

1 **Climate change and cetacean health: impacts and future directions**

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9

10 **Abstract (max 200 words)**

11 Climate change directly impacts the foraging opportunities of cetaceans (e.g., lower prey
12 availability), leads to habitat loss, and forces cetaceans to move to other feeding grounds. The
13 rise in ocean temperature, low prey availability, and loss of habitat can have severe
14 consequences for cetacean survival, particularly those species that are already threatened or
15 those with a limited habitat range. In addition, it is predicted that the concentration of
16 contaminants in aquatic environments will increase due to Arctic meltwater and increased
17 rainfall events leading to higher rates of land-based runoff in downstream coastal areas.
18 These persistent and mobile contaminants (PMCs) can bioaccumulate in the ecosystem, and
19 lead to ecotoxicity with potentially severe consequences on the reproductive organs, immune
20 system, and metabolism of marine mammals. There is a need to measure and assess the
21 cumulative impact of multiple stressors, given that climate change, habitat alteration, low
22 prey availability and contaminants do not act in isolation. Human-caused perturbations to
23 cetacean foraging abilities are becoming a pervasive and prevalent threat to many cetacean
24 species on top of climate change associated stressors. We need to move to a greater
25 understanding of how multiple stressors impact the metabolism of cetaceans and ultimately
26 their population trajectory.

27 Introduction

28 The change in climate during the past decades is having a devastating effect on our ecosystem
29 with a gradual change in temperature, ocean circulation, ice coverage, sea level, and acidity
30 and with more sudden increases in extreme weather events. In their 1996 paper, MacGravin
31 & Simmonds predicted that climate change will affect cetaceans by both a reduction in prey
32 availability and a shift in the distribution of prey species. They speculated that this will be
33 caused by changes in water temperature, turbulence, and surface salinity of our oceans [1].
34 Over the last two decades, Arctic surface air temperature has indeed increased by more than
35 double the global average, resulting in loss of sea ice but also a disproportionate increase in
36 global ocean heat [2]. For example, in 2014, the Pacific Decadal Oscillation changed to a
37 positive phase with a rise in sea surface temperatures, and coastal upwellings weakened as a
38 result [3]. Coinciding with this climate event, a massive lens of warm water developed in the
39 North East Pacific and moved east in the summer of 2014, spreading along the shelf of North
40 America and coastal Alaska [4]. This led to sea surface temperature increases greater than
41 +3°C in certain areas [5]. This marine heatwave had detrimental impacts on the marine
42 ecosystem, recording not only mass strandings of marine mammals and seabirds but also a
43 geographical shift of species [5]. Extreme climatic events, which are predicted to increase in
44 frequency as a result of climate change [6], can induce ecosystem change and alter patterns
45 of resource availability, as observed in a habitat shift of bottlenose dolphins (*Tursiops*
46 *truncatus*) following seagrass die-off from the 2011 La Niña event [7].

47 Using quantitative models to estimate global terrestrial, freshwater, and marine diversity
48 scenarios containing information on extinctions, changes in species abundance, habitat loss,
49 and distribution shifts indicate that there will be a continuous decline in biodiversity over the
50 21st century [8]. For example, the overexploitation of important fish stocks to top marine
51 predators in combination with this rise in ocean temperature can cause a decline in the
52 availability of fish. In Europe, a shift has been observed in the trophic-web of fish communities
53 and a decline in mean trophic level [9]. In addition, the increase in harmful algal blooms is
54 associated with climate change [10–12]. These algal blooms can produce biotoxins and can
55 further bioaccumulate in filter-feeding shellfish, transferring toxins to higher trophic levels
56 [13]. Recurring harmful algal blooms are also linked to loss of foraging fish and a decline in
57 plankton dynamics [14], leading to an overall decline in prey availability for marine top

58 predators. In addition, these biotoxins produced by the harmful algal blooms can impact
59 physiological functions and lead to an overall decline in health and body condition of marine
60 mammals [15,16].

61 Changes in ocean temperature and prey availability can have particularly dramatic
62 consequences for marine mammals [17] and trait-based approaches show that threatened
63 species or local resident populations are the most vulnerable to climate change [18, Sousa et
64 al. 2020]. Species may be impacted, for example, by the loss of suitable habitat for functional
65 behaviors. For example, many currently occupied humpback whale (*Megaptera*
66 *novaeangliae*) breeding grounds are predicted to be unsuitable (>28°C) by the end of the 21st
67 century [19]. Genetic data combined with predictive habitat models for the year 2100 also
68 predicts that gray whales (*Eschrichtius robustus*) will expand beyond their habitat to the
69 Atlantic, potentially via Arctic migration routes [20]. Similarly, beluga (*Delphinapterus leucas*)
70 habitats are predicted to continue to decline for the year 2100, resulting in a distribution shift
71 northwards and leading to a population decline in some populations [21]. Shifts in distribution
72 ranges appear to have been successfully employed in the past in response to climate change,
73 at least in some species. For example, ancient DNA revealed that the bowhead whale (*Balaena*
74 *mysticetus*) lineage survived the change in the Late Pleistocene climate by shifting habitats
75 northwards [22]. Foote *et al.* predict that the response to climate change will be species-
76 specific and suitable habitat for bowhead whales will likely be halved by the end of this
77 century. The combination of the rise in ocean temperature, low prey availability, and the loss
78 of habitat can have severe consequences for the survival of many cetacean species,
79 particularly those that are already threatened or those with a limited habitat range [23]. Here,
80 we will discuss the consequences of climate change on cetacean health by looking at impacts
81 on distribution, abundance, phenology and behavior, reproductive success, and pollutant
82 burden. Finally, we will discuss how health is currently being measured to assess
83 environmental impacts and the novel approaches taken to increase our knowledge of the
84 physiological constraints limited prey availability might cause.

85

86 **Consequences on distribution, abundance, phenology, and behaviour**

87 Changes in habitat usage/diversity and abundance are one of the most common responses of
88 marine biota to the rise in ocean temperature. Similarly, the distributions of many cetacean
89 species are expected to shift towards the poles, resulting in range contraction for polar
90 species and range expansion for warm water species, as well as changes in population size
91 [24–27]. Although effects on Arctic species are of particular concern (e.g., [28–30]), climate-
92 driven impacts on cetaceans are projected to be global (e.g., [18,31,32]). Indeed, a recent
93 systematic review (58 articles, 29 species) on climate change and distribution, migration, and
94 habitat use showed a poleward shift for many species [33]. Habitat usage is species-specific,
95 meaning that whilst some species may move between different temperature zones, others
96 might be more constrained. For example, the white-beaked dolphin (*Lagenorhynchus*
97 *albirostris*) is a cold-water species whose relative abundance appears to be declining in
98 northwest Scotland (UK), based on both frequencies of strandings between 1992-2003 and
99 sighting surveys from 2002 and 2003 [34]. Indeed, statistical models show a negative
100 relationship between white-beaked dolphin distribution and increasing water temperature
101 [35]. On the other hand, the common dolphin (*Delphinus delphis*) has increased in abundance
102 (both stranding and sightings), reflecting increased habitat usage of the warmer waters in
103 northwest Scotland [34]. In addition, striped dolphins (*Stenella coeruleoalba*) are now
104 regularly sighted in Scottish waters, despite never being recorded before 1988 [36]. Similar
105 observations were documented in St. Mary's Bay (Canada), which historically had few
106 sightings of cetaceans. Due to an increase in the local water temperature, this became a
107 feeding ground for humpback whales in 2016 [37]. Changes in species abundance have also
108 been reported in the North Atlantic, where sightings reported over the last 14 years showed
109 an increase in humpback and fin (*Balaenoptera physalus*) whale abundance, but a significant
110 decrease in common minke whale (*Balaenoptera acutorostrata*) abundance [38,39].

111 Similar shifts in distribution and abundance were observed in bowhead whales tracked by
112 satellite between 2001-2011 in West Greenland. Bowhead whales showed a change in
113 movement pattern, and were found at higher latitudes during spring and summer [40], likely
114 due to the decrease in ice covering and the need to change their habitat usage. Bowhead
115 whales feed on krill (*Euphasia spp.*) and the sea ice edge provides shelter from predators for
116 krill and contains critical food resources (i.e., sea ice algae). As such, the receding of the sea

117 ice edge results in a decline in krill availability [41]. On the other hand, the Pacific-Arctic
118 bowhead whale was reported to be thriving during a period of rapid sea ice loss (longer
119 duration of summer open water) and changes in upwelling potential (wind stress) with
120 increased population size, body condition, and calf counts over the last 25 years [42,43]. This
121 was in combination with a substantial shift in habitat usage over those 25 years and reflects
122 the findings of the bowhead whale lineage that survived the Late Pleistocene climate by
123 shifting habitats [22]. Changes in habitat usage and abundance are not limited to colder
124 regions and were also observed in cetaceans inhabiting tropical and subtropical regions of the
125 Pacific Ocean. For example, the abundance of Bryde's whales (*Balaenoptera edeni*) increased
126 between 2000 and 2010 in the Southern California Bight (USA), which was likely driven by
127 prey availability [44]. Similarly, unusual sightings of Clymene dolphins (*Stenella clymene*) have
128 been recorded on the northern coast of Spain [45], the Patagonian Coast (Argentina) [46],
129 and the Brazilian coast [47], outside their usual habitat in the tropical waters of the Atlantic
130 Ocean, Caribbean Sea and the Gulf of Mexico. Range shifts are believed to correlate with
131 habitat expansion, leading to a functional feeding response of cetacean species to changes in
132 the marine environment [39]. If climate-change impacts accelerate, such regime shifts are
133 thought to become more widespread [48]. In general, range shifts are believed to be an
134 indirect effect of climate change, as cetaceans adapt to changes in the distribution of prey
135 (e.g., Víkingsson et al. 2015). However, a recent study showed that pilot whales shifted
136 polewards at a strikingly high rate that correlated with thermal niche, rather than shifts in
137 prey distribution, thus suggesting a direct response to warming waters [49]. This decoupling
138 between predator and prey distribution may potentially influence trophic interactions,
139 reshaping marine communities and affecting cetacean populations. Future studies
140 quantifying the rate of distribution shift in other populations and species will be crucial
141 towards our understanding of the direct effects of climate change on cetaceans and the
142 ecosystem-level consequences of these range shifts.

143 Environmental changes can impact food-web dynamics and may change entire marine
144 ecosystems. They may lead, for example, to the introduction or increased occurrence of top
145 predators, with consequences propagating through the entire food chain. For example, as the
146 Arctic sea ice cover diminishes as a result of warming waters, killer whales (*Orcinus orca*) are
147 expanding to ice-free areas of Hudson Bay (Canada) [50]. These animals are reported to feed

148 on other marine mammals including seals and other whales (e.g. narwhal (*Monodon*
149 *monoceros*) and bowhead whales) [51,52]. The expansion of inhabitable Arctic water is likely
150 to continue to lead to an increasing presence of those killer whales that prey on marine
151 mammals, putting severe pressure on marine mammals stocks and the Arctic marine
152 ecosystem [51]. Behavioural studies of belugas, narwhals and bowhead whales show that in
153 the presence of killer whales, these species change their habitat usage which can lead to
154 increased stress and decreased fitness [53–55]. Such nonconsumptive effects on prey species
155 may cause cumulative consequences for energy acquisition in habitat that may already be of
156 poorer quality due to climate change effects on resource availability. In addition, the shift of
157 cetaceans to new feeding grounds can have an impact on the body condition of other non-
158 cetacean species (e.g., Adelie (*Pygoscelis adeliae*) and Emperor penguins (*Aptendytes*
159 *forsteri*)) [56].

160 Phenology and behavioural changes have also been reported as a result of climate changes.
161 For migratory species, the impacts of climate change can be particularly challenging as these
162 species time their migration to maximise exploitation of prey in feeding areas, which is only
163 available temporarily. Changes in the period of prey availability will lead to mismatches
164 between the arrival of migrants and the availability of prey, leading predators to shift their
165 migration timing. However, there may be limits to the degree to which such timings can be
166 adjusted before other important functional behaviours are affected. Baleen whales that
167 migrate between feeding and breeding grounds provide an excellent example of these
168 impacts. For example, in the Gulf of St. Lawrence, fin and humpback whales were shown to
169 shift arrival date over a period of 30 years, arriving and leaving earlier to and from their
170 feeding grounds (Ramp et al. 2015). While both species were initially able to maintain
171 temporal niche separation, there were indications of increasing temporal overlap, leading to
172 higher competition for prey resources. The high rate of change in migration timing observed
173 also suggested that if environmental changes continued at the same pace, both species would
174 need to substantially change their annual life cycle to adapt to the timing of prey availability.
175 Similar changes in migration timing have also been observed in other species [33].
176 Additionally, changes in behaviour as a result of climate change have also been reported, such
177 as in group size. For example, bottlenose dolphins in the Moray Firth (UK) and killer whales in
178 Johnstone Strait (Canada), seemed to change their group size in relation to changes in ocean

179 climate over a period of 9-11 years [57]. Climate indicators correlated with local prey
180 abundance and smaller groups were observed during periods of lower salmon availability in
181 both areas. This seemed to recur each 2 years after a low phase of North Atlantic and Pacific
182 Decadal Oscillations [57].

183 Clearly, climate change can impact not only the distribution range and abundance of
184 cetaceans but also impact migration timing and behaviour, all of which may eventually lead
185 to poorer health due to decreased access to preferred prey or decreased foraging success.
186 Those cetacean species that are limited by their habitat usage may face a greater challenge
187 to cope with the temperate change, and thus may lead to extinction events. In contrast, those
188 that can change their habitats, such as the bowhead whale, may ensure the survival of the
189 species as demonstrated by historical climate events. Shifts in habitat usage will lead to
190 increased sightings of uncommon species in some areas, which could have repercussions
191 across the food chain, and ultimately alter whole ecosystems. As such, monitoring schemes
192 and policy makers should take into account the predicted trajectory of habitat usage and
193 those species that have a limited range when managing Marine Protected Areas.

194

195 **Consequences on reproductive success**

196 The rise in ocean temperature can impact the metabolism of marine mammals and their
197 overall health. For example, following a heat wave, Indo-Pacific bottlenose dolphins (*Tursiops*
198 *aduncus*) inhabiting Shark Bay (Western Australia) showed a significant decline in female
199 reproductive rates [58]. Those that use tools for foraging had a higher survival rate compared
200 to those that did not. The lower survival rate persisted post-heatwave and Wild *et al.*
201 speculate that habitat loss may prolong negative impacts on higher trophic level marine
202 predators. Wild *et al* also speculate that the decline in population numbers is likely due to (1)
203 females spending more time foraging leaving calves open to predators; (2) a trade-off
204 between energy available and reproduction; and 3) suppression of the reproductive system
205 due to low body weight.

206 The amount of energy available (e.g., fat) is tightly linked to the ability to invest in
207 reproduction, and blubber thickness is linked to reproductive success [59–63]. When in
208 poorer body condition (e.g., due to low prey availability) early term abortion or less

209 investment in foetus growth has been observed in cetaceans as a measure to save energy and
210 protect the mother's survival [60,61,64]. In addition, suppressed ovulation or delayed sexual
211 maturity may also occur when females are below a certain threshold of body weight [65]. As
212 such, the impact of climate change may have long-term effects on reproduction rates and
213 lead to severe population declines over longer periods. For example, coinciding with the
214 changes in the Pacific Decadal Oscillation and other climate events, the mother-calf rates of
215 humpback whales sighted at Au'au Channel Maui (Hawaii) dropped by 76.5% between 2013-
216 2018, showing a rapid decline in reproductive rates [66]. There has been a decline in
217 abundance and apparent survival rates of fin whales over the last 35 years [67] and a
218 reduction in the reproductive success of humpback whales at the Gulf of St Lawrence
219 (Canada) [68]. In humpback whales observed between 2004-2018, 39% of the identified
220 pregnancies were unsuccessful over this 15 year period [68]. Both species also displayed
221 changes in their migratory timing [69]. One of the likely drivers for these changes is the
222 reduced prey availability caused by environmental shifts as a result of reduced sea ice extent
223 [67].

224 Continued increasing water temperatures and sea ice reduction may also have major effects
225 on ecosystem energy flux altering the ratio of phytoplankton and zooplankton species
226 production [70]. With a gradual shift in the composition of Atlantic zooplankton species, lipid
227 rich prey species such as amphipods may contain less energy [71]. Marine predators such as
228 common minke whales feeding on these less-energy rich species then fail to build up energy
229 reserves for migration to breeding areas and may lead to a decline in producing offspring [72].
230 Similar patterns are observed with the southern right whale (*Eubalaena australis*) preying on
231 krill [73]. Data collected between 1997 and 2013 showed a strong correlation between whale
232 breeding success in southern Brazil and krill density. During that period, krill density was
233 correlated with global climate indices and thus reduced krill is likely to slow down the current
234 recovery rate of these historically overexploited species [73].

235 For some cetacean predators, consequences of environmental changes may be stronger due
236 to low flexibility for dietary shifts. For example, population trends of killer whales in the north
237 eastern Pacific Ocean are strongly correlated with the availability of their principle prey, the
238 Chinook salmon (*Oncorhynchus tshawytscha*) [74]. The lack of this key prey is associated with
239 low reproductive success and high rates of unsuccessful pregnancies in the Southern Resident

240 killer whale population [75]. Although other prey exists in the environment, the strong
241 preference for this specific prey species can lead to population demographic consequences in
242 killer whales. This dependence on a single prey species stems from fixed behavioural
243 traditions within a pod, acting as important social isolating mechanisms which ultimately lead
244 to the evolution of genetically distinct populations [76]. Thus, genetic diversity is also
245 threatened under climate change. The decline in population size allows for inbreeding
246 depression by reducing the genetic diversity and increasing recessive homozygotes created
247 by consanguineous mating [77–79]. That would lead to a weakened resilience of populations
248 against climate change effects and other anthropogenic pressures [80].

249 Prey switching to provide sufficient energy when other sources are low may not be an optimal
250 response either, as it can lead to a decrease in body condition if suboptimal prey are
251 consumed. Beluga whales in the eastern Beaufort Sea (Arctic region) primarily prey on Arctic
252 cod, which is a fish species sensitive to climate change. Data collected between 2011-2014
253 showed that the diet of belugas containing cod declined and a prey switch occurred to capelin.
254 The lowest body condition (maximum girth and blubber thickness) measured in 2014
255 coincided with the lowest consumption of cod and the highest of capelin, and this
256 predominantly affected females and juveniles [81,82].

257 Climate change impacts reproductive success indirectly by reducing the food availability and
258 thus worsening body condition. Given the trade-off between survival and reproducing when
259 fat stores are low, climate change can lead to less offspring being born and thus could lead
260 over-time to an overall population decline. In addition, those species that migrate to their
261 breeding grounds may encounter a loss of those grounds, change their migratory patterns, or
262 fail to reproduce as migration can be energetically costly.

263

264 **Consequences on pollutant burden**

265 Climate change has the potential to impact the current environmental distribution of
266 chemical toxicants and their associated biological effects on the marine ecosystem (see
267 review [83]). With the increase in arctic ice melting and change in regional precipitation
268 patterns, the concentration of contaminants in the meltwater and aquatic environments will
269 increase [84,85]. As a warmer atmosphere can hold more water vapor, climate change models

270 predict an intensification and an increase of rainfall events in certain areas [86–89]. This can
271 lead to higher rates of land-based runoff in downstream coastal areas, elevating pollutant
272 concentrations. Over time, this could contribute to increased contaminant exposure on
273 cetaceans and affect survival rates of entire populations [90,91]. For example, model
274 forecasts predict that >50% of world killer whale populations are threatened by PCB-
275 mediated effects [92]. This is likely to be more severe in coastal populations, that are and will
276 be exposed to higher concentrations of pollutants than those with an oceanic habitat.
277 Persistent and mobile contaminants (PMCs) are globally distributed, persist long after their
278 emissions (most banned in 1960s) and can bioaccumulate in the ecosystem, leading to
279 ecotoxicity [93]. Environmental exposure to these PMCs can continue for years and decades,
280 with long-lasting adverse health effects on many organisms including marine species [94].
281 These effects include immunotoxicity and endocrine disruptions, which leads to changes in
282 reproductive success [94–96].

283 Cetaceans are particularly vulnerable to these pollutants as they are apex predators, feed on
284 top of the food chain and have a thick blubber layer where these chemicals bioaccumulate
285 [97]. These contaminants then recirculate in periods of low prey availability (using energy
286 stores), exposing vital organs to toxic risks [98]. Further, the immunosuppressive effects of
287 PCBs make it more likely for an individual to die from infectious disease [99]. Although there
288 has been a general decline in POPs since the 1980s in blubber samples of cetaceans [100,101],
289 the current change in climate could lead to a resuspension and reintroduction of these
290 contaminants into the aquatic environment. Especially those species inhabiting coastal and
291 Arctic regions may be most at risk of an increased contaminant exposure and there is evidence
292 of PMCs transferring maternally in several species [102–105]. For example, following a severe
293 weather event in 2011 resulting in an influx of contaminated freshwater into coastal waters
294 in Queensland (Australia), unusually high mortality was observed in several dolphin species
295 [90]. A rise in DDT, PCB and HCB levels (i.e. POPs) in blubber samples was also recorded
296 between 2011-2015 following this event in coastal Australian humpback dolphins (*Sousa*
297 *sahulensis*) and Australian snubfin dolphins (*Orcaella heinsohni*) [106]. Further, sustained
298 periods of elevated freshwater discharge may contribute to a higher mortality of resident
299 inshore cetaceans [90]. This could potentially impact their health and reproductive success

300 due to the increased exposure to infectious pathogens [107] and contaminants with
301 immunosuppressive effects [108], making the animal more vulnerable to disease.

302 Shifts in habitat usage and prey, due to the low availability of preferred prey, may also result
303 in higher exposure to pollutants [109]. Pollutant burdens are strongly influenced by
304 geographical distribution, [110], and the shift of species to new feeding grounds/habitats
305 could expose cetaceans to higher levels of pollutants.

306

307 **Measuring health in cetaceans: current and novel approaches**

308 The ability of an animal to reproduce is highly dependent on the amount of energy that is
309 available to invest in reproduction. When fat reserves are low, one's own survival is prioritised
310 with a shut-down of processes related to reproduction. Therefore, the amount of fat stores
311 is widely used in mammals to assess body condition or used as a health proxy [111–113],
312 including in cetaceans (i.e. blubber thickness) [114]. However, using blubber thickness alone
313 to infer body condition has led to inconclusive results (see review [63]). In some cetacean
314 species, blubber thickness may not reflect whether individuals are in negative energy status
315 or not [115–120]. This is likely because blubber also serves other functions than an energy
316 storage, such as buoyancy aid, insulator and gives structural support. For example, bowhead
317 whale blubber thickness did not vary with seasons or life stages but showed an increase in
318 structural fibre density within the blubber layers [121]. As such, blubber thickness did not
319 change but the morphology of the blubber did, with a reduced fat cell size. In addition,
320 dolphins exhibit a unique fasting profile after 24h, with a rapid switch to lipids and amino
321 acids as fuel [122]. This is in agreement with Kershaw *et al.* (2017) who argued that muscle
322 mass may be used as fuel during periods of starvation to protect the blubber's other functions
323 [123]. As such, novel approaches are being developed that consider other metrics than
324 blubber thickness to infer health/body condition in cetaceans (see reviews [124,125]). As
325 Castrillon *et al.* (2020) extensively reviewed traditional and other approaches in evaluating
326 cetacean body condition, we will here focus on the recent developments in molecular
327 approaches.

328 We currently do not fully understand how the physiological system in cetaceans responds to
329 low food availability and new insights in this complex system wide response are emerging

330 [122]. For example, nucleic acid-derived indices have recently been successfully applied as
331 ecophysiological indicators in bottlenose dolphins and pilot whales, showing differences
332 between species and animals with different residency patterns (Alves et al. 2020). This
333 approach shows promise and may have wide future applications, as it can be used in samples
334 obtained via biopsy, a technique widely used for tissue sampling of several cetacean
335 species. With recent advances in technology, we are also now able to characterize many
336 thousands of genes, metabolites, lipids and proteins associated with phenotypic traits and
337 this is key to the discovery of health biomarkers in for example human diseases (see reviews
338 [126–130]). Omics technologies are now emerging as novel methods in the field of cetacean
339 health research and to unravel how their metabolism may cope with stressors. For example,
340 evidence for a Dynamic Network Marker (DNM), originally created for early human disease
341 detection, emerged within the plasma metabolomic network of 24h fasted dolphins [122].
342 This DNM hinted that dolphins may enter a “fat conservation” state more rapidly than
343 expected and shows a tipping point is emerging in energy state transitions [122]. Managed or
344 stranded cetaceans can be used as “model species” to create a more comprehensive
345 understanding of cetacean health and the physiological/metabolic response to stressors as a
346 way to create biomarkers to assess wild populations [122,131–137]. For example, in managed
347 whales, a correlation was found between lipidomics (i.e. lipid profile) and blood parameters
348 related to metabolism [133]. As such, lipidomics shows great promise to assess the change in
349 energy body reserves and thus body condition in free ranging cetaceans [98,131,138,139].
350 Other omics approaches such as proteomics and metabolomics are also emerging as novel
351 methods to increase our understanding of cetacean metabolism [135,140–143]. Finally, we
352 also lack an understanding of how cetacean metabolism and nutrient requirements influence
353 feeding ecology. For example, selective feeding, whereby only certain portions of the prey
354 are eaten or only certain prey are targeted, may be driven by nutrient balancing, rather than
355 simple maximisation of energy intake [144]. Lipid-rich or protein-rich prey or parts of prey
356 may be preferred, depending on the nutrient needs of predators. Climate change may impact
357 not only prey availability but also prey nutrient composition, thus affecting the nutrient
358 balance required by cetacean predators. Thus, a shift in the focus of future studies away from
359 only caloric measurements and applying a nutrient geometry framework may be useful to
360 further our understanding of the impacts of climate change on feeding decision-making of
361 cetacean predators and its consequences to their health.

363 Conclusion

364 The impacts of climate change on cetaceans are species or population-specific, with some
365 being able to expand their habitat while others are forced to constrain their habitat range.
366 Those with a limited habitat range may suffer from declining population sizes mainly caused
367 by a range shift in prey availability across the food chain. Impacts may also differ depending
368 on habitat type, however knowledge on the effects of climate change in populations
369 inhabiting oceanic or remote areas is still lacking. However, conclusive to most cetaceans is
370 that with rising ocean temperature, food availability is declining and thus so is body condition.
371 This will lead to a change in metabolism with a negative energy status and thus lead to a
372 decline in reproductive rates. This is attributed to the trade-off between survival and
373 reproduction as cetaceans cannot invest in reproduction when energy reserves are already
374 low. Finally, changes in precipitation and sea ice loss caused by a warming and changing
375 climate can resuspend or introduce contaminants in the water column, potentially causing
376 adverse effects on cetacean metabolism (e.g., endocrine disruption). The worsened body
377 condition resulting from low food availability and the pollutants bioaccumulated in the thick
378 blubber layer can impact cetacean health.

379 There is a need to measure and assess the cumulative impact of multiple stressors, given that
380 climate change, habitat alteration, low prey availability and contaminants do not act in
381 isolation. Human-caused perturbations to cetacean foraging abilities are becoming a
382 pervasive and prevalent threat to many cetacean species on top of climate change associated
383 stressors. Multiple stressors can lead to a decline in population growth by reducing the
384 amount of energy that is available to invest in reproduction, which may lead to extinction
385 events. Approaches such as modelling and/or trait-based methods for assessment of climate
386 change vulnerability can be helpful in identifying local or regional management units that are
387 at particular risk. As such, monitoring schemes and policy makers should take into account
388 the predicted trajectory of habitat usage and those species that have a limited range when
389 managing Marine Protected Areas and their exposure to anthropogenic stressors. We need
390 to begin to address the knowledge gaps regarding the interactions between multiple stressors
391 and unravel the complex physiological mechanisms regulating cetacean metabolism,
392 reproduction, and body condition to better understand the consequences of future

393 environmental changes. With approximately 25% of cetacean species classified as threatened
394 (IUCN December 2020), it is critical to understand the physiological effects of climate change
395 on these apex predators to protect vulnerable cetacean species. The field of omics is showing
396 great potential for biological markers to assess health in free ranging cetaceans.

397 Lastly, the majority of the papers focus on the impact of climate change on prey availability
398 and cascading through the food-web, but little work has been done to discuss the direct
399 consequences of oceanic acidification for cetaceans. It is important to point out that with an
400 increase in atmospheric CO₂ levels, the ocean plays an increasing role in the carbon cycle with
401 a higher biological uptake of CO₂ per unit area [145]. This can have indirect effects on
402 cetaceans via their food chain by altering the quality of food available for cetaceans. However,
403 very little is known what the direct impacts of increased CO₂ levels may be on cetacean's
404 metabolism. There is indication from experimental work on other species that ocean
405 acidification directly impacts metabolism. For example, molluscs show a substantial change
406 to their energy metabolism with a shift in metabolic pathways when exposed to parameters
407 mimicking ocean acidification [146]. In large pelagic fish, elevated CO₂ increased resting
408 oxygen uptake rates compared to fish with normal conditions [147]. Other work on
409 notothenioid fish suggests that some species may require a physiological trade-off to
410 compensate for the energetic costs of acclimations to both temperature increase and CO₂
411 changes [147]. If the rise in ocean acidity requires cetaceans to increase their resting oxygen
412 uptake levels with potentially extra energetic costs, this could lead to cetaceans having to rely
413 more on their stored energy reserves. The change in acidification could lead to a reduced
414 body condition, reduced reproductive success and an increased susceptibility to diseases. As
415 mentioned earlier, climate change associated impacts such as change in temperature,
416 increased ocean acidification and a decline in prey availability are cumulative. We need to
417 move to a greater understanding how multiple stressors impact the metabolism of cetaceans
418 and ultimately their population trajectory.

419

420 **Author contributions**

421 DD contributed to the design and concept of the manuscript. DD and AK wrote the
422 manuscript. FS provided intellectual input. All authors contributed to manuscript revision,
423 read, and approved the submitted version.

424

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429

430 **Conflict of Interest**

431 The authors declare that the research was conducted in the absence of any commercial or
432 financial relationships that could be construed as a potential conflict of interest.

433

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