Pilot Whales, *Globicephala* spp.

Pilot whales are highly social and are usually found in large schools averaging 20–90 individuals, and their social structure is thought to be similar to that of killer whales [74]. Long-finned pilot whales (*Globicephala melas*) appear to live in permanent matrilineal social groups where offspring do not disperse from their natal group, and males are thought to mate outside of their group [75]; less is known about short-finned pilot whales (*Globicephala macrorhynchus*), but they also appear to live in long-term social groups. In both species, older adult females apparently have a role other than solely reproduction; short-finned pilot whales show evidence of complete female reproductive senescence [76], and long-finned pilot whales show a decline in fecundity with age but not a complete cessation of reproduction [77]. It has been suggested that the death of an older mother could substantially reduce the survival probabilities of several dependent young and perhaps other close relatives [78]. Cooperative foraging and food provisioning have been

suggested as benefits that postreproductive females could give to stable social groups [79], and this is supported by evidence of lactation in females that are no longer reproductively active (also true of sperm whales). Norris and Pryor [80] suggested that postreproductive females in pilot whale schools could also be repositories of cultural information, such as the whereabouts of feeding grounds.

Long-finned pilot whales have been hunted in the Faroe Islands since at least the 10th century. The strong social bonds of pilot whale schools allow an entire school to be herded and driven ashore (or at least into coastal shallows) and killed. Catches in the Faroese drive fishery have averaged ~1000 whales per year for the last 300 years, which indicates that the level of removal is sustainable. Studies have found significant differences in pollutant concentrations [81, 82] and parasite burdens [83] between schools of pilot whales landed on the Faroe Islands at different times and locations. This means that the schools spend different proportions of their time in different areas, which makes it possible that there is more than one stock of long-finned pilot whales in the North Atlantic, and in fact more than one stock subject to hunting in the Faroe Islands. Systematic surveys in the North Atlantic were conducted in 1987 and 1989, and abundance of long-finned pilot whales in Faroese survey blocks in 1987 (a year with more survey effort around the Faroe Islands) was 64,779 (CV = 0.454) [84]; a catch of 1000 whales per year represents ~1.5% of that abundance estimate. The most extensive survey of the North Atlantic was completed in 1989, with a total abundance estimate of 778,000 (CV = 0.295) [84]. Summing abundance over only survey blocks in the eastern half of the survey area (blocks 10, 20, 36, 40, 50, and 88) results in a total of 421,000; a catch of 1000 whales per year represents ~0.2% of that abundance estimate. It remains unclear exactly what abundance the Faroe Islands catch should be compared to, but the evidence that multiple stocks (or at least whales from multiple regions) are taken suggests a broader area than just the immediate waters around the Faroe Islands. If this is the case, the catch may have been sustainable because the population(s) from which it is taken is (are) large enough to support that removal (which would probably represent less than 1% of the population size).

Another potential factor is the nature of the hunt, which is a drive fishery that kills entire schools or aggregations of pilot whales found together. This would result in the least amount of social disruption to the remaining whales (as compared to removing a small percentage of individuals from many different social groups each year). There is no way to determine whether this has been an important factor in the sustainability of this hunt, but it is a plausible, or at least interesting, hypothesis. An alternative interpretation would be that matriline-based knowledge or foraging specializations become lost during a hunt where a whole matriline is completely removed [71]. In essence, this is how Whitehead and Rendell [22] interpreted the differential foraging success of sperm whale matriline during El Niño events.

Long-finned pilot whales were also subject to a drive fishery in Newfoundland from 1947 to 1972, and this fishery apparently reduced the stock to very low levels [85–87]. It also frequently took entire social groups [88] in a fashion

similar to that of the Faroe Islands drive fishery. Abundance at the onset of the fishery was estimated to be about 60,000 animals from an analysis using the catch record and data from the squid fishery [85]. Hay [86] conducted an aerial survey in 1980 in eastern Newfoundland and Labrador waters, and estimated 13,167 whales (95% CI: 6731 to 19,602, not corrected for diving whales or whales missed by observers). During the height of the fishery from 1951–1960, an average of ~4000 whales were killed per year; this declined in the next decade (1961–1970) to an average of ~1300 per year, with the drive fishery apparently collapsing after 1967 [85]. Thirteen hundred is ~10% of the survey abundance of 13,167, and 4000 is ~7% of the 60,000 preexploitation size estimated by Mercer [85], so this population appears to have been overexploited. Nelson and Lien [87] concluded the population had not yet recovered given the relatively low abundance estimated by Hay [86] and others, and the lack of recovery was speculated to be due to a relatively low rate of population increase and insufficient passage of time.

Short-finned pilot whales are killed in Japan in drive fisheries, crossbow fisheries, and small-type whaling, but they have not been the main targets of any of these hunts [89]. There has been a moderate decline in total catches over time [89, 90]. An average of 246 whales were taken per year from 1995 to 2004, well below the quota of 450. It is not clear if the decline in catches and the failure to reach the quota should be interpreted as a decline in the population. Recent catches averaged ~1.2% of estimated pilot whale abundance, while earlier catches averaged ~1.8% of abundance [90], but interpretation of these values is problematic due to the uncertainties about population structure.

Pilot whales of both species are among the cetaceans most frequently involved in mass strandings in which the entire group dies. Although a number of hypotheses have been proposed for the cause of these mass strandings, the one thing that is certain is that strong social bonds exist within pilot whale schools [74]. This may make pilot whales particularly vulnerable to the removal of certain individuals from social groups.

## 7. Eastern Tropical Pacific Dolphin Populations

Tropical and temperate-region oceanic dolphins are thought to live in fission-fusion societies, where small social units (such as mother/calf pairs) aggregate in schools of hundreds or even thousands of individuals. The composition of these schools can change rapidly from day to day as the school splits or joins other schools. Beyond the obvious social unit of mother/calf pairs, other longer-term social associations, such as juvenile subgroups and adult male alliances, have been described in several closely related and well-studied (coastal or island-associated) odontocetes such as bottlenose dolphins [91–93] and spinner dolphins [94].

Dolphins of several species are incidentally killed during tuna purse-seine fishing in the eastern tropical Pacific (ETP). Fishermen use the dolphins to locate schools of tuna, and chase and encircle the dolphins in nets to facilitate the catch of tuna that swim below [95–97]. Over the period 1960 to

1972, more than 4 million dolphins were killed by purse-seine vessels fishing for yellowfin tuna (*Thunnus albacares*) in the ETP [98]. At least two dolphin populations—northeastern offshore pantropical spotted dolphins *S. attenuata attenuata* and eastern spinner dolphins *S. longirostris orientalis*—are estimated to have been reduced to 40% and 20% of their pre-exploitation levels, respectively, because of high mortality from purse seining during the 1960s and early 1970s [99].

Although spotted and spinner dolphins in the ETP do not appear to live in long-term stable social groups, they do show signs of a relatively complex social structure. The proximity of individuals in aerial photographs of spotted dolphins suggests subgroups of 2 to 8 individuals within large schools [100]. Observations of spotted dolphins captured in purse seines suggest a variety of types of subgroups within schools, including groups of females with their young, triads (two adult females and a calf), groups of juveniles, and groups of adult males [100]. At a larger scale, two types of schools have been observed in the ETP. The first type is the breeding school, often numbering a few hundred animals, that contains more females with young and fewer juveniles than expected from a stable age distribution. The second type is often smaller and consists of mostly male or mostly juvenile dolphins [100]. These schools can themselves temporarily fuse into even larger aggregations.

In a recent assessment of trends in dolphin populations in the ETP, Gerrodette and Forcada [101] concluded that, despite reductions in fishing mortality spanning two orders of magnitude, neither the population of northeastern offshore spotted dolphins nor that of eastern spinner dolphins had increased in abundance by the year 2000. Thus, neither stock was considered to be recovering, even though reported kills in the fishery had been reduced from a high of hundreds of thousands per year to fewer than 1000 per year, which represented much less than 1% of the best estimate of population size. Wade et al. [99] estimated that both populations remained depleted. They compared models intended to be indicative of hypotheses to explain why neither dolphin stock had recovered, with results giving equal support to those attributing to the lack of recovery to effects of the fishery and those attributing it to changes in the ecosystem. Their conclusion was that the purse-seine fishery could well be affecting the dolphin populations in other ways than simply removal of relatively small numbers of individuals as bycatch, but that the degree to which cryptic effects are having population-level consequences is unknown.

Despite the major reduction in dolphin kills, the number of intentional sets on dolphins has not declined; the decline in kills has occurred primarily because of a major decline in the number of dolphins killed per set, which is due, in turn, to increased effort by the fishermen to release the dolphins. The number of dolphins chased, captured, and released during fishing operations is high [102], and individual northeastern offshore spotted dolphins interact with the fishery between 2 and 50 times per year, depending on size of the school [103]. This rate of interaction likely has negative effects on survival and/or reproduction through

increased energetic demands from chase, elevated stress from chase and encirclement [97, 104], and increased predation risk on release from encirclement [105].

Behavioural changes in swimming and schooling dynamics occur during the tuna-fishing process. Separation of individuals in a group can occur during the chase (due to different swimming speeds or splitting into subgroups during evasive manoeuvres), during encirclement (due to individuals ending up inside or outside the net), and during release (due to confusion and flight responses as the dolphins are slowly released from the net). Perhaps the most dramatic separation occurs between mothers and calves [102]. Estimated long-term sustainable speed is about 1 m/s for neonates compared to about 2.5 m/s for adults, and power estimates for 2-year-old spotted dolphin calves are about 40% higher than power estimates for adults needed to maintain the same speed [106]. Under normal circumstances, these higher demands are generally offset by calves drafting their mothers and using other energy-saving strategies, but the relatively high speeds associated with flight and evasion during and after tuna sets likely make this more difficult. Noren and Edwards [107] suggest that evasive behaviour of mothers during chase, coupled with the developmental state of calves, provides a plausible mechanism for mother-calf separations and subsequent mortality of calves, and that the potential for separation is highest for dolphins in their first year, becoming progressively lower with age as immature dolphins approach adult stamina levels and attain independence. Archer et al. [102] found a deficit of calves relative to the number of lactating females killed in 24%–32% of spotted-dolphin sets and in 13%–19% of spinner-dolphin sets examined. Archer et al. [108] extended this analysis over a longer time series and estimated that from 75% to 95% of the lactating females killed were unaccompanied by a calf, and it is assumed that their orphaned calves would not survive without their mothers. Over the time series, total kill was estimated to be 14% higher per year when missing calves were taken into account.

Exploitation may also have an effect on spinner dolphins through disruption of their mating system. Differences in testes size indicate that eastern spinner dolphins have a more structured polygynous mating system than other subspecies of spinner dolphins; relatively few adult eastern spinner males participate in mating. Perrin and Mesnick [109] found that only 4 out of 699 (0.6%) eastern spinner males examined had testes plus epididymides weighing more than 700 grams, the level at which all epididymides contained sperm. They interpreted this finding to indicate that only this tiny fraction of the male population was capable of successful mating. This could mean that eastern spinner dolphins are exceptionally vulnerable to perturbations caused by chase and capture in the tuna purse seine fishery, for example, breaking up schools and disrupting social bonds by altering the spatial distribution of animals within schools [109]. If few males participate in mating, the removal of important individuals could suppress reproduction. Calf production has been declining since at least 1987 for both eastern spinner and northeastern offshore spotted dolphins [110], suggesting that some aspect of interaction with the fishery could be the cause.

Given these different lines of evidence, various authors have concluded that it is plausible that the chase and encirclement of dolphin schools by the fishery has hindered or perhaps completely prevented recovery of the depleted populations [97, 99, 101]. Both populations were estimated to be increasing at less than 1% per year, a significantly lower rate than expected for dolphins (3–4% per year). It is likely that other species of social odontocetes would be similarly affected if exposed to decades of repeated harassment and social separation during a hunt that involves a relatively long chase of the group. Although the interaction between the tuna fishery and dolphin populations is an exceptional case, the indirect effects of the chase and encirclement of dolphin schools by the tuna purse-seine fishery may be taken to imply that there are similar effects from other types of direct exploitation of odontocete populations that involve pursuit.

## 8. Discussion

Our review has clearly been limited by the sparseness of data on abundance, trends in abundance, exploitation levels, and population structure as well as by not having a full understanding of social systems in most odontocete species. Nonetheless, the results are thought-provoking. We found little evidence of strong recovery for decades after the phase of intense exploitation had ended in any of the depleted populations examined. There is little evidence for recovery of sperm whale populations except perhaps in the northwestern Atlantic. Belugas have declined in many areas, and in at least five, and perhaps as many as seven, areas they show no signs of significant, sustained recovery. At least three killer whale populations have not recovered as expected, and the same is true of two dolphin populations in the eastern tropical Pacific. Only in pilot whales did we find evidence of a region (Faroe Islands) where substantial exploitation over a long period of time has been sustained; in other regions (e.g., Newfoundland, possibly Japan), pilot whales appear to have been overexploited and their extent of recovery is unknown. We hasten to add that the hunting of belugas and narwhals in some parts of the Arctic has, like the hunting of pilot whales in the Faroes, been sustained over centuries, with the whale populations remaining large and healthy (e.g., Mackenzie Delta, western Hudson Bay, Bristol Bay, and eastern Canadian Arctic), but some populations of these species also have collapsed after hunting escalated to involve commercial ventures in relatively recent times.

The documented recovery of many populations of baleen whales is striking when compared to the lack of evidence for recovery of odontocete populations. Some of the difference is likely due to the relative lack of good monitoring data for odontocetes [19]. Also, in many cases the history of odontocete populations is probably confounded by continued exploitation through bycatch or unreported deliberate removals. Their relatively low population potential rates of increase mean that odontocete populations can be overexploited with take rates of only a few percent per year.

However, in several species of highly social odontocetes there is evidence that exploitation could have effects beyond

the simple dynamics of individual removals (Table 1(a)). Four species showed evidence of a decrease in birth rates following exploitation, from mechanisms that include a deficit of adult females, a deficit of adult males, and disruption of mating systems dominated by a few individuals. The prolonged dependence of calves in social odontocetes (lactation can last up to four or five years, and a 13-year-old sperm whale with milk traces in its stomach provides an extreme example [111]) increases the risk of mortality from the physical separation, and sometimes orphaning, of calves from their mothers during chasing and harassment from directed hunting or fishing operations. In contrast, calves of baleen whales are generally weaned and fully independent by 6–9 months of age.

Several other mechanisms that could affect recovery of odontocete populations can be predicted from their social systems (Table 1(b)). In every species reviewed here, it seems plausible that a loss of cultural knowledge of feeding grounds, prey, or foraging techniques could result from the removal of older individuals, perhaps particularly older females in matriarchal societies. The magnitude of this effect could be determined by the rarity of the environmental conditions that challenge a population. Populations may gain the most benefit from the presence of older individuals in years or periods when environmental conditions occur that have not been experienced for a long time. For example, older individuals in a group of narwhals or belugas might help the group avoid ice entrapment, a benefit that would be especially important when entering colder periods in climate cycles.

Beyond the loss of cultural knowledge, there may be other effects from the loss of older individuals. Postreproductive individuals in stable societies might play important roles in recruitment, such as the nursing of calves by postreproductive females (“nannies”) suggested in pilot whales. In sperm whales (and other species), the disruption or fragmentation of social groups may compromise protection from predation. Unrelated adults may no longer be available to “babysit” or the group may become too small to physically defend smaller animals from attack by killer whales. More speculative but interesting are other extended ramifications, such as the possible collapse of social networks through the removal of key individuals [70, 71], leading to the formation of new groups and dispersal of individuals, potentially causing higher mortality rates, as observed in wolves under heavy hunting pressure [18].

## 9. Confounding Factors and Alternative Hypotheses

In some, possibly many, cases, the history of a population is confounded by undocumented continued exploitation, understood to include fishery bycatch as well as direct hunting. This could apply equally to mysticetes and odontocetes although it might be argued that the incidental mortality of small odontocetes is more cryptic than the mortality of large, relatively conspicuous mysticetes. The likelihood of documentation also would vary depending on remoteness

of the region, the distance from shore, and the relative intensity of monitoring effort. In particular, entanglement of small odontocetes in set-gill-net and drift-net fisheries is an issue of widespread conservation significance [112, 113]. In many areas, where monitored, bycatch in fisheries exceeds sustainable limits for dolphins, porpoises, and small whales, but many if not most regions of the world lack adequate monitoring [114]. The lack of recovery for many populations of odontocetes may be due, at least in part, to ongoing bycatch.

There are other alternative hypotheses to explain an apparent failure of an odontocete population to recover from overexploitation. For example, tissue concentrations of persistent organic pollutants (POPs) differ markedly, on average, between the mysticetes and the odontocetes [115], with mysticetes carrying much lower burdens consistent with feeding at lower trophic levels. In contrast, some odontocetes, such as killer whales, are found to have some of the highest burdens measured in any cetacean [65]. Indeed, a lack of recovery by St. Lawrence River belugas has been partly attributed to POPs in combination with observations of disease-associated deaths [116]. Moreover, odontocetes often compete for prey with fisheries. In general, odontocetes rely on fishes, elasmobranchs, crustaceans, and cephalopods as prey, whereas some mysticetes (e.g., balaenids and blue whales) are obligate planktivores and others (e.g., sei (*Balaenoptera borealis*), fin (*Balaenoptera physalus*), and Bryde’s (*Balaenoptera edeni*), and humpback whales) prey on a mix of zooplankton and nekton. This could mean that differences in resilience to exploitation are at least partly driven by exploitation competition for prey resources [117], with odontocetes more typically engaged in such competition with fisheries (e.g., [118]). In the case of resident killer whales along the west coast of North America, prey populations of salmonids are greatly reduced from pre-exploitation levels [62], and killer whale survival rates have been correlated with indices of Chinook salmon abundance [63], so the lack of sustained or full recovery by resident killer whale populations may be related more to this factor than to social disruption. On the other hand, the combination of a naturally low reproductive rate, a reduced food supply, social disruption from removal of key individuals, and high levels of contaminants may be a potent combination that has a greater cumulative effect than any single component.

## 10. Conclusions

We are the first to admit that the data summarised in this paper are only suggestive and that firm conclusions linking social and behavioural factors to nonrecovery or compromised recovery of odontocete populations would be premature. We cannot say with certainty that populations of social odontocetes are less resilient to exploitation than populations of mysticetes due solely or mainly to social and behavioural factors. We have, however, sought to summarise the available information in a way that allows such a hypothesis to be articulated with greater clarity so that both scientists and managers can consider its merits and

TABLE 1: Possible mechanisms by which direct exploitation affects odontocete cetaceans, beyond the simple effect on population dynamics of removing individual animals.

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(a) Mechanisms for which there is some evidence

Deficit of reproductive-age females (killer whales)

Deficit of adult males leading to lower pregnancy rate in females (sperm whales)

Lowered birth rate from disruption of mating systems (spinner and pantropical spotted dolphins)

Physical separation of cow/calf pairs from chase and encirclement leading to death of calves (spinner and spotted dolphins)

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(b) Additional mechanisms suggested by the species' social systems

Loss of cultural knowledge concerning, for example, types of alternative prey, areas where prey can be found, and ways to capture different types of prey under varying circumstances (killer whales, sperm whales, belugas, narwhals, and pilot whales)

Increased risk of ice entrapment due to loss of cultural knowledge (belugas and narwhals)

Disruption of social networks by removal of key individuals leading to dispersal and potentially higher mortality rates (bottlenose dolphins and killer whales)

Loss of an important nonreproductive role played by older females (pilot whales, killer whales, and sperm whales)

Increased predation risk due to loss of social connection and "babysitting" by nonrelatives (sperm whales)

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perhaps even "test" it. Further, we have established that, regardless of the cause, there are few examples of populations of social odontocetes that have sustained or recovered from intensive exploitation, and this stands in stark contrast to the documented recoveries of numerous heavily exploited mysticete populations.

We have made no attempt here to discuss the other highly social species of odontocetes for which there are even fewer data. By analogy with the species we have considered, however, we predict that at least some additional species would be vulnerable to the same kinds of effects. For example, the social systems of killer whales and pilot whales are likely similar in some ways to those of false killer whales (*Pseudorca crassidens*), pygmy killer whales (*Feresa attenuata*), melon-headed whales (*Peponocephala electra*), and Risso's dolphins (*Grampus griseus*). Similarly, the effects of exploitation discussed for spotted and spinner dolphins may apply to other dolphins as well.

Most management of the exploitation of wildlife populations focuses on numbers and on the evaluation of catch levels relative to the population dynamics of the exploited species. Other aspects of the species' biology are not entirely ignored—for example, spawning aggregations of fish may be fully protected, and hunting may be prohibited during the mating seasons of terrestrial mammals. For the most part, however, behaviour and social systems, per se, are rarely considered in determining how (or if) a wildlife population is to be exploited. There have been many calls in recent years for a change from single-species management to ecosystem-based management where, at a minimum, the ecological consequences of exploitation by humans are considered explicitly. We suggest that a similar shift in thinking may be warranted for managing the exploitation of highly social mammals, such that explicit consideration is given to the consequences of disruption of social systems and behaviour.

This review leaves managers faced with a conundrum. On one hand, in the absence of widespread direct evidence that social and behavioural traits make odontocetes more vulnerable to exploitation, it could be argued that there

is no justification or basis for attempting to incorporate consideration of these traits in the management of odontocete exploitation. On the other hand, the evidence for a lack of recovery by many exploited odontocete species and populations suggests that the exploitation has been poorly managed, and that future management should be more precautionary, whatever the reason might be for the apparent nonresilience of these animals.

Our review suggests a number of plausible mechanisms to explain why social and behavioural traits would cause odontocetes to be less resilient than mysticetes to exploitation. In light of those mechanisms, we believe it would be prudent for managers to consider these traits. As a start, rather than just setting a quota or a maximum allowable take level, more consideration should be given to how the animals are removed from the population, and a goal should be to minimize social disruption. For example, it may be preferable for a hunt to take an entire social group, rather than spread the same number of removals across many social groups, particularly when the hunt itself is highly disruptive of the animals' normal behaviour and activities. Further, it may be necessary to reduce the absolute number of removals to account for the indirect effects of hunts on social mammals, though how to do this in a quantitatively rigorous way is unclear given the lack of good empirical, quantitative data on such effects. Haber [18] suggested that eusocial, cooperative predators, such as wolves and Cape hunting dogs (*Lycaon pictus*), should not be hunted at all because they are so poorly suited to exploitation. According to Haber, many terrestrial mammalian herbivores exhibit behaviour that is better suited to exploitation, as their interactions between individuals and generations are relatively simple. Also, because they have existed as prey throughout their evolutionary histories, such species are used to experiencing the disruptive effects of being hunted and then resuming normal activities once they are safe.

The arguments of Haber [18] might also apply to the highly social odontocetes that appear poorly suited to exploitation. The apparent resilience of mysticetes to

exploitation, at least in comparison to odontocetes, is interesting to contemplate. Mysticetes, like many herbivorous terrestrial mammals, have relatively simple interactions between individuals. Also, mysticetes differ from odontocetes in generally not maintaining long-term social bonds or in not having long periods of dependency after birth. There is little evidence of social bonds in mysticetes other than the relationship between mothers and offspring. These traits, along with their life history, may account for the relatively strong recovery seen in many mysticete populations.

As a final point, we emphasize that our ability to reach firm conclusions regarding the resilience of odontocetes to exploitation are hampered by the shortage of data on population trends. Also, in many cases we lack the necessary information on other, potentially confounding factors, such as hidden mortality (e.g., bycatch) or habitat degradation (e.g., reduced prey populations). Despite the difficulties involved, we stress the importance of monitoring depleted odontocete populations for evidence of recovery, or otherwise, in order to shed further light on the issues raised in this paper.

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## Research Article

# Summary of Reported Whale-Vessel Collisions in Alaskan Waters

Janet L. Neilson,<sup>1</sup> Christine M. Gabriele,<sup>1</sup> Aleria S. Jensen,<sup>2</sup> Kaili Jackson,<sup>2</sup>  
and Janice M. Straley<sup>3</sup>

<sup>1</sup>Division of Resource Management, Glacier Bay National Park and Preserve, P.O. Box 140, Gustavus, AK 99826, USA

<sup>2</sup>Office of Protected Resources, National Marine Fisheries Service, P.O. Box 21668, Juneau, AK 99802, USA

<sup>3</sup>Department of Biology, University of Alaska Southeast Sitka Campus, 1332 Seward Avenue, Sitka, AK 99835, USA

Correspondence should be addressed to Janet L. Neilson, janet\_neilson@nps.gov

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Here we summarize 108 reported whale-vessel collisions in Alaska from 1978–2011, of which 25 are known to have resulted in the whale's death. We found 89 definite and 19 possible/probable strikes based on standard criteria we created for this study. Most strikes involved humpback whales (86%) with six other species documented. Small vessel strikes were most common (<15 m, 60%), but medium (15–79 m, 27%) and large ( $\geq 80$  m, 13%) vessels also struck whales. Among the 25 mortalities, vessel length was known in seven cases (190–294 m) and vessel speed was known in three cases (12–19 kn). In 36 cases, human injury or property damage resulted from the collision, and at least 15 people were thrown into the water. In 15 cases humpback whales struck anchored or drifting vessels, suggesting the whales did not detect the vessels. Documenting collisions in Alaska will remain challenging due to remoteness and resource limitations. For a better understanding of the factors contributing to lethal collisions, we recommend (1) systematic documentation of collisions, including vessel size and speed; (2) greater efforts to necropsy stranded whales; (3) using experienced teams focused on determining cause of death; (4) using standard criteria for validating collision reports, such as those presented in this paper.

## 1. Introduction

Ship strikes are a source of injury and mortality for whales worldwide but documenting these events and their outcomes is a significant challenge. The rate at which whale-vessel collisions occur, the types of vessels involved, and the extent to which they affect particular populations of whales are largely unknown, especially in remote areas such as Alaska. Accurate documentation of whale-vessel collisions is difficult for several reasons, ranging from cases where vessel operators are unaware that collisions should be reported, or operators who do not report for fear of reprisal, to incomplete data gathering on the details surrounding the collision and difficulties inherent in accurately assessing a free-ranging whale's condition following a collision. In addition, a large ship may strike a whale and the crew may be unaware that the collision occurred. Determining that a stranded whale died from a collision is especially difficult in Alaska because of the logistical challenges of performing complete necropsies

(e.g., [1]) on stranded animals. These challenges include the remote location of most carcasses, frequent inclement weather, large tides, concerns for human safety when bears are present, limited daylight at some times of the year, and a lack of personnel trained in identifying ship strike injuries.

An overarching challenge in accurately estimating the rate of ship strikes not only in Alaska, but globally, is that there are no universal, standardized criteria for evaluating eyewitness collision reports or stranded whales to determine which cases represent *bona fide* collisions and which reports should be rejected due to a lack of certainty. Other investigators have compiled accounts of ship strikes regionally and worldwide using variable criteria, terminology, and types of evidence [2–20].

Informed management of whale stocks relies upon accurate estimates of the rate of serious injuries and mortalities from ship strikes. In the United States, the Marine Mammal Protection Act (MMPA) [21] defines a serious injury as any injury that will likely result in mortality. The

National Oceanic and Atmospheric Administration (NOAA) is responsible for marine mammal stock assessment reports for all species of cetaceans and all species of pinnipeds except walrus, including an estimate of the annual human-caused mortality and serious injury of each stock by source (e.g., commercial fishing, ship strike, etc.). Internationally, the International Whaling Commission (IWC) considers the number of mortalities from ship strikes with estimates of fisheries bycatch in developing recommendations for large whale conservation. The need for a standardized quality control system to validate collision reports has been recognized by the IWC Vessel Strike Data Standardization Group (VSDG), which formed in 2005 to examine the issue of ship strikes with cetaceans. Since 2007, the group has been developing a global ship strike database that aims, among other things, to identify the level of uncertainty associated with individual records based on strandings and eyewitness collision accounts [22]. The IWC database classifies collision reports into six categories (definite ship strike, probable ship strike, possible ship strike, not a ship strike, whale initiated collision, and rejected report); however, these categories do not yet have standardized definitions (D. Mattila, pers. comm.). Each report is reviewed by the VSDG, and an incident is only classified as a “definite ship strike” if all members are unanimous.

At the individual level, the MMPA contains a general prohibition on the “take” of marine mammals, defined as “to harass, hunt, capture, or kill, or attempt to harass, hunt, capture, or kill any marine mammal.” NOAA regulations implementing the MMPA further describe the term “take” to include “the negligent or intentional operation of an aircraft or vessel, or the doing of any other negligent or intentional act which results in disturbing or molesting a marine mammal” [23]. In 2001, NOAA implemented regulations in Alaska limiting approaches to humpback whales to minimize disturbance that could adversely affect individual animals and to manage the threat to these animals caused by increasing vessel traffic and a growing whale watch industry in Alaska. These regulations prohibit vessels from approaching within 91 m (100 yards) of a humpback whale and require vessels to operate at a “slow, safe speed” near humpback whales [24]. This speed is not specified beyond the definition for “safe speed” in 33 US Code 2006, “every vessel shall at all times proceed at a safe speed so that she can take proper and effective action to avoid collision and be stopped within a distance appropriate to the prevailing circumstances and conditions.” In addition, since 1979, more protective regulations have existed in Glacier Bay National Park in southeastern Alaska to reduce the risk of humpback whale-vessel collisions and disturbance in park waters. These regulations include limits on the number of vessels allowed to enter Glacier Bay, a 463 m (one-quarter nautical mile) approach limit to humpback whales, and vessel speed and course restrictions in areas where whales are concentrated [25]. For species other than humpback whales, no specific regulations exist in Alaska, although vessel operators are advised to follow a general marine mammal viewing “Code of Conduct” which recommends remaining at least 91 m (100 yards) from marine mammals and avoiding

excessive speeds. These guidelines are intended to prevent mariners from accidentally harassing or injuring whales in violation of the MMPA and US Endangered Species Act (ESA).

Vessel strikes are a significant concern from other perspectives as well. In Alaska, recovering whale populations and increasing vessel traffic are creating a persistent problem. Collisions are costly and dangerous to humans and they can harm mariners’ reputations. From commercial whale watching to subsistence whaling, whales are economically and culturally valuable to Alaska residents and visitors. In addition, one can argue that we have an ethical obligation to address the ship strike issue. For example, in 2007 an injured humpback whale (*Megaptera novaeangliae*) with a grossly inflated tongue and deformed head was observed alive in southeastern Alaska for three days before dying. A necropsy revealed that the probable cause of death was blunt trauma [26]. From an animal welfare perspective, it is our human responsibility to learn how to mitigate our actions—in this case, prevent collisions—such that whales are not subject to extended periods of suffering before dying from ship strike injuries.

Vessel traffic in Alaska overlaps with 14 whale species known to occur in waters around the state: humpback whale<sup>1</sup>, fin whale (*Balaenoptera physalus*)<sup>1</sup>, gray whale (*Eschrichtius robustus*), bowhead whale (*Balaena mysticetus*)<sup>1</sup>, minke whale (*Balaenoptera acutorostrata*), blue whale (*Balaenoptera musculus*)<sup>1</sup>, sei whale (*Balaenoptera borealis*)<sup>1</sup>, North Pacific right whale (*Eubalaena japonica*)<sup>1</sup>, sperm whale (*Physeter macrocephalus*)<sup>1</sup>, beluga whale (*Delphinapterus leucas*)<sup>2</sup>, killer whale (*Orcinus orca*), Cuvier’s beaked whale (*Ziphius cavirostris*), Stejneger’s beaked whale (*Mesoplodon stejnegeri*), and Baird’s beaked whale (*Berardius bairdii*) [27, 28]. Population estimates are not available for most of these species in Alaska waters; however, most of the baleen whale stocks are known or thought to be recovering following the end of commercial whaling in the North Pacific in the 1960s and 1970s. For example, stocks of humpback, fin, bowhead, and gray whales are estimated to be increasing at 3–7% per year [29–32]. A notable exception is the North Pacific right whale, which remains extremely rare with a current population estimate of 31 animals (95% CL 23–54; [33]) and an unknown population trend [28]. The majority of right whale detections have occurred in the southeastern Bering Sea [33], with a smaller number of detections in the Gulf of Alaska south of Kodiak Island [34]. On the other end of the spectrum, a minimum of 12,000 humpback whales are found in high densities in spring through fall in southeastern Alaska, the eastern Aleutian Islands, along the Bering Sea continental shelf edge and break and in the Gulf of Alaska (primarily near the Shumagin Islands, Kodiak Island and from the Barren Islands through Prince William Sound) [28, 31].

The whale strike risk for various vessel types relies on a number of factors, including the number of vessels on the water and their geographic overlap with each whale species. Much of the vessel traffic in Alaskan waters is highly seasonal and concentrated in coastal areas of southeastern and south central Alaska during the summer months, where private

and commercial recreational vessels (e.g., charter vessels, commercial whale watch vessels, tour boats, and cruise ships) are prevalent. Other types of vessel traffic in Alaskan waters are more likely to occur year-round and/or over broader geographic areas, including both near shore and offshore waters (e.g., commercial fishing vessels, freighters/tankers, passenger ferries, etc.), where they may overlap with a variety of near shore and offshore species [28]. In general, there is less vessel traffic off western and northern Alaska compared to other parts of the state, although these trends are already changing with climate change-driven decreases in sea ice in the Bering, Chukchi, and Beaufort seas.

Vessel speed and size appear to be important factors in predicting whale-vessel collisions and their outcomes. For example, the probability of a cruise ship having a close encounter with a humpback whale increases with the speed of the ship (especially at speeds >11.8 kn) [35], and Silber et al. [36] demonstrated that during close encounters, reduced ship speeds may reduce the probability of a collision. Further evidence comes from an analysis of worldwide collision records with large whales, in which Laist et al. [8] found that most lethal and severe injuries involve ships traveling 14 kn or faster and ships 80 m or longer. Likewise, Vanderlaan and Taggart [37] analyzed collision records, modeled the probability of lethal injury to a large whale based on vessel speed, and concluded that the chances of a lethal injury exceed 50% at speeds higher than 11.8 kn.

The summary reported here represents the most comprehensive compilation of whale-vessel collision records in Alaska that has yet been assembled [38, 39]. All records included here were evaluated using our newly developed standardized system for classifying collision records (witnessed at sea or based on strandings) into four confidence categories (definite strike, probable strike, possible strike and rejected report). Our primary goals were to (1) summarize the circumstances surrounding whale-collisions in Alaska, (2) recommend ways to improve data collection and validation, and (3) identify measures to help reduce collision risk.

## 2. Methods

Our study area included all waters of Alaska. We considered records that involved any species of cetacean within 370 km (200 nautical miles) of Alaska except for dolphins and porpoises. Reports of whale-vessel collisions originated from a variety of sources, including NOAA, the US Coast Guard (USCG), vessel owners, tour operators, the media, and anecdotal accounts. These reports were collected opportunistically by the National Park Service (NPS) and the University of Alaska Southeast (UAS) since 1978 and systematically by NOAA since the Alaska Marine Mammal Stranding Network was formed in 1985 [40]. We evaluated records where the whale species was uncertain or unknown on a case-by-case basis. If the species was reported as uncertain but “likely” or “probable” species X and the report was plausible given the seasonal and geographic distribution of species X, then we attributed the report to species X. We counted all other reports where the species was unknown as “unidentified

species.” We rejected reports when there was insufficient information to verify that an actual strike occurred.

To analyze seasonal occurrence in collisions, we assigned a month to each record based on when the strike occurred or the carcass was found. Similarly, we assigned a year to each record based on when the strike occurred or when the carcass was found. We assigned one record from the “late 1980s” to the year 1989. We used linear regression to examine the trend in the number of reports over time and log-linear regression to estimate the average annual rate of increase in reports.

*2.1. Ship Strike Confidence Categories.* The reports were based on (1) collisions witnessed at sea and (2) strandings in which a dead whale was found with evidence of collision injuries. We did not consider reports of whales striking vessels after being shot or harpooned because these collisions are atypical and including them in our analysis would not contribute to our understanding of typical whale-vessel collisions. We error-checked each record against all available documentation and entered the records into a relational database. To avoid potential duplicate reports, we did not include sightings of live whales with visible propeller scars unless the collision that caused the propeller injuries was witnessed. We assigned each record to one of four confidence categories: definite ship strike, probable ship strike, possible ship strike, or rejected report (Table 1).

*2.2. Sex and Age Class of Struck Whales.* We determined the sex of stranded whales from necropsy reports. It was not possible to determine the sex of live animals; however, in two cases, we knew that individually identified humpback whales were female because we had documented them in previous years with calves (NPS and UAS unpublished data). In one case, we knew that an individually identified humpback whale was male based on genetic analysis (NPS and UAS unpublished data).

We assigned the whale in each report to one of the following age classes: calf, juvenile, adult, or unknown. We based most of our assessments on empirical measurements of dead whales’ lengths using guidelines from the scientific literature for each species [41–45]. For humpback whales, we defined calves as <1 year old and juveniles as whales  $\geq 1$  year old but <5 years old [46]. We determined that one dead individually identified humpback whale was an adult based on its  $\geq 5$ -year sighting history (UAS unpublished data). We used the following guidelines to classify dead humpback whales based on body length: calves are typically 4–4.5 m in length at birth [47, 48], grow to 7–8 m in length by late summer [49], attain body lengths of 8–10 m at independence [48], and reach sexual maturity (adulthood) at approximately 12 m in length [50]. We classified an 8.2 m humpback whale that was found dead on March 13, 2005 as a juvenile, even though its length fell within the typical range for calves because it was too big to be a calf based on the date it was found. Also, anisakid nematode parasites were found in the whale’s small intestines, indicating that it was feeding on fish, not milk ([51]; F. Gulland, pers. comm.).

TABLE 1: Ship strike confidence categories.

Confidence category	Definition	
Definite strike	<i>There is evidence that a strike occurred beyond a reasonable doubt. For example:</i> Strike was witnessed by the vessel operator/crew or by the operator/crew of a nearby vessel <i>or</i> Strike was not witnessed but whale has massive blunt impact trauma (defined by disarticulated vertebrae or fractures of one or more heavy bones including skull, mandible, scapula, vertebra or adult rib, and a focal area of severe hemorrhaging) <i>or</i> Strike was not witnessed but carcass has apparent propeller wounds <sup>1</sup> (i.e., deep parallel slashes or cuts into the blubber) on the dorsal aspect <i>or</i> Strike was not witnessed but carcass has propeller wounds on the ventral and/or lateral aspect which a necropsy confirms were produced ante mortem <i>or</i> Strike was not witnessed but carcass has an amputated appendage (e.g., fluke or flipper) which a necropsy confirms occurred ante mortem due to a sudden and traumatic laceration (versus an entanglement injury causing a slow, ischemic loss of the appendage) <i>or</i> Strike was not witnessed but evidence of a collision was found on the vessel (e.g., whale skin or tissue) <i>or</i> Whale was found on the bow of a ship ..... >Subcategory: Whale struck stationary vessel Vessel was stationary at the time of the collision (i.e., anchored or drifting) <sup>2</sup>	
	Probable strike	<i>The report is likely to be true; having more evidence for than against, but some evidence is lacking. For example:</i> Vessel operator/crew or operator/crew of a nearby vessel believes that a strike occurred but cannot confirm the strike with absolute certainty <i>or</i> Strike was not witnessed, and the whale is a calf with smaller broken bones (e.g., ribs) that could have been fractured by another animal rather than by a vessel <i>or</i> Strike was not witnessed and the whale shows partial evidence of a collision other than as defined under definite strike. For example: (i) Whale has a focal area of severe hemorrhaging but no known broken bones; therefore, it is possible the trauma was caused by another animal rather than by a vessel; (ii) Carcass has propeller wounds on the ventral and/or lateral aspect; however, the necropsy is not able to determine if they were produced ante mortem
		Possible strike

TABLE 1: Continued.

Confidence category	Definition
	<i>or</i>
	Strike was not witnessed, and the whale shows partial evidence of a collision other than as defined under definite or probable strike, such as damage to an appendage or skin, but the necropsy is incomplete or there is no close examination of the whale (e.g., whale is viewed from a distance only)
	<i>The report is not credible. For example:</i>
	Third-hand report
	<i>or</i>
Rejected report	No credible eyewitnesses <sup>3</sup>
	<i>or</i>
	Lacking sufficient detail or documentation to be credible
	<i>or</i>
	Necropsy determines an alternate cause of death

<sup>1</sup>We only included whales with propeller wounds where there was evidence that the strike occurred in Alaska (i.e., the propeller wounds had to be from a strike that was witnessed and/or the propeller wounds had to be fresh (bleeding) or assessed to be fresh by a trained observer.)

<sup>2</sup>We counted collisions involving kayaks and canoes under this subcategory unless the kayak/canoe was known to be traveling at >0 kn.

<sup>3</sup>The credibility of the eyewitness(es) was assessed on a case-by-case basis. The most credible eyewitness is someone who had “something to lose” in reporting the collision (e.g., the captain and/or the crew of the vessel that struck the whale) because it is presumed they would not risk reporting the collision if it had not occurred. The least credible eyewitness is a passenger on a commercial vessel (e.g., whale watch vessel, cruise ship, etc.) who reports a collision, but there is no supporting evidence (photos, observation of wound, blood, etc.) or other eyewitnesses. In these cases, the report was rejected unless the passenger was an experienced observer and/or additional eyewitnesses were available to corroborate the report (assessed on a case-by-case basis).

Most observations of live whales were classified as age class unknown; however, we classified two live sightings of humpback whales made by knowledgeable observers as calves based on their close, consistent affiliation with an adult whale, presumed to be the mother (after [52]; J. Neilson, pers. obs.; commercial whale watch captain, pers. obs.). Similarly, we classified one live sighting of a humpback whale as a juvenile based on the animal’s very small body size (J. Neilson, pers. obs.). We determined that three live individually identified humpback whales were adults based on their  $\geq 5$  year sighting histories (NPS, UAS, and Kewalo Basin Marine Mammal Laboratory unpublished data).

**2.3. Vessel Characteristics.** We assigned each report to one of the following vessel categories: private recreational, non-motorized recreational (e.g., kayaks and canoes), commercial recreational (e.g., charter vessels, tour boats, and commercial whale watch vessels), cruise ship, cargo (e.g., oil tankers, container ships, and landing craft), commercial fishing, research, USCG cutter, state ferry, or unknown. After Laist et al. [8], we classified vessel lengths as small (<15 m), medium (15–79 m), large ( $\geq 80$  m), or unknown. We searched the USCG’s Port State Information Exchange (PSIX) online database [53] and commercial vessel operator’s websites to fill in missing vessel lengths when the vessel name was reported.

We evaluated the vessel’s activity *prior to the collision* by assigning each record to one of the following categories: anchored or drifting with engine off, slow travel (<12 kn), fast travel ( $\geq 12$  kn), travel at unknown speed, whale watching, intentionally approaching whales (e.g., whale research), intentionally ramming whales, commercial longline fishing and unknown. Similarly, we evaluated the vessel’s activity

*at the time of the collision* by assigning each record to one of the following categories: anchored or drifting silently, slow travel (<12 kn), fast travel ( $\geq 12$  kn), decelerating from fast travel, decelerating from unknown speed, travel at unknown speed, and unknown. We classified vessel speed at the time of the collision as anchored or drifting, 1–11 kn,  $\geq 12$  kn, or unknown. Separating vessel activity into these two components allowed us to link particular vessel behavior with collision risk and to assess the outcome of the collision with some knowledge of the force with which the whale was struck.

**2.4. Fate of Whales.** We evaluated the fate of the whale after the collision by assigning each report to one of the following categories: minor injury (presumably not life threatening—e.g., no blood reported in water), severe injury (potentially life threatening—e.g., blood reported in water), dead, or unknown. We described dead whales’ injuries as unknown, blunt trauma, or sharp trauma [54, 55].

**2.5. Human Toll and Property Damage from Collisions.** We assessed the human toll and/or property damage resulting from each collision by counting the number of reports in which passengers onboard the vessel were knocked down, injured, or thrown into the water. To avoid double-counting reports, passengers who were knocked down and injured were only counted as injured. However, passengers who were injured and thrown into the water were counted in both categories because we were interested in the frequency of both of these two outcomes. We also counted the number of reports in which there was significant damage to the vessel or the vessel sank. We defined significant damage as that which required repairs for continued use of the vessel.

**2.6. Collision Hotspots.** We used the kernel density analysis tool in ArcGIS 10.0 (ESRI Inc., Redlands, CA, USA) to identify potential high risk areas for whale-vessel collisions in southeastern Alaska. Only collisions that were witnessed at sea were included in the analysis. Dead whales where no collision was reported (including bow-caught whales where the collision was not witnessed), were excluded because the location where they were found may not be the same as the location where they were struck [8]. We set the output raster cell size to be 100 m and the search radius (kernel bandwidth) to be 20 km. For clarity, raster cell values representing extremely low collision densities ( $<0.0025$  collisions per  $\text{km}^2$ ) were excluded from the map. The remaining raster cell values (range 0.0025–0.0211 collisions per  $\text{km}^2$ ) were manually divided into 32 equal classes and displayed in colors ranging from yellow (moderate collision risk) to red (higher collision risk).

### 3. Results

We verified 108 and rejected 11 reports of whale-vessel collisions in Alaska waters between 1978 and 2011. The 11 rejected reports were not included in further analyses. Most strikes ( $n = 93$ , 86%) involved humpback whales, although six other species were documented (Table 2, Appendix 1 in supplementary material) (Supplementary Material will be available online at doi:10.1155/2012/106282). In eight reports (7%) the species was uncertain; however, we assigned seven of these records to humpback whales and one record to a Cuvier's beaked whale. In one report, a pair of humpback whales, thought to be a cow and calf, were involved in a collision but it was unknown which animal was hit; we counted this as one strike, not two, with the sex and age class of the struck whale unknown.

We found a significant increase in the number of reports over time between 1978 and 2011 (regression,  $r^2 = 0.6999$ ,  $df = 32$ ,  $P < 0.001$ ). Most strikes ( $n = 98$ , 91%) occurred in May through September and there were no reports from December or January. The majority of strikes ( $n = 82$ , 76%) were reported in southeastern Alaska (Figure 1), where the number of humpback whale collisions increased 5.8% annually from 1978 to 2011.

Most reports ( $n = 86$ , 80%) were based on collisions witnessed at sea, while the remaining 22 reports (20%) were based on dead whales where no collision was reported. The geographic location of the 22 dead whales and the dates when they were found did not correlate with any of the witnessed collisions; therefore, we do not believe we double-counted any of these reports. Three of the collisions witnessed at sea are known to have resulted in mortalities, for a total of 25 dead whales.

**3.1. Ship Strike Confidence Categories.** The majority of reports ( $n = 89$ , 82%) were assessed to be definite strikes and in 15 (17%) of these cases, a whale struck a stationary vessel. Seventy-nine (89%) of the 89 definite strikes were based on witnessed collisions, and 10 reports (11%) were based on dead whales where no collision was reported. Two (22%) of the nine probable strikes were based on witnessed collisions,

and seven reports (78%) were based on dead whales where no collision was reported. Five (50%) of the 10 possible strikes were based on witnessed collisions, and five reports (50%) were based on dead whales where no collision was reported.

Two of the nine probable strikes were thoroughly investigated, but seven reports were not and may have been upgraded to definite strikes with more complete follow-up (e.g., complete necropsies). In one of the two probable strikes that were witnessed, a dead humpback whale washed ashore within 3 km of where a 190 m cruise ship transiting at an unknown speed reported striking what they believed to be a whale three days earlier; however, there was no close examination of the whale [56]. Similarly, three of the 10 possible strikes were thoroughly investigated, but seven reports were not and may have been upgraded to definite strikes with more complete follow-up. For example, two of the vessel operators involved in witnessed collisions were not interviewed, and four of the five dead whales were not necropsied or examined closely. The fifth dead whale was necropsied; however, the necropsy did not get down to bone to look for fractures diagnostic of a collision.

**3.2. Sex and Age Class of Struck Whales.** Nine of the 25 dead whales were female, nine were male, and seven were of unknown sex (Table 3). In addition, we documented three live individually identified humpback whales (two females and one male) for a total, of 21 whales of known sex (10 males and 11 females).

There were 25 whales of known age involved in collisions: seven calves, seven juveniles, and 11 adults. Five dead whales were calves, six were juveniles, eight were adults, and six were of unknown age (Table 3). In addition, six humpback whales in witnessed collisions were assigned to age classes (two calves, one juvenile, and three adults). Six adult female humpback whales are known to have died from collisions and four of these mortalities occurred in southeastern Alaska between 2001 and 2011.

### 3.3. Vessel Characteristics

**3.3.1. Vessel Type.** In 19 cases, the type of vessel involved in the collision was unknown (18 were dead whales where no collision was reported, but one was a witnessed collision where the type of vessel was not recorded.) In the 89 cases where the vessel type was known, 35% ( $n = 31$ ) were private recreational, 35% ( $n = 31$ ) were commercial recreational, 8% ( $n = 7$ ) were cruise ships, 7% ( $n = 6$ ) were commercial fishing vessels, 4% ( $n = 4$ ) were USCG cutters, 3% ( $n = 3$ ) were cargo, 3% ( $n = 3$ ) were nonmotorized recreational, 3% ( $n = 3$ ) were research, and 1% ( $n = 1$ ) was a state ferry. The three cargo vessels were a 254-m oil tanker, a 216-m container ship, and a 10-m landing craft. The seven cases where the vessel type was known and the whale died involved large cruise ships ( $n = 5$ ) or cargo vessels ( $n = 2$ ; one container ship and one oil tanker). All three non-motorized recreational vessel strikes occurred in Glacier Bay.

**3.3.2. Vessel Length.** In 44 reports (41%) vessel length was not reported; however, in 18 of these cases we were able to

TABLE 2: Summary of whale-vessel collisions reported in Alaska 1978–2011. Rejected reports are not included.

Species	Confidence category			Total	Number of known dead
	Definite strike	Probable strike	Possible strike		
Humpback whale	78	8	7	93 (86.1%)	17
Fin whale	3			3 (2.8%)	2
Gray whale	1			1 (0.9%)	1
Sperm whale	1			1 (0.9%)	
Cuvier’s beaked whale		1	1	2 (1.9%)	2
Stejneger’s beaked whale			1	1 (0.9%)	1
Beluga whale			1	1 (0.9%)	1
Unidentified whale	6			6 (5.6%)	1
<b>Total</b>	<b>89 (82.4%)</b>	<b>9 (8.3%)</b>	<b>10 (9.3%)</b>	<b>108 (100%)</b>	<b>25</b>

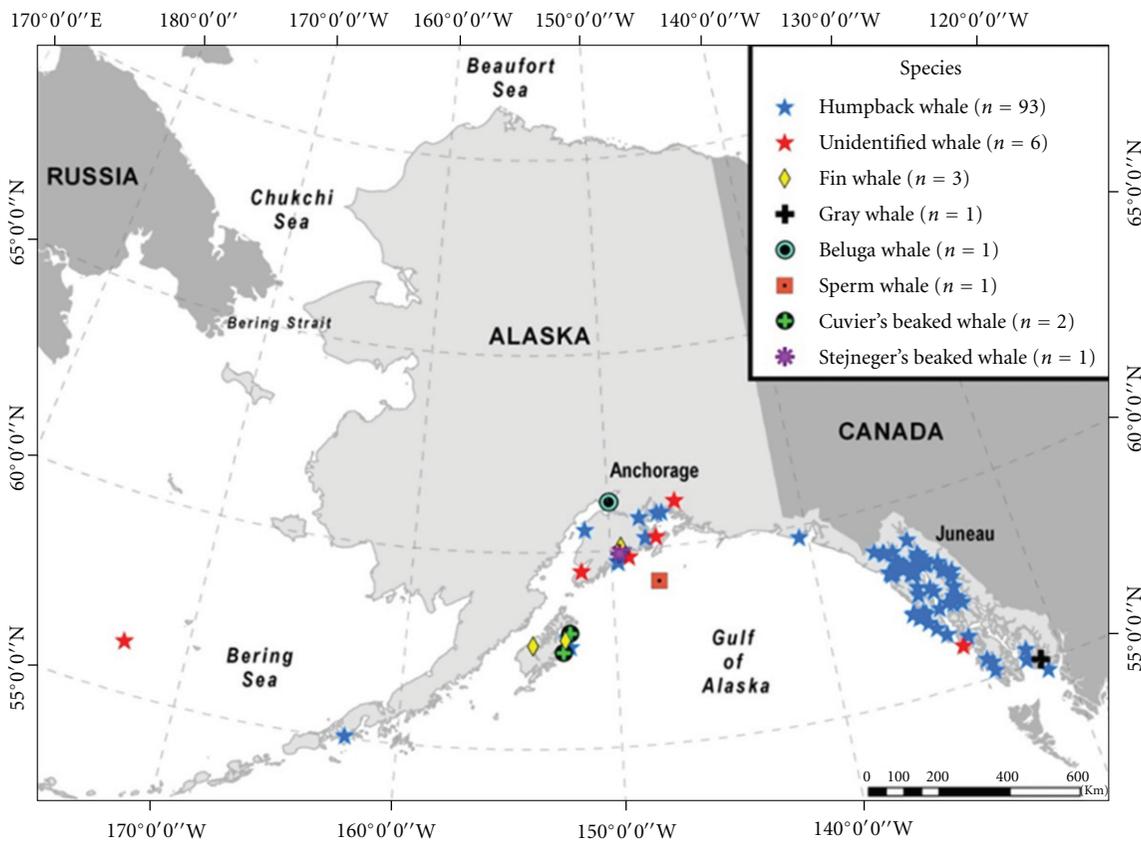


FIGURE 1: Location of whale-vessel collision reports in Alaska by species 1978–2011 ( $n = 108$ ). Rejected reports are not included.

infer the vessel’s length category based on the vessel type ( $n = 4$ , e.g., kayak and Zodiac) or look up the vessel length online using the vessel’s name ( $n = 14$ ). This left 26 reports where vessel length was unknown. Eighteen of these cases were dead whales where no collision was reported; however, eight were witnessed collisions, of which five were reported to and/or investigated by federal law enforcement officials.

In the 82 reports where vessel length was known (range 5–294 m), small (<15 m) vessels were the most commonly reported ( $n = 49$ , 60%), followed by medium (15–79 m) vessels ( $n = 22$ , 27%), and large ( $\geq 80$  m) vessels ( $n = 11$ , 13%). The difference in the number of reports in each vessel length category is significant (chi-square test for goodness of fit,  $\chi^2 = 27.976$ ,  $df = 2$ ,  $P < 0.001$ ).

TABLE 3: Sex and age classes of the 25 whales known to have been killed by vessels.

Species	Male			Female			Sex unknown		Total
	Calf	Juvenile	Adult	Calf	Juvenile	Adult	Adult	Age class unknown	
Humpback whale	4	2	1	1		6		3	17
Fin whale		1			1				2
Gray whale					1				1
Sperm whale									
Cuvier's beaked whale		1						1	2
Stejneger's beaked whale							1		1
Beluga whale								1	1
Unidentified whale								1	1
Total	4	4	1	1	2	6	1	6	25

**3.3.3. Vessel Activity Prior to Collision.** In 18 reports (17%) the vessel's activity prior to the collision was unknown or not reported. In the 90 reports where the vessel's activity was known, 44% ( $n = 40$ ) were engaged in fast travel, 16% ( $n = 14$ ) were anchored or drifting silently, 14% ( $n = 13$ ) were engaged in slow travel, 12% ( $n = 11$ ) were traveling at an unknown speed, 7% ( $n = 6$ ) were whale watching, 3% ( $n = 3$ ) were intentionally approaching whales, 2% ( $n = 2$ ) were intentionally ramming whales, and 1% ( $n = 1$ ) were commercial fishing. Note that whale watching vessels that were traveling prior to the collision were classified under one of the traveling vessel activity categories. The difference in the number of reports in each vessel activity category is significant (chi-square test for goodness of fit,  $\chi^2 = 99.867$ ,  $df = 7$ ,  $P < 0.001$ ).

**3.3.4. Vessel Activity at Time of Collision.** In 19 reports (18%) the vessel's activity at the time of the collision was unknown or not reported. In the 89 reports where the vessel's activity was known, 33 (37%) were engaged in fast travel, 19 (21%) were engaged in slow travel, 15 (17%) were anchored or drifting silently, 12 (13%) were traveling at an unknown speed, 9 (10%) were decelerating from fast travel, and one (1%) was decelerating from slow travel. The 10 vessels that reported decelerating did so in response to seeing the whale just prior to the collision, thus in some cases, their speed at the time of the collision (below) is lower (i.e., 1–11 kn versus  $\geq 12$  kn). The difference in the number of reports in each vessel activity category is significant (chi-square test for goodness of fit,  $\chi^2 = 39.157$ ,  $df = 5$ ,  $P < 0.001$ ). All 15 of the cases where a whale struck a stationary vessel involved humpback whales hitting vessels that were anchored or drifting with their engine off.

**3.3.5. Vessel Speed at Time of Collision.** In 47 reports (44%) vessel speed at the time of the collision was unknown or not reported; however, in 14 of these cases we were able to infer the vessel's speed based on other information in the report (e.g., "sailboat under power" was classified as 1–11 kn). This resulted in 75 reports (69%) where vessel speed was known (range 0–35 kn), with vessels, traveling at  $\geq 12$  kn the most commonly reported ( $n = 37$ , 49%), followed by vessels traveling at 1–11 kn ( $n = 23$ , 31%), and anchored or

drifting vessels ( $n = 15$ , 20%). The difference in the number of reports in each vessel speed category is significant (chi-square test for goodness of fit,  $\chi^2 = 9.92$ ,  $df = 2$ ,  $P < 0.05$ ).

Twenty-two of the 33 cases (67%) where vessel speed was unknown were dead whales where no collision was reported; however, 11 (33%) were witnessed collisions in which speed was not recorded. The maximum speed reported (35 kn) was a 10 m jet boat whose operator intentionally rammed a pair of humpback whales thought to be a cow and calf [57].

**3.4. Fate of Whales.** In most cases ( $n = 78$ , 72%), the fate of the whale following the collision was unknown, but 25 cases (23%) were known mortalities, and in five cases (5%) the whale was documented alive in subsequent months or years using individual identification techniques (NPS and UAS unpublished data).

**3.4.1. Minor Injuries.** In 11 cases (10%) the whale was observed with either a presumably minor injury or no visible injuries (all were humpback whales). Five of these whales are known to have survived; however, the fate of the other six whales is unknown. The five surviving whales (one calf, three adults, and one age unknown) were hit by vessels  $< 20$  m in length (range 7–19.8 m) traveling at 5 kn ( $n = 1$ ), 10 kn ( $n = 2$ ), 25 kn ( $n = 1$ ), and an unknown speed ( $n = 1$ ). The latter vessel was whale watching and was therefore likely traveling at 1–11 kn. Three of the whales had blunt trauma injuries after being struck by the bows of vessels and two had sharp trauma injuries from propellers. The collision that occurred at 25 kn was reported in 2008 by the captain of a 10 m aluminium tour boat after he struck a humpback whale as the whale came up to breathe [58]. The captain believed that the whale he hit was an individual with a uniquely marked dorsal fin that was well known to tour boat captains in the area. The speed of the vessel decreased approximately 3–4 kn after the strike, and he did not see the whale come up again, but it is unknown how long the vessel stayed on scene. Later that day, this uniquely marked adult whale was documented behaving normally and lunge feeding nearby (NOAA unpublished data), and it was observed as recently as 2011 with no visible injuries (NPS unpublished data). The calf that was struck was documented alive with its mother 75 days after being hit by an 18 m commercial fishing vessel

transiting at 10 kn (NOAA unpublished data). The other three whales that are known to have survived have been documented for a minimum of six years post-collision (NPS unpublished data).

**3.4.2. Severe Injuries.** In five cases (5%) the whale was observed after the collision with a severe injury (three humpback whales and two unidentified large whales); however, the fate of these whales is unknown. In four of these cases, blood was reported in the water. Three of these whales had sharp trauma injuries from propellers, while the type of injury sustained by the fourth whale was unknown. In the fifth case, a humpback whale punched a 1.5 m hole through the hull of an anchored 22 m wooden sailboat, sinking the vessel and leaving six plates of baleen measuring approximately 0.3 m in length held together by torn flesh inside the splintered hull.

**3.4.3. Mortalities.** In 25 cases (23%) the whale is known to have died, but vessel length and speed were known in only three of these cases. Two of the 86 collisions witnessed at sea that are known to have caused mortalities (both were adult humpback whales) involved 232 m and 243 m cruise ships traveling 14 kn and 19 kn, respectively. In a third case, a dead humpback whale was found on the bow of a 216 m container ship, and the vessel's speed at the time of the collision is unknown; however, its typical transit speed was 12–19 kn. Statewide, humpback whale vessel-strike mortalities peaked in 2010 ( $n = 4$ ) and we found an increasing trend in the number of humpback whales killed between 1978 and 2011 (regression,  $r^2 = 0.1193$ ,  $df = 32$ ,  $P < 0.05$ ).

Thirteen (52%) of the 25 dead whales were first reported floating; five were towed to shore for examination, five are known to have washed ashore on their own, and three were not towed and floated away. Seven (28%) of the dead whales were first reported beach-cast. Five of the dead whales (20%) were caught on the bulbous bows of large ships (three humpback whales, one fin whale and one unidentified large baleen whale in 2009 that appeared to be a fin, blue, or sei whale). One of the humpback whales slipped off a 243 m cruise ship's bow and sank when the ship slowed down, the other four bow-caught whales remained pinned to the ships' bows (288 m cruise ship, 294 m cruise ship, 254 m oil tanker, and 216 m container ship) until they came into port or stopped. The state of decomposition and point of collision impact on two of the whales is unknown. However, the fin whale and two of the humpback whale carcasses were fresh (not bloated) and appeared to have been struck on the dorsal side of their bodies, indicating that the whales were alive when they were hit [9, 54]. This is inferred because most large whales (except right and bowhead whales) sink when they die and then rise to the surface, ventral side up, as decomposition gases inflate the abdomen (assuming the abdominal cavity is intact and the carcass is in relatively shallow water) [18, 59, 60]. Depending on blubber thickness, some whales may float immediately upon death; in these cases, they typically will float ventral side up within approximately 24 hours as decomposition gases inflate the abdomen (F. Gulland, pers. comm.). Therefore, collision injuries on the dorsal side of a

TABLE 4: Types of injuries sustained by the 25 whales known to have been killed by vessels.

Species	Blunt trauma	Sharp trauma	Unknown injuries
Humpback whale	12	2	3
Fin whale	2		
Cuvier's beaked whale	1	1	
Stejneger's beaked whale	1		
Gray whale		1	
Beluga whale		1	
Unidentified whale			1
Total	16 (64%)	5 (20%)	4 (16%)

whale provide indirect evidence that the whale was alive (or extremely recently dead) when it was struck, otherwise the point of collision impact would be expected on the whale's ventral or lateral side ([54], F. Gulland, pers. comm.).

The first whale necropsy conducted in Alaska with a veterinarian trained in assessing ship strike injuries occurred in 2001. Since then, numerous veterinarians, stranding team members and other personnel have gained experience in assessing ship strike injuries and 13 more necropsies have found evidence that whales died from collisions. However, six of these necropsies were incomplete, meaning that the carcass was not flensed down to the bone to look for fractures. In several cases, the necropsy team ran out of time as the incoming tide covered the carcass. Overall, 11 humpback whales, two fin whales, and one Cuvier's beaked whale with ship strike injuries have been necropsied since 2001.

Most of the 25 dead whales ( $n = 16$ , 64%) had blunt trauma injuries, five (20%) had sharp trauma injuries, and four (16%) had unknown injuries because they were not necropsied (Table 4); however, at least three (two humpback whales and one unidentified large baleen whale that appeared to be a fin, blue, or sei whale) likely suffered from blunt trauma because they were found pinned to ships' bows. The fourth whale stranded in 1978 after a cruise ship reported striking what they believed to be a whale; however, there was no close examination of this humpback whale, and it is unknown if the ship's bow or propeller(s) struck the whale.

The necropsy of an adult female humpback whale found on the bow of a 288 m cruise ship in 2010 revealed a potentially complicated history [61]. A necropsy was conducted, and both gross and internal assessments of the carcass were made; however, the necropsy was limited by an incoming tide. Though it was not possible to strip the carcass entirely to the bone, the animal was found to have a sharp trauma injury (amputated pectoral flipper cut cleanly at 0.8 m in diameter), acute degenerative myopathy in several muscle tissues (indicating severe ante mortem stress and muscle exertion), and a large area of missing inframandibular tissue, indicating that the whale may have been fed on by killer whales. Elevated saxitoxin levels were also detected, which could have caused the whale to behave abnormally, making it more vulnerable to being struck. It has been proposed

that the whale may have been struck initially by a different large vessel, shearing off the pectoral fin and causing debility and/or death, followed by possible predation by killer whales, and eventual postmortem entrapment on the bow of the cruise ship. However, in initial photos of the carcass on the ship's bow, the whale does not appear to be bloated and the point of collision impact is on the dorsal thorax, indicating that the whale may have been alive when it was struck. We include the details of this particular report to illustrate the complexities involved in piecing together case histories and determining cause of death.

**3.5. Human Toll and Property Damage from Collisions.** In 37 reports (34%) the passengers and vessel were not affected by the collision, in 36 reports (33%) there was some kind of human toll and/or property damage resulting from the collision, and in 35 reports (32%) the outcome of the collision for the passengers and vessel is unknown. There were 19 reports in which passengers were knocked down (affecting a minimum of 41 people), 10 reports in which passengers were injured (affecting a minimum of 18 people), 9 reports in which passengers were thrown into the water (affecting a minimum of 15 people), 20 reports of significant property damage, and three reports of private recreational vessels sinking. Two of the vessels that sank (a 10 m fiberglass sailboat and a 22 m wooden sailboat) were anchored or drifting with their engine off when they were rammed by humpback whales. The third case involved a 8 m polyethylene powerboat that sank after striking an unidentified large whale while transiting at 19 kn.

**3.6. Collision Hotspots.** We identified several high risk areas for whale-vessel collisions in southeastern Alaska (Figure 2). All of the high risk areas were located in the northern portion of southeastern Alaska. The areas with the highest collision densities centered around Point Adolphus in Icy Strait and around North Pass in lower Lynn Canal, both popular whale watching destinations. Medium-risk areas centered around the Inian Islands in Cross Sound and in Sitka Sound. Other areas where we identified a collision risk included eastern Icy Strait near Hoonah, the lower West Arm of Glacier Bay, upper Stephens Passage, and eastern Frederick Sound.

## 4. Discussion

The great majority of ship strikes in Alaska occur with humpback whales in southeastern Alaska. This area is primarily comprised of protected waters and supports a genetically distinct feeding aggregation of 3,000–5,000 humpback whales [31]. The number of humpback whale collisions detected in this region increased by 5.8% annually from 1978 to 2011, which closely matches the 6.8% annual growth rate of the humpback whale population in southeastern Alaska between 1986 and 2008 [62]. Although the problem at present may not be resulting in population level impacts, a collision with a large whale is considered a “take” under the MMPA and is therefore a cause for concern, as are other considerations such as human safety. Our results showing

an increase over time in whale and vessel collisions are susceptible to several biases inherent in the dataset, yet we believe that this conclusion is valid based on the seasonal overlap of high densities of humpback whales and vessels and an increasing whale population trend in southeastern Alaska.

**4.1. Reporting Biases.** Although we attempted to capture all whale-vessel collisions throughout Alaska, the number we report here represents a minimum level of occurrence due to under-reporting of witnessed collisions and the significant challenges involved in investigating cause of death in whale mortalities in a large and remote state. We know that under-reporting of witnessed collisions occurs; for example, a survey of recreational boaters in southeastern Alaska documented that at least three out of four whale-vessel collisions in this region were not reported (J. Straley, pers. comm.), and similar rates of under-reporting have been found among professional mariners in Hawaii [63]. This lack of reporting could be due to fear of possible repercussions or simple ignorance that collisions should be reported to NOAA. In 2009, NOAA implemented a toll-free Marine Mammal Stranding Hotline in Alaska, which increased public awareness about the existence of a stranding network and the agency's interest in collecting ship strike information and may have led to an increase in reports in recent years. One only has to engage in casual conversation with nearly any Alaskan boater to hear anecdotal stories of whale strikes that happened to them or someone they know. Most of these reports lack so many critical details such as vessel speed, location, and the fate of whale that although they would contribute to a better understanding of the true frequency of whale-vessel collisions, they might not advance our knowledge of the specific factors leading to collisions or their outcomes.

We documented collisions with seven of the 14 whale species known to occur in Alaska, with 86% of the reports involving humpback whales and none involving bowhead, minke, blue, sei, North Pacific right, Baird's beaked, or killer whales. We recognize that the records compiled here may be biased towards humpback whales because the authors are based in southeastern Alaska; however, the overwhelming number of live and dead reports involving humpback whales indicates that they are the most heavily impacted species, at least in terms of absolute numbers. The seasonal trend in collisions, with 91% of reports occurring in May through September, is not surprising because these are the months when humpback whales, which migrate in winter to lower latitudes, are most common in Alaska. The number of humpback whales that are known to have died from collisions in Alaska ( $n = 17$ ) is much higher than in Washington from 1980–2006 ( $n = 1$ ) [18] or British Columbia from 1995–2007 ( $n = 0$ ) [64], despite both areas being important summer habitat for this species. The reason for this difference is unknown, but Douglas et al. [18] were surprised by the virtual absence of dead ship-struck humpback whales in Washington.

When a dead whale is reported in Alaska, there are limited resources and personnel to respond and conduct a

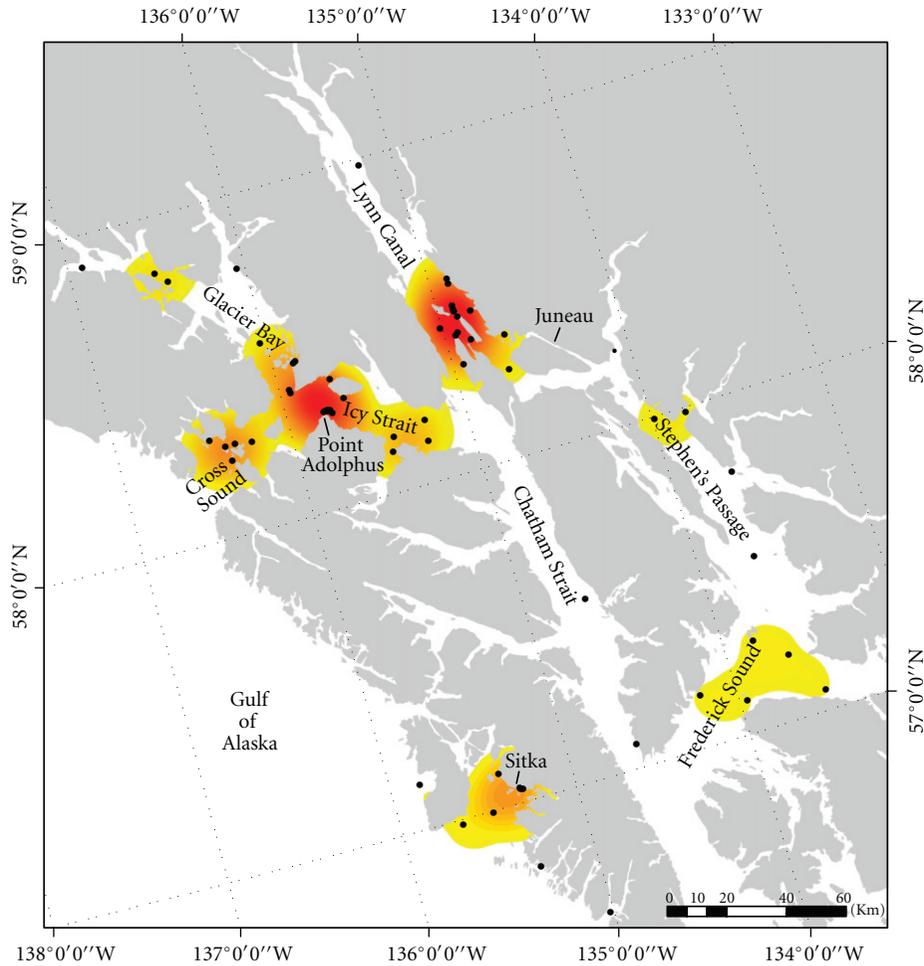


FIGURE 2: Whale-vessel collision hotspots in southeastern Alaska based on kernel density estimation. Yellow indicates moderate collision risk and red indicates higher collision risk. The locations of the collision reports used to create the map are displayed.

necropsy. Whether a necropsy is pursued or not depends on a variety of factors, including the condition of the carcass (ranging from fresh to skeletal), location and accessibility, safety, weather, available expertise, and whether the carcass is secured (such that it will not be washed away by the tide before a team can respond). Priority may be given to species listed under the ESA, species which are rarely encountered or for which little data exists (i.e., beaked whales), or incidents where there is a likelihood of human interaction (e.g., suspected ship strike, entanglement, shooting, etc.).

We were surprised to find so few collisions with fin whales ( $n = 3$ ) given their abundance and widespread distribution in many parts of Alaska [28], especially compared to other studies, which have found them to be the most common species struck by vessels [8, 9, 18]. One reason so few fin whale collisions were observed is that fin whales are rare in the inside waters of southeastern Alaska frequented by vessels and occur more commonly offshore where a dead whale is less likely to be noticed. Collisions with gray whales ( $n = 1$ ), sperm whales ( $n = 1$ ), and killer whales ( $n = 0$ ) were also rare compared to trends documented elsewhere [8, 18, 64].

Although vessel collisions with beaked whales have been documented in other areas [15, 17, 65], we were surprised to find three fatal strikes involving two Cuvier's beaked whales and one Stejneger's beaked whale because these species are observed rarely and typically inhabit offshore waters [27, 28].

We acknowledge several geographic biases in the records we compiled. The records are likely biased towards southeastern Alaska and there is a statewide bias towards human population centers (e.g., Juneau, Anchorage, Seward, and Kodiak) where there are more observers on the water. However, this goes hand-in-hand with more vessels on the water, so these areas probably do have a higher collision risk. Our dataset, like other ship strike datasets [9], is biased towards species that inhabit near shore waters, such as humpback whales, because carcasses of near shore species are more likely to be found (and subsequently examined) compared to offshore species. Furthermore, carcasses reported floating far offshore are unlikely candidates for towing to shore for necropsies given the long distances involved. In addition, whales that die offshore in water depths greater than 1,000 m may not float to the surface because the hydrostatic pressure at these

depths limits the generation of buoyant decomposition gases [60]. There is generally more vessel traffic in near shore areas compared to offshore areas, which likely puts near shore species at a higher risk for collisions. We propose that a better understanding of the geographic extent of ship strikes in Alaska could be obtained by an effort to actively solicit information about past events from resource managers, law enforcement officers, the media, and the maritime community throughout the state. Maintaining NOAA's current focus on systematic data collection about ship strikes as they occur will also help facilitate equal representation of all parts of Alaska.

*4.2. Ship Strike Confidence Categories.* We recommend that the standardized system we developed to classify collision records into four confidence categories (definite strike, probable strike, possible strike, and rejected report), or a similar detailed system, be universally adopted to reduce uncertainty in interpreting ship strike data. Other investigators have employed similar tiered classification systems for dead whales with evidence of ship strike injuries (e.g., [10, 13, 15, 16, 18]); however, our definitions contain a higher level of detail which we feel makes our approach more useful as a classification tool. Also, unlike other classification systems, ours includes criteria for classifying eyewitness collision reports. We recognize that our definitions err on the side of classifying strikes as definite when it is possible that some of these collisions occurred postmortem; however, we surmise that postmortem strikes of large whales are unlikely and consequently rare, given that floating carcasses are, in most cases, significantly bloated and therefore highly visible to the naked eye and radar ([15]; F. Gulland, pers. comm.). To rule out misclassifying postmortem collisions, we recommend that whenever possible, samples from stranded whales be collected and analyzed using histochemical techniques that can detect fat emboli diagnostic of ante mortem bone fractures and severe soft-tissue damage [66, 67].

We acknowledge that including possible and probable strikes in our analyses positively biased the number of ship strike records; however, like Van Waerebeek et al. [15], we chose to include these reports in our analysis because (a) we are trying to quantify a problem that we know is under-reported and (b) we feel that the confidence codes are generally conservative, meaning that the majority of the probable and possible strikes are likely to have been genuine collisions but incomplete followup and/or necropsies precluded classifying many of them as definite strikes.

Along with a standardized system to evaluate the level of certainty associated with individual collision reports, we also recommend that a universal standardized reporting form for collisions witnessed at sea would improve the quality of ship strike data by reducing the number of reports lacking key information such as vessel size and speed at the time of the collision. An outreach campaign to the public and to the resource protection agency personnel likely to respond to reported collisions will help ensure systematic reporting of the salient details of collisions. Currently, the

NOAA National Marine Mammal Stranding Database does not accept ship strike records, thus recording and cataloguing methods vary among NOAA regions across the country. Regions typically record collision reports on a general marine mammal stranding reporting form rather than using a specialized ship strike reporting form that prompts for key details. The latter approach is needed both nationally and internationally to ensure more systematic documentation of collisions and their outcomes.

*4.3. Sex and Age Class of Struck Whales.* We did not detect any difference in the collision risk for male versus female whales, but did find that calves and juveniles appear to be at higher risk of collisions than adult whales, which is consistent with other studies [3, 7, 8, 13, 14, 17, 18]. Our age class data are biased towards dead whales; therefore, it is unknown if young animals are overall more likely than adults to be struck (based on differences in their behavior, sightability, or other factors). It is also plausible that young animals are more likely to die from collisions because of their smaller body size.

*4.4. Vessel Characteristics.* All types and sizes of vessels collided with whales; however, small (<15 m) recreational vessels were the most common. This result contrasts with other studies that have concluded that small vessels are less likely than larger vessels to strike whales [8]. We found more private recreational vessel strikes and fewer commercial recreational vessel strikes than in Hawaii, where the majority of recorded collisions with humpback whales involved commercial whale watch vessels [14], but this result might be biased by different numbers of private versus commercial whale watch vessels in the two areas. The number of large vessels that we documented is presumably an underestimate because compared to smaller vessels, the crews of large vessels may be less likely to see collisions when they occur due to limited visibility around their bows, and the impact of a collision is less likely to be felt in larger vessels [8]. Undetected collisions with large vessels presumably account for some of the 22 cases where dead whales were found but no collision was reported. Alternatively, these collisions may have been witnessed but not reported. We recognize that the majority of records were based on witnessed collisions and that our conclusions regarding the types of vessels that hit whales are likely to be biased by different reporting and detection rates between vessel types. For example, some user groups may be more wary of reporting collisions to federal officials, and overall some user groups are more aware than others that collisions should be reported. For instance, in recent years, there has been a high level of awareness in the Alaska cruise ship industry about whale collision avoidance and reporting, but other user groups may not be as aware of the issue, leading to under-reporting.

It is notable that all 15 stationary vessels that were struck by humpback whales were drifting with their engine off or anchored. This suggests that the whales did not detect the vessels and that being in a silent vessel may increase the risk of a collision. Further evidence comes from a study of sailing vessel collisions with cetaceans, which found that 79%

of collisions occurred when the vessels were under sail, as opposed to motoring [19]. Many boaters erroneously assume that whales are aware of their presence and location at all times. Increasing public outreach and education programs that emphasize that sperm whales are the only large whale species that uses echolocation could be beneficial in reducing collision risk.

**4.5. Fate of Whales.** Our data support previous findings that collisions are more likely to be lethal when they involve large ships and higher vessel speeds [8, 37]. In the three mortalities where both vessel length and speed were known, the ships ranged from 216–243 m in length and were traveling 12–19 kn. Four other mortalities involved 190–294 m ships traveling at unknown speeds. In addition to these seven mortalities, there were eight more dead whales whose massive injuries (e.g., fractured skulls) indicate that they were likely struck by large ships in collisions that were either not detected or witnessed but not reported. Conversely, four of the five cases in which struck humpback whales were known to have survived provide evidence that collisions with smaller, slower moving vessels are less likely to inflict serious or fatal injuries [8, 37]. We know of at least 23 other humpback whales in southeastern Alaska that have survived collisions based on live sightings of 15 different whales with healed propeller wounds and eight whales with deep gashes and other wounds that appear to be from vessel collisions (NPS, UAS, NOAA, and Alaska Whale Foundation unpublished data). The vessel types, sizes, and speeds involved in these nonfatal collisions are unknown, but all of the propeller wounds appear to be from relatively small vessels based on the size and close spacing of the propeller scars.

The majority (80%) of the collision records were based on strikes witnessed at sea, with the fate of the whale unknown in most (72%) cases. However, over half (49%) of the witnessed collisions occurred at vessel speeds  $\geq 12$  kn, and therefore some of these collisions may have been fatal, though the smaller size of most of the vessels presumably means that lethal collisions were less likely [8, 37]. We found that vessel operators are often exceeding a “slow, safe speed” near humpback whales as required in Alaska [24] and that overall, vessels engaged in fast travel are at a greater risk of striking a whale. In the majority of cases, the collisions were accidental, with little or no time for evasive action. In a few cases ( $n = 10$ ), vessel operators reported decelerating just prior to hitting the whale.

**4.5.1. Mortalities.** We found blunt trauma injuries (e.g., broken bones and a focal area of hemorrhaging) to be more than three times as common as sharp trauma injuries (e.g., propeller wounds) in whales that died from ship strikes in Alaska, whereas propeller injuries dominate among dead ship struck right whales along the US Atlantic and South African coasts [8] and gray whales in Washington [18]. Blunt trauma injuries were prevalent in ship struck balaenopterids examined in Washington [18] and in ship struck fin, blue, and sei whales along the US Atlantic and French coasts

[8]. Models indicate that whales at the water’s surface are more likely to be hit by the bows of ships than whales submerged near the surface, which are more likely to suffer propeller strikes [36]. The majority (12 of 16) of the blunt trauma injuries in our sample were sustained by humpback whales. Humpback whales in Alaska typically make short, shallow dives [68] and spend a relatively high proportion of their time feeding, socializing, and resting at the surface (NPS unpublished data). This behavior pattern may make humpbacks more susceptible to bow strikes than propeller strikes, explaining why we found more blunt trauma injuries than sharp trauma injuries. In contrast, North Atlantic right whales spend the majority of their time submerged 0.5–2.5 m below the water’s surface, which may explain why vessel collisions in general, and propeller injuries in particular, are so common in this species [69]. Douglas et al. [18] proposed two other possible explanations for the greater percentage of blunt traumas found in some species: (1) deep propeller wounds may open the body cavity and make the whale more likely to sink and not be recovered; (2) bow-caught whales (i.e., blunt trauma cases) are more likely to be transported to coastal waters where they can be recovered and examined. Both of these hypotheses may apply to our observations, but neither fully explains our findings. Note that in our dataset, 15 of the 16 whales with blunt trauma injuries were found floating or beach-cast, not bow-caught. However, some of these whales may have been bow-caught originally but then slipped off after the ships slowed down or stopped. Ships displacing 1600 or more gross tons are required to test their forward/astern propulsion within 12 hours of entering or getting underway in US waters [70], which could increase the chances of a bow-caught whale slipping off before it is detected.

A total of five dead whales were reported caught on the bulbous bows of large ships (three humpback whales, one fin whale, and one unidentified large baleen whale that appeared to be a fin, blue, or sei whale). Previously, stocky whale species such as humpback whales were not thought to be susceptible to being pinned to the bows of ships compared to longer, sleeker rorquals such as fin whales [8]. This conclusion was based on a single known case from Alaska of a humpback whale draped over a cruise ship’s bulbous bow, and this whale slipped off the bow and sank when the ship slowed down [8, 71]. A second case, reported to have occurred in Alaska in 2006 and cited by Van Waerebeek et al. [15], was misidentified in the media as a bow-caught humpback whale, but this was actually a fin whale [72]. In addition to the single bow-caught humpback whale case already reported in Laist et al. [8], we documented two new verified cases in which humpback whales were caught on the bows of ships. In both cases, the whales did not slip off when the ships stopped; in fact, in one case, it was difficult to dislodge the whale from the bow [61].

The 25 whales that we concluded had died from ship strikes from 1978–2011 represent the minimal number of whale mortalities from ship strikes in Alaska during this time period. Over the same time span, 516 large whales (i.e., baleen whales and sperm whales) were reported dead in Alaska (NOAA Alaska Region Stranding Database

unpublished data). Thirty-two (6%) of these carcasses were necropsied, with 13 of the whales classified as ship strikes in this study. Excluding two bow-caught whales (because they are not representative of the typical floating or beach-cast dead whale), 37% (11 of 30) of the large whales necropsied in Alaska since 1978 have died from ship strikes. Similar high rates of ship strike mortalities have been found along the U.S. East Coast in some whale species (e.g., one-third of stranded northern right whales and fin whales) [8]. It is unknown how many more dead sank whales in Alaska were scavenged, floated offshore, and/or sunk without being located, but considering the remoteness of the state's coastline and offshore areas, 516 dead whales presumably represents a small fraction of the true number of dead whales over this 34-year period. Studies in the Gulf of Mexico suggest that on average, only 2% (range 0–6.2%) of cetacean carcasses are recovered [73], and low detection rates (range <1%–17%) have also been documented in several other cetacean species in other areas [74–77]. The high rate of ship strike mortalities in Alaska, as indicated by the available necropsy data (37%), suggests that many ship strike mortalities are likely going undetected in floating and beach-cast whales that are not examined.

In recent years, there has been improvement in the investigation of cause of death in whale stranding mortalities in Alaska, due to increased resources and expertise within the state, from sources such as the Prescott Marine Mammal Stranding Grant Program, the Alaska SeaLife Center, and additional veterinary support within the Alaska Marine Mammal Stranding Network. These improvements may explain some of the apparent increase in humpback whale ship strike mortalities over time. For example, 72% (24 of 32) of the large whale necropsies conducted in Alaska since 1978 occurred between 2001 and 2011 (NOAA Alaska Region Stranding Database unpublished data), which reflects NOAA's increased commitment to necropsy whales over the past decade. Despite these improvements, limited resources and personnel, combined with the logistical challenges of responding to remote carcasses, continue to result in missed opportunities to investigate the cause of death in many whale strandings. While federal resource agencies in Alaska strive to promote and facilitate necropsies led by experienced teams, ideally veterinarians, to investigate cases of whale mortality, additional resources are recommended to increase capacity and infrastructure in necropsy response to improve cause of death investigations. For instance, establishing a statewide network of vessels that are available to tow floating whale carcasses to shore would reduce the number of missed opportunities for necropsies. In many cases, multiday necropsies may be needed to flense a carcass down to bone to examine the skeleton for fractures, especially because necropsy sites in Alaska are generally too remote for heavy equipment to assist with maneuvering large carcasses [1]. It may be beneficial to involve northern Alaska Eskimo subsistence whalers, who are highly skilled in flensing whales without the aid of machines, in large whale necropsy teams. Alternatively, returning to inspect carcasses over time to look for newly exposed broken bones may be helpful, although postmortem damage to bones on weather-beaten shores

may confuse matters. Responding to whale strandings in Alaska will always be more challenging than in less remote areas where necropsy rates may be as high as 69% [18], but continuing to increase efforts to perform complete necropsies (e.g., down to bone to examine for fractures, Table 1) using experienced teams focused on determining cause of death [1] is needed to allow for a more accurate determination of the rate of ship strike mortality in Alaska.

Performing full necropsies on ship struck whales is also important because they can reveal underlying factors such as disease, biotoxins, parasites, prior injuries, and entanglements in fishing gear that may have compromised a whale and predisposed it to being hit by a vessel [8, 15]. Researchers investigating northern sea otter (*Enhydra lutris*) mortalities from vessel collisions in Alaska have found that many of the struck otters had underlying health issues such as bacterial infections and biotoxins that may have made them more susceptible to being hit (V. Gill, pers. comm.). In our sample, one adult humpback whale was found to have elevated saxitoxin levels that may have caused it to behave abnormally, which could have made it more vulnerable to being struck [61]. Systematic sample collection in all necropsies to test for an array of underlying factors is needed to gain a better understanding of how often these other stressors may be contributing to collisions. Recognizing that the pathology results from necropsies are often not available for weeks or months after the stranding, detecting the proximate and ultimate causes of vessel strikes will require stranding network personnel ensure that these results are systematically entered into the main record for each stranding in such a way that meta-analyses are possible. Storing these data in a usable fashion may require modifications to the national stranding database structure.

**4.6. Human Toll and Property Damage from Collisions.** The discovery that one-third of collisions resulted in some kind of human toll and/or property damage highlights that whale-vessel collisions are a human safety issue. To date, there have been no confirmed human fatalities from collisions in Alaska, although in one of the reports we rejected, a 5 m skiff reportedly struck a gray whale, and the operator died after falling into the water [78]. The human fatality was confirmed but we could not confirm that the accident was caused by a collision with a whale. Threats to human safety posed by collisions have been documented elsewhere [8, 17, 19, 79], but the frequency of human injuries and property damage we documented may be positively biased because presumably these cases are more likely to be reported than other collisions. Increased attention to systematic documentation of human injuries and/or property damage in all collision reports is needed to allow for a more quantitative assessment of the problem. Regardless, the number of documented incidents indicates that boaters in Alaska, especially those operating small open vessels where the likelihood of being thrown into the water from a collision is high, would benefit from public outreach and education programs that raise awareness of the risks posed by collisions and how these risks can be minimized (e.g., slow down, keep a sharp lookout for whales, always wear a life-jacket, etc.).

*4.7. Management Recommendations.* As we have shown in our analyses, the problem of whale-vessel collisions is clearly one that can be detrimental to whales and humans. Conversely, avoiding whale-vessel collisions is mutually beneficial, but the challenge is to understand how best to reach and advise each user group, given the tangle of human factors that influence vessel operators' decisions. These factors include, but are not limited to: economics, convenience, knowledge and tolerance of risk, and whether they are professional or recreational vessel operators. For the professional mariner, the recently published International Whaling Commission and International Maritime Organization collision avoidance leaflet [80] gives practical advice (e.g., pay attention, avoid areas where you know there are whales, and slow down) in an appealing and respectful format. Available on the internet in six languages, this leaflet also highlights the importance of reporting collisions to foster an understanding that will help avoid future incidents. Wide distribution of this leaflet in the international maritime industry will highlight the issue and create an ongoing dialog on whale avoidance in the industry that seems likely to alleviate some collision risk.

For recreational boaters, we suggest that the most effective approach for raising awareness of the issue would occur in nonregulatory settings using contemporary modes of communication including social networking, to inform people how to avoid collisions, and the need to report incidents when they occur. A key message for operators of small boats in Alaska is that the likelihood of colliding with a whale is increasing, and that people can get hurt, costly vessel damage can occur and the whale can be injured or killed. Simple but specific preventive measures that encourage vigilance and the willingness to use slow speeds in high-density whale areas should be made widely available in a sound-byte format that is easy to digest. Creating and distributing these messages is a step toward creating a culture where people understand the risks and will do what they can to avoid collisions with whales.

Collision hotspots (Figure 2) are areas that warrant special attention in the form of vessel speed limits, public service announcements, increased law enforcement presence or other measures. The map we created for this paper is the first regional look at the geography of collisions in Alaska, and may be a useful approach for analysis of other collision datasets outside Alaska. High-risk areas need to be closely examined and coupled with predictive modeling to assess areas where conservation action (e.g., vessel speed limits) may be targeted to prevent future vessel collisions with whales in Alaska. For example, a recommendation to reduce speed at night in known hotspot areas may be particularly relevant for large ships (such as cruise ships) which routinely transit at night. Commercial vessels may want to consider marketing "whale friendly" voyages by advertising and adhering to lowered speeds as part of their standard operations, along with increased care and attentiveness in hotspot areas. Reduced speeds have been used successfully in Glacier Bay National Park for many years (termed "whale waters"), where the park superintendent implements vessel course and speed restrictions in areas where whale

concentrations have been detected [25]. Protective measures applied to relatively small areas with reliably high whale densities may yield a disproportionately large reduction in collision risk for humpback whales in southeastern Alaska and presumably impact fewer vessel operators compared to other mitigation measures [81]. As whale populations and vessel traffic continue to change throughout the state, improved data collection and validation of collision reports will enhance our understanding of collisions, with the ultimate goal of reducing the frequency of whale-vessel collisions in Alaska.

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## Endnotes

1. Listed as endangered under the ESA.
2. Listed as endangered under the ESA (Cook Inlet stock only).

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## Review Article

# Cetaceans and Marine Debris: The Great Unknown

**Mark Peter Simmonds**

*Science Directorate, Whale and Dolphin Conservation Society, Brookfield House, 38 St Paul Street, Chippenham, Wiltshire SN15 1LJ, UK*

Correspondence should be addressed to Mark Peter Simmonds, mark.simmonds@wdcs.org

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Plastics and other marine debris have been found in the gastrointestinal tracts of cetaceans, including instances where large quantities of material have been found that are likely to cause impairment to digestive processes and other examples, where other morbidity and even death have resulted. In some instances, debris may have been ingested as a result of the stranding process and, in others, it may have been ingested when feeding. Those species that are suction or “ram” feeders may be most at risk. There is also evidence of entanglement of cetaceans in marine debris. However, it is usually difficult to distinguish entanglement in active fishing gear from that in lost or discarded gear. The overall significance of the threat from ingested plastics and other debris remains unclear for any population or species of cetaceans, although there are concerns for some taxa, including at the population level, and marine debris in the oceans continues to grow. Further research including the compilation of unpublished material and the investigation of important habitat areas is strongly recommended.

## 1. Introduction and Background

Marine litter has been characterized as an environmental, economic, human health and aesthetic problem, posing a complex and multidimensional challenge with significant implications for the marine environment and human activities all over the world [1]. Much has been written about this pervasive pollution problem in recent years, and there are various international initiatives now striving to address it, including the United Nations Environment Program (UNEP) Global Initiative on Marine Litter. Part of the problem derives from the accumulation and fragmentation of plastics, “one of the most ubiquitous and long-lasting recent changes to the surface of our planet” [2]. In the marine environment, typically 40–80% of the larger categories of marine debris items are plastic. Much of this is packaging, carrier bags, footwear, cigarette lighters and other domestic items and much originates from land, as a recent study in Central and South America showed [3]. Lost or discarded fishing gear can also be important, particularly along continental shelves and remote islands.

Thirty-one species of marine mammals have previously been reported to have ingested marine debris [4], and

it has been suggested that even small ingested quantities can have large effects [5]. In addition to interference with alimentary processes, another effect could be that the plastics lodged somewhere in the alimentary tract could facilitate the transfer of pollutants into the animals’ bodies. The chemicals contained within plastics debris include polychlorinated biphenyls (PCBs), polycyclic aromatic hydrocarbons, petroleum hydrocarbons, organochlorine pesticides (2,2’-bis(*p*-chlorophenyl)-1,1,1-trichloroethane, hexachlorinated hexanes), polybrominated diphenyl ethers, alkylphenols, and bisphenol A, at concentrations from sub ngg<sup>-1</sup> to μgg<sup>-1</sup> [6]. Some of these compounds are added during plastics manufacture, while others are adsorbed from the surrounding seawater. Concentrations of these absorbed contaminants showed distinct spatial variations, reflecting global pollution patterns. Model calculations and experimental observations consistently show that polyethylene accumulates more organic contaminants than other plastics such as polypropylene and polyvinyl chloride.

“Microplastics” are a related concern and defined by the United States’ National Oceanic and Atmospheric Administration (NOAA) Marine Debris Program as plastic debris pieces in the size range of 0.3–5 mm. “Primary microplastics”

are either intentionally produced for direct use, such as scrubbers in cleaning products, or as precursors to other products, such as preproduction plastic pellets. “Secondary microplastics” are formed from the breakdown of larger plastic materials. These small pieces of plastic are difficult to remove from the environment, and, because they have the potential to be ingested by a wider range of organisms than larger pieces microplastics may clog the feeding apparatuses or the digestive systems of a variety of species. Microscopic pieces may also be taken up from the gut into other body tissues [2].

In 2003, UNEP established a “Global Initiative on Marine Litter” to facilitate international cooperation on marine litter. This is coordinated by UNEP’s Regional Seas Programme (RSP) and the Global Programme of Action for the Protection of the Marine Environment from Land-based Activities (GPA). Most recently, in March 2011, UNEP and NOAA organized the Fifth International Marine Debris Conference in Honolulu, Hawai’i. This meeting, which brought together 440 participants representing 38 countries, agreed the Honolulu Commitment, which outlines 12 actions to reduce marine debris and also produced the *Honolulu Strategy*, a comprehensive global framework strategy to prevent, reduce, and manage marine debris [10].

An investigation was made of the published scientific and other literature in order to assess the current state of knowledge with respect to cetaceans. This review focuses on incidents recorded after the review authored by Laist in 1987, when he first raised substantive concerns about this threat for marine wildlife [8].

## 2. The Behaviour of Debris at Sea

Many studies have been carried out across the world to try to quantify marine debris, and most of these have focused on large (macro) debris. These studies show that marine debris is ubiquitous in the world’s oceans and on its shorelines [4]. Many plastics are buoyant, and plastic items are commonly found at the sea surface or washed up on the shoreline [2]. Distribution at sea is affected by local wind and current conditions, coastal geography and point of entry; enclosed seas tend to have higher concentrations.

Higher quantities are found in the mid-latitudes and tropics, with particular concentrations associated with shipping lanes, fishing areas, and ocean convergence zones. About 2000 items of anthropogenic debris are found on north Atlantic shores per linear km per year and 500 per linear km per year on south Atlantic shores. More than half of this debris is plastic. By comparison, more than six times as much plastic has been reported washing ashore annually in the Mediterranean Sea. Observed global trends include a sustained and considerable increase over time and an increase in the associations of macroplastics with some wildlife (e.g., in bird nests and stomachs, and entangling seals) [2].

Some plastics sink when they first enter the water column, and others do so after accumulating a layer of fouling organisms and sediment. Considerable spatial variability affects plastic debris below the sea surface, and distribution

is strongly affected by hydrodynamics, geomorphology, and human factors [2]. Plastics have now been found on the seabed of all seas and oceans across the planet, although macrodebris is still very rare in the Southern Ocean. It is now apparent that even those species that typically feed at significant depth will not avoid exposure to plastic debris, indeed they may actually be exposed in some areas to very high concentrations. Submersibles conducting investigations at depths beyond the continental shelf have encountered substantial quantities of debris, including high densities in coastal canyons (up to 112 items per kilometer, of which 70% were plastics) [2].

Concentrations of marine debris may occur in areas that are important for cetaceans, such as convergence zones where prey may be abundant. For example, in 1997 and 2000, surveys were conducted on the floating debris in the Ligurian Sea, a subbasin of the Mediterranean Sea which includes the Ligurian Cetacean Sanctuary [11]. Debris densities were determined to be 15–25 objects/km<sup>2</sup> in 1997 and 1.5–3 objects/km<sup>2</sup> in 2000. The authors noted that there was a difference in sampling methodology between the two surveys but also suggested that meteorological factors played a role in creating real differences in the densities reported and noted that the factors affecting distribution need to be better understood.

Williams et al. [12] have recently mapped the at-sea distributions of both marine debris and eleven marine mammal species in the waters of British Columbia to identify areas of overlap. They commented that such areas were often far removed from urban centers, and this suggested that the extent of marine mammal-debris interactions would be underestimated from opportunistic sightings and stranding records. They urged that high-overlap areas should be prioritized by stranding response networks.

There are two primary types of impact for marine wildlife: entanglement and ingestion and whilst cetaceans, pinnipeds, turtles and seabirds are all known to suffer from entanglement, it has been suggested that pinnipeds are particularly affected [4]. Entanglement in marine debris is also well established as a health problem for some marine birds and turtles [5]. Entanglement may be confused with bycatch, which is the ensnaring of nontarget animals in active fishing apparatus. It may be difficult to diagnose from retrieved bodies whether they were caught in active gear or lost gear, and marks on bodies may be misidentified as net marks when they are actually the result of entanglement in marine debris.

## 3. Ingestion

*3.1. Odontocetes.* Walker and Coe made an extensive survey of foreign body ingestion by odontocetes [7]. They commented that the pathologic effects on foreign body ingestion on captive cetaceans are well known and provide details of materials ingested in captivity. They also investigated the situation for wild cetaceans and solicited information from relevant institutions covering the period between 1963 and 1986. Due to variations in data recording and pathology techniques, they were unable to determine frequency of

occurrence of debris ingestion, but they did identify 43 examples of ingestion in stranded animals primarily from the east and west coasts of North America. Table 1 summarizes the incidents reported by Walker and Coe in 1990, including some records where ingestion of debris might have been of health significance [7]. Plastic bags and plastic sheeting were the most common items ingested (62.5% of ingested materials) [7]. Other miscellaneous plastic items such as drinking straws, bottle caps, discarded fishing net, synthetic rope, and a small container occurred in 17.5% of cases.

Walker and Coe concluded that odontocete cetaceans were affected to an unknown degree by the ingestion of oceanic debris but that the sperm whale, *Physeter macrocephalus*, seemed to be particularly affected. They suggested that mistaken ingestion of debris due to its resemblance to prey is unlikely in odontocetes because of their echolocation skills and that for these species at least, ingestion happens incidentally to feeding or may be part of the stranding syndrome. They also commented that “naturally occurring disease factors may predispose” some animals to ingest abnormal items [7].

A number of other authors have reported more recently on incidents of ingestion. For example, the first account of ingestion causing mortality in sperm whales was recently published: in 2008, two male sperm whales stranded along the northern California coast with large amounts of fishing net scraps, rope, and other plastic debris in their stomachs [5]. One animal had a ruptured stomach, the other was emaciated, and gastric impaction was suspected as the cause of both deaths. There were 134 different types of nets in these two animals, all made of floating material, varying in size from 10 cm<sup>2</sup> to about 16 m<sup>2</sup>. The researchers concluded that the variability in size and age of the pieces suggested that the material was ingested from the surface as debris. They also mentioned several other incidents of ingestion including two pygmy sperm whales, *Kogia breviceps*, with stomachs occluded by pieces of plastic bags and three bottlenose dolphins, *Tursiops truncatus*, asphyxiated by laryngeal entrapment by ingested fishing lines.

In November 1993, an emaciated juvenile female pygmy sperm whale was found stranded in Great Inlet, Longport, New Jersey, and taken into a rehabilitation facility [13]. The whale survived and exhibited various symptoms over a 42-day period. These included being unable to submerge successfully and indications that it had a digestive problem which led to a gastroscopic investigation. Foreign material was observed and, over a six-week period, using endoscopic procedures, a 20 cm × 22.5 cm sheet of black plastic, a portion of a plastic garbage bag, a cellophane wrapper, cigarette box wrapper, portion of a mylar balloon, and some other small pieces of plastic were extracted. The animal's appetite then improved, it put on weight and was ultimately released, tracked for several days, and appears to have survived.

In December 2009, a pod of seven male sperm whales stranded on the Adriatic Coast of southern Italy [14]. Stomach contents consisted mainly of highly digested cephalopod beaks and foreign bodies, including fishing gear and hooks, ropes, and several plastic objects. No evident obstruction or perforation of the alimentary tract was noted.

Beaked whales have also been suggested to be especially vulnerable [15]. Walker and Coe in 1990 reported debris from Baird's beaked whales, *Berardius bairdii*, taken at two localities in the Pacific coastal waters of Japan [7]. In these animals, the incidence of debris in 86 stomachs was 26.7% and off northern Hokkaido, in the southern Okhotsk Sea, incidence of debris in 20 stomachs was 15.0%. Prey data indicated that the lower frequency of debris ingestion reflected differences in feeding strategy. The high vulnerability of beaked whales may result from their reliance on suction-feeding for prey capture and some species in some regions, such as Cuvier's beaked whales, *Ziphius cavirostris*, in the northeast Atlantic, seem to have particularly high incidences of ingestion of and death from plastic bags [15]. MacLeod commented that “currently plastic bags are known to affect beaked whales at the individual level and may be of sufficient prevalence to affect some species at the local aggregation and population levels. As yet, it does not seem likely that plastic bag ingestion affects any beaked whales at the species level. However, this may be a possibility for some species with limited geographic ranges close to high concentrations of humans” [15].

An immature male Cuvier's beaked whale that stranded at Biscarosse, Landes, France, on January 29, 1999 was found to be emaciated, with a blubber layer almost half that expected for an animal of its age, sex, and size [16]. The stomach was found to be full of plastic, weighing approximately 33 kg when wet, and estimated to consist of 378 separate plastic items. A subsample of the plastic (786 g) consisted of seven supermarket plastic bags and two plastic sheets. A small number of cephalopod and fish remains were also found in the stomach, but no fresh prey. The debris was covered with dark viscous fluid, possibly from erosion of the stomach lining and resulting hemorrhaging, which was suggested as the cause of death.

Santos et al. report on the stomach contents of three Cuvier's beaked whales, two of which stranded in Galicia, northwest Spain, in 1990 and 1995 and the other in North Uist, Scotland, in 1999 [17]. Both the whales that stranded in Galicia had plastic remains in their stomachs, and the Scottish animal contained the remains of at least six plastic bags or refuse sacks, one of which was recorded as “tightly screwed up and apparently jammed in the entrance to the stomach.”

Santos et al. [18] later analyzed stomach contents from another group of beaked whales which mass-stranded shortly after a naval exercise conducted in the Canary Islands in September 2002. Samples from seven Cuvier's beaked whales, a single Blainville's beaked whale, *Mesoplodon densirostris*, and a single Gervais' beaked whale, *Mesoplodon europaeus*, were examined. All the whales were reported to have appeared to have been in good body condition with the exception of one of the male Cuvier's beaked whales. This animal was “visibly emaciated,” and necropsy showed a high nematode parasite burden load in the stomach and also a plastic sheet. The stomach of this specimen was also the only one that did not contain fresh food remains.

The stomach contents of 23 cetaceans stranded in the Canary Islands between 1996 and 2006 were examined,

TABLE 1: Summary of incidents of ingestion by cetaceans of plastics and other debris reported in Walker and Coe between 1963 and 1986 with notes indicating where ingestion was indicated to be of significance [7].

Species	Number of incidents	Locations	Notes
Sperm whale, <i>Physeter macrocephalus</i>	3	Florence, OR, New Jersey and Newfoundland	One animal of 38 examined from a mass stranding in Oregon had one liter of tightly packed trawl net in its stomach
Dwarf sperm whale, <i>Kogia sima</i>	1	Corolla, NC	
Pygmy sperm whale, <i>Kogia breviceps</i>	3	Sullivan's Island, SC, Galveston, TX, and Brevard Co., Florida	The Texas animal had "pounds of plastic bags clogging its stomach chambers"
Cuvier's beaked whale, <i>Ziphius cavirostris</i> ,	3	San Diego, CA, Assawoman, VA and Seaford, VA	
Blainville's beaked whale, <i>Mesoplodon densirostris</i>	1	East Hampton, NY	
Gervais' beaked whale, <i>Mesoplodon europaeus</i>	2	Hatteras Island, NC and Cape May, NJ	The NJ animal had its stomach full of plastic
Short-finned pilot whale, <i>Globicephala macrorhynchus</i>	1	Corolla, NC	
Rough-toothed dolphin, <i>Steno bredanensis</i>	3	Maui, HI and 2 from Sandbridge, VA	
Pacific white-sided dolphin, <i>Lagenorhynchus obliquidens</i>	4	Three from Santa Monica, CA, one from Long Beach, CA	The forestomach of the Long Beach animal was half full of four plastic bags, two plastic bottle caps, and various organic materials
Common dolphin, <i>Delphinus delphis</i>	4	Two from Los Angeles County, CA, one from Malibu, CA, and the other from Hermosa Beach, CA	The LA County animal had one partial red balloon (3 × 13 cm), one piece of clear plastic (8 × 13 cm), and kelp fronds in its stomach
Bottlenose dolphin, <i>Tursiops truncatus</i>	9	All from the California coastal population—stranded on various CA shores	Along with other organic and plastic debris, three of the animals contained hooks
Risso's dolphin, <i>Grampus griseus</i>	2	Martha's Vineyard, MA and Manhattan Beach, CA	The animal from MA was recorded as having a plastic bag in its throat
Striped dolphin, <i>Stenella coeruleoalba</i>	1	Cape Point, NC	
Northern right whale dolphin, <i>Lissodelphis borealis</i>	2	Los Angeles County, CA and Santa Monica, CA	
Harbour porpoise, <i>Phocoena phocoena</i> .	1	Corolla, NC	
Dall's porpoise, <i>Phocoenoides dalli</i>	3	Venice Beach, CA, and two from Santa Barbara, CA	The Venice Beach animal had its stomach "jammed with debris" including 13 pieces of clear plastic sheet, 3 heavy clear plastic bags, 2 plastic bread bags, and two plastic sandwich bags

and five of the animals examined had plastic debris in their stomachs with big plastic items being taken by deep diving teuthopagus whales [19]. The sample set comprised 5 sperm whales, 2 pygmy sperm whales, 1 Gervais' beaked whale, 1 Risso's dolphin, *Grampus griseus*, 2 short-finned pilot whales, *Globicephala macrorhynchus*, 1 Fraser's dolphin, *Lagenodelphis hosei*, 3 Atlantic spotted dolphins, *Stenella frontalis*, 3 striped dolphins, *Stenella coeruleoalba*, 1 bottlenose dolphin, 1 rough-toothed dolphin, *Steno bredanensis*, 3 common dolphins, *Delphinus delphis* and 1 Cuvier's beaked whale. One of the sperm whales had a plastic bag in its stomach. One of the pygmy sperm whales contained a plastic filament. One of the Gervais' beaked whales had a complete

plastic bag (44 × 24 cm) and pieces of another two in its stomach. The Frazer's dolphin contained some small plastic pieces, and finally one of the striped dolphins had ingested a plastic filament around 10 cm long. All the animals that had ingested plastic also had food remains in their stomachs. In addition, in February 2004, a Cuvier's beaked whale was found washed ashore on the Isle of Mull, Scotland. The entrance to this animal's stomach was found to be completely blocked by a cylinder of tightly packed shredded black plastic bin liner bags and fishing twine [20].

A North Atlantic bottlenose whale, *Hyperoodon ampullatus*, which stranded in August 2006 in Skegness, UK, was found to have ingested some plastic [21]. The fundic stomach

contained copious brownish watery fluid, a piece of plastic, and a section of some green netting (resembling fishing gear). The mucosal lining at the base of the stomach (area in direct contact with the plastic) was reddened and haemorrhagic in appearance, and a single round mucosal ulcer with a red haemorrhagic base (measuring 1–1.5 cm diameter) was noted towards the entrance to the stomach. The UK Cetacean Strandings Investigation Programme (CSIP) examined 18 stranded whales from the Ziphiid family between 2005 and 2010. Two (a North Atlantic bottlenose whale and a Sowerby's beaked whale, *Mesoplodon bidens*) had ingested debris [21].

Accounts of plastic ingestion by beaked whales outside of the North Atlantic also exist. For example, there is a published report on a Blainville's beaked whale washed ashore in Brazil with a blueish bundle of plastic threads occupying a large part of its main stomach chamber [22]. This whale had not fed for some time. In addition, a Gervais' beaked whale stranded on the southeastern coast of Puerto Rico was recently found to have more than ten pounds (4.5 kilos) of twisted plastic inside its stomach, and its death was attributed to the plastic preventing it obtaining adequate nutrition [23].

There are scattered reports of ingestion of marine debris by other odontocete cetaceans. For example, in September 1997, a small harbour porpoise, *Phocoena phocoena*, (probably not yet weaned) was found dead near Pictou, Nova Scotia. It was visibly emaciated and its stomach and intestines were empty, apart from small amounts of bile-stained liquid [24]. Upon examination of the oesophagus, a balled-up piece of black plastic (about 5 by 7 cm) was found adjacent to the junction with the stomach. Cranially to this was a mass of fish bones and flesh and three intact fish. The authors noted two earlier published reports of plastic ingestion by this species and several other unpublished records of the same. CSIP has recorded 10 out of 459 harbour porpoises examined between 2005 and 2010 had ingested marine debris [21].

The stomach contents of 42 harbour porpoises that were either bycaught or stranded between April and June in 2002 and 2003, on the Turkish western Black Sea coast, were examined [25]. Plastic debris was found in five stomachs and in one of these, a bycaught female 130 cm long, this consisted of plastic bags and sheeting with dry weight of 40.9 g.

An adult male rough-toothed dolphin, *Steno bredanensis*, that stranded alive on Poço da Draga Beach, Fortaleza, Ceará State, northeastern Brazil, was found to have ingested two plastic bags, and four pieces of sea sponges were found in the forestomach chamber, where the mucosa had several ulcers [26].

CSIP has also reported marine litter ingestion by 3 out of a sample of 128 short beaked common dolphins stranded in the UK [21].

Plastic debris ingestion was examined in a large sample of Franciscana, *Pontoporia blainvillei*, incidentally captured in the artisanal fisheries of the northern coast of Argentina [27]. Twenty-eight percent of the 106 dolphins sampled had plastic debris in their stomachs, but no ulcerations or obstructions were recorded. Plastic ingestion was more frequent in the dolphins using an estuarine environment rather than those

living in a fully marine environment, but the type of debris was similar in both. Packaging debris (cellophane, bags, and bands) was found in 64.3% of the dolphins which had ingested plastics, with a lesser proportion (35.7%) ingesting fishing gear fragments (monofilament lines, ropes, and nets). Twenty-five percent had ingested plastics from unknown sources. No obstructions or ulcers were found in any of these animals, and the researchers commented "that the small number and size of the fragments found in healthy dolphins suggest that this material is not lethal... [but] cannot be ruled out as a potential cause of death." They also noted that sublethal effects, such as partial obstruction of the gastrointestinal tract and reduction of feeding stimulus might occur. This large sample size also revealed that there is a potential relationship between age and plastic ingestion. The Franciscana of north Argentina are weaned between 2 and 7 months of age, and it is suggested that the sharp increase of plastic ingestion that occurs during the weaning phase could be a consequence of the learning process in the young animals as they start to catch prey by themselves [27].

**3.2. Mysticetes.** In 2000, a Bryde's whale, *Balaenoptera edeni*, was found on the shore in Cairns, Australia with a considerable amount of plastic in its stomach including 30 whole plastic bags and three lengths of plastic sheeting [28]. The plastic when stretched out was reported to cover an area of 6 m<sup>2</sup>.

In April 2002, a dead minke whale, *Balaenoptera acutorostrata*, washed up on the Normandy Coast of France, was found to have 800 kg of plastic bags and packaging, including two English supermarket plastic bags in its stomach [29].

CSIP has not reported ingestion of plastic in any of the 13 baleen whales examined in the UK between 2005 and 2010 [21].

## 4. Entanglement

The first comprehensive review of the impacts of marine debris globally was undertaken by Laist [8], and he revisited this issue ten years later [9], when he was of the opinion, based on the available data, that entanglement was a greater threat to marine mammals than ingestion. Laist reported that fishing gear (monofilament line, nets, and ropes) was found to be the most significant source of entanglements in all documented records regarding sea turtles, coastal and marine birds, marine mammals, fish, and crabs. Most of this material originated from commercial fishing operations, although recreational fishing and cargo ships were also considered potential sources. He estimated that 100,000 marine mammals died every year from entanglement or ingestion of fishing gear and related marine debris. Laist's reviews are summarized here in Table 2 alongside the literature compiled here. One hundred and thirty-six marine species have been reported in entanglement incidents in the wider United States area, including 6 species of sea turtles, 51 species of seabirds, and 32 species of marine mammals [30].

Lambertsen et al. commented on the "imperfect nature of our understanding of the impact of marine debris on mysticete species" whilst also theorizing that fouling of

TABLE 2: Overview of entanglement and ingestion in cetaceans.

Species	Laist 1987 [8]	Laist 1997 [9]	This review (Ingestion only)
Mysticete whales			
<i>Balaena mysticetus</i> (bowhead whale)		I/E	
<i>Eubalaena glacialis</i> (northern right whale)	E*	E*	
<i>Eubalaena australis</i> (southern right whale)		E*	
<i>Megaptera novaeangliae</i> (humpback whale)	E*	E*	
<i>Eschrichtius robustus</i> (gray whale)		E*	
<i>Balaenoptera physalus</i> (fin whale)	E*		
<i>Balaenoptera acutorostrata</i> (minke whale)	E*	I/E*	I
<i>Balaenoptera edeni</i> (bryde's whale)			I
Odontocete whales			
<i>Physeter macrocephalus</i> (sperm whale)	I	I/E*	IM
<i>Kogia sima</i> (dwarf sperm whale)		I	
<i>Kogia breviceps</i> (pygmy sperm whale)	I	I	I
<i>Berardius bairdii</i> (Baird's beaked whale)		I	
<i>Ziphius cavirostris</i> (Cuvier's beaked whale)	I	I	I?M
<i>Mesoplodon europaeus</i> (Gervais' beaked whale)		I	IM
<i>Mesoplodon densirostris</i> (Blainville's beaked whale)		I	I
<i>Globicephala macrorhynchus</i> (short-finned pilot whale)		I	I
<i>Globicephala melas</i> (long-finned pilot whale)		I	
<i>Steno bredanensis</i> (rough-toothed dolphin)	I	I	I
<i>Pseudorca crassidens</i> (false killer whale)		I	
<i>Orcinus orca</i> (orca or killer whale)		E*	
<i>Lagenorhynchus obliquidens</i> (Pacific white-sided dolphin)		I	
<i>Delphinus delphis</i> (common dolphin)		I	I
<i>Tursiops truncatus</i> (bottlenose dolphin)		I/E*	I
<i>Grampus griseus</i> (Risso's dolphin)		I	
<i>Stenella coeruleoalba</i> (striped dolphin)		I	I
<i>Lissodelphis borealis</i> (northern right whale dolphin)		I	
<i>Phocoena phocoena</i> (harbour porpoise)		I/E*	I
<i>Phocoenoides dalli</i> (Dall's porpoise)		I/E	
<i>Pontoporia blainvillei</i> (Franciscana)		I	I
<i>Sotalia fluviatilis</i> (tucuxi dolphin)		I	
<i>Stenella frontalis</i> (Atlantic spotted dolphin)			I
<i>Lagenodelphis hosei</i> (Fraser's dolphin)			I
<i>Hyperoodon ampullatus</i> (North Atlantic bottlenose whale)			I
<i>Mesoplodon bidens</i> (Sowerby's beaked whale)			I

Key: I: ingestion recorded; E: entanglement recorded; IM: mortality reported as associated with ingestion; I?M: mortality resulting from ingestion likely.

\*Entanglement in fishing gear where it is not clear if it was in use or lost at the time of entanglement.

the baleen may prove lethal, as it could interfere with the particular feeding mechanism used by these animals [31]. They added that this may be a significant factor in the declining survival probability of the northern right whale, *Eubalaena glacialis*, because as continuous ram feeders, they face a higher risk than rorquals of encountering various forms of marine debris with their mouths open.

As a means of trying to quantify entanglement, there have been a number of studies of nonlethal entanglements of whales using the pattern of scarification photographed on their bodies. For example, Neilson et al. found that 52–78% of humpback whales, *Megaptera novaeangliae*, in the

northern part of southeastern Alaska had been nonlethally entangled at some point in their lives [32]. Calves were less likely to have entanglement scars than older whales, and males may be at higher risk than females. Entanglement of marine mammals in fishing gear has been documented widely and may affect a significant proportion of some populations of baleen whales (e.g., [32–35]). However, it remains unclear as to what percentage of entrapment arises from marine debris as opposed to entrapment from fishing gears, that were still in active commercial use. This seems to be general and significant problem in terms of determining the source of impacts.

In a similar study to that of Neilsen et al., nine minke whales from a photo catalogue of 74 known individuals which were known to regularly return to the waters in the west of Scotland were observed entangled, or with scars suggesting previous entanglement in marine debris, including pieces of discarded or “ghost” net [36]. Two whales, photographed in May 1997 and May 1999, had plastic packing straps wrapped around their rostrums. These plastic strips were trapped in the baleen in the upper jaws and appeared to be cutting into the whale’s skin. Another whale, photographed in September 1999, had a white scar thought to be caused by a packing strip or twine. Three minke whales appeared to have evidence of creel ropes wrapped around their heads, and it was suggested that some of the other wounds seen on the whales were probably caused by marine debris. These investigations by Gill et al. provide a rare example where debris can be categorically shown to be causing entanglement. By contrast, there is a considerable literature on entanglement of cetaceans in fishing gear but given the problem of determining whether the gear was in use or not, entanglement is not further reviewed here or included in the third column of Table 2.

## 5. Conclusions

It has long been held that marine wildlife entanglement in and ingestion of synthetic marine debris are insidious and cryptic threats [8]. As Williams et al. put it “if death from debris entanglement or ingestion occurs at sea, documentation of the event generally requires the carcass to come close to shore to be detected by a person, reported to the competent authority, and subjected to a full necropsy before the carcass decays” [12]. There are, therefore, several processes at work that reduce the likelihood of the event being detected, and this may be further exacerbated by the probability that some of the deeper sea dwelling whales (i.e., the ziphiids) are particularly impacted. Then there are diagnostic problems, such as the fact that some ingestion of pebbles, sand, and debris seems to be part of the stranding process [37, 38] and the issue of trying to determine the extent to which entangled animals have become ensnared by operational rather than lost fishing gear.

It is difficult to attribute any trends to the published literature because of differences in sampling procedures and other factors such as the changes over time and variations that may exist for difference regions and cetacean populations. Table 2 shows that ingestion of debris is now known for several more species than when last reviewed, and there are incidents where it has clearly caused mortality. Deep diving whales are also strongly represented in the reports. More records from surfacing dwelling dolphin species might be indicative of a growing problem for them, but this may also be affected by sampling effort.

Nonetheless, it is clear that marine debris is an increasing problem, and there is growing evidence of impacts on cetaceans. There are now numerous recorded incidents where ingested debris has caused pathology and a growing concern especially for deep water suction feeders and arguably ram feeders as well, noting that marine debris has

also been proposed as significant threat for the critically endangered northern right whale. Whilst it is strongly suggested in the literature that the small cetaceans living in surface waters are less likely to ingest harmful materials than other species, it is also apparent that this may change where there is substantial debris at the surface, as reported off northern Argentina.

However, apart from a small number of systematic surveys involving larger numbers of animals, the relevant data are generally scattered and rather scant. During research onto this topic, it became apparent that many cetologists and some institutions around the world hold some records of ingestion or entanglement in marine debris but, as these are frequently observations on one or just a few individual animals, they rarely bring them forward for publication. Nonetheless, if such records were compiled, they would probably help us better understand the scale and significance of this problem, and this may also help to pinpoint particular problem areas or populations that are being particularly impacted. The importance of appropriate pathology of stranded and bycaught cetaceans in order to investigate this issue is also apparent and likewise the desirability of developing approaches to determine if fishing gear was active or discarded when entanglement occurred.

Further consideration of where vulnerable cetaceans and marine debris may be converging—for example, the deep water canyons used as core habitat by beaked whales—is also recommended. Overall, in comparison to the level of understanding that exists for some other marine species such as turtles and albatrosses, the current level of understanding of the threat posed by marine debris to cetaceans is poor, and it is strongly recommended that this be addressed.

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## Review Article

# The Painful Side of Trap and Fixed Net Fisheries: Chronic Entanglement of Large Whales

**Michael J. Moore and Julie M. van der Hoop**

*Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA*

Correspondence should be addressed to Michael J. Moore, [mmoore@whoi.edu](mailto:mmoore@whoi.edu)

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Concern over the well-being of marine mammals at sea has focused on intentional harvests, both in terms of individual welfare and population sustainability. Unintentional mortalities from fishing gear entanglement are primarily seen as a risk to population viability. Additionally, larger whales breaking free of, and subsequently carrying, fixed trap and net gear are subject to a very slow demise, averaging 6 months in the case of the North Atlantic right whale (*Eubalaena glacialis*). Chronic cases can involve impaired foraging, increased drag, infection, hemorrhage, and severe tissue damage. The individual suffering of these cases appears to be extreme. Thus management measures should go beyond legally mandated conservation measures to include avoidance of such scenarios. Seafood consumers could succeed, where laws have failed, to demand fishing practices that do not kill whales in this manner. The effective absence of such demands would seem to reflect the cryptic nature of these cases to most consumers.

## 1. Introduction

Current debate [1] within animal welfare includes the concept that living conditions can be incrementally enhanced (Protectionism) versus the belief that such approaches only prolong animal suffering and that there needs to be a paradigm shift whereby animals are no longer owned and used (Abolitionism). Such debate focuses primarily on captive animals, both in the laboratory and on farms. However, there are parallels for wildlife, both terrestrial and marine. A number of factors need to be considered regarding the welfare of wildlife, including the nature of the harm caused, its duration, the numbers of animals affected, and their capacity for suffering [2]. These authors point out that most of the wildlife in the world today are under human influence, and we therefore have an obligation to consider their welfare in addition to that of domesticated animals. We quote Sainsbury et al. [3]: “the use of anticoagulant rodenticides, myxomatosis in rabbits, the poisoning of wildfowl by ingested lead shot, the contamination of seabirds with fuel oil, the effects of shooting, injuries due to collisions with road and vessel traffic and predation by domestic cats all severely compromise the welfare of large numbers of wild animals.”

Feral cats provide a particularly poignant counterpoint, between concerns for their welfare, versus their impact on other wildlife such as song birds, and the impacts of trap, neuter, and return programs [4].

With regard to marine mammals, their welfare has been discussed in terms of their maintenance in captivity for display [5], especially in the context of the effects of long-term commercial confinement on *Orcinus orca*. Life expectancy has been reduced [5] in captive killer whales, and concern has been raised over behaviors of jaw popping and chewing of gate bars, which result in chronic dental decay [6], as well as periodic lethal aggression towards trainers [7]. The costs and benefits of marine mammal rehabilitation and release have also been reviewed [8]. For marine mammals in the wild there has been substantial concern about the sustainability of fishery bycatch [9]. There has, however, been less focus on the welfare concerns facing marine mammals at sea. Most such concern has focused on the various methods used in directed marine mammal harvests [10–12] where questions about the humane nature of such harvests have often been overlain and obfuscated with concerns about their sustainability. Previous papers have alluded to these welfare issues [13–15].

Drowning of small cetaceans and pinnipeds is of course a less than ideal manner of death, but it is at least usually quite quick, although substantially prolonged when compared to land mammals, given marine mammal adaptations for sustained diving [16]. Stress related to short-term entanglement of dolphins with mortality or subsequent release from tuna seines has also been widely studied [17, 18]. In contrast, entanglement in debris and fishing gear can have a far longer time course for the most powerful larger species. Cassoff et al. [19] have detailed the pathobiology of chronic large whale entanglement in 21 cases from 4 species of baleen whale in the NW Atlantic.

Here the types and timelines of trauma documented by Cassoff et al. [19] are reviewed, and then discussed in the context of marine versus terrestrial animal welfare concerns and the differences in our societal responses to such trauma: when it is out of sight, at sea, compared to where it is to be in plain view on land.

## 2. The Nature of Large Whale Entanglement

**2.1. Drowning.** If the animal is entangled in sufficient gear that it cannot break free of or swim the gear to the surface to breathe, it will drown. The evidence for this usually shows acute entanglement impact. Lesions often include one or more rope impressions, with the texture of the rope imprinted on the skin. Such imprints may be faint, and their detection can require a thorough external examination, often becoming less cryptic with different incident angles of light, and with the skin surface drying. Rope texture imprints, however, may be missing if the rope has been sawing back and forth as the animal struggles, causing deep skin, blubber, and muscle lacerations even down to the underlying bone, as has been modeled in the laboratory [20, 21]. The carcass may or may not remain entangled on discovery. It may be found anchored in the gear, though animals are often cut loose postmortem to enable gear retrieval. Internal examination often reveals very little change. The trachea may have substantial froth, but there is usually an absence of inhaled water. Thus these drownings typically reflect asphyxiation. Often there is substantial bruising and edema underlying the areas compressed by the entangling gear, reflective of a functional circulation for some time after the initial entanglement but before death. Given that these species can all normally dive for tens of minutes, this is not surprising.

**2.2. Emaciation.** Entanglement involving the head region has been observed in 67% of all lethally entangled whales described by Cassoff et al. [19] and is the most common point of attachment for right whales [22]. This can result in direct reduction in feeding efficiency. Full wraps around the rostrum are not uncommon and can restrict mouth opening. Rope may foul the baleen filter, disrupt flow patterns, and limit the movement of the lips and tongue having direct impacts on feeding ability [23].

**2.3. Increased Drag.** Whales swim at a low drag coefficient [24–26], suggesting that the added drag of towing accessory

gear could substantially affect the energy budget of an entangled large whale through time, as has been described for entangled fur seals [27]. Such an energy drain likely significantly contributes to the emaciation commonly seen with chronic entanglement [19]. Additionally, Lambersten et al. [23] have suggested that disruption of the oral seal, holding the lower mandible closed, could have a significant impact on propulsion efficiency and energy expenditure.

**2.4. Infection and Severe Tissue Damage.** Laceration and consequent infection can be another cause of death in chronic entanglement of large whales, with secondary bronchopneumonia [19]. Cases reported in North Atlantic right whales [19, 28] have included a taut line over the back between both axillae, dissecting off a 1.5 m sheet of blubber pre-mortem. Commonly, where line is fixed to more than one body part, such as baleen and with multiple wraps around a flipper, the continual swimming motion of the animal induces a chronic laceration down to the limb bones, often the radius and ulna, with a subsequent massive proliferation of loose fibroosseous new periosteal bone (see cases 7, 8 and 11 in Cassoff et al., online supplement [19]).

**2.5. Time Frame.** Where drowning does not occur, lethally entangled right whales tend to die over periods of about 6 months [13, 19]. There are cases where entanglement can persist for multiple years [29].

## 3. Marine versus Terrestrial Contexts

Many humans who are directly exposed to the realities of the pathology of the cases summarized above tend to be severely shocked by the inherent pain and suffering that they presumably represent for the individual animals in the time between initial entanglement and final demise. Documenting these case histories will lead to questioning all fishing practices responsible for such long drawn out trauma, pain and suffering. Thus it is worth reviewing the relevant legal and moral basis for why this situation persists in areas where powerful large whales, such as North Atlantic right whales, encounter anchored traps and nets.

North Atlantic right whale conservation is driven in the United States by attempts to conform to the Marine Mammal Protection Act of 1972 (MMPA) and the Endangered Species Act of 1973. In Canada, the recently enacted Species at Risk Act of 2003 is the legal mandate for right whale conservation, along with other endangered organisms. The MMPA does require consideration of humane treatment for specific scenarios, where “humane” is defined as “the least possible degree of pain and suffering practicable.” Under the MMPA, the importation of a marine mammal must be humane and various sections allow that, in order to issue taking permits, the manner of the “take” must be humane. The U.S. Animal Welfare Act of 1996 as amended dictates suitable management of vertebrates in research and teaching contexts. However, the primary enforcement of all these laws for marine wildlife has been avoidance of species loss with little to no focus on the welfare aspects of incidental take in fisheries.

Porter [30] classes cetaceans in the highest category of animals on a scale of sensibility to pain and suffering, from mollusks to primates. He describes them as sentient, highly intelligent and precognitive, in the same category as primates and carnivores. The degree to which it is possible to infer pain and suffering in wild animals has been reviewed by Kirkwood et al. [2]. These authors suggest summarizing cause, effect, level of stress and pain, and magnitude of the problem. In the case of large whale entanglement mortality, the cause is irreversible entanglement in fishing gear, the effect is ultimately lethal trauma through a drawn-out cumulative loss of body condition and constriction of body parts, with or without secondary infection, and the level of pain and stress is presumably extreme.

In a recent analysis (van der Hoop et al. unpublished data) entanglement was the leading cause of death in a suite of large whale species off the North American eastern seaboard. In addition, Knowlton et al. [31] have analyzed entanglements in North Atlantic right whales from photographs of entanglement scar incidence through time on living animals at sea. Between 1980 and 2004 at least 73% of 493 individuals were entangled at least once. The number of entanglements ranged from 1 to 6 per individual. Thus most self-disentangle or are disentangled by humans [32], with the entangling gear leaving visible, persistent scars. In the Knowlton study [31] the number of newly entangled animals in a given year ranged from 4 to 33% of the population. In SE Alaska at least 52% of humpback whales have been entangled at least once, with an average of 8% of the population getting new entanglements every year [33]. Thus the lethal entanglement events are the extreme, and relatively infrequent end of a more widespread, persistent, and repetitive problem. The cost of nonlethal entanglement in terms of energy, stress, and pain, may significantly reduce fecundity in North Atlantic right whales, as this species reproduces at lower rates than southern right whales (*Eubalaena australis*) [34].

Consider the likely difference in response if the results of long standing right whale entanglements (i.e., emaciation, starvation, chronic pain, and infection) were observed on a daily basis by humans as they went about their lives in urban, suburban or rural communities rather than remaining out of sight at sea. If the equivalent of fixed fishery traps and nets was to be set on land, with a comparably slow and painful death for wildlife, the responsible industry could be subject to consumer revolt, irrespective of whether there was an actual law concerning such an interaction. However, a terrestrial precedent, that of coyotes conflicting with farming or ranching, where coyotes are poisoned and trapped, often with federal support, suggests that the politics of these interactions are very complex, and not necessarily based upon the welfare of individual wild animals.

The history of repeated attempts to ban leg-hold traps for terrestrial wildlife is salutary as reviewed by Gentile [35]. More than 450 antitrapping bills have been filed in the US Congress since 1900, but Gentile concluded that “the 99.98% failure rate of antitrapping legislation can be attributed more to the inability of anti-trappers to unite than to a lack of

popular support for their goal.” Leg-hold traps are currently banned or restricted in only eight US states.

#### 4. Conclusion

Chronic large whale entanglement, while unintentional, is cruel. Efforts to remedy the situation [36] have largely failed. Alternative remedies are available, specifically: consumer action, including boycotts, active publicity campaigns, and seafood certification. However, such efforts, such as the Marine Stewardship Council (MSC-<http://www.msc.org/>), to protect wild resources, can bring mixed results. The MSC has been criticized by environmental groups for certifying fisheries with debatable records and is currently considering providing certification to the lobster fisheries in the Gulf of Maine which have entangled large endangered whales. Better information about the nature and magnitude of the problem needs wider publicity and public awareness to begin to resolve these complex issues.

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## Review Article

# River Cetaceans and Habitat Change: Generalist Resilience or Specialist Vulnerability?

**Brian D. Smith<sup>1</sup> and Randall R. Reeves<sup>2</sup>**

<sup>1</sup>*Ocean Giants Program, Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, NY 10460, USA*

<sup>2</sup>*Okapi Wildlife Associates, 27 Chandler Lane, Hudson, QC, Canada J0P 1H0*

Correspondence should be addressed to Brian D. Smith, bsmith@wcs.org

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River dolphins are among the world's most threatened mammals, and indeed the baiji (*Lipotes vexillifer*), a species endemic to China's Yangtze River, is likely extinct. Exploitation for products such as meat, oil, and skins has been a lesser feature in the population histories of river dolphins compared to most large mammals. Habitat factors are therefore of particular interest and concern. In this paper we attempt to describe the population-level responses of river dolphins to habitat transformation. We find circumstantial but compelling evidence supporting the view that, at a local scale, river dolphins are opportunists (generalists) capable of adapting to a wide range of habitat conditions while, at a river basin scale, they are more appropriately viewed as vulnerable specialists. The same evidence implies that the distributional responses of river dolphins to basinwide ecological change can be informative about their extinction risk, while their local behaviour patterns may provide important insights about critical ecological attributes. Empirical studies are needed on the ecology of river cetaceans, both to inform conservation efforts on behalf of these threatened animals and to help address broader concerns related to biodiversity conservation and the sustainability of human use in several of the world's largest river systems.

## 1. Introduction

In this paper, we attempt to evaluate the ability of river dolphins to adapt to environmental change. This evaluation is necessarily speculative and largely theoretical. Our goal is to develop ideas and terminology that will facilitate a rigorous debate and stimulate field researchers and resource managers to look at these animals with fresh eyes.

Our evaluation is far from academic because the fluvial systems occupied by dolphins have been and continue to be subjected to dramatic environmental changes associated with water development, a general decline in the availability and quality of fresh water, and global climate change. Regarding this last, although global warming will generally result in increased precipitation, the effects will be spatially and temporally uneven, and declines are expected in some areas [1]. Also, sea-level rise is expected to result in the loss of dolphin habitat in the lower reaches of rivers due to salinity encroachment and increased sedimentation [2].

The recent extinction of the Yangtze River dolphin or baiji *Lipotes vexillifer* [3] adds a sense of urgency for understanding the vulnerability and resilience of freshwater dolphins to environmental change. Although fishery interactions were probably the primary cause of the baiji's precipitous decline [4], the construction of extensive flood control, hydropower, and irrigation projects in the Yangtze River and its tributaries, resulting in extensive habitat loss [5], was almost certainly a contributing factor [6].

This paper consists of three main parts. First, we introduce the species, their taxonomic and ecological groupings, habitat selection, and social ecology. Next, we attempt to analyze the adaptability of these animals to variable environmental conditions, and, by inference, we consider whether they are better described as generalists or specialists according to particular criteria. Finally, we identify ways in which river dolphins might and might not be regarded as indicator species or, alternatively, as informative species.

## 2. The Species and Their Habitat

**2.1. Systematics and Taxonomy.** Adaptation to fluvial habitat provides an organizing principle for our concept of river dolphins in this chapter. Cassens et al. [7] described the river dolphins as “a wastebasket nonmonophyletic ... taxon consisting of relict dolphin lineages from the Eocene, Oligocene, and early Miocene” that developed extreme ecological specialization. Those authors were referring to what are sometimes regarded as the “true” river dolphins belonging to four extant families: Platanistidae, Lipotidae (although this family is now likely extinct), Iniidae (Table 1), and Pontoporiidae. Although the systematics and taxonomy are still unsettled, for convenience, we accept Rice’s [8] synthesis. He considered each of the four families to contain only a single living species, each endemic to a well-defined and restricted geographic setting. In two cases, he designated subspecies. Thus, Platanistidae consists of the “blind” dolphins of the South Asian subcontinent: species *Platanista gangetica*, subspecies *P. g. gangetica* (Ganges or gangetic dolphin), and *P. g. minor* (Indus dolphin); Iniidae consists of the species *Inia geoffrensis* of South America, with the subspecies *I. g. geoffrensis* (Amazon dolphin or boto), *I. g. humboldtiana* (Orinoco dolphin), and *I. g. boliviensis* (Bolivian dolphin of the Madeira River drainage). In both families, there is ongoing debate on whether multiple species should be recognized. No such debate surrounds the other two families—Lipotidae, consisting of *Lipotes vexillifer*, the baiji, and Pontoporiidae, consisting of *Pontoporia blainvillei*, the franciscana or La Plata dolphin. The latter is anomalous as it lives in estuarine and coastal marine, not fresh, waters along the eastern coast of South America and is not considered further here. Its inclusion among the “true” river dolphins is based on superficial similarities of skull features and body morphology, probably the result of convergent evolution from inhabiting a similarly turbid environment [7].

Although perhaps not as extreme, the adaptations to life in fresh water exhibited by several other primarily marine cetacean taxa are noteworthy. These, what we call facultative (as opposed to obligate) river cetaceans (Table 2), are dolphins of the genus *Orcaella* and genus *Sotalia*, and the narrow-ridged finless porpoises (*Neophocaena asiaeorientalis*). The systematics and taxonomy of these genera have been and remain in considerable flux. *Orcaella* was divided recently into two species, the Irrawaddy dolphin *O. brevirostris* and the snubfin dolphin *O. heinsohni* [9] but only the former has freshwater-living populations (in the Irrawaddy, Mekong, and Mahakam rivers of Southeast Asia). *Sotalia*, too, was divided recently into two species [10], with the tucuxi *S. fluviatilis* apparently confined to the Amazon system (which would make it an obligate freshwater species) and the Guiana dolphin *S. guianensis* occurring in coastal marine waters of northeastern South America and eastern Central America but also far up the Orinoco River of Venezuela (making it a facultative freshwater species). Due to the close taxonomic affinity of these two species and recent splitting of them (which means that most of the literature lumps them together) and their distinct evolutionary differences from the “true” river dolphins, which all have much longer

species’ histories and occupy their own families, we provisionally treat both the tucuxi and the Guiana dolphin as facultative freshwater species. We acknowledge, however, that this situation presents an exception to the concept of obligate (or “true”) versus facultative freshwater cetaceans and may challenge our theory (explained below) about their respective differences as resilient generalists or adaptive specialists. A similar situation exists for the finless porpoises. One population of the narrow-ridged species (subspecies *N. a. asiaeorientalis*) occurs throughout the Yangtze River system in China. It was sympatric with the baiji and its historic range extended all the way from Three Gorges to the South China Sea, including large appended lakes (Poyang and Dongting).

**2.2. Anatomical and Behavioural Adaptations to a Running-Water Environment (Including River-Appended Lakes and Flooded Forests).** The three living forms of “true” river dolphins that inhabit rivers and lakes share superficial morphological traits, including reduced eyes, large paddle-like flippers, unfused cervical vertebrae (which allows considerable neck movement), and a long, narrow rostrum (beak) with numerous sharply pointed teeth. Considering the early divergence of the “true” river dolphins within the order Cetacea [11, 12], these shared features offer an excellent example of convergent evolution.

The loss of visual acuity is presumably related to its high metabolic cost and the limited usefulness of vision in the highly turbid waters that generally distinguish the habitat of these dolphins. As implied earlier, the Ganges and Indus dolphins are functionally blind: their eyes lack a crystalline lens. They are likely able to distinguish up from down during daylight but otherwise depend on a sophisticated auditory sense, including echolocation, to navigate, avoid obstacles, and capture prey.

A long, narrow beak, large flippers, and flexible neck provide obvious foraging advantages in freshwater environments, which are generally characterized by a greater degree of structural complexity, including local hydraulics, compared to coastal and pelagic marine waters. In the case of botos, these traits enable the animals to take advantage of foraging opportunities that arise as rivers spill over their banks and inundate the surrounding forest [13]. They enter the forest and chase and capture fish (and other organisms such as molluscs, crustaceans, and young turtles) among submerged roots, branches, and tree trunks. Botos are unique among toothed cetaceans in having differentiated teeth, with the posterior ones cusped and capable of crushing armoured catfish that are included in their catholic diet [13]. Whether the other river dolphins similarly foraged in the same kind of habitat before the surrounding land was deforested and the rivers were entrained by embankments and infested with other water regulation structures is unknown. In South Asian river dolphins, an extraordinarily long beak, sometimes curved to one side at the tip, is sexually dimorphic to females [14]. These dolphins have been observed rooting around with their beaks in the nooks and crannies of woody debris, attempting to catch fish associated with this type of microhabitat structure [15].

TABLE 1: Details on the conservation status, behavior, and ecology of the obligate freshwater dolphins (i.e., “true” river dolphins). Information on Ganges and Indus dolphins from [16–20]; Amazon dolphin or boto from [13, 21–26]; Yangtze dolphin or baiji from [4, 6, 27–29]. EN: endangered, DD: data deficient, CR: critically endangered, and PE: possibly extinct.

Species	IUCN Red List status and justification*	Aggregation size <sup>†</sup>	Seasonal movements	Habitat preferences	Observations of sociality	Prey
Ganges and Indus dolphins	EN—Reduction in population size of more than 50% in three generations (60 years) inferred given that dam construction associated with the range declines of both subspecies occurred after 1944.	Alone or in clusters of 2–3, but occasionally as many as 25 present in the same area.	Range expansion into smaller tributaries and sometimes into irrigation channels as water levels rise.	Countercurrents and deep pools located downstream of channel confluences and sharp meanders. Generally in the deepest river channel and less common in secondary channels.	Few observations reported except for mother-young associations, and observations of mating.	At least 36 teleost fishes and four crustaceans.
Amazon dolphin or boto	DD—Previously listed as VU but it is now considered DD due to limited information on threats, ecology, and population numbers and trends.	Variable from solitary to small groups.	Some resident to specific areas year-round whereas others move several tens to hundreds of km.	Prefers river edges, confluences, and seasonally flooded lakes and channels off the main rivers. At high water, many animals utilize fish resources of the flooded forest.	Sometimes form loose groups that fish in a coordinated fashion. Interspecific play in the wild and food sharing in captivity. Male-on-male aggression common.	Wide variety of prey including at least 43 fishes, generally bottom feeders and including armoured catfish, as well as small turtles.
Yangtze dolphin or baiji	CR (PE)—Total number of mature individuals <250, a continuing decline is projected and all individuals belong to a single population. Recent survey found no animals.	1–4 but occasionally as many as 10, although broken up into several subgroups.	Range apparently expanded upstream when water levels were high and then contracted downstream when water levels were low.	Generally found in eddy countercurrents below meanders and channel convergences. Also, historically in lakes appended to the Yangtze mainstem.	Little information available but side-by-side swimming has been reported, with a group of four individuals splitting apart when disturbed but rejoining later.	Various fishes, including surface and bottom feeders. Only limitation appears to be size (<6.5 cm in width and <250 gm in weight).

\* See IUCN (2001) for details on Red List categories. <sup>†</sup> The term “aggregation” includes both social groups and clusters that form due to the common use of habitat. In practice, these are often difficult to tell apart on the basis of surfacing behavior and the context of “group size estimates” is often unclear in the literature.

TABLE 2: Details on the conservation status, behavior, and ecology of riverine populations of the facultative freshwater cetaceans. Information for the Yangtze finless porpoise from [30, 31]; tucuxi from [32–34]; Irrawaddy dolphin from [2, 35–38]. VU: vulnerable.

Species/subspecies	IUCN Red List status and justification	Group sizes or aggregations	Seasonal movements	Habitat preferences	Observations of sociality	Prey
Yangtze finless porpoise	EN—Population <2,500 mature individuals with a continuing decline and all individuals in a single subpopulation.	3–6 but occasionally as many as 20 in the Yangtze	Indirect evidence from changes in density that some porpoises move upstream during the high-water season.	Nearshore waters in the Yangtze.	Little socializing observed on the surface. Chasing observed in captivity.	Opportunistic feeder on wide variety of demersal fishes, cephalopods, and crustaceans.
Amazon and Orinoco tucuxi	DD—Lack of basic information (e.g., abundance, population structure, bycatch rates).	Generally 1–6 with a mean in the Amazon of 3.3 and maximum of 30.	May enter lake systems during high water but generally avoids flooded forests.	Similar to boto, tucuxis show a distinct preference for river junctions.	Group feeding observed.	A wide variety of fishes (at least 28 species), mostly small schooling species.
Irrawaddy dolphin	VU—At least a 30% reduction in the rangewide population size over three generations (45–48 years) inferred from increasing bycatch and habitat degradation. Five geographically isolated populations (including three riverine) are CR.	2–6 but up to 15 when two or more groups come together.	Some evidence of range expansion into smaller tributaries during high-water season. Seasonal movements in response to changes in freshwater flow in the Sundarbans Delta. Apparent small home ranges and individual fidelity to confluences in the Mahakam River.	Deep pools of large rivers and nearshore marine environments (including appended lakes or lagoons) with freshwater inputs.	Fission-fusion group dynamics with frequent social interactions. Cooperative feeding, both intraspecific and with cast-net fishermen, reported in the Ayeyarwady River.	At least seven fishes (two Pangasiidae and five Cyprinidae) and various shrimps in the Mekong. Probably many more based on catches of cooperative fishermen in Ayeyarwady River.

A striking feature of the boto's habitat is its dramatic seasonal variability. As summarized by Martin and da Silva [13] referring to the central Amazon, Brazil, "from low to high water the main rivers lose sandbanks and associated shallows, lowland forest is flooded to a depth of several metres, and floodplain depressions become lakes. All these changes are matched by large-scale movements of fish." In contrast to Amazonia (and Orinoquia, the other major aquatic system occupied by botos; cf. [39]), the fluvial systems currently inhabited by the South Asian river dolphins and (until recently) baijis have been transformed by centuries of human occupation and endeavour. Although considerable seasonal flux in water levels and riverbed morphology still occur in these latter systems, the scale, timing, and complexity of that flux have unquestionably changed as a result of deforestation, the construction of dams and embankments, and a declining water table. It is nevertheless reasonable to assume that selective forces broadly similar to those of the Amazon have helped shape the socioecology of Asian river dolphins on an evolutionary timescale.

Life for cetaceans in running-water environments is more energetically demanding than in oceanic environments because these animals must constantly swim upstream just to maintain their position along the river's axis. A behavioural response exhibited by river dolphins to this challenge is a distinct preference for occupying countercurrent pools where they find refuge from downstream currents and where much of the biological productivity is concentrated. Their affinity for countercurrents is probably most pronounced in the far upstream reaches of their range (i.e., in low-order tributaries) where the forces of downstream flow, due to a relatively steep geomorphic slope, are most intense (e.g., in the Karnali River, Nepal [15]), and least pronounced in the mainstem of large rivers where countercurrents are less circumscribed (e.g., in the Brahmaputra [40]). A strong affinity for countercurrents has also been noted for Ganges River and Irrawaddy dolphins at the ecotonal limit of the downstream range of the former species and the upstream range of the latter species in the Sundarbans mangrove forest, where tidal currents also contribute to the hydraulic structure of their running-water habitat [2, 41].

With regard to social ecology, is there anything in the social organisation or affiliative behaviour of river cetaceans that might be interpreted as an adaptation to living in a riverine, or indeed lacustrine, environment? Factors that could influence sociability are (a) defence against predation or bullying, (b) foraging efficiency (e.g., resource partitioning, cooperation in detection of food patches, cooperative capture of prey), (c) enhancement of reproductive success (e.g., communal care of young, territoriality), and (d) avoidance of inbreeding (i.e., enhancing genetic fitness).

Although the individual and group behaviour of the "true" river dolphins has been little studied, available information suggests they are generally less sociable than most marine cetaceans. Their group sizes are generally small (especially compared to most other toothed cetaceans); few interspecific interactions, with the exception of mating and in the case of botos male-on-male aggression, have been reported; the sole attractive force for animal clusters, with the

exception of mother-young pairs, appears to be the concentrated nature of resources and hydraulic refuge in river systems, including appended water bodies.

Far from being maladaptive, the relatively low sociability of these species probably confers distinct advantages for a large, mobile predator living in riverine and backwater environments. With the exception of humans, river dolphins have no known predators, so the protective advantages of group living are largely irrelevant. Although temporally and spatially variable, the locations of their food are predictable at a river basin level according to hydrological cues from the seasonal flood pulse and at a local level according to geomorphic, hydraulic, and vegetative structure. This means that the detection of food patches is probably not an important factor selecting for sociability. The argument could be made that communal defence of food patches selects for group living. However, the temporal dynamism, three-dimensional character, and physical properties of lotic systems (which limit the potential range of sensory perception despite the fact that river dolphins are equipped with highly adaptive and effective echolocation abilities) imply that establishing and maintaining defensible territorial boundaries would be difficult at best, regardless of whether the animals occurred in groups or as individuals. In terms of reproductive success, including avoidance of inbreeding, the predictable but dynamic and difficult-to-defend patches of hydraulic refuge and food and the higher travel costs (see [42]) associated with running waters (which would particularly affect newborn animals) suggest that nongregariousness would be adaptive to the circumstances of life in a riverine environment.

A caveat is that the difference in sociability between the "true" river dolphins and the facultative freshwater species, which are more inclined towards group living, might imply that selective forces affecting river cetaceans can be attractive as well as repellent (even in the same rivers—e.g., the Orinoco and Yangtze where obligate and facultative freshwater species are, or once were, sympatric or partially so), depending on a species' evolutionary niche. Irrawaddy dolphins, tucuxis, and possibly finless porpoises are notably more social than the "true" river dolphins. For example, Irrawaddy dolphins exhibit cooperative feeding behaviour [35, 43], as well as fission-fusion activity, meaning that, during only a few surfacings, the animals split into multiple groups and then coalesce into a single group and then split apart again into some other configuration [44]. Tucuxis also forage in groups, converging simultaneously around a fish school, as well as alone [32].

In the case of the Sundarbans mangrove forest where the ranges of Ganges River and Irrawaddy dolphins meet, the former clearly dominate in freshwater areas and the latter are generally limited to areas with salinity levels greater than about 5 ppt, with distinct environmental partitioning between the two species, according to isohaline gradients. This might imply that the upstream range of Irrawaddy dolphins is more constrained by interspecific competition with Ganges river dolphins than by a dependence on a particular salinity threshold [2]. In fact, Irrawaddy dolphins occur far upstream in three other large Asian rivers (Ayeyarwady,

Mekong and Mahakam; see [45]) that are not inhabited by Ganges or Indus river dolphins.

### 3. Are River Dolphins Specialists or Generalists?

In exploring the subject of specialist versus generalist tendencies, we are well aware of the difficulty of defining “river dolphin” and therefore of the risk of painting our story with too broad a brush. In other words, there is danger that generalist resilience ascribed to one species could be mistakenly extrapolated to another species simply because both are cetaceans living in freshwater systems. One might expect, *a priori*, that the boto, baiji, and South Asian river dolphins, found solely in freshwater habitat, would be more specialized than the Guiana and Irrawaddy dolphins and finless porpoises, all of which occur across the spectrum of habitats from marine to estuarine to fluvial.

Although the emphasis of this paper is on the obligate river dolphins, comparisons with the facultative freshwater species provide some of the most compelling evidence supporting the view that, at a local scale, the obligate species are opportunists (generalists) capable of adapting to a wide range of environmental conditions while, at a river basin scale, they may be pushing the limits of their ecological resilience, more closely resembling specialists.

Similar to the other “true” river dolphins, baijis had an awkward appearance and their swimming performance and respiration rates were described as relatively slow compared to those of the much more streamlined and active finless porpoises [27, 46]. The slower swimming speed and longer dive times of baijis were probably related to their strong affinity for deep pools located within the hydraulic refuge of countercurrents [28]. Less is known about the habitat selection of finless porpoises, but they appear to be far more flexible in terms of the riverine environments they occupy.

Numerous surveys in the Yangtze River have indicated a declining population of finless porpoises, especially in the upper reaches where baijis seem to have disappeared earlier than in the middle and lower reaches [47]. The immediate cause of the precipitous decline of baijis was probably direct mortality from entanglement in gillnets, snagging on long-lines with multiple hooks, and electrocution from illegal fishing with electricity. However, the massive alteration of their riverine habitat caused by water engineering projects (see [5]) was almost certainly a contributing factor. One of the primary impacts of such projects was the simplification of river channels (i.e., countercurrents were reduced in size or eliminated as waterways became more canal-like in their geomorphic structure). It is possible that, at a local level, the affinity of baijis for countercurrents promoted generalist tendencies, allowing the animals to take advantage of the high diversity of prey supported by the abundant microhabitats occurring within these hydraulically complex nodes. However, at a river-basin level, their dependence on these fluvial features probably put them at increased risk as humans transformed the river and its appended lake systems. In contrast, finless porpoises may be somewhat better adapted (due in part to their more streamlined body

shape) to survive in running waters with reduced hydraulic refuge. Admittedly, this supposed difference is based solely on circumstantial evidence. If true, however, it would mean that baijis could be considered generalists at a local scale, which might help explain why they managed to survive in much of the Yangtze River system from the middle Miocene (see [11]) to the present day (almost), despite centuries of relatively intense and prolonged human activity on and along the river. In contrast, they would have to be considered specialists at the basin scale, having finally proven unable to adapt to the wholesale transformation of the Yangtze system achieved by human activity in the 20th century. Finless porpoises, on the other hand, appear to exhibit generalist tendencies at both local and river basin scales. This would imply that their conservation prospects in the Yangtze are at least somewhat more favorable than those of the baiji, although even the most resilient generalists have their ecological limits, as humans in some areas are beginning to find (e.g., with famines in much of sub-Saharan Africa transforming previously productive lands into barren deserts). Also, as Zhao et al. [47] emphasized, the continuing threat of incidental mortality in fisheries may yet prove sufficiently potent to nullify any resilience the porpoises may have in terms of adapting to environmental change.

No facultative freshwater cetaceans occur within the range of Ganges and Indus dolphins, except as mentioned above in a very narrow, seasonally mobile band of distributional overlap between Irrawaddy and Ganges dolphins in the Sundarbans mangrove forest. This situation might be expected, given that *Platanista* (a sister taxon to all other members of the Odontoceti suborder [11]) has had since the late Neogene, when it remained in shrinking epicontinental seas as sea levels receded, to finely tune its adaptations to a running-water environment. This long evolutionary history probably allowed *Platanista* to become an unrivalled freshwater specialist, occupying a wide range of ecological niches that might otherwise be available for potential range extensions of facultative freshwater cetaceans (e.g., Irrawaddy dolphins or finless porpoises that inhabit adjacent coastal waters). Indeed, Miller [48] distinguished *Platanista* as the most highly modified species within the order Cetacea. It follows that the other obligate river dolphins appeared much later in the middle Miocene and share their habitat today with facultative freshwater cetaceans. Interestingly, the only large, mobile predator that may have rivalled the dominance of *Platanista* in the Ganges and Indus rivers is the gharial *Gavialis gangeticus*, a critically endangered [49], exclusively riverine, and piscivorous crocodylian that, similar to Ganges and Indus river dolphins, is a monotypic, relict species with a highly modified long snout—another striking example of convergent evolution.

The apparent contradiction between *Platanista*'s identification as a running-water specialist, and at the same time as a species with generalist tendencies allowing it (both subspecies) to essentially monopolize the ecological niches available for secondary occupancy by other cetaceans, may be resolved by considerations of scale (river-basin versus habitat). Support for considering Ganges and Indus dolphins to be resilient generalists at the habitat scale but vulnerable

specialists at the river-basin scale can be inferred from their population-level responses to habitat modification. Extensive flow regulation structures were built, mostly in the 1950s through 1980s, in both the Ganges (at least 19 high dams (defined as an artificial barriers with a height of 15 m or more that are constructed across a watercourse to impound water and regulate flow for generating hydroelectricity and flood prevention) and 23 barrages (defined as low-gated dams used to divert water for irrigation, flood control, and/or navigation purposes; normally the gates remain closed during the low-water season and are opened during the high-water season with differing levels of regulation in between)) and Indus (at least 8 high dams and 17 barrages) systems [5]. Prior to that construction binge, the distribution of both subspecies reportedly extended to the Himalayan foothills where rocky barriers, high water velocity, or shallow water blocked farther upstream movement by dolphins [50]. Not surprisingly, marked declines have occurred in the ranges of both subspecies since the 19th century.

In the Indus, dolphins historically occurred in approximately 3,400 km of the main channel and its tributaries, but they are now found in only about 1,000 linear km of downstream reaches in the main channel, with 99% confined to a 690 linear km segment [16]. In the Ganges system, the situation is less clear, but substantial portions of the dolphins' range, particularly in upstream areas, have been lost. For example, no dolphins have been reported in recent years in a river segment approximately 100 km long between the Madhya Ganga Barrage and the Bhimgoda Barrage, at the upstream limit of their historical range in the Ganges [51]. In recent years, dolphins have not been reported in the Yamuna River above the Chambal River confluence during the dry season but that segment might still be occupied during the high-water season [51]. Historically, dolphins were found year-round in the Yamuna River about 400 km upstream to Delhi [50]. Finally, Ganges dolphins apparently have also been extirpated from a 300 linear km segment of the Son River, above and below the Indrapuri Barrage (at least during the dry season) and upstream of the Ganges confluence [52].

It is difficult to differentiate between the impacts of population fragmentation [53] and habitat degradation [54] caused by dam construction, but a clear pattern of extirpation from upstream segments, where the animals are probably more dependent on hydraulic complexity, is evident from the reported range declines summarized above. In the middle and lower reaches of the main channel, where the animals may have more flexibility in how they use habitat due to the less circumscribed nature of countercurrents and the greater availability of hydraulic refuge induced by minor geomorphic features (e.g., slight sinuosity) and where greater productivity is generally realized from the seasonal flood pulse, "densities" of both species remain quite high. For instance, a mean encounter rate of 1.8 dolphins/linear km was reported for the Vikramshila Gangetic Dolphin Sanctuary [17] in approximately the middle of the Ganges River, and 3.6 dolphins/km in the Sindh Dolphin Reserve between the Guddu and Sukkur barrages slightly downstream of approximately the middle of the Indus River [16]. In the latter, the dolphin population is believed to be increasing,

due to either unidirectional immigration from upstream segments of the river (as dolphins move downstream through barrage gates but presumably have difficulty returning due to high-velocity, turbulent flows), increased recruitment within the Guddu-Sukkur segment following implementation of a ban on hunting in 1972, or some combination of both [16].

The dramatic range declines of both Ganges and Indus dolphins constitute a significant threat to the survival of *Platanista* (which, as was the case with the baiji, means the survival of an entire mammalian family). Nonetheless, their apparently high population densities where suitable habitat remains, in many cases despite local factors threatening both subspecies (e.g., incidental catches, illegal hunting, pollution), suggest that these dolphins are fairly resilient (albeit within limits) as generalists at a habitat scale but exceedingly vulnerable as specialists at a river basin scale. Also, it again implies that the distributional responses of *Platanista* populations to basin-wide ecological impacts (whether human-induced or natural) are informative about their extinction risk, as well as about declines in associated biotic diversity, while their local behaviour patterns may provide important insights about the ecological characteristics of their habitat.

#### 4. River Dolphins as Indicator or Informative Species

Zacharias and Roff [55] differentiate between "compositional indicators," which signify a particular habitat, community, or ecosystem, and "condition indicators," which are used for biological monitoring of environmental changes resulting from anthropogenic and natural disturbances. At face value, river dolphins make poor compositional or condition indicators. Indeed, the species often appear to satisfy their life history needs in environmental conditions that are "in every sense marginal" [56], and their life history characteristics are opposite of what are generally considered necessary for scientifically defensible indicators, including occupation of a highly specific ecological niche (see [57]). However, as large, mobile predators, the manner by which river dolphins satisfy their life history needs (e.g., movement patterns, habitat use, foraging behaviour, etc.), may give them particular value for identifying ecologically significant attributes, including local aggregations of biological productivity for site-based protection, and for monitoring changes in these parameters. We suggest that using the indicator properties of cetaceans (i.e., observable adaptive responses), rather than simple measures of animal presence-absence or relative abundance, makes it possible to turn the concept of indicator species on its head. In other words, the very plasticity of cetaceans, which is a feature that in some ways undermines their utility as conventional compositional or condition indicators, can be used for making certain ecological inferences.

The term generalist carries the unfortunate connotation of haphazard indifference to habitat, whereas the concept of adaptive resilience implies an ability to exquisitely apply an array of specific survival and reproductive strategies under a range of environmental conditions. Thus, even though the basic resources needed by a generalist for survival may

be generic—food, refuge from energy-draining, and injurious environmental forces, reproductive opportunities the strategies river dolphins use to gain access to such resources and their adaptive responses to changing conditions can be informative about critical habitat features. One advantage of cetaceans (versus most other aquatic species) as informative species is that they can be observed, counted, and tracked. One can tell where they are located and to a certain degree what they are doing simply by surface observations and also by listening (both above the water surface, where their respiration sounds are often heard, and underwater, where their vocalizations are virtually constant).

*Homo sapiens*, a quintessential generalist, can hardly be considered an indicator or informative species nowadays. We sequester and consume vastly more resources than are needed to sustain and perpetuate our own species, and we have suppressed or obliterated many of the ecological feedback processes that might be informative, if not also indicative. However, in looking back on our days as hunter-gatherers, it could be argued that ours was, at that time, an informative species. As just one example, the controlled burning of grasslands by nomadic or seminomadic hunters would have demonstrated the importance of open forests and meadows to large herbivorous wildlife.

Understanding the habitat preferences of freshwater cetaceans and tracking changes in their fine-scale distribution has strong potential for informing us about habitat quality and perhaps, at least indirectly, the population status of other biota. By investigating and monitoring the physical and biological dependencies of river cetaceans and how these change in the context of altered environmental conditions, much can be learned about the conditions needed to conserve and maintain high levels of biological diversity and productivity in the river systems where these animals occur.

In assessing a species' value as an ecological indicator, it is necessary to differentiate between or among geographic scales. As generalists, freshwater cetaceans make poor indicator species, *per se*, but, at a local level, their adaptive resilience makes them particularly informative for understanding critical habitat features. For instance, at the far upstream range of their distribution, the wide variety of foraging strategies exhibited by Ganges River dolphins in the Karnali River provides information on the role of hydraulic complexity in structuring habitat and demonstrates the importance of woody debris for maintaining biological productivity in low-order tributaries that do not enjoy the same magnitude of nutrient influx from flood recession as downstream river segments. Similarly, information on the catholic diet of botos and their sexually dimorphic patterns of habitat use (see [21]) provide valuable clues about the local movements and environmental requirements of their diverse prey.

Meanwhile, at a river-basin level, the specialist tendencies of “true” river dolphins can be informative about critical ecological processes. These species are profoundly tied to the physical characteristics of their environment. Besides their need for osmotic regulation, they require sufficient freshwater flow to allow movement between deep pools and they need access to hydraulic refuge from high-velocity currents [54]. Their movement patterns and fine-scale distribution

may therefore be informative about the hydrologic regimes (e.g., timing and magnitude of the seasonal flood pulse) and sediment dynamics (e.g., erosion and deposition patterns) needed for maintaining native species diversity and abundance in large floodplain rivers, which are coming under increasing stress from human use and abuse. For instance, understanding and monitoring the ecology of Ganges River and Irrawaddy dolphins in the Sundarbans mangrove forest may provide useful insights on the impacts of declining freshwater supplies and sea-level rise [2]. Such insights may, in turn, contribute to the development of adaptive management strategies that allow biodiversity to be conserved even as human communities themselves struggle to adapt and survive in a rapidly changing environment.

## 5. Conclusion

As mentioned at the beginning, the aim of this paper was to develop ideas and stimulate debate concerning the generalist and specialist characteristics of river cetaceans and to point out ways that observations of these animals might be informative concerning the environments where they live. Among the topics discussed were the importance of considering geographic scale, probable differences in the resilience to environmental change between the obligate and facultative freshwater cetaceans, and the relative value of both species groups for identifying and monitoring habitat attributes and ecosystem processes.

Each of the obligate freshwater dolphin species is uniquely situated along a spectrum of human-induced disturbance and species endangerment, with the position (or status) of the boto being the most favourable, albeit still vulnerable, within the comparatively undisturbed Amazon, Madeira and Orinoco basins. The Ganges and Indus dolphins are endangered within the highly modified Indus and Ganges river basins, and the baiji is functionally if not entirely extinct, having been drawn into what might be described as a classic extinction vortex in the extremely modified and degraded Yangtze Basin. Regardless of how discouraging this interpretation of the situation may be, it allows one to see how the various species might be used to inform freshwater conservation and management. Thus, the boto might be regarded as a “control” of sorts, the Ganges and Indus dolphins as subjects of experimental manipulation (living as they do in highly modified systems but with remaining patches of relatively high-quality habitat), and the baiji as an extreme demonstration of the limits of resilience or, put another way, an example of the inevitable consequences of complacency and inaction.

Perhaps the most definitive conclusion that can be drawn from this paper is that more empirical studies are needed on the habitat preferences and ecology of freshwater cetaceans (although for the baiji, this would have to be a retrospective analysis), both to inform conservation efforts on behalf of these endangered animals (whether as generalists, specialists or, depending on geographical scale, both) and to help address broader concerns related to biodiversity conservation and the sustainability of human use in several of the world's largest rivers systems.

Two promising initiatives exemplify how these types of studies have already been used for conservation planning: the South American River Dolphin Protected Area Network and the Bangladesh Cetacean Diversity Protected Area Network, the latter also including marine species [58]. Both initiatives seek to conserve freshwater cetacean diversity (Amazon, Bolivian, Orinoco, Guiana, and tucuxi dolphins in the former; Ganges and Irrawaddy dolphins in the latter) at a variety of spatial scales and to use ecological information from priority habitat to better understand alterations in river-basin processes, due to water development and climate change, and inform adaptive conservation management.

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