

Marine mammal behavior: a review of conservation implications

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PB initiated the review and with assistance and comments from SRXD developed the submitted the revised manuscript.

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Abstract

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The three orders which comprise the extant marine mammals exhibit a wide range of behaviors, varying social structures and differences in social information use. Human impacts on marine mammals and their environments are ubiquitous; from chemical and noise pollution, to marine debris, prey depletion and ocean acidification. As a result, no marine mammal populations remain entirely unaffected by human activities. Conservation may be hindered by an inadequate understanding of the behavioral ecology of some of these species. As a result of social structure, social information use, culture and even behavioral syndromes, marine mammal social groups and populations can be behaviorally heterogeneous. As a result responses to conservation initiatives, or exploitation, may be complex to predict. Previous commentators have highlighted the importance of incorporating behavioral data into conservation management and we review these considerations in light of the emerging science in this field for marine mammals. Since behavioral canalization may lead to vulnerability, whereas behavioral plasticity may provide opportunity for resilience, we argue that for many of these socially complex, cognitive species understanding their behavioral ecology, capacity for social learning and individual behavioral variation, may be a central tenant for their successful conservation.

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10 **Abstract**

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12 varying social structures and differences in social information use. Human impacts on marine
13 mammals and their environments are ubiquitous; from chemical and noise pollution, to marine
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22 lead to vulnerability, whereas behavioral plasticity may provide opportunity for resilience, we argue
23 that for many of these socially complex, cognitive species understanding their behavioral ecology,
24 capacity for social learning and individual behavioral variation, may be a central tenant for their
25 successful conservation.

26 **1 Introduction**

27 The extant marine mammals are found in three Orders *Cetacea*, *Sirenia* and *Carnivora* (including
28 suborder *Pinnipedia*, Family *Mustelidae* and Family *Ursidae*). These species inhabit a diverse range
29 of habitats from river, brackish, mangrove and estuarine habitats, to coastal shallows and pelagic
30 seas, with some even foraging at the edge of the abyssal plain. In addition, they have a diverse range
31 of food items, from seagrass or zooplankton, through to fish, penguins and other marine mammals.
32 As a result of their diverse niches, they exhibit a wide range of behaviors. Some of their behaviors
33 have been studied in detail, whereas others remain more mysterious. For example, the exceptional
34 migration of the baleen whales is well documented, while details about the more subtle, small-scale
35 behavioral differences between marine mammals social groups is only now starting to emerge.

Marine mammal behavior: conservation implications

36 The importance of incorporating behavioral ecology into conservation efforts has long been argued
37 for terrestrial mammals (Candolin and Wong, 2012; Caro and Durant, 1995; Sutherland, 1998),
38 particularly where manipulations of the wild environment are possible to assist conservation efforts.
39 The challenge that remains is to determine how insights into behavioral ecology can best be used to
40 inform conservation efforts in the more alien marine environment.

41 Sociality and social learning are undoubtedly important considerations when conserving marine
42 mammals. In 2010 Whitehead suggested that several factors complicate the conservation of species
43 that learn socially, such as the rapid spread of novel behavior, the evolution of maladaptive behavior,
44 or the inhibition of adaptive behavior (Whitehead, 2010). He argued that such factors have an
45 influence on habitat suitability, responses to anthropogenic change and even genetic structures. This
46 is reflected in an analysis which revealed that of the toothed whales (*Odontoceti*), four species
47 showed evidence of decrease in birth rates following exploitation, highlighting the effects beyond the
48 dynamics of individual removals (Wade et al., 2012).

49 Behavioral variation among populations and individuals also has the potential to influence responses
50 to management efforts and to enhance or hinder conservation. For example, understanding sperm
51 whale (*Physeter microcephalus*) depredation of sablefish from demersal longlines across the Alaskan
52 fishery has only been possible with emerging knowledge about the scale and spread of this behavior
53 and whether noise from fishing vessels may be providing an acoustic cue for these whales (Thode et
54 al., 2015). While research on killer whale (*Orcinus orca*) response to an acoustic harassment device,
55 to prevent long-line depredation, indicated habituation to the device (Tixier et al., 2015). However,
56 despite being habituated to the device, exposure to the sound it produces while depredating lines may
57 result in potentially harmful hearing damage (Tixier et al., 2015).

58 In 1998, Sutherland noted that ‘The exciting research developments in animal behavior over the last
59 two decades have had a negligible impact on conservation’. He then reviewed 20 subjects in which
60 the study of behavioral ecology could make a significant contribution to conservation (Sutherland,
61 1998). Here we review this list specifically for marine mammal conservation, in light of the
62 subsequent 18 years of research, and suggest some potential additions to the list.

63 **2 Small population extinctions**

64 Genetic, ecological and behavioral factors can all contribute to making small populations particularly
65 vulnerable to extinction. One of the most significant challenges for marine mammal conservation is
66 determining demographically independent conservation units, based on acoustic, taxonomic, genetic,
67 geographic, behavioral, social or ecological features (Parsons et al., 2015). In highly social species,
68 behavior may play a particularly important role in differentiation between units to conserve and in
69 understanding the mechanisms of population persistence or decline.

70 Social species may benefit from the presence of conspecifics in a number of ways including
71 predation risk dilution, collective anti-predator vigilance, ‘selfish herd’ effects, predator confusion,
72 cooperative foraging, resource defense, increased availability of suitable mates, allo-parental care and
73 reduction of inbreeding (Krause and Ruxton, 2002; Stephens et al., 1999). Whilst a handful of marine
74 mammal species are solitary, many are social for at least part of their life cycle and as numbers
75 decrease the ability to raise the alarm, defend against predators, forage or breed cooperatively also
76 generally declines. The Allee effect (Allee, 1931), which may result in precipitous decline, is defined
77 as a positive relationship between any component of individual fitness and density of conspecifics
78 (Stephens et al., 1999). But it is necessary to differentiate between component Allee effects (at the

79 level of individual fitness) and demographic Allee effects (at the level of mean fitness), which may
80 be important for predicting the persistence of small populations, particularly where a decrease in
81 numbers results in reduced opportunities for cooperation. For example, obligate cooperative breeders
82 rely on a minimum group size to subsist and studies in terrestrial mammals suggest that cooperative
83 breeders (see Section 3) may be particularly susceptible to Allee effects. A new conceptual level, the
84 group Allee effect, has been suggested for cooperative breeders (Angulo et al., 2013).

85 Smaller populations may also place limitations on the ability to find a suitable mate. This may be the
86 result of changes in operational sex ratio as the population declines, which may be related to
87 population density and changes in habitat, but other sexual selection pressures, such as the specifics
88 of mate choice, may also have an influence on population growth rates, making smaller populations
89 more prone to extinction. For example, there is evidence from sperm whaling records that following
90 the reduction in abundance of larger males, that fertility rates were reduced (Clarke et al., 1980;
91 Whitehead et al., 1997). Whether this reduced fertility rate was the result of female mate choice or
92 other selection pressures is unknown.

93 Nevertheless, it has been suggested that in baleen whales, since male song may influence female
94 mate choice, that preference for local or known dialects could theoretically cause pre-zygotic
95 isolation between species, potentially a precursor to speciation (Beltman et al., 2004; Thornton and
96 Clutton-Brock, 2011). Conversely, it has also been suggested that to avoid inbreeding depression
97 female humpback whales may have a preference for novelty in song, which itself may drive the
98 evolution of the males' song (Parsons et al., 2008).

99 The matter of how to define a 'small population' has conventionally been resolved on genetic or
100 geographic parameters (or both). Nevertheless, from the perspective of determining the influence of
101 behavior for conservation efforts, delimiters based on specific behaviors may also be relevant for
102 predicting population persistence. For example, Southern sea lions (*Otaria flavescens*), which have
103 declined by over 90% in the Falkland Islands since the 1930s, exhibit two discrete foraging
104 strategies; inshore and offshore. These strategies appear to be independent of intraspecific
105 competition and are thought to be influenced by foraging site fidelity (Baylis et al., 2015). Using
106 feeding strategies as a boundary between smaller sub-sets of the population may be a vital
107 conservation tool.

108 In addition, of the three distinct populations of false killer whales (*Pseudorca crassiden*) recognized
109 around the Hawaiian Islands, a significant difference in fisheries related scarring has been identified
110 between these populations. This suggests that fisheries interactions are occurring at a higher rate in
111 one population, with a bias towards females, suggesting that fisheries-related mortality is likely to be
112 disproportionate across these distinct populations (Baird et al., 2014). Thus behavior is relevant for
113 determining 'distinct population segments' (DSP) and it has been argued that attempts to limit DSPs
114 to purely 'evolutionarily significant units' could compromise management efforts, since the use of
115 demographic and behavioral data would be reduced (Pennock and Dimmick, 1997).

116 **3 Mating systems and inbreeding depression**

117 Some marine mammal species, such as sperm whales, killer whales and elephant seals (*Mirounga* sp)
118 exhibit dramatic sexual dimorphism, with the males being considerably larger than the females. It has
119 been speculated that species which exhibit communal displays, such as leks may be more prone to
120 small population extinctions (Sutherland, 1998) (see Section 2). Whilst there is only limited data on
121 the mating display of some marine mammals (particularly for those species where mating occurs

Marine mammal behavior: conservation implications

122 underwater), sexual dimorphism may provide some clues. In sperm whales it is not known whether
123 copulation is forced by males, chosen by females or determined by other processes (Whitehead,
124 2003). Nevertheless, there is some evidence that the sexual dimorphism in sperm whales (males
125 being three times the mass of females) tips the balance in favor of ‘roving’ in higher latitudes among
126 the males (up to 27 years), before moving to warmer waters when they begin effective breeding. It
127 has been suggested that the advantages of continuing to feed and grow before seeking out females
128 outweighs the opportunity to breed sooner (Whitehead, 1994), indicating some competitive
129 advantage for larger males. In addition, it has been suggested that difference in feeding ecology
130 between males and females in resident, fish-eating killer whales of the northeastern Pacific Ocean
131 may either be a driver or consequence of sexual dimorphism in this species (Beerman et al., 2016).

132 Similarly, Northern elephant seals feed separately with males travelling north closer to shore,
133 whereas females migrate west from the coast into the open ocean. Males also forage during benthic
134 dives, whereas female foraging is characterized by pelagic dives interspersed with trips to the sea
135 floor. It has been suggested that this resource partitioning is the result of sexual dimorphism, with the
136 females’ smaller size necessitating foraging in areas with less predators (Le Boeuf et al., 2000).

137 Mating behavior clearly has implications for potential inbreeding and conservation. In Antarctic fur
138 seals (*Arctocephalus gazella*), the territoriality of males and the behavior of females searching for
139 suitable pupping locations are thought to combine to be responsible for the low re-mating frequency
140 (Bonin et al., 2016). Whilst, Wade et al. (2012) noted that in four odontocete species examined there
141 was evidence of a decrease in birth rates following exploitation. Suggested mechanisms include a
142 deficit of adult females, a deficit of adult males, and disruption of mating systems (Wade et al.,
143 2012). In addition, research on California sea lions (*Zalophus californianus*) suggests that inbreeding
144 may also increase susceptibility to some pathogens (Acevedo-Whitehouse et al., 2003).

145 It is important to understand the relationship between different breeding systems and inbreeding
146 depression (Sutherland, 1998). Inbreeding depression is the result of non-random mating of close
147 relatives, with a resultant lowering in population fitness. However, the effects of inbreeding are
148 controversial and not always easily predicted (Huisman et al., 2016), as evidenced by the case of the
149 recovering Northern elephant seal (*Mirounga angustirostris*) population. Despite at one point being
150 reduced to a population of likely less than 20 individuals, this species exhibits significant inbreeding
151 with little genetic diversity and yet the populations do not yet show any obvious signs of inbreeding
152 depression (Weber et al., 2004).

153 In contrast, the Northern right whale (*Eubalaena glacialis*) which suffered similar population
154 decimation, failed to make a similar recovery following whaling, with the total minimum population
155 currently estimated at 465 (NOAA, 2015). Research suggests that this population is suffering from
156 reduced fertility, fecundity, and juvenile survivorship. It has been suggested that these factors may be
157 the result of low genetic diversity (in comparison to other right whale populations) (Kraus et al.,
158 2001; Schaeff et al., 1997), but that the low genetic variability in this species may be the result of
159 slow but continual erosion of alleles during the last 800 years of the population’s decline (Waldick et
160 al., 2002). In addition, there is evidence for post-copulatory gamete selection in right whales,
161 thought to be the result of genetic incompatibility arising from two potential mechanisms: fetal
162 abortion when the offspring are too similar to the mother; or increased fertilization rates and
163 successful pregnancy from genetically dissimilar gametes (Frasier et al., 2013). This may further
164 complicate the influence of mate choice on genetic diversity.

165 Also in contrast to the Northern elephant seal populations, a small population of Weddell seals at
166 White Island in Antarctica, estimated to be around 80 individuals, is thought to have been founded by
167 only three females and two males. This population exhibits such profound inbreeding that it results in
168 low pup survival (Gelatt et al., 2010).

169 Nevertheless, along with the Northern elephant seal, Juan Fernandez fur seals (*Arctocephalus*
170 *philippii*), is another species that has recovered significantly despite reaching the brink of extinction.
171 Variability in response to inbreeding across marine mammals indicates that some species may be
172 more sensitive to inbreeding depression than others (Hoelzel et al., 2009).

173 **4 Species Isolation**

174 Behavior, and in particular social learning, may be drivers for speciation (Beltman et al., 2004). But
175 species isolation may cause genetic bottlenecks to develop or create independent evolutionary
176 trajectories. Behavior itself, and particularly social information use, may cause effective population
177 isolation to develop for population segments in sympatry (Riesch et al., 2012).

178 Extirpation has the potential to remove localized adaptations and potentially eliminate unique
179 evolutionary paths. It has been suggested that for the morphologically and genetically distinct
180 Maritimes walrus (*Odobenus* sp) localized extinction as a result of hunting, curtailed an evolutionary
181 trajectory that would have enabled this species to evolve along a different path to other north Atlantic
182 walrus (McLeod et al., 2014).

183 However, hybridization, a spontaneous phenomenon which is suspected in several cetacean (Brown
184 et al., 2014; Hodgins et al., 2014) and pinniped (Lancaster et al., 2010) species also has conservation
185 implications. Depending on the fitness of the hybrids, hybridization may alter gene flow and species
186 boundaries (Lancaster et al., 2010). The effects of hybridization may be difficult to predict in a
187 rapidly changing marine environment (for a review see Schaurich et al., 2012). For sympatric species
188 (living in the same or overlapping habitat), behavioral diversity, such as different habitat use
189 resulting from foraging specializations, may help to reduce encounter rates between species and
190 maintain discrete gene pools (Sobel et al., 2010).

191 **5 Dispersal in fragmented populations**

192 The degradation of habitats can lead to the fragmentation of populations and remains an ongoing
193 conservation issue. Key causes of population fragmentation in marine mammals are displacement,
194 through noise, fishing, harassment or some other environmental stressor, or change in prey
195 abundance or dispersal. Some species may be better equipped to adapt to differing food availability,
196 for example through adapting foraging specializations (Ansmann et al., 2012; Tinker et al., 2008).
197 But other species don't have this flexibility, sirenians are obligate seagrass feeders and thus may
198 disperse into fragmented populations in search of new food patches following extensive damage to
199 seagrass beds (Prins and Gordon, 2014).

200 Key to predicting how populations may fragment as a result of habitat degradation is an
201 understanding of the range of possible dispersal behaviors. Sutherland (1998) noted a need for a
202 better understanding of how animals search, sample and select new patches (or boarder habitat) and
203 this remains a significant question for marine mammals. This is not only true for resident populations
204 – versus more transient cohorts - but may also be relevant for understanding changes to migration
205 patterns between critical feeding and breeding habitats. But interpreting responses to disturbance can

206 be complex. Bejder et al. (2006) argue that incorrect application of the term habituation may result
207 from situations where more sensitive individuals have already left a disturbed study area before
208 assessment.

209 Fragmentation of social groups may be caused by other anthropogenic effects, such as hunting,
210 bycatch or harassment. Dispersal behavior is also relevant to the rate and extent of the spread of
211 disease. The rate of infection is dependent upon the frequency with which susceptible individuals
212 come into contact with uninfected individuals. For example, elucidation of dispersal and social
213 interactions may be important for predicting transmission of the phocine distemper virus epidemics
214 across harbor seal populations (*Phoca vitulina*) in north-western Europe (Bodewes et al., 2013).

215 **6 Predicting the consequences of environmental change**

216 Predicting the consequences of environmental change is best understood by looking at the patterns of
217 density dependent processes (Sutherland, 1996) i.e. how vital rates (such as mortality and fertility)
218 are regulated by population density. To understand the role of behavior in some density dependent
219 processes it is necessary to have data on the type of breeding systems, social structure and the
220 transmission of social information within and between populations, as well as an understanding of
221 individual decision making. Such data can be difficult to collect in the marine environment.
222 Nevertheless, some studies provide insights into these processes and may provide opportunities for
223 predicting the consequences of human-induced rapid environmental change (HIREC) (Sih et al.,
224 2011) in marine environments.

225 For example, understanding how population density influences competition (and resource depletion)
226 within feeding habitats may provide some useful insights into the effects of environmental change
227 (Sutherland, 1995). It has also been argued that there are many modulating factors that can influence
228 how wildlife respond to disturbance including; age, antipredator strategy, habitat type and even
229 timing of the disturbance. As a result of these many confounding factors, some of which appear to
230 have non-linear and complex effects, the difficulty of finding general patterns may be amplified at
231 higher levels of organization towards populations and species (Tablado and Jenni, 2015).

232 Arguably the most pressing environmental issue of this era, which is increasingly being regarded as
233 the 'Anthropocene' (Waters et al., 2016) - because within this epoch human activities are having
234 significant global impact - is the rising atmospheric carbon dioxide and the resultant change in
235 climate. This is producing discernable shifts in marine ecosystems, particularly in relation to
236 temperature, circulation, stratification, oxygen content and acidification (Doney et al., 2012). From
237 the perspective of marine mammal conservation, it has long been thought that these effects will be
238 most acutely felt in the polar regions, which are particularly vulnerable to sea-ice retreat and which
239 may be the destination of species migrating towards the poles as temperatures rise (Kovacs et al.,
240 2011) . Whilst some marine mammals may be able to adapt more readily to rapid change, others may
241 not (Moore and Huntington, 2008). For example, killer whales are now able to access new regions of
242 the Arctic as a result of receding sea ice. But as apex predators their presence may have an influence
243 on other marine mammal populations such as beluga (*Delphinapterus leucas*) and bowhead whales
244 (*Balaena mysticetus*) (Ferguson et al., 2010). It remains unknown whether this expansion of their
245 range is opportunistic, or the result of undocumented environmental pressures.

246 However, whilst there has been a focus on the effects of climate change on polar and tropical marine
247 ecosystems (such as reef habitat), the effects may be more ubiquitous than first anticipated, with
248 potential range shifts likely to occur across wider latitudes (Lambert et al., 2011) . Other species,

249 such as some of the river dolphins and the beaked whales (about which less is known), may also face
250 significant challenges as a result of the effects of climate change on their habitat.

251 Polar bears (*Ursus maritimus*), have become the flag-ship species for climate change, precisely
252 because they are so vulnerable to changes in sea ice coverage (for a review see Stirling and Derocher,
253 2012). However, of the 19 subpopulations, there is increasing evidence that response to the loss of
254 sea ice may vary considerably temporally and geographically and may be related to density-
255 dependent effects (Rode et al., 2014). This variability among sub-populations highlights the difficulty
256 of providing accurate general population projections, where perhaps sub-population projections
257 would be more helpful, especially in light of the rate of change within the summer and winter sea-ice
258 coverage.

259 **7 Reducing predation**

260 Whilst introducing predators is not common practice in the marine environment, reduced predation
261 from marine mammals can be a goal for some fisheries. One solution is the culling of predators,
262 which has ethical and welfare considerations and its efficacy is controversial (Yodzis, 2001) .
263 Invariably, it is more appropriate to deploy non-lethal methods to manipulate predator behavior, such
264 as seal scarers, an acoustic repellent system (for examples see: Schakner and Blumstein, 2013).
265 Successful outcomes are dependent on an accurate assessment of the interaction between predator
266 and fishery (which can be elusive) (Morissette et al., 2012) and the deployment of such a device may
267 also cause disturbance, or displacement, for other marine mammals besides the target species. In such
268 cases, maintaining fish stocks for exploitation is, strictly speaking, not a conservation goal but rather
269 an industry goal, which often neglects the importance of diversity within food webs and ecosystems,
270 or the implications of the impact of commercial fisheries on marine mammal populations (DeMaster
271 et al., 2001).

272 Sutherland (1998) argues that research on individual or social learning can have an important role in
273 tackling conservation issues associated with predation (Sutherland, 1998). Research on dugong
274 avoidance of sharks showed, unsurprisingly, that in relatively dangerous shallow habitat, dugongs
275 avoided continuous series of resting bouts in the presence of these predators. Whereas, in deeper
276 water habitats their response to the presence of sharks were more modest (Wirsing and Heithaus,
277 2012). Data on the range of natural responses to predators may be particularly useful for addressing
278 conservation issues associated with excessive predation of endangered species.

279 Population size may also be an important factor in relation to predicting the consequences of
280 predation. For example, when Steller sea lions (*Eumetopias jubatus*) were less abundant in the
281 Aleutian Islands (1990s) and in Southeast Alaska (1960s) predation by killer whales was thought to
282 influence population projections. However, predation by killer whales seemed to have little effect
283 when the populations became more abundant (Guénette et al., 2006).

284 **8 Retaining cultural skills**

285 Research on non-human culture has progressed a pace, particularly in cetaceans since Sutherland
286 (1998) identified these original 20 areas of interest (see for example Rendell and Whitehead, 2001;
287 Whitehead and Rendell, 2015). Social learning is a prerequisite for culture, which can be defined as:
288 ‘*information or behavior - shared within a community – which is acquired from conspecifics through*
289 *some form of social learning*’ (Whitehead and Rendell, 2015, p.12). Social learning and culture are
290 not only relevant to terrestrial conservation in terms of ensuring that captive-bred or translocated

Marine mammal behavior: conservation implications

291 animals have the rights skills to survive in the wild (as Sutherland (1998) suggests), but culture is
292 also now recognized as having important implications for the conservation of wild populations
293 (CMS, 2014; Whitehead, 2010).

294 Whilst there are many types of learning, social learning is arguably the most relevant to the
295 consideration of the conservation of marine mammals. Social learning can entail fewer costs to the
296 individual than individual learning and enables novel behavior to spread rapidly, so adaptation can
297 occur faster than through genetic change alone (Boyd and Richerson, 1985). HIREC may provide a
298 number of novel cues and opportunities for social learning for marine mammals, generating unique
299 selection pressures. It has been argued that ‘a cognitive mechanism that causes avoidance of novel
300 food is as encumbering as a specialized feeding apparatus that prevents an animal from eating that
301 food’(Greggor et al., 2014, p.490). It can similarly be argued that the learning of a social norm and
302 the drive to conform may likewise inhibit the spread of adaptive behavior, in a similar manner to
303 neophobia (fear or dislike of anything new or unfamiliar).

304 But the occurrence and consequences of innovations can be difficult to predict. Malthus (1798)
305 famously predicted that the projected increase in human populations would lead to ‘vice and misery’,
306 but failed to account for the fact that humans had the capacity to innovate and socially transmit
307 methods for increasing their own food supply (Davies et al., 2012). Nevertheless, caution should be
308 applied when predicting how social learning may assist or hinder wildlife adaptation to change as
309 there may be anthropogenic (Donaldson et al., 2012), ecological, cognitive (Greggor et al., 2014) or
310 cultural (Whitehead, 2010) interactions and constraints in play. There is also evidence for individual
311 variation in social learning within species and a continuum of phenotypic plasticity (i.e. a range of
312 ways in which the genes can manifest in different environments) has been suggested (Mesoudi et al.,
313 2016).

314 Social learning in marine mammals is most famously evidenced in the transmission of humpback
315 whale song (*Megaptera novaeangliae*) (Garland et al., 2011; Noad et al., 2000) and more recently
316 through the spread of a novel feeding method, known as ‘lobtail feeding’ (Allen et al., 2013). The
317 occurrence of these two apparently independent elements of social learning suggest that this species
318 can maintain more than one independently evolving culture (Allen et al., 2013).

319 Social transmission and cultural constraints may influence conservation outcomes. North Atlantic
320 right whales (*Eubalaena glacialis*) have shown a very poor recovery following intensive whaling
321 during the 16th and 17th Centuries. Right whales are now almost entirely absent in the waters of
322 Labrador (Katona and Kraus, 1999). It is thought that whilst oceanic climate change may play a role
323 in this lack of recovery, perhaps the removal of such a significant proportion of the population
324 through whaling destroyed cultural knowledge about critical habitat, or other significant cultural
325 knowledge that may be inhibiting recovery (Whitehead et al., 2004).

326 Also, since baleen whale calves are thought to learn migratory routes and likely other habitat
327 knowledge from their mothers, such as the location of critical feeding or breeding habitat, or areas of
328 high predator density, some may be more reluctant to explore new areas, culminating in slower range
329 recovery following extirpation (Baker et al., 2013; Carroll et al., 2011, 2014; Clapham et al., 2008). It
330 has been suggested that loss of cultural knowledge and resultant limited range recovery may be one
331 factor inhibiting a recovery of the North Atlantic right whale population (Mate et al., 1997). This has
332 been demonstrated for southern right whales (*Eubalaena australis*) where, following extensive
333 whaling, the remaining populations are now limited to two distinct feeding areas as a result of

334 maternally directed site fidelity, despite the availability of other suitable feeding habitat (Carroll et
335 al., 2014, 2016).

336 Research on the social structure of migrating beluga whales (*Delphinapterus leucas*), an odontocete
337 species, also suggests that cultural conservatism enables social groups to learn migratory routes.
338 However, a potential cost may be that this conservatism could impede the re-colonization of
339 extirpated areas (Colbeck et al., 2013).

340 As well as ecological cultural knowledge, conservative cultures, in which individuals must conform
341 in order to ‘fit in’, may lead to the suppression of novel behaviors. Conformist cultures may inhibit
342 adaptive learning, with preference for cultural norms potentially suppressing ecologically useful
343 behavioral adaptations, or leading to valuable habitats being overlooked (Whitehead, 2010). A
344 striking example of this is provided by the southern resident population of killer whales which feed
345 preferentially on chinook salmon (*Oncorhynchus tshawytscha*) (Ford and Ellis, 2006). It is argued
346 that since these killer whales seem very reluctant to use a variety of other prey-items available to
347 them, this conformist prey specialization may be a constraint on the population’s resilience, since it is
348 contingent on the availability of the salmon (Ford et al., 2010; Whitehead, 2010). In addition to prey
349 preferences, cultural conformism may also inhibit an individual’s adaptive use of space, through
350 dispersal or migration. For example, it has been suggested that killer whales may continue to use
351 traditional areas despite increases in chemical and noise pollution (Osborne, 1999).

352 Whitehead suggest that in some instances cultural behavior may be maladaptive (Whitehead, 2010)
353 and that mass stranding of species such as the highly social pilot whales may be at least partly be
354 associated with conformist cultures (Rendell and Whitehead, 2001). Nevertheless, there are many
355 other possible causes of mass stranding and the difficulty in such instances is to separate out
356 anthropogenic, cultural and other natural causes.

357 Sutherland (1998, p.804) noted: ‘A better understanding of cultural evolution would have
358 considerable consequences for conservation’. Although social learning has been identified in many
359 terrestrial mammals (Thornton and Clutton-Brock, 2011), research on social learning and
360 investigation into potential unique cultures in other marine mammals species besides cetaceans is
361 limited. This is an area where directed examination of social transmission across all marine mammal
362 species would likely benefit conservation efforts in the future.

363 **9 Behavioral manipulations**

364 Many terrestrial conservation projects involve manipulating behavior (Sutherland, 1998). This is
365 rarer in the marine environment, where such manipulations can be more challenging. As far as the
366 authors are aware, there are no conservation schemes to alter the migration routes of marine
367 mammals, or reserves set up with the sole intention of attracting marine mammals to a formerly
368 uninhabited area. Instead there is emphasis on reducing environmental threats and identifying critical
369 habitat (particularly breeding or feeding habitat) for protection (Hoyt, 2011).

370 Nevertheless, non-lethal deterrents are used to manipulate marine mammal behavior, with efforts
371 focused on reducing bycatch and depredation from fisheries. Such deterrents act by creating the sense
372 of a perceived risk associated with utilizing the resource, often with the use of sound (Schakner and
373 Blumstein, 2013). But such manipulations could be improved with insights from comparative
374 cognition (Greggor et al., 2014).

Marine mammal behavior: conservation implications

375 Successful mitigation of environmental threats and identification of critical habitat requires a good
376 understanding of the behavioral ecology of the species and population specific behavior. Some
377 instances of behavioral manipulation in marine mammals arise as the result of opportunistic
378 interaction with humans, although these may not necessarily be directly associated with conservation
379 efforts, they may have conservation implications.

380 Interactions with human activities, such as co-operative fishing (Daura-Jorge et al., 2012), trawling
381 (Ansmann et al., 2012; Chilvers et al., 2001; Pace et al., 2011), depredation (i.e. taking fish from
382 fishing gear) (Esteban et al., 2016b), provisioning or begging (Donaldson et al., 2012; Mann and
383 Kemps, 2003), can provide a novel foraging niche, which marine mammals can learn to utilize
384 through social transmission. As a result there is a risk of social groups becoming dependent on these
385 human activities, in what has been termed ‘anthropo-dependence’ (CMS, 2014).

386 **10 Release schemes**

387 Release of marine mammals into the wild is relatively rare (in comparison with terrestrial mammal
388 breeding and release schemes), but sea otter recovery from near extinction in the 1700s and 1800s
389 has been facilitated by conservation release schemes. Nevertheless, recovery to the full extent of their
390 former range has been sporadic, possibly as a result of problems with habitat quality and research on
391 the influence of age, sex or social structure on dispersal into new habitat may enable predictions of
392 future distribution (Lafferty and Tinker, 2014).

393 For other marine mammals species release is more common in relation to rescue and rehabilitation.
394 Whilst there are strong welfare motivations for rescue and release - and rescue and release can be
395 successful (Sharp et al., 2016) - a number of significant issues associated with the release of marine
396 mammals have been identified. These include: potential conflict with fisheries, ignorance of recipient
397 population ecology, genetic disparity and the potential for the spread of novel or anti-biotic resistant
398 pathogens (Moore et al., 2007). In addition, depending on the circumstances and longevity of the
399 rehabilitation period, there are potential issues associated with finding suitable social units with
400 corresponding culture or social knowledge for a release candidate. Also, for young rescued and
401 rehabilitated mammals, such as harbor seal (*Phoca vitulina richardii*) pups, there is evidence that a
402 developmental window associated with learning specific behaviors from their mothers may be missed
403 if rehabilitation occurs during the nursing period (Gaydos et al., 2013). This highlights the need to
404 integrate a species behavioral ecology into decision making about rescue and release schemes for
405 marine mammals.

406 **11 Habitat requirements of species of conservation concern**

407 In order to determine habitat requirements for any marine mammal of conservation concern, it is
408 essential to have information on the diversity of prey, home range, sensitivities to specific
409 anthropogenic threats (such as noise from vessel traffic, entanglement etc.) and knowledge about
410 breeding behavior. Understanding social structure and dispersal behavior are also likely to be
411 important. But for some marine mammal species (particularly those that exhibit some degree of
412 foraging plasticity), it is important to ensure that protected habitats are sufficiently diverse (for
413 example by including steep sloping habitat) that they offer opportunities for new foraging strategies
414 or prey items, to provide resources for resilience to HIREC through innovation and social learning.

415 Under the United States Endangered Species Act of 1973 (ESA; 16 U.S.C. § 1531 et seq.), critical
416 habitat should provide the physical and biological features essential to the conservation of

417 endangered or threatened species. For marine mammals these features include: space for individual
418 and population growth and normal behavior; shelter; food, water, air; and sites for breeding and
419 rearing offspring. In addition, critical habitat may also include areas beyond the species range at the
420 time of listing, but which are considered essential to their conservation.

421 Killer whales have been shown to be more vulnerable to disturbance from vessels when they are
422 feeding, rather than when resting, travelling or socializing, leading to the recommendation that
423 protected area management strategies should target feeding ‘hotspots’, thus prioritizing the protection
424 of habitat used for the behavior in which a species is most vulnerable to anthropogenic disturbance
425 (Ashe et al., 2010).

426 Defining critical habitat for migratory species can be particularly challenging. Different types of
427 habitat may have several functions for some migratory species. For example, in humpback whales it
428 has been suggested that subarctic feeding grounds provide not only an opportunity for foraging but
429 also for song progression and exchange and may act as opportunistic mating grounds for migrating or
430 overwintering whales (Magnúsdóttir et al., 2015).

431 **12 Minimum area necessary for reserves**

432 There are many challenges associated with determining the size and composition of marine protected
433 areas or reserves for highly social marine mammal species. Among the various threats to marine
434 mammals which reserves can help to mitigate are fisheries entanglement, bycatch, prey depletion and
435 ship strikes. Protecting cetacean habitat from anthropogenic noise may be a particularly salient
436 consideration in relation to behavioral ecology (see Section 21.2), particularly where noise overlaps
437 with communication or echolocation (Melcón et al., 2012; Veirs et al., 2015).

438 Sound can travel much greater distances in water than in air and the range over which some of the
439 larger marine mammals may be in social contact with each other may even extend to the level of
440 ocean basins (Whitehead and Rendell, 2015). As a result marine protected area networks and zoning
441 are an essential tool for ensuring the integrity of marine mammal populations (Hoyt, 2011).
442 Protecting ‘opportunity sites’ has also been suggested to capitalize on protecting important wildlife
443 habitat that already has low anthropogenic noise (Williams et al., 2015).

444 Behavior is clearly relevant in relation to delineation of marine protected areas. The challenge is
445 determining which behavior is either the best indicator, or the most vulnerable to anthropogenic
446 threats (see Section 11). For example, Bryde’s whales (*Balaenoptera edeni*) around the coast of
447 Brazil may use coastal areas for feeding and migrate to deeper oceanic habitat for breeding
448 (Gonçalves et al., 2015), highlighting the need for protected areas to encompass the range of lifecycle
449 events associated with vital rates, with connectivity between critical habitat.

450 Since culture can evolve faster than genetic lineages, marine mammals that exhibit social learning
451 and the transmission of culture may also require more regular review of marine protected areas and
452 their efficacy: as behaviors change and culture evolves, habitat requirements may change. Whilst
453 some cultures may be very stable and may last many generations, some cultures may evolve more
454 rapidly in response to changes in the environment. Where possible, this should be accounted for at
455 the outset, by ensuring that protected areas are large enough to accommodate such shifts and by
456 ensuring management plans include areas with flexible high protection zones (Hoyt, 2009, 2011).
457 This type of adaptive and dynamic management (Bengtsson et al., 2003; Game et al., 2009) is

458 important for resilience. For example, if dramatic shifts in behavior as a result of rapid social learning
459 occur that have implications for conservation, plans can be adapted.

460 In addition, it has been argued that during designation of marine protected areas, attention should be
461 paid to the wider ecosystem and how this supports specific habitat and behaviours. For example, for
462 killer whale populations that feed on salmon, consideration should not only be given to the habitat in
463 which these whales are feeding, but also to the river systems which support their prey (Ashe et al.,
464 2010; Hoyt, 2009, 2011).

465 **13 Captive breeding**

466 Captive breeding for marine mammals is fraught with difficulty, largely as a result of the challenges
467 associated with successfully reproducing the unique physical and social environment required for
468 these species, particularly those with extensive home ranges. For example, researchers recorded a
469 killer whale travelling from the Antarctic Peninsula to Brazil and back again over the course of just
470 42 days, a journey of some 9,400km (Durban and Pitman, 2012).

471 But the physical limitations of the captive environment are only part of the picture. Providing the
472 right social environment for mating and successful rearing of offspring of highly socially marine
473 mammals may be particularly challenging. For example, in the wild, killer whales live in multi-
474 generational societies, with distinct ecotypes differing in morphology, communication, prey and
475 foraging strategies (Pitman et al., 2010; Riesch et al., 2012). These complex societies cannot be
476 replicated in the captive environment and although killer whales of different ecotypes may produce
477 viable offspring in captivity, these hybrids are unlikely to be suitable for release. It is argued that the
478 failure to successfully reintroduce the captive killer whale known as Keiko back into the wild, who
479 more readily associated with dolphins than killer whales from his own pod, suggests that correctly
480 assimilating cultural traditions could be age specific (Riesch et al., 2012; Simon et al., 2009).

481 As a result, compared with fertility rates in the wild, captive breeding rates and survival to age
482 milestones for some species, such as killer whales, are poor (Jett and Ventre, 2015; Small and
483 Demaster, 1995). The emerging knowledge on the behavioral ecology of many of the larger marine
484 mammals is unlikely to ameliorate this problem, but instead serve to demonstrate lack of suitability
485 for successful captive breeding and re-introduction (see also section 10).

486 **14 Reproductive behavior and reproductive physiology**

487 Sutherland (1998) posits that opportunities for manipulating reproductive behavior and physiology in
488 wild populations are underexplored. Whilst this remains true for many marine mammal species, this
489 approach has many practical difficulties, particularly for those marine mammals that live their entire
490 lifecycle in the water. But even for those species that spend some time on land, from the perspective
491 of practicality and economics, there is likely more merit in exploring the conditions, both social and
492 environmental, required for optimal breeding in the wild.

493 Reproductive behavior in marine mammals includes polygyny and promiscuity and pinnipeds species
494 that breed on land compete for reproductively active females by defending breeding territories.
495 Notably, those pinnipeds that breed in the water or on ice (walrus and ice seals), which may have
496 more difficulty defending an unstable environment, tend to be less polygynous. Cetaceans exhibit a
497 range of mating strategies. Toothed cetaceans tend to exist in social groups, which may indicate an
498 important role for others in the rearing of offspring (allo-parental care). Whereas, the basic social unit

499 in baleen whales is considered to be the cow-calf pair, with shorter periods of maternal care than in
500 the toothed cetaceans (for a full discussion of marine mammal mating systems see: Berta et al., 2015).
501 Nevertheless, the role of a male or female ‘escort’ to a humpback whale cow-calf pair remains under
502 debate and highlights the need for further research on some aspects of marine mammal mating
503 systems in order that conservation efforts can target optimal conditions for breeding.

504 **15 Census techniques**

505 For marine mammals that spend most or all of their life cycle in the water, census techniques have to
506 make assumptions about the likelihood of being ‘caught’ (for example during mark recapture
507 techniques). Better understanding of surfacing behavior, or regularity and range of vocalizations, as
508 well as knowledge of dispersal across patchy habitat, may enhance the resolution of some census
509 techniques, particularly for more cryptic species, such as the beaked whales (Yack et al., 2013). One
510 technique in particular, which aims to quantify song dynamics and identify individual humpback
511 whales by their distinct vocalizations, holds promise as a population identifier for monitoring trends
512 across vast habitat (Garland et al., 2013) and the use of environmental DNA (eDNA) in marine
513 habitats may also assist in understanding dispersal, by detecting the presence or absence of some
514 species (Foote et al., 2012). In addition, molecular census techniques used to elucidate dispersal
515 patterns and fragmentation in cryptic terrestrial mammals, such as the giant panda (*Ailuropoda*
516 *melanoleuca*) (Zhan et al., 2006) may have application for marine mammals, where adequate fecal
517 sampling is practical.

518 **16 Exploitation**

519 Patterns of exploitation are influenced by the behavior of both hunters and their prey (Sutherland,
520 1998). Similarly, the distribution of whaling vessels has been compared with the ecological theory of
521 ideal free distribution, in which the number of individuals that will aggregate in various patches of
522 resource is proportional to the amount of resource available in each patch. However, records of sperm
523 whaling in the Galapagos Islands in the 1800s, suggest a violation of the ideal free distribution. It is
524 speculated that this may be a result of inaccuracies in the information available to these early
525 whalers (Whitehead and Hope, 1991).

526 For many marine mammals the history of hunting is well chronicled, but the numbers taken is often
527 less well documented (Ivashchenko and Clapham, 2015; Ivashchenko et al., 2011). As a result
528 determining pre-exploitation abundance can be challenging and controversial. For example, models
529 for mDNA sequence variation provide estimates for North Atlantic fin (*Balaenoptera physalus*
530 *physalus*) and humpback (*Megaptera novaeangliae*) whale populations 6 to 20 times higher than
531 present day populations (Roman and Palumbi, 2003).

532 One important potential behavioral issue of concern for exploited marine mammals is the buffer
533 effect, where at low densities individuals concentrate in the best habitat, but at higher densities are
534 more dispersed over a wider area (Brown, 1969). This can give a false indication of abundance to
535 hunting communities searching in localized areas of high density, whilst the overall population may
536 be in decline. This may be an important consideration in the geo-political wrangling between
537 whalers, scientists and governments, and in decision making on protection of polar bear habitat
538 (Rode et al., 2014). Sutherland (1998) contends that it is precisely this effect that led to the
539 confidence of the fishing community which brought about the collapse of the Atlantic cod (*Gadus*
540 *morhua*) fishery off the eastern-coast of Canada. Marine mammal conservation efforts will doubtless

541 benefit from improved knowledge of dispersal trends, particularly in relation to changing
542 environments and patchy distribution of resources.

543 **17 Increase in human population**

544 Sutherland (1998) notes: ‘the overwhelmingly important problem to humanity and biodiversity is the
545 increase in human population’. Since the paper’s publication in 1998 there are around 1.4 billion
546 additional humans on the planet and although the growth rate has dropped a little, the total human
547 population is likely to rise to around 9.6 billion by 2050 (UNFPA, 2011). While reproductive
548 decision making is a behavioral ecology issue, even within our own species (Sutherland, 1998), there
549 are also many socio-economic issues related to the decision processes and this topic remains both
550 largely taboo (a cultural issue) and the single biggest threat to conservation efforts.

551 The human population explosion, combined with the procurement and use of fossil fuels - in
552 particular the ubiquitous use of plastics, which accumulate in the marine environment - remains one
553 of the largest threats to marine mammal populations (Simmonds, 2012). This is particularly true for
554 species inhabiting coastal areas where the impacts are often more concentrated (Brakes and
555 Simmonds, 2013). But solutions to problems such as marine debris are not always straight forward. It
556 was hoped that the introduction of biodegradable plastics would go some way towards curbing the
557 marine plastics issue. However, it is now thought that the biodegradation of plastics occurs in
558 conditions rarely met in the ocean environment (Kershaw, 2015) and that other solutions must be
559 sought.

560 **18 Discounting**

561 It has been asserted that discounting by human decision-makers favors the over-exploitation of long-
562 lived species as the long-term benefits of sustainable yield once discounted, may be less than the
563 short-term benefit of overexploiting (Clark, 1990; Henderson and Sutherland, 1996). Discounting is
564 potentially a problem for some marine mammal species, which are often long-lived and lowly
565 fecund. Whilst sustainability of resource use into the future may in some cases temper over-
566 exploitation, the basic discounting principle that the opportunity to utilize a resource now, combined
567 with the risk that these resources may not be available in the future, can drive over-exploitation of
568 marine mammals populations (Ivashchenko and Clapham, 2015; Ivashchenko et al., 2011) and may
569 be a motivation for under reporting . Whilst there are some legal and practical conservation measures
570 designed to prevent over exploitation, the uncertainty associated with the potential effects of climate
571 change and other threats to marine mammal populations could potentially lead hunters to favor
572 higher discount rates, particularly if the likelihood of population persistence into the future is
573 uncertain.

574 **19 Increase in Conservation Concern**

575 Sutherland (1998) predicted that public and media interest in behavioral ecology has a considerable
576 role in encouraging interest in conservation and shaping the views of the next generation of
577 biologists. Indeed, public interest in animal behavior in wild populations has only increased in the
578 last 15 years with improvements in technology and a proliferation of media outlets for wildlife
579 documentaries and news. Insight into the lives of marine megafauna has benefitted from this
580 revolution as the deployment of affordable remote monitoring technology continues to burgeon. This
581 is leading to a golden age of discovery of the lives and habits of many marine mammals species.

582 Research comparing public attitudes towards wildlife between the United States, Japan and Germany
583 highlighted that differing attitudes are the result of biogeographical and cultural difference between
584 countries (Kellert, 1993). Later research on public attitudes towards dolphins suggested that these
585 species remain poorly understood by the wider public with potentially harmful behaviors towards
586 wild dolphins being widespread (Barney et al., 2005). More recent research in the Caribbean island
587 of Aruba, where there is not yet a whale watching industry, indicates that support for marine mammal
588 conservation among residents is high, whilst knowledge about species richness and identity is low,
589 suggesting that detailed knowledge is not necessarily a prerequisite for positive public attitudes
590 towards conservation (Luksenburg and Parsons, 2014).

591 **20 Conserving behavior**

592 It has been argued that specific behavior, such as wildebeest (*Connochaetes* sp) migrations or bathing
593 in hot springs by Japanese Macaques (*Macaca fuscata*) may be of sufficient interest to warrant
594 conservation in itself (Sutherland, 1998). Whilst the emphasis of conservation bodies such as the
595 IUCN is on maintaining genetic diversity, there is a strong argument that maintaining behavioral
596 diversity may also play a central role in ensuring sufficient variety for resilience to environmental
597 change.

598 It can perhaps further be argued that some non-human cultures, such as some of those exhibited by
599 whales and dolphins, may be worthy of preservation for their own intrinsic value, irrespective of their
600 potential facility to species conservation. UNESCO (the United Nations Education, Scientific and
601 Cultural Organization) argues that cultural heritage extends not only to objects and monuments, but
602 also encompasses behaviors inherited from our ancestors including ‘oral traditions, performing arts,
603 social practices, rituals, festive events, knowledge and practices concerning nature and the universe
604 or the knowledge and skills to produce traditional crafts’ (UNESCO). Whilst many of these remain
605 uniquely human cultures, there is strong evidence among whales and dolphins for culture including,
606 vocal dialects, the transmission of migratory routes and knowledge about tool use (Whitehead and
607 Rendell, 2015) (see section 8). If we consider that knowledge may be as vital a currency as genes for
608 some social species, maintaining the diversity of non-human intangible cultural heritage may be as
609 important for some marine mammals as it is for humans.

610 **21.1 Consequences of environmental changes on behavior**

611 The implications of behavior for conservation of marine mammals have been reviewed here
612 extensively. But Sutherland (1998) also argued that it is important to consider the implications of
613 environmental change on behavior itself. Specifically it is important to consider how environmental
614 change, including exploitation, may create selection pressures that may influence marine mammal
615 behavior.

616 Acknowledging the limitations of the data reviewed, Wade et al. (2012) argue that odontocetes
617 (toothed cetaceans) may be less resilient than mysticetes (baleen whales) to overexploitation. In
618 contrast, research on the restructuring of a dolphin population following a change in human use of
619 the environment from trawling to post-trawling periods within Moreton Bay, Australia, showed that
620 since the reduction in trawling the social networks of the two social groups had become less
621 differentiated and that previous partitioning into two communities disappeared (Ansmann et al.,
622 2012). These contrasting findings highlight the complexity with which social dynamics may be
623 influenced by differing anthropogenic environmental change and how some species and populations
624 may demonstrate adaptability and be more robust to change, whereas others may be less resilient.

625 This complexity may be further compounded by the synergistic manner in which some anthropogenic
626 threats may operate, making forecasting the consequences for behavior a greater challenge.

627 Marine mammals inhabit a vast array of habitats and as a result threats from HIREC are myriad. It is
628 also important to consider the spatio-temporal scale of the species in question when assessing
629 changes in behavior as a result of environmental factors (Lomac-Macnair and Smultea, 2016).

630 **21.2 Noise and behavior**

631 One anthropogenic threat, not singled out by Sutherland (1998) but of specific relevance to marine
632 mammal behavior, is noise. Sound travels more than four times faster in water than in air and noise,
633 whether natural or anthropogenic, can interfere with marine mammal communication, sociality,
634 navigation and foraging (particularly for those species that echolocate). Nevertheless, whilst noise is
635 a natural phenomenon in the oceans, there is evidence that humpback whales may not be able to cope
636 with an increase in anthropogenic noise in the same way that they offset fluctuations in natural noise
637 (Dunlop, 2016).

638 As anthropogenic ocean noise increases there is concern that the effects of auditory masking may be
639 having far reaching effects for some marine mammals populations (Erbe et al., 2015). The effects of
640 noise may not be limited just to the receiver. The Lombard (1911) effect predicts that noise may elicit
641 anti-masking behavior in the sender, for example changing call rate or frequency. For example,
642 research on fin whale (*Balaenoptera physalus*) 20-Hz song showed that male fin whales modify song
643 characteristics under increased background noise resulting from shipping and seismic air guns
644 (Castellote et al., 2012).

645 Several theories have been posited as to the cause of the decline in tonal frequencies of blue whale
646 song, such as increasing ocean noise, sexual selection, increasing population recovering following
647 exploitation, competition with other species, such as fin whales and even ocean acidification
648 (McDonald et al., 2009). However, it has also been suggested that social learning may have played a
649 role in this now worldwide phenomenon (Whitehead and Rendell, 2015), which may be the result of
650 anti-masking behavior.

651 Potential effects of noise on the lower frequency communication of the baleen whales has been under
652 discussion for some time, but there is now evidence that the range of frequencies emitted by various
653 types of shipping traffic within coastal areas include higher frequency noise within the range used by
654 killer whales for both communication and echolocation (Veirs et al., 2015).

655 **22 Further considerations**

656 Whilst the synergies between behavioral ecology and conservation science have blossomed in the
657 years since Sutherland (1998) raised the issue of disconnect between these two fields, the
658 examination of his 20 key areas of interest shows that there is still a considerable way to go for
659 behavioral ecology to be fully incorporated into conservation science and policy making for marine
660 mammals.

661 In addition to the 20 key areas raised by Sutherland, there are arguably a number of other emerging
662 issues in behavioral ecology that also warrant consideration for marine mammals, including different
663 social learning mechanisms, social structure, social role and personality.

664 Social information and fine scale social structure (Esteban et al., 2016a; Kurvers et al., 2014;
665 Williams and Lusseau, 2006) may strongly influence social dynamics and potentially vital rates.
666 These influences may be synergistic or opposing and warrant a more sophisticated approach towards
667 managing social species, particularly those which exhibit social transmission.

668 How social segments within marine mammal populations are connected and how information flows
669 between them also requires further elucidation (for example see: Filatova et al., 2013; Rendell et al.,
670 2012), particularly since multi-level societies may have differing behavioral responses to
671 anthropogenic change (Cantor et al., 2015; Whitehead et al., 2012). The roles of individuals within
672 their social groups and even the ontogeny of senescence may have important implications for
673 survivorship and conservation (Brent et al., 2015).

674 Since maintaining behavioral diversity is important for adaptation to novel environments, one of the
675 principle goals of conservation, beyond conserving genetic biodiversity, should also be to conserve a
676 wide range of behaviors and in some populations this may also include protecting discrete cultural
677 units.

678 Understanding behavioral plasticity is also undoubtedly an important consideration for predicting
679 how a species may respond to changes in their environment. The degree of plasticity within
680 behavioral repertoires may provide important opportunities for adaptation (Ansmann et al., 2012;
681 Mann et al., 2012). Although resilience as a result of behavioral plasticity may act as a buffer to
682 ecological change, there is also concern that behavioral adaptation could mask emerging ecological
683 issues. For example, whilst a species may switch prey in the face of ecological pressures, if such
684 buffers then become exhausted the consequences of change could be more rapid (CMS, 2014). This
685 highlights the need to monitor changes in prey choice for endangered species that exhibit a high
686 degree of behavioral plasticity.

687 In addition to the more general characterization of a species overall behavioral plasticity, behavioral
688 syndromes, consistent individual differences in behavior (CIDs or personality variation) may
689 influence individuals' ability to cope with novel conditions (Sih et al., 2004). For example,
690 individuals with flexible, exploratory, bold or aggressive behavioral tendencies may be able to cope
691 better with HIREC (Sih et al., 2011). However, in captivity there are concerns that reduced
692 behavioral diversity and selection for personality traits that better suit the captive environment may
693 lead to propagation of personality types and behavior that is ill-suited for the wild, potentially
694 reducing viability for successful release (Carere and Maestriperi, 2013).

695 For a discussion on the consequences of animal personality for population persistence and social
696 dynamics see (Wolf and Weissing, 2012). However, empirical studies into personality variation in
697 wild marine mammals are rare (see for example: Estes et al., 2003; Twiss et al., 2012) and are likely
698 to remain so for some of the more enigmatic species, such as the beaked whales. But even for those
699 more accessible marine mammals whose behavioral repertoires and ecology are well researched it is
700 important not to conflate behavioral polymorphism with personality variation. An empirical
701 framework for evaluating personality variation has been suggested to avoid such pitfalls (Dall and
702 Griffith, 2014).

703 **23 Conclusion**

704 There is no doubt that a better understanding of the behavioral ecology of many marine mammals is
705 important for their conservation. It is difficult to envision any approach towards conserving a

706 population of modern humans, which merely preserved their genetic integrity and did not also
707 consider their behavior. We have some understanding and experience of the complexity of human
708 decision making: amid our different cultures, environments and circumstances we make choices
709 about what to eat, who to socialize with, where to live, how many offspring to have etc. All of which
710 can influence our fertility rates and survival.

711 Similarly, while efforts to conserve marine mammal biodiversity focus strongly on maintaining
712 genetic integrity and diversity, the emerging evidence indicates that sociality and behavioral diversity
713 may also be central to individual, social group and population viability. The challenge ahead is
714 teasing out the most relevant factors and understanding how to incorporate this new knowledge into
715 management models and conservation efforts for marine mammals.

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Marine mammal behavior: conservation implications

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Marine mammal behavior: conservation implications

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