

An Update on Captive Cetacean Welfare

Lori Marino^{1,2}, Catherine Doyle³, Heather Rally⁴,
Lester O'Brien⁵, Mackenzie Tennison⁶, Bob Jacobs⁷

¹ Whale Sanctuary Project, Washington, DC, 20003. [marinolori@outlook.com]

² Animal Studies Program, Department of Environmental Studies, New York University, New York, NY, 10012

³ Performing Animal Welfare Society, P.O. Box 849, Galt, CA, 95632. [cdoyle@pawsweb.org]

⁴ Foundation to Support Animal Protection, Norfolk VA, 23510. [heatherrally@gmail.com]

⁵ Palladium Elephant Consulting Inc., 2408 Pinewood Dr. SE, Calgary, Alberta Canada, T2B1S4. [obrienology@icloud.com]

⁶ Department of Psychology, University of Washington, Seattle, WA 98195. [macten@uw.edu]

⁷ Neuroscience Program, Colorado College, Colorado Springs, CO 80903. [bjacobs@coloradocollege.edu]

Corresponding Author:

Lori Marino, Whale Sanctuary Project, marinolori@outlook.com

30 **Abstract:** The welfare of captive cetaceans (i.e., dolphins, whales, and porpoises) has garnered
31 increasing attention over the years as **captivity** presents significant challenges for these long-
32 lived, highly intelligent, wide-ranging, and socially complex animals. This paper **provides** an
33 overview of the current state of captive cetacean welfare, examining captive facilities, recent
34 improvements, persistent problems, and the clinical/behavioral/neural consequences of
35 confinement. We specifically address both quantitative and qualitative **aspects** of captive
36 space, sociocognitive factors, feeding, and welfare concerns such as **stereotypies**, physical
37 health, reproduction, and lifespan. The contrast between the **restrictive** nature of captive
38 **environments** and the dynamic, multifaceted characteristics of **the** natural environment
39 highlights the difficulties faced by cetaceans in captivity. Despite **efforts** by some facilities to
40 improve conditions, serious welfare challenges persist, raising critical ethical concerns about the
41 well-being of captive cetaceans.

42
43

44

45

46

47

48

49

50

51

52

53

54 1. Introduction

55 Cetaceans (i.e., dolphins, whales, and porpoises) have long been considered challenging and
56 ethically problematic candidates for captivity (Carter, 1982; Goldblatt, 1993; Lott & Williamson,
57 2017; Rose et al., 2017; Hosey et al., 2020; Marino, 2020; Marino et al., 2020; Marino & White,
58 2022; McGillian, 2023). Typically, only odontocetes (i.e., toothed whales) are held in captivity because
59 mysticetes (i.e., baleen whales) are too large and have feeding habits that make captivity particularly
60 challenging. The 2013 film *Blackfish*, directed by Gabriela Cowperthwaite, played a key role in
61 changing public sentiment about captive cetaceans, particularly orcas (“killer whales”) by focusing
62 on the disturbing personal history of the orca Tilikum (Parsons & Rose, 2018; Boissat et al., 2021).
63 Increasingly, the public in many parts of the world has become more concerned about the welfare
64 of captive cetaceans and less favorable towards captivity itself (Giovos et al., 2019; Naylor &
65 Parsons, 2019). Wasserman et al. (2018) found that, when accounting for some biases in previous
66 surveys of visitor attitudes, support for orca shows and swim-with-dolphins (SWD) programs in
67 their survey was well below what had been reported in previous studies conducted on behalf of
68 captive cetacean attraction operators. Clegg (2021) argued that captive cetacean facilities will
69 need to respond to these changing social ethics to survive into the future.

70
71 This increase in public concern has led to several legislative efforts around the world to limit or
72 eliminate keeping cetaceans for entertainment. Canadian Bill S-203 (Parliament of Canada, 2025),
73 passed in 2019, bans the breeding and use of captive cetaceans for pure entertainment. In 2021, the
74 French government decreed a trading and breeding ban, which will end whale and dolphin
75 captivity by 2026 (Berry, 2021). More recently, Belgium has officially become the seventh
76 country worldwide and the fourth in Europe to enact a permanent ban on dolphinariums (The
77 Brussels Times, 2024). The above mentioned legislation requires alternative housing options be
78 in place that would improve the animals' welfare (see discussion of authentic sanctuaries in
79 Section 6). The U.S.-based SWIMS Act (2024), a federal bill to phase out captive cetacean
80 entertainment in the United States, was last reintroduced in 2024.

81
82 Nevertheless, captive cetacean entertainment persists across 50 countries in the world, with most
83 facilities found in China, the U.S., Mexico, Japan, and Russia (Cetabase, 2024). The scope of the
84 issue of captive cetacean welfare is broad. In China, the captive cetacean entertainment industry

Commented [A1]: This start is very much framed as a “some people say” argument. I would recommend a more balanced approach where objective measures are considered. Where the authors must rely on “some people say” arguments more effort should be put into discussing the peer reviewed rebuttals to these papers and arguments.

Commented [A2]: Be specific here.

Commented [A3]: Both studies were based on limited social media samples that were not global. I would be cautious to frame this appropriately.

Commented [A4]: As the authors are trying to frame this paper as an update on the state of captive animal welfare, it is incomplete to just mention this legislation without discussing some of the impacts of it. Including the failure to establish potential relocation plans before some of these laws went into effect, leading to dire welfare conditions for animals in both Canada and France.

Commented [A5]: Can you point to any data that shows animals in GFAS sanctuaries have better welfare than pool counterparts? Is there perhaps data from a C-well assessment that can be used to compare the welfare of little white and little grey when in the sea pen and when in their pool? An assumption of better welfare is not sufficient, data are necessary before any other animals move into these GFAS accredited sea pens.

85 has been growing precipitously over recent years (Ong, 2017). Globally, more than 3,500
86 cetaceans are housed in concrete tanks or small pens in ~350 marine parks, zoos, and military
87 facilities (Cetabase, 2024). The most abundant cetacean species in captivity are common
88 bottlenose dolphins (*Tursiops truncatus*, ~87% of all cetaceans; Brando et al., 2018), beluga whales
89 (*Delphinapterus leucas*), and orcas (*Orcinus orca*), but also includes pilot whales (*Globicephala*
90 *macrorhynchus*), Commerson's dolphins (*Cephalorhynchus commersonii*), white-sided dolphins
91 (*Lagenorhynchus obliquidens*), and several other species and hybrids (Cetabase, 2025). In North
92 America alone, there are ~480 bottlenose dolphins, ~60 belugas, and 18 orcas in captivity
93 (Cetabase, 2025).

94
95 Animals in zoos and marine parks in the U.S. are covered by minimal regulations set forth under
96 the Animal Welfare Act (2025), which are often under-enforced (Winders & Chilakamarri, 2018).
97 Accrediting organizations (e.g., Association of Zoos and Aquariums, AZA; ~40 members/facilities
98 housing cetaceans) set welfare standards for their members. More broadly, some associations
99 specifically focus on aquatic animals (e.g., Alliance of the Marine Mammal Parks and Aquariums,
100 AMMPA; ~50 members; European Association for Aquatic Mammals, EAAM). In addition, the World
101 Association of Zoos and Aquariums (WAZA; ~400 members) provides a platform for collaboration
102 among institutions and sets ethical guidelines but does not serve as an accrediting body. However, even
103 under the highest standards, there remain unique challenges in meeting the essential needs of the
104 animals (Morgan & Tromborg, 2007; Shepherdson & Carlstead, 2020). Moreover, only a
105 relatively small number of existing zoos and aquatic parks around the world are accredited,
106 potentially indicating widespread problems in welfare for the majority of captive entertainment
107 facilities.

108
109 Recently, a series of nine articles known as the Cetacean Welfare Study examined captive
110 cetacean welfare measurements across 43 accredited zoos and aquariums in seven countries
111 (Lauderdale et al., 2021a-e; Miller et al., 2021a-d). It was designed to identify factors related to
112 the welfare of bottlenose dolphins (*Tursiops truncatus*), Indo-Pacific bottlenose dolphins
113 (*Tursiops aduncus*), beluga whales (*Delphinapterus leucas*), and Pacific white-sided dolphins
114 (*Lagenorhynchus obliquidens*). This project did not examine unaccredited facilities or those
115 housing other cetaceans. These studies focused on which welfare factors of captive dolphins

Commented [A7]: What do you mean by small? Do you have data that size of sea pen positively correlates with welfare?

Commented [A7]: This language seems biased and fairly subjective.

Commented [A8]: Yes. But there are other accreditation groups such as the American Humane Society, EAZA, The Alliance of Marine Mammal Parks and Aquariums and the International Marine Animal Trainers Association (which accredits facilities based on their use of positive reinforcement techniques). As in the previous paragraphs the authors would be best served going into detail the number of facilities accredited and the nature of those accreditations quantitatively by region (given the proposed scope of this paper). After all, one wouldn't necessarily expect that facilities all over the world are accredited by organizations who mostly operate within the US.
<https://www.ammmpa.org/membership/standards-guidelines>, <https://www.aza.org/assets/2332/aza-accreditation-standards.pdf>, <https://eaam.org/wp-content/uploads/2019/06/EAAM-Standards-and-guidelines-2019.pdf>, <https://www.eaza.net/assets/Uploads/Standards-and-policies/2020-10-EAZA-Standards-for-Accommodation-and-Care.pdf>. There are also guidelines present from groups like WAZA. https://www.waza.org/wp-content/uploads/2020/05/ENG_WAZA-Guidelines-for-AVI_FINAL_April-2020.pdf

Commented [A8]: Do the authors have a sense of this? How many cetacean housing facilities are accredited? I do not believe it is a "small" number. It would be better to be precise on issues like this to give a good update on the state of captive welfare in cetaceans.

116 were determined to be most important, and which ones could be implemented in the future.
117 Identified factors included habitat characteristics and management practices (Lauderdale et al.
118 2021c,d; Miller et al., 2021b), environmental enrichment (Lauderdale et al., 2021e), health
119 reference intervals (Lauderdale et al. 2021a), biomedical markers (Lauderdale 2021a; Miller et
120 al., 2021d) social behavior (Miller et al., 2021b), and behavioral diversity (Miller et al., 2021a).
121 The findings of these studies are integrated in the present review where relevant.

122
123 The science of captive wild animal well-being thus continues to be informative about the needs
124 of various species held in zoos, marine parks and aquaria (Whitham & Wielebnowski, 2013;
125 Clegg & Delfour, 2018; Shepherdson & Carlstead, 2020). Yet, several species, including cetaceans,
126 still face significant challenges in captive settings (Clubb & Mason, 2003; Morgan & Tromborg,
127 2007; Mason, 2010; Fischer & Romero, 2018; Limin et al., 2025). There are numerous markers of
128 poor welfare (e.g., stereotypies, defined as unchanging repetitive actions; Mason, 1991; Jacobs et
129 al., 2021) and, too, ways to determine positive welfare (Lauderdale et al., 2021b). The Cetacean
130 Welfare Study, for example, found that environmental enrichment programs and social management
131 factors were positively associated with positive welfare (Lauderdale et al., 2021b). Importantly, good
132 welfare is not simply equivalent to the absence of negative welfare markers (Miller et al., 2020).
133 There are several factors such as diet, shelter, health, ability to express species-specific behaviors,
134 and choice, that provide positive well-being (Vicino & Miller, 2015).

135
136 The objective of the present review is to examine the current well-being of captive cetaceans. To that
137 end, we review the literature to examine how well the care of captive cetaceans around the world
138 aligns with their needs, aiming to identify remaining challenges. This includes an overview of
139 behavioral and clinical factors in cetacean captivity, particularly in managed settings. Our focus is
140 on the most recent research and representative facilities, many (but not all) of which hold
141 accreditation from one or more professional organizations, presumably indicating higher welfare
142 standards. Finally, we discuss the ethical implications of our findings. And we are concerned with
143 several species held in captivity, not just bottlenose dolphins.

144 2. Literature review methodology

Commented [A10]: I can understand the citations for Whitham and Wielebnowski and Shepherdson and Carlstead as they make arguments for new paradigms in how to study zoo animal welfare. But Jacobs et al is speculative with convincing rebuttals in the press (<https://doi.org/10.3390/ani13172707>). I recommend removing Jacobs et al here.

Commented [A11]: This again seems very one sided. There are a series of articles now discussing enhanced welfare in captive cetaceans both in measures of behavior and in terms of longevity. A more even discussion of the literature would provide readers with a better sense of the state of captive cetacean welfare. See: <https://doi.org/10.1371/journal.pone.0255506>, <https://doi.org/10.1371/journal.pone.0250687>, <https://doi.org/10.1371/journal.pone.0252010>, <https://doi.org/10.1371/journal.pone.0253688>, [10.1098/rspb.2023.1895](https://doi.org/10.1098/rspb.2023.1895), <https://doi.org/10.1111/mms.12601>

Commented [A13]: I would also cite [10.3390/ani13172707](https://doi.org/10.3390/ani13172707) here as this paper specifically addresses the complexity of how to consider an animal in good welfare in a way these authors seem to want to focus on.

146 Our methodology involved conducting a scoping review of the literature (Munn et al., 2018) on
147 captive cetacean welfare and related topics such as: body condition, dietary preferences, health,
148 stereotypies, disease, maturation, sociality, reproduction, housing, management, enrichment,
149 performance, space, complexity, and behavioral diversity. After a review of that literature we
150 organized the review into dimensions of the captive setting important to cetacean welfare: a)
151 enclosures, space and exercise, b) complexity and sensory-perceptual experience,
152 c) sociality, d) feeding and cognitive demands, and e) performances and interactions with
153 humans, as well as specific welfare topics: brain and behavior (e.g., stereotypies, aggression) and
154 physical health (e.g., nutrition and metabolism, skin health, dental disease, digestive and
155 gastrointestinal disease, infections, reproduction, longevity, survival rates, and mortality rates).
156 We examined and included data on free-living and captive cetaceans.

157
158 We conducted our primary searches using Google Scholar. We used our own papers and
159 referencesd from published scientific papers as well. We selected only publications for which we
160 could obtain the complete article/chapter (as opposed to just an online abstract). Given that the field of
161 cetacean welfare advances rapidly, we focused on articles published since 2000 with only a few
162 exceptions.

163
164 We used 282 substantiated sources of information in this review. These included 215 peer-
165 reviewed papers, 27 chapters in edited books, and six scientific books. We used 34 sources of gray
166 literature (e.g., conference proceedings, white papers, government documents, accrediting
167 organization websites). We gave priority to the most recently dated findings. Eighteen citations
168 were for publications prior to the year 2000, 176 published between 2000-2019, and 88 between
169 2020-2025. We obtained information about standards and recommended practices published by
170 professional organizations from their websites. Moreover, we did not omit findings that
171 demonstrated improvements in welfare or positive views of captive cetacean welfare because our
172 aim was to generate an accurate, comprehensive and current picture of the status of captive
173 cetaceans. To confirm that our search was comprehensive and inclusive, we examined reference
174 lists of all articles we used. Finally, findings from secondary sources (e.g., review articles, online
175 web pages) were confirmed in primary sources whenever possible.

176

Commented [A14]: Do the authors mean to imply that if a paper was behind a paywall they did not utilize it? That would be unacceptable. Also many of the papers that are omitted here are open access.

Commented [A15]: I think there is an effort here to imply that this is a comprehensive review. I would argue it is not and that these methods were not robust toward achieving a comprehensive review for the purposes of determining the objective state of captive cetacean welfare (if such a thing is even possible given the variety of housing conditions current cetaceans in captivity find themselves).

177 **3. The captive environment**

178 Captivity in the present context is the state of being confined to an artificial environment (usually
179 designed for human benefit), which is typified by zoos, aquaria, and marine parks but also
180 includes research laboratories and military facilities (Hancocks, 2002; Marino, 2018; Marino &
181 White, 2022). Authentic sanctuaries (discussed in Section 6) are also a form of captivity,
182 designed for animals who cannot be released or returned to the wild (Doyle, 2017). They differ
183 in that an authentic sanctuary prioritizes the well-being of each resident over human interests in
184 an entirely non-exploitive setting more consistent with their evolutionary history and needs
185 (Marino et al., 2025).

186
187 Across these managed establishments, there are significant differences in terms of space allotted,
188 quality of veterinary care, level of visitor interactions, inclusion of demonstrations/performances,
189 and several other factors (Shepherdson & Carlstead, 2020). The captive environment is
190 multifaceted, influencing both physical and behavioral aspects of welfare. Key factors include
191 space and complexity, movement, sensory experiences and mental stimulation, diet, and social
192 interactions.

194 **3.1a Enclosures, Space, Exercise**

195 Although some cetaceans are kept in sea pens and netted off areas in a lagoon or bay adjoining
196 the ocean, most are kept in land-based concrete tanks. Individuals housed in enclosures
197 continuous with the ocean tend to fare somewhat better than those in tanks (see below; Ugaz et
198 al., 2009, 2013). In the Cetacean Welfare Study, ~58% of dolphins lived in zoo/aquarium habitats and
199 ~42% lived in habitats connected to ocean water (Lauderdale et al., 2021e). Cetaceans are also often
200 managed by holding them in various pools for training, medical procedures, and to separate
201 aggressive individuals. There are also quarantine pools and maternity pools that allow for
202 separation and enhanced control over the animals. Moreover, some tanks have lifting floors that
203 allow the animal to be lifted out of the water to be physically restrained by trainers and
204 veterinarians (Couquiaud, 2005). The Cetacean Welfare Study found that most facilities had five
205 or fewer areas that were separated by gates (Lauderdale et al., 2021e).

Commented [REDACTED] These terms are subjective and are being used to hide the fact that a GFAS sanctuary is another form of captivity that must be evaluated solely on its welfare implications for the captive animals who live within it. This whole section needs to be reframed with far less bias.

Commented [A19]: This definition needs a citation. Captivity is the condition of being confined. Whether the environment is artificial or not. The rest of this definition seems to imply that only zoos are captive environments when, even by the authors' own admission, a large sea pen sanctuary is still captivity (which is defined as a naturalistic environment).

Commented [REDACTED] These criteria are not exclusive to sanctuaries. Marine parks, zoos and aquariums also house animals that cannot be returned to the wild.

Commented [REDACTED] So citing Marino 2025 is like citing "because I said so". Marino 2025 is a commentary. While it may be peer-reviewed it's a peer-reviewed opinion. It is NOT sufficient to cite your opinion as evidence that accredited zoos and aquariums do not prioritize the welfare of their animals over the needs of guests.

Commented [A20]: How are these determined? The Cetacean Welfare study argues space is not a significant factor relative to trainer and conspecific social interactions.

Commented [A21]: These statements need to be contextualized with The Cetacean Welfare Study <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0250687>

Commented [REDACTED] This is not what was meant by contextualizing this with the CWS. One should contextualize this finding with the contrasting findings of the CWS.

207 In this context, it is important to acknowledge that cetaceans have evolved for efficient, long-
 208 distance swimming (Buchholtz, 2001; Gillet et al., 2019), with certain species specialized for
 209 deep diving (Piscitelli et al., 2013; Hindle 2020), activities that are severely curtailed in captivity. |
 210 There is considerable variation in tank size across captive facilities. Many tanks are too small or
 211 shallow to allow natural swimming behaviors, especially for larger cetaceans (Corkeron, 2009; Lott &
 212 Williamson, 2017). For instance, orcas are the largest odontocetes held in captivity, with adult
 213 males ranging up to 9 meters in length and weighing close to 7,000 kg (Baird, 2002). Despite
 214 this, under the federal Animal Welfare Act (2025), which is enforced by the United States Department
 215 of Agriculture, the minimum size standard for orca enclosures is 15 m for minimum horizontal
 216 distance (i.e., length and width) and 4 m for minimum depth, which would limit animal movement if
 217 facilities of that size existed for orcas (Joseph & Antrim, 2010; Rose et al., 2017). Thankfully no
 218 facility exists with such dimensions. One of the largest pools in the world housing orcas is the
 219 Port of Nagoya Public Aquarium in Japan. It is 12 m deep, 60 m long and 30 m wide, resulting in
 220 an overall water volume of ~13,499 m³. By comparison, the Salish sea, the primary home range
 221 to J Pod orcas, is ~18,000 km² in area and contains ~2 x 10¹² m³ of water (MacCready et al.,
 222 2021). Within these large home ranges, orcas “routinely swim multiple kilometers in straight
 223 lines and are capable of travelling as many as 225 km a day for up to 30–40 days without rest”
 224 (p. 46, Rose et al., 2017) reaching up to 9,400 km in 42 consecutive days (Durban & Pitman,
 225 2012). To put this in perspective, a distance of 225 km would require ~1,518 laps of the Nagoya
 226 Public Aquarium. In terms of depth, the deepest recorded dive for an orca is 1,087 m (Towers et
 227 al., 2019), although they typically dive much shallower (~200-400 m; Miller et al., 2010; Wright
 228 et al., 2017; Tennessean et al., 2019). |
 229
 230 Similar ranges and depths have been documented for beluga whales as well. For example, the
 231 summer core range for the Eastern Beaufort Sea population has been estimated to be 36,349 km²;
 232 the actual home range is much larger, consisting of the Amundsen Gulf, the eastern Beaufort Sea
 233 shelf, shelf and slope regions west and north of Banks Island into M’Clure Strait and Viscount
 234 Melville Sound (Hauser et al., 2014). These whales are also known to swim >50 km/day (Hauser
 235 et al., 2014), and dive as deep as ~900 m (Hauser et al., 2015).

Commented [REDACTED] Yes. But it seems that belugas (n=2) stress out when put in large sea pens after living in pools for a long time. Consequently it may not matter what the animals “evolved” to do. This is why it was important to take seriously the comments about explaining the concerns with the GFAS sanctuary model.

Commented [REDACTED] Do you have any data that shows that captive animals from pools would want to engage in these behaviors? Are you assuming they would?

Commented [REDACTED] But you are comparing starving orcas who waste away searching for food burning untold calories to provisioned and monitored animals. I just don’t think this is a great comparison in context. Are you arguing that J-pod is experiencing better welfare than orcas at Sea World? I think that is probably wrong and in this case highly speculative. I get that you are trying to avoid having to discuss that the sizes for pools actually exceed the USDA standards, but I don’t think this is an effective way to do that.

Commented [REDACTED] Same problem as above. You assume the animals want that kind of space when there is at least some data suggesting that they don’t. I would recommend a discussion of how we don’t know how animals who have lived in pools would react to super enlarged enclosures, and that those reactions could be negative. If not, it’s the naturism fallacy.

Commented [A28]: Are any American facilities housing orcas at those dimensions? Perhaps discuss what the current digestions are for orcas under captive conditions in the US relative to these standards.

Commented [REDACTED] See recommended highlighted changes.

237 For captive dolphins in the Cetacean Welfare Study, Lauderdale et al. (2021e) found that mean
 238 habitat length was 41.28 m (width was not reported) and the mean maximum habitat depth was
 239 7.66 m, allowing access to 2,610 m³ at night, and 2,540 m³ during the day. Bottlenose dolphin
 240 home ranges vary considerably, from 20 km² to 344 km² (Nekolny et al., 2017), and they are
 241 known to travel 33-89 km a day while making journeys of up to 4,200 km (Wells et al., 1999;
 242 Wells & Scott, 2009). Although coastal bottlenose dolphins (e.g., in Sarasota Bay) remain in
 243 relatively shallow waters (<4 m; Wells et al., 2013), offshore bottlenose dolphins regularly dive
 244 deeper than 500 m and sometimes as deep as 1,000 m (Fahlman et al., 2022). There does not
 245 appear to be any research on the daily distances covered by dolphins in captivity, although
 246 Lauderdale et al. (2021d) measured average distance traveled per hour (ADT). They found that
 247 captive dolphins traveled an average of 2.32 km/hr during the day, slightly above the rates of
 248 wild bottlenose dolphins on the Pacific Coast of the United States (Irvine et al., 1981). However,
 249 Lauderdale et al. (2021d) did not track movement at night, noting that captive dolphins, unlike
 250 their wild counterparts (Shorter et al., 2017), exhibit reduced activity at night. Using a 3D video-
 251 tracking system, Rachinas-Lopes et al. (2018) found that captive bottlenose dolphins spent most
 252 of their time at the surface in the deep area of their pool, presumably because they have more
 253 stimuli (e.g., trainers, objects, food) at the surface. They also suggested that wild dolphins in
 254 their natural habitat might have more incentive than captive dolphins to explore deeper waters
 255 (Rachinas-Lopes et al., 2018). This would seem to be confirmed by Cetacean Welfare Study,
 256 which found that dolphins in managed ocean habitats swam in the top third of the water column
 257 less often than dolphins in managed zoo/aquarium habitats, presumably because they were
 258 exploring the more natural ocean environment (Lauderdale et al., 2021b; Miller et al. 2021b).
 259
 260 Factors other than the amount of space can also affect cetacean welfare. Miller et al. (2021b,
 261 2021c) found that type and timing of enrichment can sometimes be more important than tank size
 262 for captive bottlenose dolphins. Specifically, captive dolphins on a more predictable schedule of
 263 enrichment activities were more socially interactive than those on a random schedule. Similarly,
 264 Lauderdale et al. (2021c, d) found that environmental enrichment and predictable training schedules
 265 were more strongly associated with how dolphins used their habitat (e.g., time in bottom third of
 266 enclosure) and with distance traveled (as measured by ADT) than were habitat characteristics (e.g.,
 267 tank size, water volume availability). Moreover, given orders of magnitude difference between

Commented [REDACTED] How many offshore dolphins are in captivity?

Commented [REDACTED] I think this entire section is predicated on this idea that swimming great distances is preferable to not. I'm not sure there is an established welfare benefit to swimming in this way for captive cetaceans. I think there is a romanticized view of freedom typified in swimming great distances, but one would need to assess the willingness captive animals would have for this if placed in large sea pens as the authors prescribe. I reject this assumption of increased welfare benefit to vast swim distances without data to support it. I also think it is very difficult to make these comparisons in general given the differences in movement and activity patterns across numerous populations and species of cetaceans. It can very easily lead to cherry picking populations (knowing that most captive dolphins in the US are near shore coastal vs. open ocean, for example).

Commented [REDACTED] This is what the paper actually said: "Results showed that both animals spent about 85% of the time in the Deep Area of the pool, but mostly at the surface, and only 7% in the Bottom, near the 5 meters maximum depth. This is not surprising since these animals have more stimuli at the surface, e.g. the trainers, food and toys. In the Bottom, on the contrary, the animals find only a canvas surface. While in natural environments dolphins may feel motivated to explore deeper, in captivity the animals may prefer to spend less time near the bottom, and that kind of information could be relevant when planning new habitats." I would reword this to make it clear that there is no assumption on Rachinas-Lopes et al.,'s part that pool dolphins would behave like wild dolphins if put in that environment. Suggested edits made to document.

Commented [A33]: Can you discuss under what conditions this is true? If it is the conclusion of Miller et al., 2021 that this is always the case consider removing the qualifier.

Commented [REDACTED] Authors should also discuss findings related to ocean vs. pool housing.

268 captive pools and the extensive natural home ranges for which many cetaceans have evolved,
 269 there is potential confound (i.e., a floor effect) with conclusions about how tank size affects
 270 movement and social behavior. In the Cetacean Research Study, for example, the magnitude of
 271 habitat change in length from the smallest measure to the largest is 13.13; in depth, it is 6.4
 272 (Lauderdale et al., 2021e, Table 5). These are miniscule changes compared to the change from
 273 the captive to the natural habitat. Not only the size of a species' native habitat for which it
 274 evolved, but also the actual size of a species (e.g., a goldfish vs. an orca) may affect its
 275 perception of enclosure size/complexity (de Azevedo et al., 2023). As such, it could be that the
 276 different sizes and complexities of captive enclosures do not constitute a meaningful difference
 277 for cetaceans. Studies incorporating significantly larger areas could potentially find associations
 278 between enclosure size/complexity and welfare outcomes. In conclusion, the strong mismatch
 279 between their natural aquatic behavior and captive enclosures, along with the complexities of
 280 habitat issues themselves, indicate that welfare in captive cetaceans is impacted by an array of
 281 interwoven factors.

283 3.1.b Complexity and sensory-perceptual experience

285 Sensory-perceptual experiences are largely determined by the physical features of captive
 286 enclosures, which are relatively limited and unchanging. Remark on the lack of complexity in
 287 captive environments, Jaakkola (2024, p.2) stated: "in contrast to the situation in the wild, these animals
 288 live in highly predictable and structured environments." Most captive cetacean tanks are painted light
 289 or bright blue and designed to maximize the ability of visitors to observe them. Underwater
 290 windows, if present, may further decrease the opportunity for captive animals to find refuge from
 291 visitor gaze. To ensure ease of maintenance and cleaning, tanks have smooth concrete surfaces
 292 and substrates and are relatively featureless as opposed to naturalistic textures (Couquiaud, 2005;
 293 Rose et al., 2023). Water clarity and cleanliness is typically achieved through filtration, ozonation,
 294 and chlorination (Couquiaud, 2005).

296 The acoustic properties of concrete tanks, which are affected by tank size, depth, surfaces, and
 297 configuration, can be problematic for cetaceans, who are highly reliant on sound to
 298 perceive/navigate their environment (Au, 1993; Pack et al., 2002; Branstetter & Mercado, 2006), and

Commented [A43]: Which for those animals is a doubling of size.

Commented [A44]: Right. Which could be, and may already have been in Iceland, too overwhelming. Hence why authors of this paper have talked about different techniques for staging animals in increasing sized sea pens.

Commented [A45]: They may have evolved there, but they didn't grow up there. I think if you are going to make welfare prescriptions you should have data to support the idea that nature wins this battle.

Commented [A46]: That is pretty speculative. Again, if space is a pancia, why are Little White and Little Grey in a staging pool instead of their sea pen after over 5 years of being in Iceland?

Commented [A47]: And one should not assume the directionality of those.

Commented [A48]: At no point did the authors provide any evidence that increased space is tantamount to improved welfare (or any welfare consequence).

Commented [A44]: The authors spend some time stating that there are a variety of enclosures, yet refer to them as immutable limited and unchanging. This dissonance weakens the paper.

Commented [A45]: What are the benefits of naturalistic textures? I would imagine fake rock work would also be for the guests rather than the animals.

Commented [A46]: I am seeing a lot of assumptions around the benefits of environmental complexity in cetacean welfare, but I see no data. Can the authors please present data or studies that use data that discuss how welfare in a pool differs than that of a lagoon or sea pen as a function of environmental complexity? The CWS has such data.

Commented [A47]: Can you please highlight where this is a problem? Is excessive chlorination common in modern cetacean holding facilities? What would be excessive chlorination?

299 for socialization/communication (Janik et al., 2006; Janik, 2014). Anthropocentric noise in captive
 300 settings, for example, has been shown to alter acoustic behavior in bottlenose dolphins (Therrien et al.,
 301 2012) and to disrupt communication involved in performing a cooperative task (Sørensen et al., 2023).
 302 Persistent, anthropogenic noise from nearby construction, traffic or amusement park rides, if not
 303 dampened sufficiently, can increase stress and negatively impact welfare (i.e., increase levels of
 304 cortisol, a stress hormone; Monreal-Pawłowsky et al., 2017; Yang et al., 2021) but more research is
 305 needed to determine how prevalent this issue is for captive cetaceans. Acoustic noise is also exacerbated
 306 by the shallowness of the tank due to "...greater reflection off substrate and the shallow longitudinal
 307 wavelengths of low-frequency sounds" (p. 6, Stevens et al., 2021). Moreover, any sharp angles in a tank
 308 can cause potentially stressful reverberations (Wright et al., 2007; Huettner et al., 2021). In this
 309 regard, it has been suggested that smooth tank surfaces may result in reverberations that lead to
 310 reduced rates of echolocation (Rose et al., 2023). In addition, several alterations in cetacean
 311 vocal patterns have been noted in captivity. Irrawaddy dolphins exhibited a reduction in whistles
 312 after years in captivity (Svarachorn et al., 2016). Following transportation to a new facility,
 313 beluga whales exhibited a significant and prolonged reduction in vocalizations, suggesting stress-
 314 related suppression in acoustic activity (Castellote & Fossa, 2006). Bottlenose dolphins exhibited
 315 changes in the structural characteristics of signature whistles in association with staff presence
 316 and food-anticipatory activity, indicating increased arousal (Probert et al., 2021). The effects of a
 317 captive environment on cetacean acoustic behavior is an area where additional research is needed
 318 (Stevens et al., 2021), with some researchers suggesting that acoustic behavior could be used to
 319 evaluate cetacean welfare (Jones et al., 2021; Winship & Jones, 2023).

3.1.c Sociality

322 Although there is variability across cetacean species in terms of level and type of sociality (i.e.,
 323 the ways in which groups are structured and held together), the species usually kept in captivity (e.g.,
 324 common bottlenose dolphins, orcas, beluga whales) are highly social. They have extensive
 325 juvenile periods during which they learn cultural practices within a complex social network that
 326 is maintained throughout their lives in the wild (Williams & Lusseau, 2006; O'Corry-Crowe et
 327 al., 2020; Whitehead & Rendell, 2021). Bottlenose dolphins can form nested alliances within
 328 complex social networks (King et al., 2018). Free-living orcas live in nested pods within clans
 329 that are bonded by dialect and other behavioral traditions (Williams & Lusseau, 2006; He, 2023).
 330 In the wild, beluga whales live in small groups that join, from time to time, with larger

Commented [REDACTED] Yeah. But that was not noise common to facilities. It basically took a power washer almost on top of them before they made significant mistakes.

Commented [REDACTED] I choose to interpret the author's misrepresentation of our words charitably. Stevens et al., 2021 does not imply anything about tank noise with this statement taken out of context. The actual paragraph that this comes from says. "The propagation of anthropogenic noise varies by the depth of water, and the intensity of sound depends on the geophysical constitution of the location that it is produced in, as well as its source. In shallow water, there is greater noise pollution due to greater reflection off substrate and the shallow longitudinal wavelengths of low-frequency sounds. In noisy areas of the Ganges River, vessel sound pollution increased the ambient noise levels by 14 dB, with an average water column height decrease of 1.5 m during the dry season [45]. Although deeper natural river channels may act as a buffer to some of the increased vessel noise during times with low water levels, river dolphins require full use of shallow and deep areas for resting and foraging [45]. During louder times, marine cetaceans may retreat into deeper waters, but river dolphins and cetaceans restricted to shallow waters in sea-side lagoons or sea pens may not have such opportunities. The quote you have taken applies to wild or natural soundscapes with massive acute vessel noise. Kindly remove.

Commented [REDACTED] I can't determine why this paper is cited here. This was in no way the thrust or data associated with Tim's study.

Commented [REDACTED] This is speculation and is discussed in Bruck, 2024 with a way of studying this.

Commented [REDACTED] That is correct. This paper did say that. And sanctuaries are also part of what we were talking about here...

Commented [REDACTED] To help contextualize this section with a paper you must have read because you cited it here. Here are some aspects you should include here on how some concerns with noise are likely not as dire as they are highlighted in this section. From Stevens et al., 2021 "In human care facilities, anthropogenic noise composition depends on multiple factors including, but not limited to, facility type, amount of exposure to the ocean, life support machinery, presence of shows, and location. Facilities that house marine mammals in pools do not have additional oceanic anthropogenic noise, but their enrichment devices

[... [1]

Commented [A54]: This is all very speculative. This is supposed to be a state of the current captive situation for these animals. Are there any data the authors can utilize to contribute to this? If those data are not available perhaps the authors can highlight where opportunities exist for further study. See [10.3390/ani11113312](https://doi.org/10.3390/ani11113312). The authors will later endorse the use of sea pen sanctuaries (defined [... [2]

331 aggregations of hundreds or thousands of individuals (O'Correy-Crowe et al., 2020). Adult females
332 are strongly bonded with their newborns as well as with older offspring. These triads stay
333 together and join with others to form large nursery groups. Generally, group composition is fluid
334 and underwritten by complex vocalizations and a variety of other characteristics (O'Correy-Crowe,
335 2009).

336
337 In captivity, by contrast, cetaceans live in managed collections that largely forgo opportunities
338 for choice in relationships (Waples & Gales, 2002). Clegg & Butterworth (2017) noted that
339 social group composition in captive facilities is largely artificial and under the control of zoo
340 management rather than the animals themselves. Animal welfare scientists have stated that
341 "keeping animals in appropriate social groupings, and with the required space and complexity to
342 allow individuals to choose to spend time together or apart, is likely to be the most important
343 welfare consideration" (Brando & Buchanan-Smith, 2018, p 85). After the minimum weaning
344 age, captive cetacean mothers and offspring living in marine parks may be separated, as are other
345 socially bonded individuals (Rose et al., 2023). Because captive cetacean groups do not resemble
346 social groups in the wild there may be long-standing repercussions for the psychosocial well-being
347 of calves. Lott and Williamson (2017, p. 166) state: "In captivity, because of the artificial nature of the
348 environment and the fact that calves of a number of cetacean species held in captivity
349 are often separated from their mothers at a young age, whales and dolphins cannot
350 learn the skills important to survival or essential nursing skills necessary to care for their
351 own young (Rose et al. 2009). High rates of neonatal mortality are considered a major
352 problem in captivity (Van Lint et al., 2006)." The limited space available to groups of captive
353 cetaceans may also impact their ability to use dispersal to keep intra-group aggression to a
354 minimum, but this possibility has not been systematically studied. |

356 3.1.d Feeding and cognitive demands

357 Feeding is not just about fulfilling dietary requirements; it also encompasses vital cognitive and
358 physical challenges that are essential to well-being. Consistent with the notion that the cognitive
359 demands of feeding are integral parts of welfare, Clegg et al. (2023b) found that when captive
360 bottlenose dolphins are presented with cognitively enriched foraging opportunities, they exhibit

Commented [A55]: And yet the Cetacean Welfare Study qualitatively showed something different with regard to space. A discussion of the differences here in conclusions would be helpful to the readers.

Commented [A56]: This again is vague. How often is this practice enacted currently. I know of no facility that regularly separates pre-weaned animals from their mothers. In fact one might argue that cetaceans today remain in the presence of their mother's too long given a cursory evaluation of CetaBase and inferences from Sarasota and Shark Bay.

Commented [A57]: Multi-generational populations are not a rule. Nor are preferences for kin associations (see https://www.sciencedirect.com/science/article/pii/S0376635715300930?casa_token=qgqX_wvHzkAAAAA:g7JA198MRbRNRj5czc4Y9tNOITltuM7cSIWkOVymp9Z9Kn3IMPvA19ZJBwwe2JALdY2WqOibOJAhttps://q.bstatic.com/data/bsuitewi/f277d42400017e09095fed934aab6b6d86fabf49.pdf) Especially in bottlenose dolphins which are now to have social units termed as "groups" rather than "pods" given their social fluidity. That being said there are many instances of alloparenting in zoological populations. Perhaps a discussion of these examples would strengthen the paper. <https://www.aquaticmammalsjournal.org/wp-content/uploads/2022/11/48-6-dudzinski.pdf>.

Commented [REDACTED]: Please let me know what modern accredited zoo separates calves at a young age.

Commented [A59]: This citation is a general review article speaking about social integration and wild survival rates (with implications for humans). It says nothing about the status of captive cetacean groups and the only intent reference to dolphins is: "In some species, juvenile survival may also be linked to the ability to socially integrate into mixed-age social groups (49, 50)." Whereas 49 is a reference to a dolphin paper. The only other reference in the paper is in figures where comparisons are used to discuss comparative network centrality with the dolphin data based on that same one wild study. This sentence implies that Snyder-Mackler et al makes claims about dolphins that frankly aren't made. This must be reworded to more accurately reflect the citation so it is not assumed the citation here is evidence for the authors' claims about dolphins.

Commented [REDACTED]: Do you have a source for this that isn't about 20 years old? Given the increases in captive lifespans over the years I would argue you really don't want to cite anything on this older than 5 or 10 years.

361 more positive (e.g., greater engagement and healthy appetite) and fewer negative (e.g.,
362 stereotypes, excessive logging) welfare behaviors.

363 |
364 Dietary preferences and needs vary widely across cetacean species and across communities
365 within species. For instance, southern resident orcas in the Pacific Northwest have a diet that
366 consists of nearly 80% chinook salmon, depending on the season. The emphasis on chinook is
367 not just a preference; it is a vital aspect of their culture (Hanson et al., 2021). Orcas off the coast
368 of New Zealand, on the other hand, specialize in eating stingrays, requiring a high level of skill in
369 processing before they are ingested because of the danger of stingray spine penetrations (Duignan et
370 al., 2000). Orcas can also eat highly varied diets, sometimes including mammals, sea birds, and
371 fish (Samarra et al., 2018). Other species, like common bottlenose dolphins, also have quite
372 diverse diets (Gannon & Waples, 2004). Captive cetaceans are fed a narrower selection of
373 commercially available dead fish and occasional invertebrates (Rosen & Worthy, 2018). Rosen and
374 Worthy (2018, p. 719) note “both a lack of diet diversity and the reliance on frozen foods present
375 potential nutritional challenges.” Although the fish are generally of high quality (i.e., freshly frozen
376 and thawed, free from contaminants, regularly tested, and meeting balanced nutritional requirements),
377 they are delivered to them in a manner (i.e., thrown directly into their mouths above water) that
378 requires little to none of the cognitive activity relevant in natural hunting and feeding. In addition,
379 the freezing and thawing of fish results in significant nutrient loss; for this reason supplements are often
380 supplied (Brando et al., 2018). The lack of stimulation from the way food is delivered must be countered
381 by the implementation of other methods of cognitive enrichment. One reason for providing a limited
382 selection and uniform delivery is to maintain records of how much each individual is eating, as
383 appetite is an important indicator of health. |

384
385 It must be understood that animals are evolutionarily driven to seek the most accessible and
386 abundant food resources for survival. However, the routine consumption of readily available
387 food sources, such as occurs in fish provisioning, ecotourism, or in the captive setting, does not
388 satisfy the biological drive to engage complex cognitive and physical faculties inherent in
389 foraging, which involves travelling to locate food along with capturing and consuming the prey. These
390 activities present opportunities and challenges that are collectively enriching and consume a

Commented [A62]: This is a good addition. The authors should also consider discussing Jaakkola, 2024 here as it also speaks to opportunities for cognitive enrichment.

Commented [A65]: Animals frequently defy this pattern. Even cetaceans like wild orcas will engage in arduous hunts of large baleen whales only to eat tongues and livers. Many animals will forgo easy food sources to pursue preferred food sources. GUDs are a rich literature in this regard.

Commented [REDACTED]: This is still a really bad way to argue about something from an evolutionary perspective. If you absolutely need this statement argue it from an energetics perspective.

Commented [REDACTED]: How do those references make this point in cetaceans?

large percentage of cetaceans' time budget in the wild (Neumann, 2001; Stockin et al., 2009; Noren & Hauser, 2016).

Commented [A68]: These statements need citations or data.

3.1.e Interactions with Humans

Captive cetaceans are often required to interact with humans in different ways, for husbandry, training, and entertainment of the public – all of which have an effect on welfare. Standards that safeguard animal well-being in interactions with visitors (e.g., dolphin assisted therapy and other swim programs, petting pools, and public feeding activities; Stewart & Marino, 2009) vary. In many respects, standards implemented by the U.S. Animal Welfare Act (2025), AMMPA (2020), AZA (2025), and EAAM (2019) mirror one another. However, an important difference is found in standards for interaction time. The Animal Welfare Act (2025) requires that interaction time (i.e., designated interactive swim sessions) for each cetacean cannot exceed two hours per day, with at least one period of at least 10 continuous hours without public interaction within a 24-hour period. AMMPA, EAAM and AZA standards do not require a similar 2-hour cap. The AMMPA (2020) requires that each cetacean have at least one period of at least 10 continuous hours without public interaction in each 24 hour period, and EAAM (2019) standards require one period of at least 12 continuous hours without public interaction within a 24-hour period. Under AMMPA and EAAM standards, a cetacean can be exposed to extended hours of interaction time. The AZA (2025) standards require that certain staff determine interaction time based on various factors. Another difference is in the ratio of human participants to cetaceans. The Animal Welfare Act (2025) states that the ratio of human participants to cetaceans shall not exceed 3:1. The AMMPA (2020), AZA (2025), and EAAM (2019) do not provide a specific ratio; their standards require that the ratio of human participants to cetaceans should be appropriate to the type of interactive activity offered, although they require approval of the ratio by certain staff.

Training for interactions with the public (as well as husbandry and veterinary care) is conducted through positive reinforcement methods in which the animals are rewarded with something they like, typically food, for performing a requested behavior. Trainers may also use a secondary reinforcer known as a “bridge”, usually a whistle, that indicates correct responses to a trainer’s commands (Feng et al., 2016). It has been suggested that training and performance are a form of environmental enrichment for captive cetaceans (Westlund, 2014; Jaakkola et al., 2023; Melfi &

Commented [A69]: It would be beneficial to the stated goals of the authors to provide more detail here. What specifically are the arguments here. Again, I would discuss Jaakkola, 2023 and 2024- but there is a rich literature in cetaceans and other species that the authors should consider.
<https://pmc.ncbi.nlm.nih.gov/articles/PMC2859718/>,
<https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0253688>,
<https://doi.org/10.1016/j.applanim.2013.04.011>,
Ramirez K. Animal training: successful animal management through positive reinforcement. Chicago, IL: Shedd Aquarium Press; 1999.,
https://www.researchgate.net/profile/Sabrina-Brando/publication/250020474_Decrease_Stress_Train_Your_Animals_The_Effect_of_Handling_Methods_on_Cortisol_Levels_in_Harbour_Porpoises_Phocoena_phocoena_Under_Human_Care/links/00b7d52bb6399b70e9000000/Decrease-Stress-Train-Your-Animals-The-Effect-of-Handling-,
<https://doi.org/10.1016/j.applanim.2018.01.015>

422 Ward, 2020). There is some evidence to suggest that positive reinforcement training can help to
423 decrease stereotypic behavior and the stress of husbandry and medical procedures in other species in
424 captivity (Desportes et al., 2007; Coleman & Maier, 2010); however, it is unclear how and when various
425 forms of training correlate with overall enhanced enrichment and well-being for captive wildlife (Melfi,
426 2013; Fernandez, 2022). Thus, it is clear that more research is required to understand which
427 components of training and performance are indeed enriching rather than just providing
428 temporary relief from boredom, creating a distraction, or otherwise occupying the time budget of
429 captive cetaceans.

430
431 Several factors may play an important role in stress levels during interactive programs and therefore the
432 issue is very complicated. Matsushiro et al. (2021) studied only five dolphins, showing that the average
433 cortisol level of the group decreased significantly after an interaction session. But average cortisol levels
434 were significantly higher in the busy visitor season than in low visitor season in two out of three dolphins.
435 They concluded that there was little evidence that interactions caused acute stress but kept open the
436 possibility of chronic stress in dolphins participating in interactive programs during the high visitor
437 season. It should also be noted that cortisol is not necessarily harmful unless it becomes dysregulated
438 during periods of chronic stress (Sapolsky et al., 2000; Jacobs et al., 2021). One study in New Zealand,
439 with a small sample size of three dolphins, found that common dolphins significantly increased their
440 use of refuge areas when exposed to the public in SWD attractions (Kyngdon et al., 2003),
441 suggesting these sessions may be aversive or stressful. However, they found no overall decrease
442 in welfare due to SWD activities. Miller et al. (2011), however, found higher rates of behavioral
443 diversity following swim programs, which may be interpreted as a positive welfare indicator
444 (Miller et al., 2020; Brereton & Fernandez, 2022), although this has yet to be validated.

445
446 More changes in behavior have been reported during unstructured or free-style SWD sessions
447 compared to structured (staged) sessions in which there is explicit trainer regulation of interactions
448 between dolphins and human swimmers. (Brensing et al. 2005). Brando et al. (2019) found that some
449 dolphin behaviors change during swim sessions but that these changes may be due to the
450 presence or absence of trainers or disturbances in the pool rather than due to the swim session
451 itself. Therefore, although there are reasons to view interactions with humans – and in particular
452 the public – as negative for captive dolphins, it is yet to be determined which specific
453 components of those activities (and those before or after) are important factors in how dolphins

Commented [A73]: Again. And this is a theme. This is a very selective reading of this study. The authors should attempt to provide as full a depiction of this research as possible to give their readers the best information if the authors goal is to provide a comprehensive review of what is currently known about the welfare of captive cetaceans. For example, the last line of the abstract for this study reads "The SWD sessions did not appear to have a detrimental effect on the dolphins."

Commented [A74]: I would delete. Unless the authors would like to tack this qualifier on studies that support their views?

Commented [A76]: As this is meant to be a current state of captive dolphin welfare I wouldn't focus on unstructured SWD as it isn't practiced commonly in accredited facilities. The facility in question in this study is Dolphins Plus and they do not engage in this currently.

454 react. Delfour et al. (2020) developed a method of analyzing dolphin-trainer interactions during
455 training sessions that may have promising applicability to SWD sessions but is not yet fully
456 validated as a direct measure of welfare. More research on important physiological and
457 behavioral factors (i.e., oxytocin levels, more precise cortisol levels) may elucidate the nature of
458 the dolphin-trainer relationship and how it impacts dolphin welfare.

Commented [A77]: I think it is fairly clear, even from the studies cited here, that the relationship between the trainer and the dolphin plays a large role in facilitating a successful SWD program. The authors should consider calling for oxytocin studies with dolphins in relation to their interactions with trainers as a potential method for assessing this.

Commented [REDACTED]: Define what full validation would look like here.

460 3.1.f Summary

461 Above, we discuss some of the most relevant and substantive aspects of captive environments for
462 cetaceans. These include the amount of space (both horizontal and depth) provided but also the
463 complexity of the environment. Recent studies suggest that the complexity of a captive
464 environment, and not just the size, is important. The nature of sensory-perceptual experience in
465 captivity is also important for welfare and, as cetaceans are highly acoustically sensitive animals,
466 more research is needed to understand how tank size and shape affects them in terms of acoustic
467 behavior. Other relevant factors are sociality and how groupings in captivity do or do not
468 resemble natural social groups. Finally, feeding, cognitive demands, and interactions with
469 humans are discussed in terms of whether food is not only balanced and nutritional but also is
470 presented in a stimulating way.

472 4. Current Welfare Issues

473 The welfare of cetaceans, as with any animal, is multidimensional; each factor involved in their
474 overall well-being is intricately linked to several others. A deep understanding of captive
475 cetacean welfare requires appreciating that many welfare problems, particularly health
476 challenges that present a risk to welfare (e.g., infections, parasites, etc.) occur both in captivity
477 and in the wild. But the critical point is that there are numerous known reasons for illness, injury,
478 and mortality in the wild, including pollution, pathogens, predators, ships, noise, nets, and so on
479 (Bossart et al., 2003; Fair et al., 2017; Avila et al., 2018; Bossart et al., 2019; Sanganyado & Liu,
480 2022). None of these have any relevance to the captive situation and, therefore, leave open the
481 possibility that there are other factors (e.g., stress, novel pathogen and chemical exposure,
482 neurobiological harm) unique to or exacerbated by captivity that contribute to poor welfare and
483 death in captive cetaceans. For example, below we present evidence suggesting that at least some
484 common diseases of captive cetaceans are directly linked to husbandry or environmental

Commented [REDACTED]: These are not current welfare issues at least in accredited facilities. Again. You need a zoo-based co-author.

Commented [REDACTED]: They do if your captive environment has a net surrounding 100 acres of ocean.

Commented [REDACTED]: This just ignores all of the survival improvement literature you were asked to cite. Again. Not only can you not assume this, there are data specifically countering this.

485 conditions. Despite decades of housing cetaceans in captivity and efforts by accredited zoos and
486 aquaria to modify their facilities, husbandry, and preventative medical programs to reduce these
487 diseases, many of them persist.

488
489 Although sufficient evidence exists to raise concerns about the health and welfare of captive
490 cetaceans, as is detailed in the present paper, it is important to note that a great deal of data on
491 captive cetacean disease and illness is absent from the literature and is publicly inaccessible. The
492 reason for this is that the medical and behavioral records of these animals are routinely withheld
493 by the institutions housing them, including the cause of death data and necropsy reports of
494 deceased captive cetaceans. Despite the value of such records for advancing captive cetacean
495 health, husbandry, and welfare, as well as wildlife conservation efforts, federal agencies with
496 jurisdiction over these animals and facilities have routinely failed to enforce their authority to
497 obtain such records (Rally et al., 2018). Therefore, it can be expected that the information
498 available and presented herein is likely an under-representation of the true rates and etiologies of
499 morbidity in captive populations.

500
501 In this section, we describe the current well-being (mental and physical health) of captive
502 cetaceans, starting with brain and behavioral issues, various dimensions of physical health, and
503 concluding with longevity, survival, and mortality statistics. The chronic stress of coping with
504 the various dimensions of captivity over time has an impact on mental and physical health in
505 cetaceans, as it does in every other species (Marino et al., 2020). All these factors, described
506 more fully below, contribute to a generally problematic picture of captive cetacean welfare.

507 **4.1. Brain and Behavior**

508 **4.1.a. Stereotypies**

509
510 One of the more prevalent behavioral abnormalities found in captive animals is stereotypic behavior
511 (Mason & Latham, 2004; Mason & Rushen, 2008; Bacon, 2018). When present, stereotypies
512 reflect changes in the brain. The circuitry involved in motor control and stereotypies is complex
513 but, at the neural center of this circuitry, is the basal ganglia (or corpus striatum), which are
514 highly conserved across mammals, including cetaceans (Grillner & Robertson, 2016; Marino,
515

Commented Not publicly inaccessible. Just not accessible to someone who actively antagonizes zoos and aquariums. A fair minded scientist interested in working to solve any zoo-born illness would be able to access said data. So this is not accurate.

Commented Is your goal in obtaining the records to improve welfare by actively working to cure a disease of interest? Or is your goal to attack zoos and aquariums? If it is the latter are you surprised they aren't sharing these things with you? Eitherway, the absence of data are not data in this case. It is not sufficient to say, "the zoos won't give us these data so they must be hiding something". The onus is on the authors to substantiate their claims with data/facts or to not make the claims.

Commented [A85]: There have been two substitutive critiques of this paper by two different sets of authors. This paper should not be cited outside of the context of those critiques.
<https://pmc.ncbi.nlm.nih.gov/articles/PMC7401611/>,
<https://escholarship.org/uc/item/6cj9473p>

Commented Still true

Commented [A87]: Not referencing this paper is a significant omission <https://www.mdpi.com/2076-2615/14/6/949>

2022). Therefore, cetacean stereotypies, like stereotypies in other mammals, are not just behavioral issues, but also represent brain function abnormalities (Jacobs et al., 2021).

Captive cetaceans exhibit a range of stereotypies that are also found in other captive species (Clubb & Mason, 2003; Morgan & Tromborg, 2007; Mason, 2010) but not found in free-living cetaceans. Although much more in-depth research is needed on the frequency and nature of stereotypies in captive cetaceans (Gygax, 1993; Clark, 2013), oral stereotypies appear to be relatively common (Jett et al., 2017). These are observed most frequently, but not exclusively, in captive orcas and include biting, chewing, and jaw-popping on hard tank surfaces (Ventre & Jett, 2015; Visser & Lisker, 2016; Jett et al., 2017; Figure 2) Also found in captive cetaceans are circling and repetitive swimming patterns (Jett & Ventre, 2011; Ugaz et al., 2013). However, Miller et al. (2021a) did not find route tracing behavior (a form of stereotypical swimming) in the captive bottlenose dolphins they studied but rather a high rate of behavioral diversity (amount of species typical behavior), suggesting an inverse relationship between behavioral diversity and stereotypies. Continued research is necessary to validate behavioral diversity as an indicator of positive welfare for bottlenose dolphins and other captive cetaceans (Miller et al., 2020; Brereton & Fernandez, 2022).

Self-harm, whether deliberate or incidental to other abnormal behaviors like stereotypies, also occurs in captive cetaceans but, again, is largely unobserved in free-living cetaceans (although these kinds of behaviors are more difficult to observe in the wild). Examples include constantly rubbing their skin on hard objects, resulting in excessive abrasions (Lipman, 2016), or continually hitting against the side of the tank (Dima & Gache, 2004). In one well-known case, a captive orca continually hit his head against the sides of the tank until he died of a brain aneurysm in 1980 (Ringelstein, 2021). Repetitive regurgitation and reingestion is another stereotypic behavior that develops in response to boredom, illness, social isolation/instability, and/or stressful training interactions (Walsh et al., 1996; Calle, 2005). On the other end of the activity spectrum are symptoms which may indicate depression (e.g., spending more time logging or lying motionless on the surface of the water for extended periods, resting motionless on the bottom of the tank, and loss of appetite in the absence of physical illness; Dima & Gache, 2004; Jett & Ventre, 2012; Worthy et al., 2013). It should be noted that lying on the bottom of the tank is sometimes observed in

Commented [A88]: This paper has a significant rebuttal from Jaakkola. Not discussing it is problematic as that rebuttal pretty much addresses much of what is in 4.1 <https://www.mdpi.com/2076-2615/13/17/2707>

Commented [A89]: I would be much more specific here, especially when arguments from other species are used to justify conclusions in cetaceans.

Commented [A90]: I think the cetacean welfare study has addressed some of these issues from the 1993 paper if the authors want to incorporate that into this section.

Commented [A91]: There are a lot of things that aren't observed in wild cetaceans. They are hard to watch 24/7.

Commented [A93]: I would not consider a 30 year old abstract to a veterinary conference a "foundational paper". Especially when the rates of regurgitation in current populations are not properly assessed by the authors.

547 resting individuals who are not necessarily depressed. These various factors are best interpreted
548 in a more holistic way, such as assessing whether many different indicators of depression are
549 present rather than just one. Captive facilities attempt to control or diminish stereotypes
550 primarily through reinforcement of alternative behaviors, pharmacological treatment, or
551 environmental enrichment, but none are completely successful (Mason et al., 2007). However,
552 one study found that cognitive foraging enrichment led to reduced stereotypes and other
553 abnormal behaviors (Clegg et al., 2023b), suggesting that more complex enrichment formats
554 anchored in more naturalistic behaviors may be more helpful than non-cognitive forms.

556 4.1.b. Aggression

557 Although aggression towards members of one's family or social group does occur in free-living
558 cetaceans (Scott et al., 2005; Marley et al., 2013; Robinson, 2014), it is often kept from escalating by
559 dispersal and other factors (Bisther, 2002; Towers et al., 2018). But conspecific aggression can
560 sometimes be exacerbated in tanks, where space is inadequate for dispersal, is shared by
561 individuals who are not necessarily compatible, and where separation or isolation might be the only
562 recourse – all of which have welfare ramifications (Frohoff, 2004; Evans, 2015; Ventre & Jett, 2015).
563 Miller et al. (2021c) suggest that for species with dominance hierarchies, such as bottlenose dolphins, the
564 ability to have the space to separate themselves physically from other individuals may be important for
565 welfare. Likewise, direct attacks on humans by orcas and belugas in the wild are unknown (Pagel
566 et al., 2017) and there is only one record of a free-living bottlenose dolphin killing a human (who
567 was abusing him; Santos, 1997). Nevertheless, there have been hundreds of aggressive acts by
568 captive cetaceans towards humans (Lott & Williamson, 2017) and four human deaths by captive
569 orcas (Parsons, 2012). Moreover, captive bottlenose dolphins and other cetaceans, especially
570 those in interaction and feeding sessions with the public and SWD programs, also have a long
571 record of aggression towards humans, often resulting in severe human injuries (Anderson et al.,
572 2016). Maternal rejection and aggression towards calves is also not uncommon in captive
573 cetaceans (Rose et al., 2023; Marino et al., 2020). In the wild, infanticide has been observed in six
574 odontocete species and has been theorized to be motivated by sexual access to females or
575 removal of genetic competition (orcas: Towers et al., 2018; bottlenose dolphins: McEntee et al.,
576 2023).

Commented [A94]: This is not a good representation of this paper. Mason et al argues that their 2007 paper that ARBs can and should be reduced to zero.

Commented [A95]: That is a sampling bias given the proximity of dolphins in captivity to humans. These should not be evaluated as apples to apples comparisons.

Commented [A96]: I am not aware of any dolphin petting programs.

Commented [A97]: Anderson et al is an opinion piece about killer whales. Nothing to do with SWD programs. This article also argues that the reasons for increased aggression is because whales do not get unstructured time with guests and that's why they are aggressive. This is hardly an objective or well reasoned paper. <https://www.mdpi.com/2076-2615/6/8/49>, <https://www.kintocetaceans.org/robert-anderson.html>

Commented [A98]: cf Jaakkola et al 2020 and Dudzinski, et al., 2021)

Commented [A99]: In the wild infanticide motivated by increased sexual access to females with calves, or the elimination of potential genetic competition has also been proposed for delphinids. Examples include killer whales (Towers et al. 2018), Indo-Pacific humpback dolphins (Zheng et al. 2016), Guiana dolphins (Nery and Simao 2009), and bottlenose dolphins (Dunn et al. 2002, Scott et al. 2005, Kaplan et al. 2009, Robinson 2014, Perrtree et al. 2016). And maternal failure in first born calves is VERY common but it is unclear if that's a feature of maternal rejection or built up organic pollutants passed to the offspring.

578 **4.2 Physical health**

579

580 **4.2.a. Nutrition and metabolism**

581 Many diseases in captive cetaceans are associated with metabolic syndromes believed to be
582 linked to the captive diet (Rosen & Worthy, 2018). Captive bottlenose dolphins, for example, are
583 prone to developing insulin resistance and fatty liver disease, similar to type-2 diabetes in
584 humans (Colegrove, 2018). Free-living bottlenose dolphins have been found to be 15 times more
585 likely to express lower iron levels than captive dolphins (Mazzaro et al., 2012). Elevated iron found in
586 captive bottlenose dolphins as they age is a precursor to developing a disease called
587 hemochromatosis, which is known to occur in managed care populations. This suggests that captive
588 dolphins are more susceptible to non-hereditary hemochromatosis than free-living populations, which
589 can lead to liver, heart, and reproductive problems, as well as joint pain, increased cancer risks,
590 and death (Mazzaro et al., 2012; Venn-Watson et al., 2012a, 2013). Another condition likely
591 related to the captive diet is hypocitraturia, which is characterized by low levels of citrate urinary
592 excretion (Zuckerman & Assimos, 2009). This disease is four times more common in captive
593 than in free-living bottlenose dolphins and promotes the formation of kidney stones, which can
594 lead to serious complications such as renal failure and death (Venn-Watson et al., 2010). Despite
595

596 **4.2.b. Skin Health**

597 Skin disease is common in captive dolphins, with the most prevalent being tattoo skin disease
598 (TSD; black or grey stippling discoloration of the skin), caused by poxvirus, and diamond skin
599 disease (slightly raised, rhomboidal grey patches), caused by the bacterium *Erysipelothrix*
600 *rhusiopathia*. Skin diseases are also found in dolphins in the wild; for example TSD is associated
601 with poor population health (van Bressem et al., 2008). Although poxvirus is associated with
602 TSD lesions in bottlenose dolphins, the virus typically is expressed in individuals who are
603 immunocompromised from stress or concurrent illness. Van Bressem et al. (2008) reported that
604 20.6% of the 257 bottlenose dolphins held in 31 U.S. and European facilities had tattoo lesions.
605 When left untreated, active diamond skin disease lesions can progress to a serious and life-
606 threatening zoonotic bacterial infection (Tryland, 2018; Lacave et al., 2019). However, it is also
607 possible for cetaceans to develop sudden illness and death in the absence of obvious skin lesions.
608 The causative organism is found on dead fish products, the main source of infection for captive

Commented [A100]: Mazzaro et al., did not say what these authors imply here. What they said was "Compared with those in managed collections, wild dolphins were 15 times more likely to have low serum iron (100 µg/dL or less), and this measure was associated with lower haptoglobin." High serum iron was defined as levels exceeding 300 µg/dL. The Average for the study was 184 ± 132 µg/dL. In the captive data all populations are under the 300 µg/dL level considered normal. In the wild populations some are below the 100 µg/dL.
<https://pmc.ncbi.nlm.nih.gov/articles/PMC3527756/table/tbl4/>.

If one goes through just about all of these references there is a good chance similar discrepancies will be found.

Commented [A101]: And that is possible in the wild. What are the authors trying to claim here about cetacean welfare in captivity?

609 cetaceans (Lacave et al., 2019). For this reason, Erysipelas is primarily a disease of captive
610 cetaceans (Rosen & Worthy, 2018) and numerous deaths have been reported due to peracute
611 septicemic *Erysipelothrix* infection (Van Bonn et al., 2007).

614 Tooth injury resulting from stereotypical behavior is a major problem for many animals across a
615 range of species in zoo settings (Glatt et al., 2008). Mason and Latham (2004) estimated that
616 82% of wild carnivores held in zoos express stereotypical behavior, with oral stereotypies being
617 most prevalent (Bergeron et al., 2006). Tooth wear from oral stereotypies is also commonly
618 reported in captive orcas (Graham & Dow, 1990; Jett & Ventre, 2012; Ventre & Jett, 2015;
619 Almunia, 2017). Even though they are fed in a way that does not involve using their teeth (by
620 throwing fish into the back of the throat), captive orca teeth commonly exhibit extensive wear
621 and other dental pathologies such as fractures and exposed pulp cavities (Jett & Ventre, 2012;
622 Ventre & Jett, 2015; Visser & Lisker, 2016; Jett et al., 2017). The main reason for the extensive
623 dental wear and trauma in captive orcas is frequent biting and grating of the teeth against hard
624 surfaces in the tank. This stress-related stereotypy does not appear to be as problematic in captive
625 belugas and bottlenose dolphins as in orcas. In one large survey, approximately 69% of captive
626 orcas in the U.S. and Spain had fractured mandibular teeth and 24% exhibited “major” to
627 “extreme” mandibular coronal tooth wear down to the gingiva (Jett et al., 2017).

Commented [A102]: I would recommend having Dave Rosen and Geraldine Lacave look at this section.

healing mechanisms are initiated to protect the integrity of the pulp chamber, such as tertiary dentin formation (Loch et al., 2025). The superficial forms of dental wear commonly seen in free-ranging orca (e.g., attrition, abrasion, abfraction, and erosion) are gradual enough to allow for concurrent healing processes and do not result in pulp exposure and subsequent infection (Loch et al., 2025). However, in captivity, cetaceans experience different types of dental injury such as acute onset of traumatic complicated crown fractures that do pose a significant health threat, including pulp infection, tooth root abscess formation, and bacteremia (Holmstrom, 2018).

In an effort to avoid infection and health complications, captive orcas with damaged teeth are often forced to undergo a modified pulpotomy procedure whereby the teeth are drilled, and pulp and debris are removed (Ventre & Jett, 2015). To mitigate the risk of systemic infection, damaged teeth are thereafter flushed with antiseptic solutions daily and the animals are often routinely treated with antibiotics, which may result in drug-resistant pathogens (Davies & Davies, 2010; Dold, 2015) and altered immune system function (Yang et al., 2017).

4.2.d. Digestive and Gastrointestinal Disease

Diseases of the gastrointestinal tract, such as gastritis and gastric ulceration, have been seen in both wild and captive cetaceans. Gastric ulcers are one of the most common gastrointestinal diseases in captive cetaceans (Colegrove, 2018). In many cases, their etiology remains unclear; however, ulcers in captive cetaceans have been linked (or suspected to be linked) to social stress (Joseph et al., 2019), dietary factors and food quality (Geraci & Gerstmann 1966; Rosen & Worthy, 2018), foreign body ingestion (Buhrmann et al., 2023), the administration of non-steroidal anti-inflammatory drugs (Simeone et al., 2014), as well as the bacteria *Helicobacter delphinicola* (Segawa et al., 2023). A recent study of this bacterial organism in dolphinarium in Japan found a statistically significant relationship between the presence of this organism and chronic gastrointestinal disease in captive bottlenose dolphins and found evidence to suggest that transmission occurred rapidly between individuals sharing the same pool enclosure (Segawa et al., 2023). *Helicobacter* gastritis and ulceration can lead to perforation of the stomach lining (Stoskopf, 2015) and has been associated with deadly cases of stomach torsion (Begeman et al., 2013).

671 Also, repetitive regurgitation and reingestion can result in chronic irritation of the delicate
 672 mucosal surfaces of the esophagus from routine exposure to acidic stomach contents, leading to
 673 inflammation, corrosion, and even death (Walsh et al., 1996). This behavior, as opposed to
 674 simple regurgitation or vomiting, has not been reported in wild cetaceans. Intestinal volvulus (an
 675 abnormal rotation of the intestine), another deadly gastrointestinal disease found in free-living
 676 and captive cetaceans, is a common cause of mortality in both (Begerman et al., 2013). Although
 677 the etiology of this condition remains unclear in most reported cetacean deaths, a significant
 678 factor known to influence the development of intestinal torsion and volvulus in a wide array of
 679 other mammalian species is dysbiosis, or an imbalance in the natural gut microbiota (Weese et
 680 al., 2015; Hullar, 2018; Oliveira, 2024). In a variety of non-human animals, and in humans, there
 681 appears to be a strong relationship between disturbances in the gut microbiota and chronic stress
 682 and depression (Kelly et al., 2016; Peirce & Alviña, 2019; Yang et al., 2020). Additional studies
 683 are necessary to understand the impact of the various social, environmental, and husbandry
 684 factors influencing the cetacean intestinal microbiome and how these might also affect mental
 685 health. However, numerous studies have shown a clear and significant impact of captivity on the
 686 fecal microflora of captive cetaceans (Bai et al., 2021; Suzuki et al., 2021; Shah et al., 2024),
 687 which consequently impacts both gastrointestinal health and the systemic immune system
 688 (Linnehan et al., 2024).

690 4.2.e. Infectious Disease

691 Viral, bacterial, and fungal infections are found in both captive and free-living cetaceans with
 692 viral and bacterial pneumonia the most common causes of fatality in captive cetaceans (Kielty,
 693 2011; Jett & Ventre, 2012; Nelson et al., 2019). Pulmonary mycotic infection (fungal pneumonia)
 694 is also a frequent cause of death in captive and free-living cetaceans (Brando et al., 2018;
 695 Reidarson et al., 2018). At least 15 of the 22 orcas who died in U.S. marine parks between 1990
 696 and 2010 succumbed to infectious and inflammatory diseases, including pneumonia,
 697 encephalitis, bacteremia, and leptomeningitis (Kielty, 2011). In a retrospective study of the US Navy
 698 Marine Mammal Program from 1980-2010, 50% of the dolphins had histopathologically confirmed
 699 pneumonia (Venn-Watson et al., 2012b). Other infectious diseases in captive cetaceans are related to
 700 behavioural dysfunctions. For instance, it has been suggested that the increased time orcas spend
 701 floating on the tank surface increases vulnerability to mosquito-borne infections, such as St.

Commented [A106]: This is a very selective presentation of the literature and is very speculative. Are the authors aware of current rates and prevalences of digestive and gastrointestinal disease in cetaceans today? If not this would be a great opportunity to investigate that or, if necessary, call for that work. Unless you have modern papers that suggest that ulcers are common in zoos then I think this section needs to be removed or revised to suggest that work is needed here (if it's actually needed). To be fair the authors are also selectively discussing ulcers. Belugas in the Sea Life Beluga Sanctuary were found to have ulcers that correlated to their time in the sea pen and away from their tanks. This has resulted in the whales not being able to go to their sanctuary. As the authors advocate sanctuaries an even discussion of this phenomenon would be more balanced.
<https://www.mdpi.com/2076-2615/14/2/335>
<https://www.mdpi.com/2673-5636/6/1/4>

702 Louis encephalitis (Jett & Ventre, 2012). At least two captive orcas deaths from this disease have
703 been documented (St. Leger et al., 2011; Jett & Ventre, 2012).

704

705 Routine preventative administration of antibiotics and antifungals often causes an imbalance of
706 microflora and resistance to the medicines themselves (Dold, 2015; Reidarson et al., 2018; Park
707 et al., 2020). For instance, meticillin-resistant *Staphylococcus aureus* (MRSA) was reported in
708 captive dolphins in two Italian facilities, with one dolphin in each facility dying from MRSA-
709 linked septicemia (Gili et al., 2017). Another recent case demonstrated the presence of resistant
710 *Morganella morganii*, a bacterium associated with fatal sepsis in human beings, in a captive
711 bottlenose dolphin in South Korea (Park et al., 2020). *Candidiasis*, often observed in
712 immunocompromised individuals, is increasingly prevalent in captive cetaceans (Reidarson et
713 al., 2018; Ohno et al., 2019). Several other opportunistic infections (e.g., *Giardia* sp. and
714 *Cryptosporidium* spp.) have also been linked to the captive environment (Koch et al., 2018).

715

716 4.2.f. Reproduction

717 Most cases of neonatal death in captive facilities occur in young females giving birth for the first
718 time (Owen, 1990; Sweeney et al., 2010), which may be due to immaturity and lack of exposure
719 to natural mother-calf relationships (i.e., factors particularly relevant to the captive situation).

720 The same pattern is true in the wild (Henderson et al., 2014; Robinson et al., 2017; Wells et al.,
721 2025). However, the fact that these infant mortality statistics are the same in the wild and in
722 captivity – where none of the dangers or risks inherent in the wild are present – leaves open the
723 critical question of why neonatal deaths in captivity are not lower than in the wild.

724

725 Female dolphins at SeaWorld facilities are often impregnated through artificial insemination
726 (AI), an invasive procedure that requires mild sedation so that semen can be deposited inside the
727 reproductive tract through a catheter (Robeck et al., 2005; O'Brien & Robeck, 2006). AI often
728 involves multiple attempts. In the common bottlenose dolphin, the conception rate after AI using
729 frozen-thawed semen is 65–70% (Robeck et al., 2009). SeaWorld also employs AI to control the
730 sex ratio of its captive dolphin population in favor of breeding females. Out of 30 such
731 inseminations, 28 have resulted in females (Robeck & O'Brien, 2018).

732

Commented [A107]: The authors fail to contextualize this limited literature with studies that utilize captive cetaceans as the control for sick wild populations. See the body of research from Greg Bossart. The authors state in the longevity portion of this paper that meaningful comparisons cannot be made regarding captive and wild animal life spans when lifespan data is usually incomplete for wild populations. Yet the authors have no problem making that implied comparison here, without much recognition of the fact that wild cetaceans also get sick. As this paper is supposed otherwise be an update to the current state of cetacean welfare in captivity a lot of these data are also really old.

Commented [A108]: A comprehensive review of birth control is missing here. Especially given the authors' preferences for authentic/GFAS sanctuaries where that tool would be deployed. See <https://www.mdpi.com/2076-2615/14/2/335>

Orca females reach sexual maturity between 11 and 13 years of age in the wild (Ford, 2018) but reach peak fertility at around 20 years of age (Ward et al., 2009). Females typically give birth to their first viable calf at 12–14 years of age (Olesiuk et al., 2005). Calves nurse exclusively for at least a year but remain in close association with their mother for at least the first two years or longer (NOAA, 2025). Males sexually mature at the age of 15, but do not typically reproduce until age 21 (Ford, 2009). AI is used to breed captive orcas as well and several have been conceived at SeaWorld parks this way (Robeck et al., 2004, 2017).

740

Female beluga whales in the wild become sexually mature at age 8–12 years, males between 9–15 years—although there is still considerable variability in estimates (O’Corry Crowe, 2009; Suydam, 2009). Most calves continue nursing until they are 20 months old, although nursing is often available to calves for more than two years (O’Corry Crowe, 2009). Captive beluga reproduction has been a longstanding problem because of physiological and behavioral factors (e.g., they are facultative induced ovulators and seasonal breeders; Steinman et al., 2012). That is, they are not always ready to breed. Therefore, AI has been used, with uneven success, in captive beluga whales (O’Brien et al., 2008; Robeck et al., 2010).

749

750 4.2.g. Longevity, survival, and mortality rates

Although more data are needed, captive cetaceans continue to experience an equivalent or higher risk of dying compared to conspecifics from healthy, free-living populations (Montano, 2017; Jaakkola & Willis, 2019; Rose et al., 2023). These findings are difficult to explain given that cetaceans in captivity are afforded full-time veterinary care and are protected from food shortages, predators, pollution, and parasites. This situation begs the question of why illness and mortality are so high in captivity.

757

Estimates for free-living bottlenose dolphins suggest a maximum lifespan of ~25 years (Sergeant et al., 1973) whereas Wells et al. (2013) suggest an average age at death of 19.9 years. Wells & Scott (2009) suggest that female free-living bottlenose dolphins can live to more than 56 years and males to 48 years. Therefore, there is variation in estimates of maximum lifespan for free-living bottlenose dolphins. One recent study suggested that mean life expectancy for captive bottlenose dolphins is not significantly different from that in some free-living populations (Jaakkola & Willis, 2019). The

764 most recent study of longevity also indicates improvements in life expectancy and first year survival
765 rates for captive bottlenose dolphins (Tidière et al., 2023). These increases were attributed to
766 improvements in captive environments and to the fact that there were fewer wild-caught dolphins, who
767 have higher mortality rates, in the more recent time periods examined. One crucial point remains: the
768 authors acknowledge that the study “does not assess individual-level welfare or quality of life, which is
769 essential to advance animal care and develop a holistic understanding of animal welfare” (p. 7, Tidière et
770 al., 2023). Longevity for common bottlenose dolphins thus appears to have increased over time in
771 captive settings. It remains important to remember, however, that although longevity may be
772 related to quality of life, it is not the same.

773
774 For orcas, the mean life expectancy for females in the Pacific Northwest is ~46-50 years, with a
775 maximum of ~80 years (Olesiuk et al., 2005; Ford, 2018). Mean life expectancy for males is ~30
776 years but they may live to ~60 years (Ford, 2018). In contrast, of the more than 200 wild-caught
777 or captive-born orcas held since the 1960s, fewer than 15% have lived to age 30 (Rose et al.,
778 2023). Jett and Ventre (2015) found that orcas in U.S. facilities (12.0 years) demonstrated a
779 significantly higher median survival time than those in non-U.S. facilities (4.4 years), as did
780 whales entering captivity after January 1985 (11.8 years) versus those entering prior to January
781 1985 (3.9 years). Therefore, survival of captive orca cohorts has generally increased in the last
782 four decades, although survival to age milestones remain poor in captive animals in comparison
783 to free-living orcas.

784
785 For free-living beluga whales, mean life expectancy is ~20-30 years and maximum ~60 years
786 (Lockyer et al., 2007; Wells & Scott, 2009; Willis, 2012). Although definitive life expectancy
787 statistics for captive beluga whales have not yet been established, there is evidence that lifespan
788 is compromised (Woodley et al., 1997). The best estimation for maximum longevity in captive
789 beluga whales is 35 years of age (Montano et al., 2017). Survival rates in captive belugas also
790 appear to be lower than in nature (Small & DeMaster, 1995; Woodley et al., 1997). However,
791 updated research on these statistics for captive belugas is critically needed.

792 4.2.h Summary

Commented [A111]: The authors say these groups can't be compared and then proceeds to compare them. Truth is we have really good data in zoos and we have some good data for some populations in wild dolphins. The clear pattern is that male and female dolphins outlive their wild counterparts.
<https://royalsocietypublishing.org/doi/10.1098/rspb.2023.1895>. The authors should cite from peer reviewed sources rather than blogs (this is Long, 2018, <https://us.whales.org/2018/08/23/how-long-do-bottlenose-dolphins-survive-in-captivity/>).

Commented [A112]: Again we are told we can't compare spotty wild data to complete captive data. The authors need a consistent view on this.

Commented [A113]: So this way of analyzing the data forgets that there are quite a few whales that may survive past those ages. The only way this analysis is useful is if the population is extinguished and you can look back at each animal's total lifespan.

Commented [A114]: Pre 2000

Commented [A115]: Pre 2000

Commented [A116]: This is the only sentence in this paragraph that objectively true and useful. Cook Inlet belugas against captive belugas is probably a different story than it would be for Black Sea belugas. But we just don't know.

794 In the above sections, we described the mental and physical health of captive cetaceans, starting
795 with brain and behavioral issues, various dimensions of physical health, and concluding with
796 longevity, survival, and mortality statistics. Captive cetaceans, and especially orcas, exhibit
797 several abnormal behaviors in captivity, including oral stereotypies, self harm, and
798 hyperaggression towards tankmates and humans. In terms of physical health, captive cetaceans
799 suffer from all of the systemic, skin, and digestive diseases known to occur in cetaceans in the
800 wild. This finding begs the question of why they are exhibiting these diseases in a clean,
801 controlled environment. Moreover, reproduction and births remain problematic in captivity.
802 Finally, with the exception of the bottlenose dolphin, no other cetacean species lives as long in
803 captivity as in the wild.

804

805 5. Environmental Enrichment

806 Whether zoos and marine parks can, in principle, provide for the needs of cetaceans is a question
807 that has received increasing attention in the domain of environmental enrichment (Brando et al.,
808 2018; Jacobs et al., 2021). The marine park industry was the first to recognize the difficulties
809 cetaceans have in coping with the incongruity between artificial and natural environments
810 (Swaigood & Shepherdson, 2005; Morgan & Tromborg, 2007). As a result, accrediting agencies
811 require various forms of enrichment, which are implemented to “maximize psychological health”
812 (WAZA, 2025), to stimulate “natural behavior” (AZA, 2025), to allow the animal “variety and
813 choices” in the animal’s environment (AMMPA, 2025), and to provide the animal with
814 “behavioural choices” and “control over its environment” (EAAM, 2025). The requirement of
815 such ad hoc enrichment constitutes a de facto recognition that the captive environment is
816 inherently impoverished, as has been suggested by several researchers (Hancocks, 2002; Mason
817 & Burn, 2018; Jacobs et al., 2021). This claim has been refuted for accredited dolphin enclosures
818 by Jaakkola (2023), but Jaakkola does not consider facilities for larger cetaceans or those that are
819 unaccredited. Nevertheless, it should be noted that this refutation is based on an oversimplified
820 interpretation of the impoverishment-enrichment continuum used in laboratory studies whereby
821 Jaakkola isomorphically maps the laboratory paradigm onto captive dolphin enclosures. Simply
822 adding enrichment to an enclosure does not necessarily transition an impoverished environment
823 to an enriched environment (Jacobs et al., 2021).

824

Commented [A117]: Can enrichment take other forms? See Heather Browning argument. Also Lauderdale LK, Miller L.J. Common bottlenose dolphin (*Tursiops truncatus*) problem solving strategies in response to a novel interactive apparatus. Behav processes. 2019 Dec 1;169:103990. PMID:31678324

Commented [A118]: <https://www.mdpi.com/2076-2615/13/17/2707>

Commented [A119]: This study implied that captive dolphins live in impoverished environments. That just isn't quantitatively or qualitatively true. See Jaakkola, 2023.

825 Traditionally, much of the enrichment for captive cetaceans has involved the presentation of
826 plastic or rubber floating objects (i.e., toys) with which the animals can interact (Brando et al.,
827 2018; Lauderdale et al., 2021e; Jaakkola, 2024). Although such objects may initially arouse
828 interest, habituation occurs relatively quickly (Clark, 2013), which is why variable enrichment
829 schedules and novel items are recommended (Kuczaj et al., 2002). It nevertheless remains
830 unclear to what extent such objects are actually enriching (Delfour & Beyer, 2011). Other types
831 of enrichment may include submerged objects, human interaction/training, as well as food-based,
832 structural, and sensory enrichment (Brando et al., 2018), including classical music (Guérineau et
833 al., 2022). More recent efforts have focused on cognitive challenges (e.g., physical or virtual
834 puzzles and games) to the enrichment repertoire (Clark, 2013; Jaakkola, 2024). As summarized
835 by Jaakkola (2024), cognitive stimulation appears to be intrinsically rewarding and has been
836 associated with a variety of positive welfare indicators (e.g., increases in activity, decreased
837 stereotypies, increased exploratory behavior). Yeater et al. (2024) taught dolphins the concept of
838 innovation and found that the activity was intrinsically rewarding and cognitively engaging.
839 Clegg et al. (2023a) found that cognitive foraging enrichment improved welfare by increasing
840 dolphin engagement and motivation in training sessions and led to fewer stereotypic behaviors.
841 Such cognitive challenges need to account for both species and individual differences and need
842 to be at an appropriate level of difficulty to avoid negative welfare outcomes (e.g., unresolved
843 frustration; Jaakkola, 2024). Unfortunately, as of 2017, cognitive enrichment appeared to be the
844 least-used type of enrichment in captive settings (Clark, 2017). However, cognitive-focused
845 enrichment practices have grown in recent years and appear to be more effective in
846 diminishing abnormal stress-related behaviors, at least for smaller cetaceans (Perlado-Campos,
847 2017; Matrai et al., 2020).

848
849 Neuroscience research suggests that a more natural environment is better for the brain and for the
850 emotional health of the animal than are artificially enriched environments (Rosenzweig et al., 1972;
851 Lambert et al., 2015, 2016). Consistent with this notion are studies that suggest that dolphins in
852 captive environments with more natural elements (e.g., sea pens or netted off areas continuous
853 with the ocean) are less stressed and display fewer behavioral abnormalities than those living in
854 tanks. For instance, Ugaz et al. (2009) found that the same group of bottlenose dolphins engaged
855 in more active swimming and less logging in open sea pens (with access to ocean and a more

Commented [A120]: These arguments should be contextualized with Proie, 2013 which showed no differences in cortisol between captive and wild animals (with captive animals showing even less stress than wild animals under SD). I know the lead author is familiar with this work because she is in Proie's acknowledgements.

856 complex environment) than when they were in closed facilities with no ocean access. As noted
857 previously, dolphins in closed artificial environments were also found to have higher salivary
858 cortisol levels than those in open sea pens (Ugaz et al., 2013). Moreover, dolphins transferred
859 from concrete tanks to captive ocean environments spent less time in social interactions (Ruiz et
860 al., 2009). The authors suggested this finding could be due to the significant increase in space
861 available (the ocean habitat was approximately five times the size of the tanks) as well as the
862 opportunity to explore other features of the natural environment, such as fish and other
863 organisms who may be present (Ruiz et al., 2009). In a review of several studies of cortisol levels
864 in and out of captivity, Proie (2013) found evidence for higher levels in free-ranging cetaceans
865 than in captive cetaceans. However, as Proie noted, cortisol assays in the wild are done by chase
866 and capture whereas, in captivity, they are done as part of routine husbandry procedures, thus
867 making comparisons problematic: "...sampling methodology is such a pronounced confounding
868 variable it would be inaccurate to conclude that captive cetaceans have a lower resting cortisol
869 level than wild cetaceans or to assume that captive cetaceans are 'less stressed' than their wild
870 counterparts" (Proie, 2013, p. 138).

871
872 Lauderdale et al. (2021b) found that dolphins in natural ocean facilities (netted off areas
873 continuous with the ocean) spent less time swimming in the top third of the water column than
874 those in tanks. The authors suggested that, among other reasons, dolphins in ocean facilities may
875 spend more time deeper in the water column because of the presence of natural flora and fauna,
876 especially fish, who enter and exit the area (Lauderdale et al., 2021b). The above studies, while
877 far from conclusive, strongly suggest that there are welfare benefits to dolphins (and likely other
878 cetaceans) of living in a more natural ocean environment – even when captive. The current
879 literature on environmental enrichment and welfare in cetaceans indicates that much more
880 research is needed to determine if and how specific enrichment efforts can improve welfare with
881 the caveat that certain aspects of enrichment (e.g., space) often cannot reasonably be addressed in
882 traditional captive facilities. The effects of environmental enrichment can only be fully
883 understood by employing well-confirmed welfare tests (Brereton & Rose, 2023).

884 6. Discussion and Conclusion

Commented [A121]: But for a dolphin moving from a pool to a sea pen the experience may be very different.

Commented [A122]: This needs to be contextualized with the overall findings of the Cetacean Welfare Study that showed that space and whether or not the animals were in a pool or a sea pen were the weakest welfare predictors.

Commented [A123]: Well this is not true at all. One could treat this in lagoon facilities where dolphins have open ocean access and the amount of primary reinforcement it takes to get the animals to swim into the open ocean could be used as the dependent measurement to determine the effectiveness of space in improving welfare. But again. The Cetacean Welfare Study looked at this. See the numerous calls to incorporate that better into this paper. The authors are hampered here by not having a complete understanding of the diversity of captive facilities in the world.

886 In the present review, we have underscored concerns that are vital to captive cetacean welfare. For
887 cetaceans, there is a significant mismatch in amount and complexity of space available, socio-cultural
888 opportunities, and cognitive stimulation between the captive and natural environments, which
889 contributes to their difficulties coping with life confined to concrete tanks (Mason, 2010; Hosey
890 et al., 2020). Additionally, the natural characteristics of cetaceans (e.g., their need for space,
891 cognitive and social complexity) predict the welfare challenges outlined above (Clubb & Mason,
892 2007; Pomerantz et al., 2013; Hosey et al., 2020; Mellor et al., 2021). These outcomes are in
893 keeping with Mason's (2010) study of how different species respond to captivity.

895 Much of the literature we have cited acknowledges areas where further study is needed. For
896 instance, important questions remain about how amount of space and complexity interact as factors in
897 well-being, how to provide more supportive environments for nursing and rearing calves, and which
898 enrichment methods are long-lasting and the most effective, and why, among others. In addition, the bulk
899 of the cetacean welfare literature appears to be focused on dolphins and less so on the larger odontocetes
900 like orcas and beluga whales. There remain significant (practical) limits to the extent to which land-
901 based entertainment parks can provide larger, more complex, and variable environments that
902 would allow cetaceans to engage in a greater range of natural behaviors. Pierce and Bekoff
903 (2018) point out that discussions of animal welfare in zoos and marine parks often center on
904 incremental improvements while overlooking the fundamental issue of captivity itself, namely the
905 underlying incompatibility between captivity and life in the wild.

907 Welfare measures and assessments make up the bulk of the literature on captive animal welfare
908 because one can collect scientific, quantifiable data. Such studies, however, do not address an
909 important factor: quality of life. Presumably, this is because quality of life is a subjective
910 evaluation made by the non-human animal and is not something one can scientifically measure in
911 the absence of self-reporting. One can conduct choice and preference testing to help determine
912 what is important to an animal (Dawkins, 2003), but the choices provided may not discern what
913 the animal truly prefers, that is, what is actually optimal for the animal. For example, a
914 researcher may give an animal a choice between Food A and Food Z, but what the animal prefers
915 might actually be Food B at Time F, and food J at Time Y. The former option provides the
916 animal with a choice; the latter option is more reflective of true autonomy. In the Cetacean

Commented [REDACTED] This is correct. It should be applied what is known and unknown about the GFAS sanctuary model at the end of this paper.

Commented [REDACTED] Orcas are dolphins. I think you mean to change "dolphins" to "bottlenose dolphins"

Commented [REDACTED] Yes. There is an incompatibility to life in captivity and in the wild, which I think explains why releasing cetaceans doesn't work and why GFAS cetacean sanctuaries as a concept are flawed. Animals that have no experience with the wild may not be compatible with even limited amounts of it, as anyone who has watched zoo-dolphins flee from a swimming fish will attest. This is a philosophical critique because the authors make philosophical arguments. Not sure that belongs in a paper that is ostensibly about the state of cetacean welfare in zoos.

917 Welfare Study, “quality of life” is mentioned only one time: “There is a strong commitment
918 among zoos and aquariums to continuously advance an understanding of welfare across facilities
919 using scientific methods to positively impact the quality of life for the animal” (p. 2, Lauderdale
920 et al., 2021b). As such, there is an assumption or belief that improved welfare measures will lead
921 to a better quality of life (Pierce & Bekoff, 2018). However, the studies did not evaluate the
922 actual well-being of the dolphins; in fact, of the nine articles, there is only one mention of the
923 term “well-being” (Miller et al., 2021c), and then only in a quote from Shepherdson (1998). The
924 question thus remains: how can one definitively determine which welfare assessments actually
925 provide quality of life? For example, researchers would probably agree that having autonomy
926 (i.e., choice and control over the environment) should improve well-being (Jaakkola, 2023) by
927 providing captive animals with the opportunity to thrive (Vincino & Miller, 2015; Miller et al.,
928 2020). But the relationship between autonomy and quality of life in a captive setting is not
929 something one can easily quantify. As noted previously, although Tidière et al. (2023) found that
930 their data on captive animals demonstrated increased longevity in recent decades (a finding
931 typically interpreted as indicating positive welfare), the study did not address quality of life
932 itself. This issue would seem to go beyond the quantifiable bounds of science.

934 Moreover, as often appears to be the case with such welfare measurement studies, it is not clear
935 if any of the welfare measures have actually been implemented. For the Cetacean Welfare Study,
936 for example, apart from providing baseline reference measures through an iOS application (e.g.,
937 blood variables, fecal hormone metabolites; Lauderdale et al., 2021b), it remains unclear if, to
938 what extent, how, or where the welfare measures determined to be important will be incorporated
939 by captive facilities. In recent years, there have been attempts to apply comprehensive
940 assessment programs for dolphins (e.g., the C-Well Assessment for bottlenose dolphins, Clegg et
941 al., 2023a; Dolphin-WET, Baumgartner et al., 2024). These efforts reflect growing progress
942 toward embedding welfare assessments into the daily care of captive cetaceans, but concerns
943 remain regarding the quality of life for these animals (Hoy et al., 2010; Clegg & Delfour, 2018;
944 Clegg et al., 2023b).

946 Thus, from an ethical standpoint, the deeper question is whether cetaceans can truly thrive in
947 captivity, rather than merely survive. Thriving goes beyond physical health or lifespan – it

Commented [REDACTED] I’m not sure what the purpose of this section is. Do the authors wish to imply that animals under human care have a poor quality of life? If the authors agree that no claim can be made on that through science why bring it up in this context?

Commented [REDACTED] So you say that one cannot scientifically know quality of life but you assume it to be bad? This treads dangerously into the “because I said so” territory. This all really should go. I also would make sure that the authors cited would subscribe to your framing of this.

948 encompasses overall *quality* of life and well-being. This includes factors such as the ability to
 949 exercise autonomy (as highlighted in Vicino and Miller's, 2015, emphasis on choice and control)
 950 and engage in meaningful environmental challenges. Partoon et al. (2025) suggest that a positive
 951 mental state is crucial to an animal thriving, and this involves promoting positive experiences for the
 952 animal through a species appropriate diet, naturally occurring social groupings, preventative healthcare,
 953 and a species appropriate habitat. Current evidence indicates that, although marine parks and
 954 aquariums can upgrade enclosures to offer some physical and behavioral benefit, they remain
 955 limited by available space and the artificial conditions required to keep cetaceans in captivity. Certainly,
 956 they cannot replicate the conditions of a free-living life necessary for cetaceans to truly thrive.
 957 With few exceptions (i.e., when individuals are captured from the wild or rescued and held in captivity
 958 for a short while), captive cetaceans cannot be released into the wild because they lack basic
 959 survival skills. Therefore, there are limited ethical alternatives. One of the most feasible options is
 960 a sanctuary, that is, ocean-based captive enclosures where cetaceans can receive human care while
 961 experiencing more space, autonomy, and choice in a natural environment. There are currently three
 962 cetacean sanctuaries being created by the Whale Sanctuary Project, the National Aquarium, and
 963 SEALIFE TRUST (Marino et al., 2025). Authentic sanctuaries, as opposed to greenwashed or
 964 temporary sea pen facilities (Speiran, 2025), are still captive environments and therefore will share
 965 many management challenges with other captive facilities (e.g., feeding, veterinary care, funding; Bruck,
 966 2024). However, a sanctuary has different tools to mitigate the challenges of captivity such as a larger,
 967 more natural environment that offers greater complexity and enhanced sensory-perceptual experiences.
 968 As opposed to zoos, marine parks, and other entertainment venues (as well as military and
 969 scientific settings) authentic sanctuaries are not driven by objectives that often compete with
 970 animal well-being and autonomy (e.g., visitor experiences, scientific studies, breeding through
 971 AI). Accreditation standards for cetacean sanctuaries have been adopted by the Global
 972 Federation of Animal Sanctuaries (GFAS, 2025; Marino et al., 2025). Authentic sanctuaries for
 973 other wild animals, such as elephants and great apes, face many of the same challenges as
 974 cetacean sanctuaries but report improved physical and psychological health in their residents
 975 after they acclimate to their new environment (Buckley, 2009; Derby, 2009; Grow, 2020).
 976
 977 Although concerns about sanctuaries have been expressed by those who currently work with
 978 both wild and captive cetaceans (Bruck, 2024; Almunia & Canchal, 2025), it remains one of the
 979 only options available for those animals currently held in managed land-based tanks. Clearly,

Commented [A130]: Does a cetacean have autonomy if you put it in a stretcher haul it to Nova Scotia and put it in a 100 acre sea pen? Does it have a choice in that move? If you are interested in choice perhaps you could go to Dolphin Quest Bermuda where their pools are connected to the open ocean or Dolphin Research Center where the animals have open ocean experience and start testing habitat preferences. One could even use the amount of primary reinforcer is a dependent measurement when examining how willing animals are to go from place to place in these different habitats. I think the answer would surprise you. You talk later about "species appropriate habitat". I think you should consider "individual appropriate habitat". What is the habitat appropriate for this individual with this l... [4]

Commented [A131]: The authors should be very specific as to what environmental challenges they expect for the animals. And they should meaningfully contrast these enrichment experiences with specif... [5]

Commented [A132]: Can you please present data from cetaceans that shows that a free living life is necessary for cetaceans under human care to thrive? To my knowle... [6]

Commented [A133]: There are at least two publications that I am aware of that highlight serious concerns with sanctuaries proposed under the model of the Global Federation of Animal Sanctuaries. Detail is given ... [7]

Commented [A134]: There is no such thing as an authentic sanctuary. Until such a thing exists with animals living in the intended sea pen environment it is not for you to say what is greenwashing and what is legitimate. G... [8]

Commented [A135]: The point of this paper was to highlight the increased challenges associated with vast sea pens where folks try to skate a line between wild and captive. A facility with a 100 acre sea pen has MORE ... [9]

Commented [A136]: This sounds like a statement that has little informing it from actual accredited facilities. I don't know any facility where animal welfare takes a back ... [10]

Commented [A139]: The authors seem to have a view of current zoological models that assumes research with the animals or visitor interactions are implicitly negative experiences for the animals. I think rese... [11]

Commented [A140]: If you are going to discuss sanctuaries it would be appropriate to discuss the challenges associated with them. Animals not responding well to them, noise, veterinary acces... [12]

Commented [A141]: It would be necessary at this point to discuss critiques of the standards. There are a lot. It would also be important to highlight what informs these standards. I'm sorry but your readers should not hav... [13]

Commented [A142]: It is important to properly characterize the work of those you cite.

Commented [A143]: There is also the option not to move the animals into massive sea pens. At least not until compelling data suggests that they will uniformly experience improved welfare. The authors should no... [14]

980 transitioning cetaceans to an authentic sanctuary requires careful planning (e.g., priming the
 981 microbiota to buffer against novel pathogens; Dallas & Warne, 2023) and will require continued
 982 research to evaluate the welfare of transferred animals. Welfare assessments in sanctuaries will,
 983 in some ways, differ from those in zoos and aquariums as the animals will have access to and
 984 interact with more natural environments. The goal would be for animals to exhibit (1) greatly
 985 reduced or an absence of stereotypes, (2) greater engagement in natural behaviors, including
 986 those that were previously unavailable to them (e.g., exploring/interacting with natural features
 987 of the environment, foraging), (3) increased time spent in play and other positive behaviors
 988 illustrating greater behavioral diversity, (4) time budgets closer to what exists in nature, (5)
 989 decreased time spent in human-animal interactions, (6) increased autonomy and the ability to
 990 make meaningful choices, and (7) a decrease in physiological indicators of stress. These goals
 991 are consistent with the five domains model of animal welfare (Hampton et al., 2023; Partoon et
 992 al., 2025). Although none of these, in isolation, indicates that an animal is thriving, the broad
 993 confluence of all these factors would indicate more natural behavior and would help attain the
 994 goals set by accrediting agencies mentioned previously, namely: “maximize psychological
 995 health” (WAZA, 2025), stimulate “natural behavior” (AZA, 2025), allow the animal “variety and
 996 choices” in the animal’s environment (AMMPA, 2025), and to provide the animal with
 997 “behavioural choices” and “control over its environment” (EAAM, 2025).

998

999 In conclusion, the evidence clearly shows that ongoing health and welfare challenges remain for
 1000 captive cetaceans, indicating that they are generally unsuited for captivity from both practical
 1001 and ethical standpoints. Marine parks, particularly those that are accredited and have
 1002 environmental enrichment programs, have improved in their ability to provide better welfare for
 1003 captive cetaceans. Nevertheless, they still cannot fully meet the complex needs of these animals.
 1004 As interest and experience in captive animal well-being grows, it is essential to acknowledge
 1005 when certain environments fail to provide what a species needs to thrive. Moving forward,
 1006 science-based policies should be considered to determine which species should no longer be
 1007 housed or bred in zoos, aquariums, and entertainment parks.

1008

1009

1010

Commented [A149]: Perhaps one would assess the potential welfare outcomes before animals are irrevocably moved to these environments? Which I remind the authors the two belugas in Iceland were moved to and had to move back into the pool. Hence why you should properly read and discuss Bruck, 2024 and Almunia and Canchal, 2025 in this section to give a fair minded discussion of the GFAS Standards and how they relate to the animals, in theory, that should be experiencing them right now.

Commented [A150]: Even the study you mentioned on animal tracking showed little evidence for stereotypes. Where is your evidence that this is a pervasive problem that requires all cetaceans to be put in GFAS sanctuaries? From Rachinas-Lopes 2019 “The subjects showed specific movement routines that involved circular swimming over the Deep Area of the pool and used most of their habitat, performing rings with different durations and sizes. These rings presented differences between individuals and were variable across sessions, indicating that these patterns of movement are not highly stereotyped. In any case, having a baseline of the normal movements of captive dolphins facilitates the detection of bizarre behaviours that m (... [15]

Commented [A151]: Again. This is the naturism fallacy. Where in the cetacean welfare study did it show that cetaceans in ocean environments had better welfare than those in pools? Will the animals stop stress swimming at any point to engage in these behaviors? Little White and Little Grey didn’t and that’s why they are back in their stag (... [16]

Commented [A152]: This is the naturism fallacy. Why is a time budget closer to nature better for welfare? To me it seems your best case scenario is that these whales go somewhat back to wild. How would you be able to do medical care with them when their medical training collapses? The frustration is that it doesn’t take much (... [17]

Commented [A153]: Increased autonomy can lead to decreased training, decreased medical care, decreased welfare. Micheal Moore speaks eloquently about the welfare of wild animals. He does not paint the rosy picture the authors do here. Any fair-minded discussion of the state of welfare in captive cetaceans should honestly cons (... [18]

Commented [A154]: That assumes, probably erroneously, that the animals have heightened stress in human care—which was a surprise, I’m sure, for Proie and the folks from this paper who helped them. The more pressing problem is assuming that there won’t be a stress response to the noise, activity and sheer space afforded by a GFAS sanctuar (... [19]

Commented [A150]: incredibly biased language.

Commented [A151]: I’m not seeing data that shows this. In the studies cited I see opinions, but I don’t see data. The CWS, for whatever criticisms you have of it, has data and it does not show this. I would recommend softening this language to use words like “may” or “might”.

Commented [A152]: That is not a consensus opinion and has not been demonstrated from the selective use of primary materials present in this paper.

References

- Almunia J. 2017. Loro Parque vs People for the Ethical Treatment of Animals (PETA), Puerto de la Cruz, Tenerife, Spain. Case File number: 3802841120160000920, Civil Juicio Ordinario 0000187/2016'. Testimony at 02:41:03.
- Almunia J, Canchal M. 2025. Cetacean sanctuaries: Do they guarantee better welfare? *Journal of Zoological and Botanical Gardens* 6:4. <https://doi.org/10.3390/jzbg6010004>
- AMMPA. 2025. Alliance for Marine Mammal Parks Aquariums. <https://ammpa.org/sites/default/files/files/Resource%20Library/AMMPA-StandardsAndGuidelines-R072020.pdf#page=9.08>. Accessed on 1 May 2025.
- Anderson R, Waayers R, Knight A. 2016. Orca behavior and subsequent aggression associated with oceanarium confinement. *Animals* 6(8):49.
- Animal Welfare Act. 2025. <https://www.ecfr.gov/current/title-9/chapter-I/subchapter-A/part-3/subpart-E>. Accessed on 14 May 2025.
- Au WWL. 1993. *The sonar of dolphins*. New York: Springer-Verlag.
- AZA. 2025. *Association of Zoos & Aquariums*. <https://www.aza.org>. Accessed on 5 February 2025.
- Avila IC, Kaschner K, Dormann CF. 2018. Current global risks to marine mammals: Taking stock of the threats. *Biological Conservation* 221:44-58.
- Bacon H. 2018. Behaviour-based husbandry—A holistic approach to the management of abnormal repetitive behaviors. *Animals* 8:103. <https://doi.org/10.3390/ani8070103>
- Bai S, Zhang P, Zhang C, Du J, Du X, Zhu C, Liu J, Xie P, Li S. 2021. Comparative study of the gut microbiota among four different marine mammals in an aquarium. *Frontiers in microbiology* 12:769012. <https://doi.org/10.3389/fmicb.2021.769012>
- Baird RW. 2002. *Killer Whales of the World - Natural History and Conservation*. Voyageur Press, Stillwater; MN. ISBN978-0896585126
- Baumgartner K, Hüttner T, Clegg IL, Hartmann MG, Garcia-Párraga D, Manteca X, Mercera B, Montreal-Pawlowsky T, Pilenga C, Ternes K, Tallo-Parra O, Vaicekauslaite R, von Fersen L, Delfour F. 2024. Dolphin-WET—Development of a welfare evaluation tool for bottlenose dolphins (*Tursiops truncatus*) under human care. *Animals* 14(5):701. <https://doi.org/10.3390/ani14050701>

Commented [A153]: This is an opinion article with a retired Space Dynamics Laboratory member as the lead author

1042 Begeman L, Leger JS, Blyde DJ, Jauniaux TP, Lair S, Lovewell G, Raverty S, Seibel H, Siebert
 1043 U, Staggs SL, Martelli P, Keesler RI. 2013. Intestinal volvulus in cetaceans. *Veterinary*
 1044 *Pathology* 50(4):590-596.
 1045 Bergeron R, Badnell-Waters AJ, Lambton S, Mason G. 2006. Stereotypic oral behaviour in
 1046 captive ungulates: foraging, diet and gastrointestinal function. In: *Stereotypic Animal*
 1047 *Behaviour: Fundamentals and Applications to Welfare*. Wallingford UK: CABI, 19-57.
 1048 Berry G. 2021. [New law looks set to ban dolphin shows in France - *Whale and Dolphin*](https://uk.whales.org/2021/11/23/new-law-will-ban-dolphin-shows-in-france/#:~:text=New%20legislation%20in%20France%20is,orcas%20and%2012%20bottlenose%20dolphins)
 1049 [Conservation](https://uk.whales.org/2021/11/23/new-law-will-ban-dolphin-shows-in-france/#:~:text=New%20legislation%20in%20France%20is,orcas%20and%2012%20bottlenose%20dolphins). [https://uk.whales.org/2021/11/23/new-law-will-ban-dolphin-shows-in-](https://uk.whales.org/2021/11/23/new-law-will-ban-dolphin-shows-in-france/#:~:text=New%20legislation%20in%20France%20is,orcas%20and%2012%20bottlenose%20dolphins)
 1050 [france/#:~:text=New%20legislation%20in%20France%20is,orcas%20and%2012%20bott-](https://uk.whales.org/2021/11/23/new-law-will-ban-dolphin-shows-in-france/#:~:text=New%20legislation%20in%20France%20is,orcas%20and%2012%20bottlenose%20dolphins)
 1051 [lenose%20dolphins](https://uk.whales.org/2021/11/23/new-law-will-ban-dolphin-shows-in-france/#:~:text=New%20legislation%20in%20France%20is,orcas%20and%2012%20bottlenose%20dolphins). Accessed 5 May 2025.
 1052 Bisther A. 2002. Intergroup interactions among killer whales in Norwegian coastal waters;
 1053 Tolerance vs. aggression at feeding grounds. *Aquatic Mammals* 28:14-23.
 1054 Boissat L, Thomas-Walters L, Verissimo D. 2021. Nature documentaries as catalysts for change:
 1055 Mapping out the 'Blackfish Effect.' *People and Nature* 3(6):1179-1192.
 1056 <https://doi.org/10.1002/pan3.10221>
 1057 Bossart GD, Meisner R, Varela R, Mazzoil M, McCulloch SD, Kilpatrick D, Friday R, Murdoch
 1058 E, Mase B, Defran RH. 2003. Pathologic findings in stranded Atlantic bottlenose
 1059 dolphins (*Tursiops truncatus*) from the Indian River Lagoon, Florida. *Florida Scientist*
 1060 66(3):226-238.
 1061 Bossart GD, Romano TA, Peden-Adams MM, Schaefer AM, Rice CD, Fair PA, Reif JS. 2019.
 1062 Comparative innate and adaptive immune responses in Atlantic bottlenose dolphins
 1063 (*Tursiops truncatus*) with viral, bacterial, and fungal Infections. *Frontiers in Immunology*
 1064 10:1125. <https://doi.org/10.3389/fimmu.2019.01125>
 1065 Brando S, Broom DM, Acasuso-Rivero, Clark F. 2018. Optimal marine mammal welfare under
 1066 human care: Current efforts and future directions. *Behavioural Processes* 156:16-36.
 1067 <http://dx.doi.org/10.1016/j.beproc.2017.09.011>
 1068 Brando S, Buchanan-Smith HM. 2018. The 24/7 approach to promoting optimal welfare for
 1069 captive wild animals. *Behavioural Processes* 156:83-95
 1070 Brando S, Kooistra N, Hosey G. 2019. Pre and post session behaviour of captive bottlenose
 1071 dolphins *Tursiops truncatus* involved in "Swim-with-Dolphin" events. *Journal of Zoo*
 1072 *and Aquarium Research* 7(4):195-202.

1073 Branstetter B, Mercado E III. 2006. Sound localization by cetaceans. *International Journal of*
1074 *Comparative Psychology* 19(1). <https://doi.org/10.46867/ijcp.2006.19.01.05>

1075 Brensing K, Linke K, Busch M, Matthes I, van der Woude SE. 2005. Impact of different groups
1076 of swimmers on dolphins in swim-with-the-dolphin programs in two settings. *Anthrozoös*
1077 18(4):409-429.

1078 Brereton JE, Fernandez EJ. 2022. Investigating unused tools for the animal behavioral diversity
1079 toolkit. *Animals*, 12(21):2984. <https://doi.org/10.3390/ani12212984>

1080 Brereton J, Rose P. 2023. An evaluation of the role of “biological evidence” in zoo and aquarium
1081 enrichment practices. *Animal Welfare* 31:13-26.
1082 <https://doi.org/10.7120/09627286.31.1.002>

1083 Bruck JN. 2024. The cetacean sanctuary: A sea of unknowns. *Animals* 14(2):335.
1084 <https://doi.org/10.3390/ani14020335>

1085 Buchholtz, EA. 2001. Vertebral osteology and swimming style in living and fossil whales
1086 (Order: Cetacea). *Journal of Zoology London* 253:175-190.
1087 <https://doi.org/10.1017/S0952836901000164>

1088 Buckley C. 2009. Sanctuary: A fundamental requirement of wildlife management. In: Forthman,
1089 DL, Kane LF, Hancocks D, Waldau PF, eds., *An Elephant in the Room: The Science and*
1090 *Well-being of Elephants in Captivity*. Center for Animals and Public Policy, North Grafton,
1091 MA: Tufts University, 191-197.

1092 Buhrmann CA, Gridley T, Oellermann LK. 2023. Diagnosing gastric ulcers in bottlenose
1093 dolphins (*Tursiops* sp.) using gastroscopy and cytology. *Zoo Biology* 42:522–528.
1094 <https://doi.org/10.1002/zoo.21767>

1095 Calle PP. 2005. Stereotypic behavior in zoological species. In: Proceeding of the NAVC North
1096 American veterinary conference. New York.
1097 <https://www.cabidigitallibrary.org/doi/pdf/10.5555/20053197497> Accessed on 20 May
1098 2025.

1099 Carter N. 1982. Effects of psycho-physiological stress on captive dolphins. *International Journal*
1100 *for the Study of Animal Problems* 3(3):193-198.

1101 Castellote M, Fossa F. 2006. Measuring acoustic activity as a method to evaluate welfare in
1102 captive beluga whales (*Delphinapterus leucas*). *Aquatic Mammals* 32(3):325-333.
1103 <https://doi.org/10.1578/AM.32.3.2006.325>

1104 Cetabase. 2025. <https://www.cetabase.org>. Accessed 7 January.

1105 Clark FE. 2013. Marine mammal cognition and captive care: A proposal for cognitive enrichment
1106 in zoos and aquariums. *Journal of Zoo and Aquarium Research* 1(1):1-6.

1107 Clark FE. 2017. Cognitive enrichment and welfare: Current approaches and future directions.
1108 *Animal Behavior and Cognition*, 4(1), 52–71. <https://doi.org/10.12966/abc.05.02.2017>

1109 Clegg ILK. 2021. What does the future hold for the public display of cetaceans? *Journal of*
1110 *Applied Animal Ethics Research* 3(2):240-278.

1111 Clegg ILK, Borgner-Turner JL, Eskelinen HC. 2023a. C-Well: The development of a
1112 welfare assessment index for captive bottlenose dolphins (*Tursiops truncatus*).
1113 *Animal Welfare* 24(3):267-282. <https://doi.org/10.7120/09627286.24.3.267>

1114 Clegg ILK, Butterworth A. 2017. Assessing the welfare of Cetacea. In *Marine Mammal Welfare:*
1115 *Human induced change in the marine environment and its impacts on marine mammal*
1116 *welfare*. New York: Springer, 183-211.

1117 Clegg ILK, Delfour F. 2018. Can we assess marine mammal welfare in captivity and in
1118 the wild? Considering the example of bottlenose dolphins. *Aquatic Mammals*
1119 44(2):181-200. <http://doi.org/10.1578/AM.44.2.2018.181>

1120 Clegg ILK, Domingues M, Ström E, Berggren L. 2023b. Cognitive foraging enrichment (but not
1121 non-cognitive enrichment) improved several longer-term welfare indicators in bottlenose
1122 dolphins. *Animals* 13:238. <https://doi.org/10.3390/ani13020238>

1123 Clubb R, Mason G. 2003. Captivity effects on wide-ranging carnivores. *Nature* 425:473-474.
1124 <https://doi.org/10.1038/425473a>

1125 Clubb R, Mason G. 2007. Natural behavioural biology as a risk factor in carnivore welfare: How
1126 analyzing species differences could help zoos improve enclosures. *Applied Animal*
1127 *Behavior Science* 102:303-328. <https://doi.org/10.1016/j.applanim.2006.05.033>

1128 Colegrove KM. 2018. Noninfectious diseases. In: Dierauf LA, Gulland FMD, eds., *CRC*
1129 *Handbook of Marine Mammal Medicine*. CRC Press:Boca Raton, FL, 309-335.

1130 Coleman K, Maier A. 2010. The use of positive reinforcement training to reduce stereotypic
1131 behavior in rhesus macaques. *Applied Animal Behavioral Science* 1:124(3-4):142-148.
1132 <http://doi.org/10.1016/j.applanim.2010.02.008>

1133 Corkeron P. 2009. Captivity. In: Perrin WF, Würsig B, Thewissen JGM, eds., *Encyclopedia of Marine*
 1134 *Mammals* (2nd Ed.). New York: Academic Press, 183-188.
 1135 <https://doi.org/10.1016/B978-0-12-373553-9.00049-3>
 1136 Couquiaud L. 2005. Introduction to a survey of the environments of cetaceans in human care.
 1137 *Aquatic Mammals* 31:277e385
 1138 Dallas JW, Warne RW. 2023. Captivity and animal microbiomes: Potential roles of microbiota
 1139 for influencing animal conservation. *Microbial Ecology* 85:820-838.
 1140 <https://doi.org/10.1007/s00248-022-01991-0>
 1141 Davies J, Davies D. 2010. Origins and evolution of antibiotic resistance. *Microbiology and*
 1142 *Molecular Biology Reviews* 74:417e433.
 1143 Dawkins MS. 2003. Behaviour as a tool in the assessment of animal welfare. *Zoology* 106(4):
 1144 383-387. <https://doi.org/10.1078/0944-2006-00122>
 1145 de Azevedo CS, Cipreste CF, Pizzutto CS, Young RJ. 2023. Review of the effects of enclosure
 1146 complexity and design on the behaviour and physiology of zoo animals. *Animals*
 1147 13(8):1277. <https://doi.org/10.3390/ani13081277>.
 1148 Delfour F, Beyer H. 2012. Assessing the effectiveness of environmental enrichment in bottlenose
 1149 dolphins (*Tursiops truncatus*). *Zoo Biology* 31:137-150.
 1150 <https://doi.org/10.1002/zoo.20383>
 1151 Delfour F, Monreal-Pawłowsky T, Vaicekauskaitė R, Pilenga C, Garcia-Parraga D, Rödel HG,
 1152 García Caro N, Perlado-Campos E, Mercera B. 2020. Dolphin welfare assessment under
 1153 professional care: ‘Willingness to participate’, an indicator significantly associated with
 1154 six potential ‘alerting factors’. *Journal of Zoological and Botanical Gardens* 1(1):42-60.
 1155 <https://doi.org/10.3390/jzbg1010004>
 1156 Derby P. 2009. Changes in social and biophysical environment yield improved physical and
 1157 psychological health for captive elephants. In: Forthman DL, Kane LF, Hancocks D,
 1158 Waldau PF. eds., *An Elephant in the Room: The Science and Well-Being of Elephants in*
 1159 *Captivity*. Center for Animals and Public Policy, North Grafton, MA: Tufts
 1160 University, 198-207.
 1161 Desportes G, Buholzer L, Anderson-Hansen K, Blanchet AM, Acquarone M, Shephard G,
 1162 Brando S, Vossen A, Siebert U. 2007. Decrease stress; train your animals: The effect of

1163 handling methods on cortisol levels in harbour porpoises (*Phocoena phocoena*) under
 1164 human care. *Aquatic Mammals* 33:286-292. <http://doi.org/10.1578/AM.33.3.2007.286>
 1165 Dima LD, Gache C. 2004. Dolphins in captivity: Realities and perspectives. *Analele Științifice*
 1166 ale Universității, “Alexandru I. Cuza” Iași. S. 1. Biologie animală, Tom L [Scientific
 1167 Annals of “Alexandru Ioan Cuza” University of Iasi. Section 1]. *Animal Biology* 50:413-
 1168 418.
 1169 Dold C. 2015 Cetacea (whales, dolphins, porpoises). In: *Fowler's Zoo and Wild Animal*
 1170 *Medicine*. Elsevier, St. Louis, MI: Elsevier, 422-436.
 1171 Doyle C. 2017. Captive wildlife sanctuaries: Definition, ethical consideration and public
 1172 perception. *Animal Studies Journal* 6(2):55-85.
 1173 Duignan PJ, Hunter JE, Visser IN, Jones GW, Nutman A. 2000. Stingray spines: A potential
 1174 cause of killer whale mortality in New Zealand. *Aquatic Mammals* 26:143-147.
 1175 JW, Pitman RL. 2012. Antarctic killer whales make rapid, round-trip movements to
 1176 subtropical waters: evidence for physiological maintenance migrations? *Biology Letters*
 1177 8:274-277. <https://doi.org/10.1098/rsbl.2011.0875>
 1178 EAAM. 2025. European Association for Aquatic Mammals.
 1179 https://www.eaam.be/_files/ugd/ba9fb6_6f39447579634794ab70c28a1c2db26da.pdf
 1180 Accessed on 1 May 2025.
 1181 Evans SJ. 2015. Nanuq the beluga whale dies at under-fire SeaWorld Orlando after fracturing
 1182 his jaw and contracting infection while on loan. *Daily Mail*, 22 February 2015.
 1183 <http://www.dailymail.co.uk/news/article-2963937/>
 1184 Fahlman A, Moore, RBT, Stone R, Sweeney J, Trainor RF, Barleycorn AA, McHugh K, Allen
 1185 JB, Wells RS. 2022. Deep diving by offshore bottlenose dolphins (*Tursiops* spp.). *Marine*
 1186 *Mammal Science* 39:1251-1266. <https://doi.org/10.1111/mms.13045>
 1187 Fair PA, Schaefer AM, Houser DS, Bossart GD, Romano TA, Champagne CD, Stott JL, Rice
 1188 CD, White N, Reif JS. 2017. The environment as a driver of immune and endocrine
 1189 responses in dolphins (*Tursiops truncatus*). *PLoS ONE* 12(5):e0176202.
 1190 <https://doi.org/10.1371/journal.pone.0176202>
 1191 Feng LC, Howell TJ, Bennett PC. 2016. How clicker training works: comparing reinforcing,
 1192 marking, and bridging hypotheses. *Applied Animal Behaviour Science* 181:34-40.
 1193 Fernandez EJ. 2022. Training as enrichment: A critical review. *Animal Welfare* 31(1):1-12.

1194 Fischer CP, Romero LM. 2018. Chronic captivity stress in wild animals is highly species-
 1195 specific. *Conservation Physiology* 7:coz093. <https://doi.org/10.1093/conphys/coz093>

1196 Foote AD, Newton J, Piertney SB, Willerslev E, Gilbert MTP. 2009. Ecological, morphological
 1197 and genetic divergence of sympatric North Atlantic killer whale populations. *Molecular*
 1198 *Ecology*, 18(24):5207-5217.

1199 Ford JK, Ellis GM, Matkin CO, Wetklo MH, Barrett-Lennard LG, Withler RE. 2011. Shark
 1200 predation and tooth wear in a population of northeastern Pacific killer whales. *Aquatic*
 1201 *Biology*, 11(3):213-224.

1202 Ford JKB. 2018. Killer whale: *Orcinus orca*. In: Würsig B, Thewissen JGM, Kovacs KM, Eds,
 1203 *Encyclopedia of Marine Mammals* (3rd ed.). Cambridge, MA: Academic Press, 531-537.

1204 Ford JK. 2009 Killer whale: *Orcinus orca*. In: Perrin WF, Würsig B, Thewissen JGM, eds.,
 1205 *Encyclopedia of Marine Mammals* (2nd Ed.). New York: Academic Press, 650-657.

1206 Frohoff TG. 2004. Stress in dolphins. In: Bekoff M, ed, *Encyclopedia of Animal Behavior*.
 1207 Santa Barbara, CA: Greenwood Press, 1158-1164.

1208 Gannon D, Waples DM. 2004. Diets of coastal bottlenose dolphins from the US mid-Atlantic
 1209 coast differ by habitat. *Marine Mammal Science* 20:527-545.
 1210 <https://doi.org/10.1111/j.1748-7692.2004.tb01177.x>

1211 Geraci JR, Gerstmann KE. 1966. Relationship of dietary histamine to gastric ulcers in the
 1212 dolphin. *Journal of the American Veterinary Medical Association* 149(7):884-890.

1213 GFAS. 2025. [https://sanctuaryfederation.org/wp-content/uploads/2023/06/GFAS-Cetacean-](https://sanctuaryfederation.org/wp-content/uploads/2023/06/GFAS-Cetacean-Standards-2023.pdf)
 1214 [Standards-2023.pdf](https://sanctuaryfederation.org/wp-content/uploads/2023/06/GFAS-Cetacean-Standards-2023.pdf) Accessed on 10 May 2025.

1215 Gillet A, Frédéric B, Parmentier E. 2019. Divergent evolutionary morphology of the axial
 1216 skeleton as a potential key innovation in modern cetaceans. *Proceedings of the Royal*
 1217 *Society B*. 28620191771. <http://doi.org/10.1098/rspb.2019.1771>

1218 Gili C, Biancani B, Mazzariol S. 2017. Meticillin-resistant *Staphylococcus aureus* (MRSA)
 1219 associated dolphin mortality and the subsequent facility decolonisation protocol.
 1220 *Veterinary Record Case Reports* 5:e000444. [https://doi.org/10.1136/vetreccr-2017-](https://doi.org/10.1136/vetreccr-2017-000444)
 1221 [000444](https://doi.org/10.1136/vetreccr-2017-000444)

1222 Giovos I, Moutopoulos DK, Nakagun S, Vieira N, Akritopoulou E, Floriou-Servou A, Savinelli B,
 1223 Papadopoulos M, Mendez L, Calle Lobo S, Zaratva E, Garagouni M, Orfanidis G, Brito

1224 C. 2019. An international online social survey of public attitudes towards cetaceans.
 1225 *Aquatic Mammals* 45(3):327-339.

1226 Glatt SE, Francl KE, Scheels JL. 2008. A survey of current dental problems and treatments of
 1227 zoo animals. *International Zoo Yearbook* 42(1):206-213.

1228 Goldblatt A. 1993. Behavioural needs of captive marine mammals. *Aquatic Mammals* 19(3):149-157

1229 Graham MS, Dow PR. 1990. Dental care for a captive killer whale, *Orcinus orca*. *Zoo Biology*,
 1230 9(4), 325-330.

1231 Grow G. 2020. Knowing Jeannie. In: Rosenman D, ed, *The Chimpanzee Chronicles*. Santa
 1232 Fe, NM: Wild Soul, 17-30.

1233 Grillner S, Robertson B. 2016. The basal ganglia over 500 million years. *Current Biology*
 1234 26(20):R1088-R1100.

1235 Guérineau C, Lööke M, Ganassin G, Bertotto D, Bortoletti M, Caviechioli L, Furlati S, Mongillo
 1236 P, Marinelli L. 2022. Enrichment with classical music enhances affiliative behaviours in
 1237 bottlenose dolphin. *Applied Animal Behavioral Science* 254:105696.
 1238 <https://doi.org/10.1016/j.applanim.2022.105696>

1239 Gyax L. 1993. Spatial movement patterns and behaviour of two captive bottlenose dolphins
 1240 (*Tursiops truncatus*): Absence of stereotyped behaviour or lack of definition? *Applied*
 1241 *Animal Behavior Science* 38:337-344. [https://doi.org/10.1016/0168-1591\(93\)90031-J](https://doi.org/10.1016/0168-1591(93)90031-J)

1242 Hampton JO, Hemsworth LM, Hemsworth PH, Hyndman TH, Sandøe P. 2023. Rethinking the
 1243 utility of the Five Domains model. *Animal Welfare* 32.
 1244 <https://doi.org/10.1017/awf.2023.84>.

1245 Hancocks D. 2002. *A Different Nature: The Paradoxical World of Zoos and Their Uncertain*
 1246 *Future*. Berkeley, CA: University of California Press.

1247 Hanson MB, Emmons CK, Ford MJ, Everett M, Parsons K, Park LK, Hempelmann J, Van
 1248 Doornik DM, Schorr GS, Jacobsen JK, Sears MF, Sears MS, Sneva JG, Baird RW, Barre
 1249 L. 2021. Endangered predators and endangered prey: Seasonal diet of Southern Resident
 1250 killer whales. *PloS ONE*, 16:e0247031. <https://doi.org/10.1371/journal.pone.0247031>

1251 Hauser DDW, Laidre, KL, Parker-Stetter SKL, Horne JK, Suydam RS, Richard PR. 2015.
 1252 Regional diving behavior of Pacific Arctic beluga whales *Delphinapterus leucas* and
 1253 possible associations with prey. *Marine Ecology Progress Series* 541:245-264.
 1254 <https://doi.org/10.3354/meps11530>

1255 Hauser DDW, Laidre, KL, Suydam RS, Richard PR. 2014. Population-specific home ranges and
 1256 migration timing of Pacific Arctic beluga whales (*Delphinapterus leucas*). *Polar Biology*
 1257 37:1171-1183. <https://doi.org/10.1007/s00300-014-1510-1>
 1258 He Z. 2023. Social dynamics and intelligence of killer whales (*Orcinus Orca*). *Highlights in*
 1259 *Science, Engineering and Technology* 74:584-589. <https://doi.org/10.54097/4eygvh38>
 1260 Henderson SD, Dawson SM, Currey RJC, Lusseau D, Schneider K. 2014. Reproduction, birth
 1261 seasonality, and calf survival of bottlenose dolphins in Doubtful Sound, New Zealand.
 1262 *Marine Mammal Science* 30(3):1067–1080. <https://doi.org/10.1111/mms.12109>
 1263 Hindle AG. 2020. Diving deep: Understanding the genetic components of hypoxia tolerance in
 1264 marine mammals. *Journal of Applied Physiology* 128:1439-1446.
 1265 <http://doi.org/10.1152/jappphysiol.00846.2019>
 1266 Holmstrom S. 2018. Dentistry. In: Gulland FMD., Dierauf LA, Whitman KL. eds.,
 1267 *CRC Handbook of Marine Mammal Medicine*. CRC Press:Boca Raton, FL, 501-516.
 1268 Huettner T, Dollhaeupl S, Simon R, Baumgartner K, von Fersen L. 2021. Activity budget
 1269 comparisons using long-term observations of a group of bottlenose dolphins (*Tursiops*
 1270 *truncatus*) under human care: Implications for animal welfare. *Animals* 11(7):2107.
 1271 Hosey G, Melfi V, Ward SJ. 2020. Problematic animals in the zoo: The issue of charismatic
 1272 megafauna In: Angelici F, Rossi L, eds, *Problematic Wildlife II*; New York: Springer, 485-
 1273 508. https://doi.org/10.1007/978-3-030-42335-3_15
 1274 Hoy M, Murray PJ, Tribe A. 2010. Thirty years later: Enrichment practices for captive
 1275 mammals. *Zoo Biology* 29:303–316. <http://doi.org/10.1002/zoo.20254>
 1276 Hullar MAJ, Lampe JW, Torok-Storb BJ, Harkey MA. 2018. The canine gut microbiome is
 1277 associated with higher risk of gastric dilatation-volvulus and high risk genetic variants of
 1278 the immune system. *PLoS ONE* 13(6): e0197686.
 1279 <https://doi.org/10.1371/journal.pone.0197686>
 1280 Irvine AB, Scott MD, Wells RS, Kaufmann JH. 1981. Movements and activities of the Atlantic
 1281 bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. *Fishery Bulletin*
 1282 79(4):671–88.
 1283 Jaakkola K. 2023. Are dolphins kept in impoverished environments? *Animals* 13(17):2707.
 1284 <https://doi.org/10.3390/ani13172707>

1285 Jaakkola K. 2024. Minding the minds: A primer on cognitive challenge for marine mammals in
 1286 human care. *Animals* 14(6):949. <https://doi.org/10.3390/ani14060949>

1287 Jaakkola K, Brignac S, Erb L, Guarino E, Haddock A, Rodriguez A. 2023. Trainer interaction
 1288 can improve welfare outcomes of toy enrichment for isolated animals: A case study.
 1289 *Journal of Zoological and Botanical Gardens* 4(1):72-81.
 1290 <https://doi.org/10.3390/jzbg4010008>

1291 Jaakkola K, Willis K. 2019. How long do dolphins live? Survival rates and life expectancies for
 1292 bottlenose dolphins in zoological facilities vs. wild populations. *Marine Mammal Science*
 1293 35:1418-1437. <https://doi.org/10.1111/mms.12601>

1294 Jacobs B, Rally H, Doyle C, O'Brien L, Tennison M, Marino L. 2021. Putative neural
 1295 consequences of captivity for elephants and cetaceans. *Reviews in the Neurosciences*
 1296 33(4):439-465. <https://doi.org/10.1515/revneuro-2021-0100>

1297 Janik VM. 2014. Cetacean vocal learning and communication. *Current Opinion in Neurobiology*.
 1298 28:60-65. <https://doi.org/10.1016/j.conb.2014.06.010>

1299 Janik VM, Sayigh LS, Wells RS. 2006. Signature whistle shape conveys identity information to
 1300 bottlenose dolphins. *PNAS* 103(21):8293-8297. <https://doi.org/10.1073/pnas.0509918103>

1301 Jett J, Ventre J. 2011. Keto and Tilikum express the stress of orca captivity. Report available
 1302 from The Orca Project. [https://theorcaproject.wordpress.com/2011/01/20/keto-](https://theorcaproject.wordpress.com/2011/01/20/keto-tilikum-express-stress-of-orca-captivity)
 1303 [tilikum-](https://theorcaproject.wordpress.com/2011/01/20/keto-tilikum-express-stress-of-orca-captivity)
[express-stress-of-orca-captivity](https://theorcaproject.wordpress.com/2011/01/20/keto-tilikum-express-stress-of-orca-captivity)

1304 Jett J, Ventre J. 2012. Orca (*Orcinus orca*) captivity and vulnerability to mosquito transmitted
 1305 viruses. *Journal of Marine Animal Ecology* 5:9-16.

1306 Jett J, Ventre J. 2015. Captive killer whale (*Orcinus orca*) survival. *Marine Mammal Science*,
 1307 31(4):1362-1377. <https://doi.org/10.1111/mms.12225>

1308 Jett J, Visser IN, Ventre J, Waltz J, Loch C. 2017. Tooth damage in captive orcas (*Orcinus orca*),
 1309 *Archives of Oral Biology* 84:151-160. <https://doi.org/10.1016/j.archoralbio.2017.09.031>.

1310 Jones BL, Oswald M, Tufano S, Baird M, Mulsow J, Ridgway SH. 2021. A system for
 1311 monitoring acoustics to supplement an animal welfare plan for bottlenose dolphins.
 1312 *Animals* 2(2):222-233. <https://doi.org/10.3390/jzbg2020015>

1313 Joseph CA, Ollermann LK, Gridley T. 2019. An assessment of behaviour, stress, and gastric
 1314 ulcers in bottlenose dolphins (*Tursiops* sp.) at uShaka Marine World. Abstract presented

1315 at the International Association for Aquatic Animal Medicine Conference, Durban, South
 1316 Africa.

1317 Joseph B, Antrim J. 2010. Special considerations for the maintenance of marine mammals in
 1318 captivity. In: Kleiman DA, Thompson KV, Kirk Baer C, eds, *Wild Mammals in Captivity.*
 1319 *Principles and Techniques for Zoo Management.* Chicago, IL: The University of Chicago,
 1320 181-191.

1321 Kelly JR, Borre Y, O'Brien C, Patterson E, Aidy SE, Deane J, Kennedy PJ, Beers S, Scott K,
 1322 Moloney G, Hoban AE, Scott L, Fitzgerald P, Ross P, Stanton C, Clarke G, Cryan JF,
 1323 Ginan TG. 2016. Transferring the blues: depression-associated gut microbiota induces
 1324 neurobehavioural changes in the rat. *Journal of Psychiatric Research* 82:109–118.
 1325 <https://doi.org/10.1016/j.jpsychires.2016.07.019>

1326 Kieley J. 2011. Marine mammal inventory report: Killer whales (*Orcinus orca*) in captivity. St
 1327 Pete Beach, Florida, USA: The Orca Project Corp. Unpublished report.
 1328 [https://theorcaproject.files.wordpress.com/2011/03/mmir-deficiency-evaluation-killer-](https://theorcaproject.files.wordpress.com/2011/03/mmir-deficiency-evaluation-killer-whales2.pdf)
 1329 [whales2.pdf](https://theorcaproject.files.wordpress.com/2011/03/mmir-deficiency-evaluation-killer-whales2.pdf). Accessed 28 April, 2021.

1330 King SL, Friedman WR, Allen SJ, Gerber L, Jensen FH, Wittwer S, Connor RC, Krützen M.
 1331 2018. Bottlenose dolphins retain individual vocal labels in multi-level alliances. *Current*
 1332 *Biology* 28(12):1993-1999. <https://doi.org/10.1016/j.cub.2018.05.013>
 1333 <https://doi.org/10.1016/j.cub.2018.05.013>

1334 Koch MS, da Silva VDP, Bracarense APFRL, Domit C. 2018. Environmental aspects and
 1335 diseases related to immunosuppression in cetaceans: A concise review. *Semina Ciências*
 1336 *Agrárias* 39:2897-2918. <http://dx.doi.org/10.5433/1679-0359.2018v39n6p2897>

1337 Kuczaj S, Lacinak T, Fad O, Trone M, Solangi M, Ramos J. 2002. Keeping environmental
 1338 enrichment enriching. *International Journal of Comparative Psychology* 15(2):127-137.
 1339 <https://doi.org/10.46867/C4XK5N>

1340 Kyngdon DJ, Minot EO, Stafford KJ. 2003. Behavioural responses of captive common dolphins
 1341 *Delphinus delphis* to a 'Swim-with-Dolphin' programme. *Applied Animal Behaviour*
 1342 *Science* 81(2):163-170.

1343 Lacave G, Cui Y, Salbany A, Flanagan C, Grande F, Cox E. 2019. Erysipelas vaccination
 1344 protocols in dolphins *Tursiops truncatus* evaluated by antibody responses over twenty

1345 continuous years. *Diseases of Aquatic Organisms* 134:237-255.
 1346 <https://doi.org/10.3354/dao03367>

1347 Lambert KG, Hyer M, Bardi M, Rzucidlo A, Scott S, Terhune-Cotter B, Hazelgrove A, Silva I.
 1348 Kinsley C. 2016. Natural-enriched environments lead to enhanced environmental
 1349 engagement and altered neurobiological resilience. *Neuroscience* 330: 386-394.
 1350 <https://doi.org/10.1016/j.neuroscience.2016.05.037>

1351 Lambert KG, Nelson RJ, Javanovic T, Cerdá M. 2015. Brains in the city: Neurobiological
 1352 effects of urbanization. *Neuroscience and Biobehavioral Reviews* 58: 107-122.
 1353 <https://doi.org/10.1016/j.neubiorev.2015.04.007>

1354 Lauderdale LK, Walsh MT, Mitchell KA, Granger DA, Mellen JD, Miller LJ. 2021a. Health reference
 1355 intervals and values for common bottlenose dolphins (*Tursiops truncatus*), Indo-Pacific
 1356 bottlenose dolphins (*Tursiops aduncus*), Pacific white-sided dolphins (*Lagenorhynchus*
 1357 *obliquidens*), and beluga whales (*Delphinapterus leucas*). *PLoS ONE* 16: e0250332.
 1358 <https://doi.org/10.1371/journal.pone.0250332>

1359 Lauderdale LK, Mellen JD, Walsh MT, Granger DA, Miller LJ. 2021b. Towards understanding
 1360 the welfare of cetaceans in accredited zoos and aquariums. *PLoS ONE* 16:e0255506.
 1361 <https://doi.org/10.1371/journal.pone.0255506>

1362 Lauderdale LK, Shorter KA, Zhang D, Gabaldon J, Mellen JD, Walsh MT, Granger DA, Miller
 1363 LJ. 2021c. Habitat characteristics and animal management factors associated with habitat
 1364 use by bottlenose dolphins in zoological environments. *PLoS ONE* 16:e0252010.
 1365 <https://doi.org/10.1371/journal.pone.0252010>

1366 Lauderdale LK, Shorter KA, Zhang D, Gabaldon J, Mellen JD, Walsh MT, Granger DA, Miller LJ.
 1367 2021d. Bottlenose dolphin habitat and management factors related to activity and distance
 1368 traveled in zoos and aquariums. *PLoS ONE* 16:e0250687

1369 Lauderdale LK, Walsh MT, Mellen JD, Granger DA, Miller LJ. 2021e. Environmental
 1370 enrichment, training, and habitat characteristics of common bottlenose dolphins (*Tursiops*
 1371 *truncatus*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). *PLoS ONE* 16:
 1372 e0253688

1373 Limin NA, Nurfatih S, Hatta NF, Zaki NA, Yusof NNM. 2025. Abnormal behaviors in captive
 1374 wildlife: To keep or not to keep. *Science Letters* 19(1):117-140. [https://scilett-](https://scilett-fsg.uitm.edu.my/images/Volume19-1/10_manuscript_SL_2024_31_final.pdf)
 1375 [fsg.uitm.edu.my/images/Volume19-1/10_manuscript_SL_2024_31_final.pdf](https://scilett-fsg.uitm.edu.my/images/Volume19-1/10_manuscript_SL_2024_31_final.pdf)

1376 Linnehan BK, Kodera SM, Allard SM, Brodie EC, Allaband C, Knight R, Lutz HL, Carroll MC,
 1377 Meegan JM, Jensen ED, Gilbert JA. 2024. Evaluation of the safety and efficacy of fecal
 1378 microbiota transplantations in bottlenose dolphins (*Tursiops truncatus*) using
 1379 metagenomic sequencing. *Journal of Applied Microbiology*, 135(2):lxae026.
 1380 <https://doi.org/10.1093/jambio/lxae026>
 1381 Lipman S. 2016. Exclusive: Self-mutilation by a young whale at the Vancouver Aquarium.
 1382 [http://www.onegreenplanet.org/animalsandnature/exclusive-self-mutilation-by-a-young-](http://www.onegreenplanet.org/animalsandnature/exclusive-self-mutilation-by-a-young-whale-at-vancouver-aquarium/)
 1383 [whale-at-vancouver-aquarium/](http://www.onegreenplanet.org/animalsandnature/exclusive-self-mutilation-by-a-young-whale-at-vancouver-aquarium/) Accessed 16 January 2021
 1384 Loch C, Simões-Lopes PC. 2013. Dental wear in dolphins (*Cetacea: Delphinidae*) from southern
 1385 Brazil. *Archives of Oral Biology*, 58(2):134-141
 1386 Loch C, Visser IN., Stratford K, White S, Wakefield J, Bull S, Matenga L, Johnstone M,
 1387 Oliphant-Stewart R. 2025. Tooth wear and dental calculus in a group of orca (*Orcinus*
 1388 *orca*) stranded on the New Zealand southern coast. *Journal of the Royal Society of New*
 1389 *Zealand* 1-18. <https://doi.org/10.1080/03036758.2025.2491510>
 1390 Lockyer C, Hohn AA, Doidge DW, Heide-Jørgensen MP, Suydam R. 2007. Age determination
 1391 in belugas (*Delphinapterus leucas*): A quest for validation of dentinal layering. *Marine*
 1392 *Mammal Science* 33:293-304. <http://doi.org/10.1578/AM.33.3.2007.293>
 1393 Lott R, Williamson C. 2017. Cetaceans in captivity. In: Butterworth A. ed., *Marine Mammal*
 1394 *Welfare* (Vol. 17). New York, Springer: pp 161-181.
 1395 MacCready P, McCabe RM, Siedlecki SA, Lorenz M, Giddings SN, Bos J, Albertson S, Banas
 1396 NS, Garnier S. 2021. Estuarine circulation, mixing, and residence times in the Salish Sea.
 1397 *Journal of Geophysical Research: Oceans* 126:e2020JC016738.
 1398 <https://doi.org/10.1029/2020JC016738>
 1399 Marino L. 2018. **Captivity**. In: Gruen L (ed.). *Critical Terms for Animal Studies*. Chicago:
 1400 University of Chicago Press, 99-111.
 1401 Marino L. 2022. Cetacean brain, cognition, and social complexity. In: Notarbartolo di Sciara G,
 1402 Würsig B, eds. *Marine Mammals: The Evolving Human Factor*. Charn, Switzerland:
 1403 Springer Nature, pp 113-148.
 1404 Marino L. 2020. Mental health issues in captive cetaceans. In: McMillan FD, ed. *Mental Health*
 1405 *and Well-being in Animals*, 2nd ed. Oxfordshire, UK, CABI, pp 315-327.

1406 Marino L, Rose N, Visser I, Rally H, Ferdowsian H, Slootsky V. 2020. The harmful effects of
 1407 captivity and chronic stress on the well-being of orcas (*Orcinus orca*). *Journal of*
 1408 *Veterinary Behavior* 35:69-82. <https://doi.org/10.1016/j.jveb.2019.05.005>
 1409 Marino L, Vinick C, Foster K, Foster J, Hicks R, McGrath G, Racanelli J, Brewer J. 2025.
 1410 Accredited ocean sanctuaries for transforming captive cetacean care. *PLoS Biology* 23(5):
 1411 e3003166. <https://doi.org/10.1371/journal.pbio.3003166>
 1412 Marino L, White T. 2022. Cetacean personhood, rights, and flourishing. In: Notarbartolo di
 1413 Sciara G, Würsig B, eds. *Marine Mammals: The Evolving Human Factor*. Springer Nature,
 1414 375-395.
 1415 Marley SA, Cheney B, Thompson PM. 2013. Using tooth rakes to monitor population and sex
 1416 differences in aggressive behaviour in bottlenose dolphins (*Tursiops truncatus*). *Aquatic*
 1417 *Mammals* 39:107–115. <https://doi.org/10.1578/AM.39.2.2013.107>
 1418 Marx FG, Hocking DP, Park T, Pollock TI, Parker WMG, Rule JP, Fitzgerald EMG, Evans AR.
 1419 2023. Suction causes novel tooth wear in marine mammals, with implications for feeding
 1420 evolution in baleen whales. *Journal of Mammalian Evolution* 30:493–505.
 1421 <https://doi.org/10.1007/s10914-022-09645-1>
 1422 Mason GJ. 1991. Stereotypies: A critical review. *Animal Behaviour* 41(6):1015 – 1037.
 1423 [https://doi.org/10.1016/S0003-3472\(05\)80640-2](https://doi.org/10.1016/S0003-3472(05)80640-2).
 1424 Mason GJ. 2010. Species differences in responses to captivity: Stress, welfare and the
 1425 comparative method. *Trends in Ecology and Evolution* 25:713-721.
 1426 <https://doi.org/10.1016/j.tree.2010.08.011>
 1427 Mason GJ, Burn CC. 2018. Frustration and boredom in impoverished environments. In Appleby
 1428 MC, Olsson A, Galindo F. (eds.), *Animal welfare*. CABI, 114-138..
 1429 <https://doi.org/10.1079/9781786390202.0114>
 1430 Mason GJ, Clubb R, Latham N, Vickery S. 2007. Why and how should we use environmental
 1431 enrichment to tackle stereotypic behaviour? *Applied Animal Behaviour Science*,
 1432 102(3):163-188.
 1433 Mason GJ, Latham NR. 2004. Can't stop, won't stop: Is stereotypy a reliable animal welfare
 1434 indicator? *Animal Welfare* 13(Suppl):S57-S69.
 1435 Mason GJ, Rushen J. eds. 2008. *Stereotypic Animal Behaviour: Fundamentals and Applications to*
 1436 *Welfare*, Oxfordshire, England: CABI, Wallingford.

1437 Matrai E, Ng AKW, Chan MMH, Gendron SM, Dudzinski KM. 2020. Testing use of a potential
 1438 cognitive enrichment device by an Indo-Pacific bottlenose dolphin (*Tursiops aduncus*).
 1439 *Zoo Biology* 39:156–167.

1440 Matsushiro M, Kurono H Yamamoto K, Kooriyama T. 2021. Cortisol changes in bottlenose
 1441 dolphins in the dolphin interactive program. *Japanese Journal of Veterinary Research* 69:
 1442 99-108. <https://doi.org/10.14943/jjvr.69.2.99>

1443 Mazzaro LM, Johnson SP, Fair PA, Bossart G, Carlin KP, Jensen ED, Smith CR, Andrews GA,
 1444 Chavey PS, Venn-Watson S. 2012. Iron indices in bottlenose dolphins (*Tursiops*
 1445 *truncatus*). *Comparative Medicine* 62:508-515.

1446 McEntee MH, MacQueeney M, Alvarado D, Mann J. 2023. Infanticide and sexual conflict in
 1447 cetaceans. In: Würsig B, Orbach DN, eds, *Sex in Cetaceans: Morphology, Behavior, and*
 1448 *the Evolution of Sexual Strategies*. Cham, Switzerland: Springer International Publishing,
 1449 199-224.

1450 McGillian D. 2023. Orca reproduction in captivity: A review of science, ethics and welfare
 1451 concerns. *Annals of Marine Science* 7(1):014-016.

1452 Melfi VA, Ward SJ. 2020. Welfare implications of zoo animal training. *Zoo Animal Learning and*
 1453 *Training* 271-288.

1454 Melfi V. 2013. Is training zoo animals enriching? *Applied Animal Behaviour Science*. 147:299-
 1455 305. <http://doi.org/10.1016/j.applanim.2013.04.011>

1456 Mellor EL, McDonald Kinkaid HK, Mendl M., Cuthill IC, van Zeeland YR, Mason GJ. 2021.
 1457 Nature calls: Intelligence and natural foraging style predict poor welfare in captive
 1458 parrots. *Proceedings of the Royal Society B*: 288: 20211952.
 1459 <https://doi.org/10.1098/rspb.2021>.

1460 Miller LJ, Mellen J, Greer T, Kuczaj II SA. 2011. The effects of education programmes on
 1461 Atlantic bottlenose dolphin (*Tursiops truncatus*) behaviour. *Animal Welfare* 20(2):159-
 1462 172. <https://doi.org/10.1017/S0962728600002645>

1463 Miller LJ, Lauderdale LK, Bryant JL, Mellen JD, Walsh MT, Granger DA. 2021a. Behavioral
 1464 diversity as a potential positive indicator of animal welfare in bottlenose dolphins.
 1465 *PLoS ONE* 16(8): e0253113. <https://doi.org/10.1371/journal.pone.0253113>

1466 Miller LJ, Lauderdale LK, Mellen JD, Walsh MT, Granger DA, 2021b. Assessment of animal
 1467 management and habitat characteristics associated with social behavior in bottlenose

dolphins across zoological facilities. *PLoS ONE* 16(8): e0253732
<https://doi.org/10.1371/journal.pone.0253732>

Miller LJ, Lauderdale LK, Mellen JD, Walsh MT, Granger DA. 2021c. Relationships between animal management and habitat characteristics with two potential indicators of welfare for bottlenose dolphins under professional care. *PLoS ONE* 16(8): e0252861
<https://doi.org/10.1371/journal.pone.0252861>

Miller LJ, Lauderdale LK, Walsh MT, Bryant JL, Mitchell KA, Granger DA, Mellen JD. 2021d. Reference intervals and values for fecal cortisol, aldosterone, and the ratio of cortisol to dehydroepiandrosterone metabolites in four species of cetaceans. *PLoS ONE* 16(8): e0250331. <https://doi.org/10.1371/journal.pone.0250331>

Miller PJO, Shapiro AD, Deecke VB. 2010. The diving behaviour of mammal-eating killer whales (*Orcinus Orca*): Variations with ecological not physiological factors. *Canadian Journal of Zoology* 88:1103–1112. <https://doi.org/10.1139/Z10-080>

Miller LJ, Vicino GA, Sheftel J, Lauderdale LK. 2020. Behavioral diversity as a potential indicator of positive animal welfare. *Animals* 10(7):1211.
<https://doi.org/10.3390/ani10071211>

Monreal-Pawlowsky T, Carbajal A, Tallo-Parra O, Sabés-Alsina M, Monclús L, Almunia J, Fernández-Bellon H, Lopez-Bejar M. 2017. Daily salivary cortisol levels in response to stress factors in captive common bottlenose dolphins (*Tursiops truncatus*): A potential welfare indicator. *The Veterinary Record* 180(24):593.

Montano GA, Robeck TR, Steinman KJ, O'Brien J K. 2017. Circulating anti-Müllerian hormone concentrations in relation to age and season in male and female beluga (*Delphinapterus leucas*). *Reproduction, Fertility and Development* 29(8):1642-1652.

Morgan KN, Tromborg CT. 2007. Sources of stress in captivity. *Applied Animal Behavior Science* 102:262-302. <https://doi.org/10.1016/j.applanim.2006.05.032>
<https://doi.org/10.1016/j.applanim.2006.05.032>

Munn Z, Peters MDJ, Stern C, Tufanaru C, McArthur A, Aromataris E. 2018. Systematic review or scoping review? Guidance for authors when choosing between a systematic or scoping review approach. *BMC Medical Research Methodology* 18:143.
<https://doi.org/10.1186/s12874-018-0611-x>

Commented [A154]: DOI issue

1498 Naylor W, Parsons ECM. 2018. An online survey of public knowledge, attitudes, and perceptions
 1499 toward whales and dolphins, and their conservation. *Frontiers in Marine Science* 5:153.

1500 National Marine Fisheries Service. 1990. A final environmental impact statement on the use of
 1501 marine mammals in swim-with-the-dolphin programs. Office of Protected Resources,
 1502 Silver Spring, MD.

1503 Nekolny SR, Denny M, Biedenback G, Howells EM, Mazzoil M, Durden WN, Moreland L,
 1504 Lambert JD, Gibson QA. 2017. Effects of study area size on home range estimates of
 1505 common bottlenose dolphins *Tursiops truncatus*, *Current Zoology* 63(6):693–701.
 1506 <https://doi.org/10.1093/cz/zox049>

1507 Nelson TM, Wallen MM, Bunce M, Oskam CL, Lima N, Clayton L, Mann J. 2019. Detecting
 1508 respiratory bacterial communities of wild dolphins: implications for animal health.
 1509 *Marine Ecology Progress Series* 622:203-217. <https://doi.org/10.3354/meps13055>

1510 Neumann DR. 2001. The activity budget of free-ranging common dolphins (*Delphinus delphis*)
 1511 in the northwestern Bay of Plenty, New Zealand. *Aquatic Mammals* 27(2):121-136.

1512 Noren DP, Hauser DDW. 2016. Surface-based observations can be used to assess behavior and
 1513 fine-scale habitat use by an endangered killer whale (*Orcinus orca*) population. *Aquatic*
 1514 *Mammals* 42(2):1168-183. <https://doi.org/10.1578/AM.42.2.2016.168>

1515 O'Brien JK, Robeck TR. 2006. Development of sperm sexing and associated assisted
 1516 reproductive technology for sex pre-selection of captive bottlenose dolphins (*Tursiops*
 1517 *truncatus*). *Journal of Reproduction Fertility and Development* 18:319-329

1518 O'Brien JK, Steinman KJ, Schmitt T, Robeck TR. 2008. Semen collection, characterization and
 1519 artificial insemination in the beluga (*Delphinapterus leucas*) using liquid-stored
 1520 spermatozoa. *Reproduction, Fertility and Development* 20(7):770-783.

1521 O'Corry-Crowe GM. 2009. Beluga whale: *Delphinapterus leucas*. In: Perrin WF, Würsig B,
 1522 Thewissen JGM, eds., *Encyclopedia of Marine Mammals* (2nd Ed.). New York: Academic
 1523 Press, 108-112.

1524 O'Corry-Crowe GM, Suydam R, Quakenbush L, Smith TG, Lydersen C, Kovacs KM, Orr J,
 1525 Harwood L, Litovka D, Ferrer T. 2020. Group structure and kinship in beluga whale
 1526 societies. *Scientific Reports* 10:1-21. <https://doi.org/10.1038/s41598-020-67314-w>

1527 Ohno Y, Akune Y, Inoshima Y, Kano R. 2019. First isolation of voriconazole-resistant *Candida*
 1528 *albicans*, *C. tropicalis*, and *Aspergillus niger* from the blowholes of bottlenose dolphins

1529 (*Tursiops truncatus*). *Journal of Veterinary Medicine and Science* 81:1628-1631.
 1530 <https://doi.org/10.1292/jvms.18-0749>
 1531 Olesiuk PF, Ellis GM, Ford JKB. 2005. Life history and population dynamics of northern
 1532 resident killer whales (*Orcinus orca*) in British Columbia. *Canadian Science Advisory*
 1533 *Secretariat*, Fisheries & Oceans, Canada.
 1534 Oliveira HGdS, Lopes CTdA, Correa LYS, Thiesen RMC, Silva ROS, Uzal FA., Domingues
 1535 SFS, Salvarani FM. 2024. Acute fatal gastric dilatation and volvulus in a captive adult
 1536 Linnaeus's two-toed sloth (*Choloepus didactylus*) in Amazon Biome. *Animals*
 1537 14(23):3527. <https://doi.org/10.3390/ani14233527>
 1538 Ong C-E. 2017. 'Cuteifying' spaces and staging marine animals for Chinese middle-class
 1539 consumption, *Tourism Geographies* 19(2):188-207.
 1540 <https://doi.org/10.1080/14616688.2016.1196237>
 1541 Owen SJ. 1990. A retrospective study of captive breeding programs involving *Tursiops truncatus*
 1542 in south Florida. Proceedings of the International Association for Aquatic Animal
 1543 Medicine Conference. Vancouver, British Columbia, Canada.
 1544 Pack AA, Herman LM, Hoffmann-Kuhnt M, Branstetter BK. 2002. The object behind the echo:
 1545 dolphins (*Tursiops truncatus*) perceive object shape globally through echolocation.
 1546 *Behavioral Processes* 58(1-2):1-26. [https://doi.org/10.1016/S0376-6357\(01\)00200-5](https://doi.org/10.1016/S0376-6357(01)00200-5)
 1547 Pagel CD, Scheer M, Lück M. 2017. Swim encounters with killer whales (*Orcinus orca*) off
 1548 Northern Norway: Interactive behaviours directed towards human divers and snorkelers
 1549 obtained from opportunistic underwater video recordings. *Journal of Ecotourism* 16:190-
 1550 200. <https://doi.org/10.1080/14724049.2016.1273939>
 1551 Park SY, Lee K, Cho Y, Lim SR, Kwon H, Han JE, Kim JH. 2020. Emergence of third-
 1552 generation cephalosporin-resistant *Morganella morganii* in a captive breeding dolphin in
 1553 South Korea. *Animals* 10:2052. <https://doi.org/10.3390/ani10112052>
 1554 Parliament of Canada. 2025. [Public Bill \(Senate\) S-203 \(42-1\) - Royal Assent - Ending the](#)
 1555 [Captivity of Whales and Dolphins Act - Parliament of Canada](#). Accessed 4 February
 1556 2025. Parsons ECM. 2012. Killer whale killers. *Tourism in Marine Environments*
 1557 8(3):153-160.

1558 Parsons ECM, Rose NA. 2018. The Blackfish effect: Corporate and policy change in the face of
 1559 shifting public opinion on captive cetaceans. *Tourism in Marine Environments* 13(2-3):
 1560 73-83.

1561 Partoon J, Sherwen S, Riley L, Whittaker A. 2025. From concept to action: Operationalizing
 1562 animal welfare strategies in zoos and aquaria. *Preprints* 2025051354.
 1563 <https://doi.org/10.20944/preprints202505.1354.v1>

1564 Peirce JM, Alviña K. 2019. The role of inflammation and the gut microbiome in depression and
 1565 anxiety. *Journal of Neuroscience Research* 97(10):1223-1241.
 1566 <https://doi.org/10.1002/jnr.24476>

1567 Perlado-Campos E. 2017. Development, evaluation and results of a yearly enrichment plan in
 1568 bottlenose dolphins (*Tursiops truncatus*). *Modern Environmental Science and*
 1569 *Engineering*, 3:469–472.

1570 Pierce J, Bekoff M. 2018. A postzoo future: Why welfare fails animals in zoos. *Journal of*
 1571 *Applied Animal Welfare Science* 21(sup1):43-48.

1572 Perrin WF, Myrick Jr AC, International Whaling Commission. 1980. Age determination of
 1573 toothed whales and sirenians; proceedings of the *International Conference on*
 1574 *Determining Age of Odontocete Cetaceans (and Sirenians)* La Jolla, Calif. Sep 5-19,
 1575 1978.

1576 Piscitelli MA, Raverty SA, Lillie MA, Shadwick RE. 2013. A review of cetacean lung
 1577 morphology and mechanics. *Journal of Morphology* 274(12):1425-1440.
 1578 <https://doi.org/10.1002/jmor.20192>

1579 Pomerantz O, Meiri S, Terkel J. 2013. Socio-ecological factors correlate with levels of
 1580 stereotypic behavior in zoo-housed primates. *Behavioral Processes* 98:85-91.
 1581 <https://doi.org/10.1016/j.beproc.2013.05.005>

1582 Probert R, Bastian A, Elwen SH, James BS, Gridley T. 2021. Vocal correlates of arousal in
 1583 bottlenose dolphins (*Tursiops* spp.) in human care. *PLoS ONE* 16(9): e0250913.
 1584 <https://doi.org/10.1371/journal.pone.0250913>

1585 Proie S. 2013. A systematic review of cortisol levels in wild and captive Atlantic bottlenose
 1586 dolphin (*Tursiops truncatus*), killer whale, (*Orcinus orca*), and beluga whale
 1587 (*Delphinapterus leucas*). Thesis for Masters of Environmental Studies, Evergreen State
 1588 College. <https://collections.evergreen.edu/s/archives/item/2452>. Accessed 31 May 2025.

1589 Ramos RMA, Di Benedetto APM, Lima NRW. 2000. Relationship between dental morphology,
 1590 sex, body length and age in *Pontoporia blainvillei* and *Sotalia fluviatilis* (Cetacea) in
 1591 northern Rio de Janeiro, Brazil. *Revista Brasileira de Biologia* 60:283-290.

1592 Reidarson TH, García-Párraga D, Wiederhold NP. 2018. Marine mammal mycoses. In:
 1593 Gulland FMD., Dierauf LA, Whitman, KL. eds., *CRC Handbook of Marine Mammal*
 1594 *Medicine*. Boca Raton, FL: CRC Press, 389-423.

1595 Ringlestein A, 2021. The saddest show on earth: The endangered species act as applied to
 1596 captive, endangered mammals in people for the ethical treatment of animals Inc. v.
 1597 Miami Seaquarium, 32. *Villanova Law Environmental Law Journal* 303.
 1598 <https://digitalcommons.law.villanova.edu/elj/vol32/iss2/7>. Accessed on 22 May 2025.

1599 Robeck TR, O'Brien JK. 2018. Reproductive physiology. In: Würsig B, Thewissen JGM, Kovacs
 1600 KM, eds. *Encyclopedia of Marine Mammals*. New York: Academic Press, 807-811.

1601 Robeck TR, O'Brien JK, Odell DK. 2009. Captive breeding. In: Perrin WF, Würsig B, Thewissen
 1602 JGM, eds. *Encyclopedia of Marine Mammals*. New York: Academic Press, 178-183.

1603 Robeck TR, Steinman KJ, Montano GA, Katsumata E, Osborn S, Dalton L, Dunn JL, Schmitt T,
 1604 Reidarson T, O'Brien JK. 2010. Deep intra-uterine artificial inseminations using
 1605 cryopreserved spermatozoa in beluga (*Delphinapterus leucas*). *Theriogenology*
 1606 74(6):989-1001. <https://doi.org/10.1016/j.theriogenology.2010.04.028>

1607 Robeck TR, Steinman KJ, O'Brien JK. 2017. Characterization and longitudinal monitoring of
 1608 serum androgens and glucocorticoids during normal pregnancy in the killer whale
 1609 (*Orcinus orca*). *General and Comparative Endocrinology* 1:247:116-129.
 1610 <http://doi.org/10.1016/j.ygcen.2017.01.023>

1611 Robeck TR, Steinman KJ, Yoshioka M, Jensen E, O'Brien, JK, Katsumata E, Gili C, McBain J,
 1612 Sweeney J, Monfort SL. 2005. Estrous cycle characterization and artificial insemination
 1613 using frozen-thawed spermatozoa in the bottlenose dolphin (*Tursiops truncatus*).
 1614 *Reproduction* 129:659-674.

1615 Robinson KP. 2014. Agonistic intraspecific behavior in free-ranging bottlenose dolphins: Calf-
 1616 directed aggression and infanticidal tendencies by adult males. *Marine Mammal Science*
 1617 30:381-388. <https://doi.org/10.1111/mms.12023>

1618 Robinson KP, Sim TMC, Culloch RM, Bean TS, Aguilar IC, Eisfeld SM, Filan M, Haskins GN,
 1619 Williams G, Pierce GJ. 2017. Female reproductive success and calf survival in a North

1620 Sea coastal bottlenose dolphin (*Tursiops truncatus*) population. *PLoS ONE* 12:e0185000.
 1621 <https://doi.org/10.1371/journal.pone.0185000>

1622 Rose NA, Hancock Snusz G, Brown DM, Parsons ECM. 2017. Improving captive marine
 1623 mammal welfare in the United States: science-based recommendations for improved
 1624 regulatory requirements for captive marine mammal care. *Journal of International*
 1625 *Wildlife Law & Policy* 20(1):38-72. <https://doi.org/10.1080/13880292.2017.1309858>

1626 Rose NA, Soller AS, Parsons ECM. 2023. *The Case Against Marine Mammals in Captivity*,
 1627 6th edition (Washington, DC: Animal Welfare Institute and World Animal Protection).

1628 Rosen DAS, Worthy GAJ. 2018. Nutrition and energetics. In: Gulland FMD, Dierauf LA.,
 1629 GrowWhitman KL. eds., *CRC Handbook of Marine Mammal Medicine*. Boca Raton,
 1630 FL: CRC Press, 309-335.

1631 Rosenzweig MR, Bennett EL, Diamond MC. 1972. Brain changes in response to experience.
 1632 *Scientific American* 226(2):22-29.

1633 Ruiz CU, Sánchez A, Maldonado FG. 2009. Social and individual behavior of a group of
 1634 bottlenose dolphins (*Tursiops truncatus*) in open and closed facilities. *Veterinaria México*
 1635 40(4).

1636 Samarra FI, Bassoi M, Béseau J, Elíasdóttir MÓ, Gunnarsson K, Mruszczok MT,
 1637 Rasmussen M, Rempel JN, Thorvaldsson B, Víkingsson GA. 2018. Prey of killer
 1638 whales (*Orcinus orca*) in Iceland. *PloS One* 13: e0207287.
 1639 <https://doi.org/10.1371/journal.pone.0207287>

1640 Sanganyado E, Liu W. 2022. Cetacean health: Global environmental threats. In: Filho WL, AZul
 1641 AM, Brandli L, Salvia AL, Wall T, eds. *Life Below Water*. Cham, Switzerland:
 1642 Springer International Publishing, 107-120.

1643 Santos MCDO. 1997. Lone sociable bottlenose dolphin in Brazil: Human fatality and
 1644 management. *Marine Mammal Science* 13:355-356. [https://doi.org/10.1111/j.1748-](https://doi.org/10.1111/j.1748-7692.1997.tb00642.x)
 1645 [https://doi.org/10.1111/j.1748-](https://doi.org/10.1111/j.1748-7692.1997.tb00642.x)

1646 Scott EM, Mann J, Watson-Capps JJ, Sargeant BL, Connor RC. 2005. Aggression in bottlenose
 1647 dolphins: Evidence for sexual coercion, male-male competition, and female tolerance
 1648 through analysis of tooth-rake marks and behaviour. *Behaviour* 142(1):21-44.
 1649 <https://doi.org/10.1163/1568539053627712>

1650 Segawa T, Ohno Y, Kurita M, Ishibashi T, Yoshioka M. 2023. *Helicobacter delphinicola*
 1651 infection and the risk of gastric disease in common bottlenose dolphin. *Diseases of*
 1652 *aquatic organisms* 155:187–192. <https://doi.org/10.3354/dao03751>
 1653 Sergeant DE, Caldwell DK, Caldwell MC. 1973. Age, growth, and maturity of bottlenosed
 1654 dolphin (*Tursiops truncatus*) from Northeast Florida. *Journal of Fisheries and Research*
 1655 *Board of Canada* 30:1009-1011. <https://doi.org/10.1139/f73-165>
 1656 Shah SAUR, Tang B, He D, Hao Y, Ahmad M, Nabi G, McLaughlin R, Wang C, Kou Z, Wang
 1657 K. 2024. Effect of calf separation on gut microbiome and fecal metabolome of mother in
 1658 the captive Yangtze finless porpoise (*Neophocaena asiaeorientalis asiaeorientalis*).
 1659 *International Microbiology*. <https://doi.org/10.1007/s10123-024-00613-8>
 1660 Shepherdson DJ. 1998. Tracing the path of environmental enrichment in zoos In: Shepherdson
 1661 DJ, Mellen JD, Hutchins M, eds. *Second Nature: Environmental Enrichment for Captive*
 1662 *Animals*. Washington, D.C.: Smithsonian Institution Press, 1–12.
 1663 Shepherdson D, Carlstead K. 2020. Psychological well-being in zoo animals. In: McMillan FD,
 1664 ed, *Mental Health and Well-Being in Animals (2nd ed.)*, U.K., CABI International pp
 1665 302-314.
 1666 Shorter K, Shao Y, Ojeda L, Barton K, Rocho-Levine J, van der Hoop J, Moore M. 2017. A day
 1667 in the life of a dolphin: Using bio-logging tags for improved animal health and well-
 1668 being. *Marine Mammal Science* 33(3):785–802. <https://doi.org/10.1111/mms.12408>
 1669 Simeone CA, Nollens HH, Meegan JM, Schmitt TL, Jensen ED, Papich MG, Smith CR. 2014.
 1670 Pharmacokinetics of single dose oral meloxicam in bottlenose dolphins (*Tursiops*
 1671 *truncatus*). *Journal of Zoo and Wildlife Medicine*, 45(3):594–599.
 1672 <http://www.jstor.org/stable/24551187>
 1673 Small RJ, DeMaster DP. 1995. Survival of five species of captive marine mammals. *Marine*
 1674 *Mammal Science* 11:209-226.<https://doi.org/10.1111/j.1748-7692.1995.tb00519.x>
 1675 <https://doi.org/10.1111/j.1748-7692.1995.tb00519.x>
 1676 Sørensen P M, Haddock A, Guarino E, Jaakkola K, McMullen C, Jensen FH, Tyack PL, King
 1677 SL. 2023. Anthropogenic noise impairs cooperation in bottlenose dolphins. *Current*
 1678 *Biology* 33(4):749-754. <http://doi.org/10.1016/j.cub.2022.12.063>

1679 Sapolsky RM, Romero LM, Munck AU. 2000. How do glucocorticoids influence stress
 1680 responses? Integrating permissive, suppressive, stimulatory, and preparative actions.
 1681 *Endocrine Reviews* 21(1):55–89. <https://doi.org/10.1210/edrv.21.1.0389>
 1682 St. Leger J, Wu G, Anderson M, Dalton L, Nilson, Wang D. 2011. West Nile Virus infection in
 1683 killer whale, Texas, USA, 2007. *Emerging Infectious Disease* 17:1531-1533.
 1684 <https://doi.org/10.3201/eid1708.101979>
 1685 Steinman KJ, O'Brien JK, Monfort SL, Robeck TR. 2012. Characterization of the estrous cycle
 1686 in female beluga (*Delphinapterus leucas*) using urinary endocrine monitoring and
 1687 transabdominal ultrasound: evidence of facultative induced ovulation. *General and*
 1688 *Comparative Endocrinology* 175(3): 389-397.
 1689 Stevens PE, Hill HM, Bruck JN. 2021. Cetacean acoustic welfare in wild and managed-care
 1690 settings: Gaps and opportunities. *Animals* 11(11):3312.
 1691 <https://doi.org/10.3390/ani11113312>
 1692 Stewart KL, Marino L. 2009. Dolphin-human interaction programs: Policies, problems, and
 1693 practical alternatives. *Animals and Society Institute Policy Papers*. Ann Arbor, The
 1694 Animals and Society Institute.
 1695 Stockin KA, Binedell V, Wiseman N, Brunton DH, Orams MB. 2009. Behavior of free-ranging
 1696 common dolphins (*Delphinus* sp.) in the Hauraki Gulf, New Zealand. *Marine Mammal*
 1697 *Science* 25(2):283-301. <https://doi.org/10.1111/j.1748-7692.2008.00262.x>
 1698 Stoskopf MK. 2015. Environmental diseases of marine mammals. In: Line S, Moses MA, eds,
 1699 *Merck Veterinary Manual Online*. Kenilworth, New Jersey, Merck and Co.
 1700 Accessed 31 March 2021 at [https://www.merckvetmanual.com/exotic-and-laboratory-](https://www.merckvetmanual.com/exotic-and-laboratory-animals/marine-mammals/environmental-diseases-of-marine-mammals#)
 1701 [https://www.merckvetmanual.com/exotic-and-laboratory-](https://www.merckvetmanual.com/exotic-and-laboratory-animals/marine-mammals/environmental-diseases-of-marine-mammals#)
 1702 mammals/environmental-diseases-of-marine-mammals#
 1703 Suydam RS. 2009. Age, growth, reproduction, and movements of beluga whales
 1704 (*Delphinapterus leucas*) from the eastern Chukchi Sea. Unpublished Ph.D.
 1705 dissertation. University of Washington. [https://www.north-slope.org/wp-](https://www.north-slope.org/wp-content/uploads/2022/03/suydam_dissertation2009-1.pdf)
 1706 [content/uploads/2022/03/suydam_dissertation2009-1.pdf](https://www.north-slope.org/wp-content/uploads/2022/03/suydam_dissertation2009-1.pdf) Accessed 8 October 2024.
 1707 Suzuki A, Akuzawa K, Kogi K, Ueda K, Suzuki M. 2021. Captive environment influences the
 1708 composition and diversity of fecal microbiota in Indo-Pacific bottlenose dolphins,

1709 *Tursiops aduncus*. *Marine Mammal Science* 37:207–219.

1710 <https://doi.org/10.1111/mms.12736>

1711 Svarachorn T, Kettratad J, Thubthong N, Chansue N. 2016. Sound characteristics and primary

1712 descriptions of vocalizations associated with behaviours of captive Irrawaddy dolphins

1713 (*Orcaella brevirostris*). *Aquatic Mammals* 42(4):519-530.

1714 <http://doi.org/10.1578/AM.42.4.2016.519>

1715 Swaisgood RR, Shepherdson DJ. 2005. Scientific approaches to enrichment and stereotypies in

1716 zoo animals: What’s been done and where should we go next? *Zoo Biology* 24: 499-

1717 518. <https://doi.org/10.1002/zoo.20066> <https://doi.org/10.1002/zoo.20066>

1718 Sweeney JC, Stone R, Campbell M, McBain J, St. Leger JS, Xitco M, Jensen E, Ridgway S.

1719 2010. Comparative survivability of *Tursiops* neonates from three US institutions for

1720 the decades 1990-1999 and 2000-2009. *Aquatic Mammals* 36:248-261.

1721 <http://doi.org/10.1578/AM.36.3.2010.248S.4740> - 117th Congress (2021-2022): SWIMS

1722 Act of 2022 | Congress.gov | Library of Congress

1723 SWIMS Act. 2024. <https://www.congress.gov/bill/118th-congress/house-bill/7145/text>.

1724 Accessed 21 November 2024.

1725 Tennessen JB, Holt MM, Ward EJ, Hanson MB, Emmons CK, Giles DA, Hogan JT. 2019.

1726 Hidden Markov models reveal temporal patterns and sex differences in killer whale

1727 behavior. *Scientific Reports* 9:14951. <https://doi.org/10.1038/s41598-019-50942-2>

1728 The Brussels Times (November 2024). Dolphinarium in Bruges ordered to close its doors by

1729 2037. [https://www.brusselstimes.com/1315790/dolphinarium-in-bruges-ordered-to-close-](https://www.brusselstimes.com/1315790/dolphinarium-in-bruges-ordered-to-close-its-doors-by-2037)

1730 [its-doors-by-2037](https://www.brusselstimes.com/1315790/dolphinarium-in-bruges-ordered-to-close-its-doors-by-2037). Accessed on 16 February 2025.

1731 Tidière M, Colchero F, Staerk J, Adkesson MJ, Andersen DH, Bland L, Böye M, Brando S,

1732 Clegg I, Cubaynes S, Cutting A, De Man D, Derocher AE, Dorsey C, Elgar W, Gaglione

1733 E, Hansen KA, Jungheim A, Kok J, Laule G, Goya AL, Miller L, Monreal-Pawłowsky T,

1734 Mucha K, Owen MA, Petersen SD, Pilfold N, Richardson D, Richardson ES, Sabo D,

1735 Sato N, Shellabarger W, Skovlund CR, Tomisawa K, Trautwein SE, Van Bonn W, Van

1736 Elk C, Von Fersen L, Wahlberg M, Zhang P, Zhang X, Conde DA. 2023. Survival

1737 improvements of marine mammals in zoological institutions mirror historical advances in

1738 human longevity. *Proceeding of the Royal Society B* 280:20231895.

1739 <https://doi.org/10.1098/rspb.2023.1895>

1740 Towers JR, Hallé MJ, Symonds HK, Sutton GJ, Morton AB, Spong P, Borrowman JP, Ford
 1741 JKB. 2018. Infanticide in a mammal-eating killer whale population. *Scientific Reports* 8:
 1742 4366. <https://doi.org/10.1038/s41598-018-22714-x> [https://doi.org/10.1038/s41598-018-](https://doi.org/10.1038/s41598-018-22714-x)
 1743 [22714-x](https://doi.org/10.1038/s41598-018-22714-x)

1744 Towers JR, Tixier P, Ross KA, Bennett J, Arnould JPY, Pitman RL, Durban JW. 2019.
 1745 Movements and dive behaviour of a toothfish-depredating killer and sperm whale. *ICES*
 1746 *Journal of Marine Science* 76(1):298-311. <https://doi.org/10.1093/icesjms/fsy118>

1747 Tryland M. 2018. Zoonosis and public health. In: LA Dierauf, FMD Gulland, eds., *CRC*
 1748 *handbook of marine mammal medicine*. Boca Raton, Florida, CRC Press: pp 47-
 1749 61.

1750 Ugaz C, Valdez RA, Romano MC, Galindo F. 2013. Behavior and salivary cortisol of captive
 1751 dolphins (*Tursiops truncatus*) kept in open and closed facilities. *Journal of*
 1752 *Veterinary Behavior* 8:285-290. <https://doi.org/10.1016/j.jveb.2012.10.006>
 1753 <https://doi.org/10.1016/j.jveb.2012.10.006>

1754 Ugaz RC, Sánchez A, Galindo MF. 2009. Social and individual behavior of a group of bottlenose
 1755 dolphins (*Tursiops truncatus*) in open and closed facilities. *Veterenaria Mexico*
 1756 40:381-387.

1757 Van Bonn W, Poll CP, Boehm JR, Davis MR, Carmack T. 2007. Successful treatment of
 1758 erysipelas septicemia in a Pacific white-sided dolphin *Lagenorhynchus obliquidens*: A
 1759 case for the aquatic animal hygiene hypothesis? Abstract presented at the International
 1760 *Association for Aquatic Animal Medicine Conference*, Orlando, Florida, USA.

1761 Van Bresse MF, Van Waerebeek K, Flach L, Reyes JC, de Oliveira Santos MC,
 1762 Siciliano S, Echegaray M, Viddi F, Félix F, Crespo E, Sanino GP, Avila IC, Fraijia N,
 1763 Castro C. 2008. Skin diseases in cetaceans. *Scientific Committee document*
 1764 *SC/60/DW8*, International Whaling Commission, Santiago, Chile. International
 1765 Whaling Commission: Santiago.

1766 Van Lint W, de Man D, Garn K, Hiddinga B, Brouwer K. 2006. *EAZA Yearbook 2004*. EAZA
 1767 Executive Office, Amsterdam

1768 Venn-Watson SK, Benham C, Carlin K, DeRienzo D, St. Leger J. 2012a. Hemochromatosis and
 1769 fatty liver disease: Building evidence for insulin resistance in bottlenose dolphins

1770 (*Tursiops truncatus*). *Journal of Zoological and Wildlife Medicine* 43:S35-S47.
1771 <https://doi.org/10.1638/2011-0146.1>

1772 Venn-Watson SK, Daniels R, Smith CR. 2012b. Thirty year retrospective evaluation of
1773 pneumonia in a bottlenose dolphin *Tursiops truncatus* population. *Diseases of Aquatic*
1774 *Organisms* 99(3):237-242. <https://doi.org/10.3354/dao02471>

1775 Venn-Watson SK, Smith CR, Johnson S, Daniels R, Townsend F. 2010. Clinical relevance of
1776 urate nephrolithiasis in bottlenose dolphins, *Tursiops truncatus*. *Diseases of Aquatic*
1777 *Organisms* 89:167-177. <https://doi.org/10.3354/dao02187>
1778 <https://doi.org/10.3354/dao02187>

1779 Venn-Watson SK, Smith CR, Stevenson S, Parry C, Daniels R, Jensen E, Cendejas V, Balmer B,
1780 Janech M, Neely BA, Wells R. 2013. Blood-based indicators of insulin resistance and
1781 metabolic syndrome in bottlenose dolphins (*Tursiops truncatus*). *Frontiers in*
1782 *Endocrinology* 4:136. <https://doi.org/10.3389/fendo.2013.00136>

1783 Ventre J, Jett J. 2015. Killer whales, theme parks, and controversy: An exploration of the
1784 evidence. In: K Markwell, ed., *Animals and tourism: Understanding diverse*
1785 *relationships.*, Bristol, UK, Channel View Publications pp 128-145.

1786 Vicino G, Miller LJ. 2015, September. From prevention of cruelty to optimizing welfare:
1787 Opportunities to thrive. In *Proceedings of the International Ethological Conference,*
1788 *Cairns, Australia* (Vol. 19).

1789 Visser IN, Lisker RB. 2016. Ongoing concerns regarding the SeaWorld orca held at Loro
1790 Parque, Tenerife, Spain. Unpublished report. [https://www.freemorgan.org/wp-](https://www.freemorgan.org/wp-content/uploads/2016/07/Visser-Lisker-2016-Ongoing-concerns-regarding-Seaworld-orca-held-at-Loro-Parque-V1.3.pdf)
1791 [content/uploads/2016/07/Visser-Lisker-2016-Ongoing-concerns-regarding-Seaworld-](https://www.freemorgan.org/wp-content/uploads/2016/07/Visser-Lisker-2016-Ongoing-concerns-regarding-Seaworld-orca-held-at-Loro-Parque-V1.3.pdf)
1792 [orca-held-at-Loro-Parque-V1.3.pdf](https://www.freemorgan.org/wp-content/uploads/2016/07/Visser-Lisker-2016-Ongoing-concerns-regarding-Seaworld-orca-held-at-Loro-Parque-V1.3.pdf). Accessed 14 September 2021.

1793 Walsh MT, Friday RB, Johnson AB, Messinger D. 1996. Regurgitation in cetaceans: Medical
1794 implications. Abstract presented at the *International Association for Aquatic Animal*
1795 *Medicine Conference*, Chattanooga, Tennessee, USA.
1796 [https://www.vin.com/apputil/content/defaultadv1.aspx?pId=11257&catId=32261&id=38](https://www.vin.com/apputil/content/defaultadv1.aspx?pId=11257&catId=32261&id=3864210#:~:text=Allowed%20to%20persist%20the%20condition,susceptibility%20to%20disease%2C%20and%20death)
1797 [64210#:~:text=Allowed%20to%20persist%20the%20condition,susceptibility%20to%20d](https://www.vin.com/apputil/content/defaultadv1.aspx?pId=11257&catId=32261&id=3864210#:~:text=Allowed%20to%20persist%20the%20condition,susceptibility%20to%20disease%2C%20and%20death)
1798 [isease%2C%20and%20death](https://www.vin.com/apputil/content/defaultadv1.aspx?pId=11257&catId=32261&id=3864210#:~:text=Allowed%20to%20persist%20the%20condition,susceptibility%20to%20disease%2C%20and%20death). Accessed 4 September, 2024.

1799 Waples, KA, Gales NJ. 2002. Evaluating and minimizing social stress in the care of captive
1800 bottlenose dolphins (*Tursiops aduncus*). *Zoo Biology* 21:5-26.
1801 <http://dx.doi.org/10.1002/zoo.10004>

1802 Ward EJ, Holmes EE, Balcomb KC. 2009. Quantifying the effects of prey abundance on
1803 killer whale reproduction. *Journal of Applied Ecology*. 46(3):632-640.
1804 [Bibcode:2009JApEc..46..632W. doi:10.1111/j.1365-2664.2009.01647.x.](https://doi.org/10.1111/j.1365-2664.2009.01647.x)

1805 Wassermann SN, Hind-Ozan EJ, Seaman J. 2018. Reassessing public opinion of captive cetacean
1806 attractions with a photo elicitation survey. *PeerJ*, 6:e5953.

1807 WAZA. 2025. World Association of Zoos and Aquariums.
1808 https://www.eaam.be/_files/ugd/ba9fb6_6f39447579634794ab70c28a1c2b26da.pdf.
1809 Accessed on 1 May 2025.

1810 Weese JS, Holcombe SJ, Embertson RM, Kurtz KA, Roessner HA, Jalali M, Wismer SE. 2015.
1811 Faecal microbiota in *post partum* colic. *Equine Veterinary Journal* 47:641-649.
1812 <https://doi.org/10.1111/evj.12361>

1813 Wells RS, Hohn AA, Scott MD, Sweeney JC, Townsend Jr FI, Allen JB, Barleycorn AA,
1814 McHugh KA, Bassos-Hull K, Lovewell GN, Duffield DA, Smith CR, Irvine AB. 2025.
1815 Life history, reproductive, and demographic parameters for bottlenose dolphins (*Tursiops*
1816 *truncatus*) in Sarasota Bay, Florida. *Frontiers in Marine Science* 12:1531528.
1817 <https://doi.org/10.3389/fmars.2025.1531528>

1818 Wells RS, McHugh KA, Douglas DC, Shippee S, McCabe EB, Barros NB, Phillips GT. 2013.
1819 Evaluation of potential protective factors against metabolic syndrome in bottlenose
1820 dolphins: Feeding and activity patterns of dolphins in Sarasota Bay, Florida. *Frontiers in*
1821 *Endocrinology* 4:139. <https://doi.org/10.3389/fendo.2013.00139>

1822 Wells RS, Rhinehart HL, Cunningham P, Whaley J, Baran M, Koberna C, Costa DP. 1999.
1823 Long-distance offshore movements of bottlenose dolphins. *Marine Mammal Science*
1824 15:1098 – 1114. <https://doi.org/10.1111/j.1748-7692.1999.tb00879.x>

1825 Wells RS, Scott MD. 2009. Common bottlenose dolphin: *Tursiops truncatus*. In: WF Perrin,
1826 B Würsig, H Thewissen, eds, *Encyclopedia of Marine Mammals*, 2nd ed. San
1827 Diego: Academic Press, 249-255.

1828 Westlund K. 2014. Training is enrichment—And beyond. *Applied Animal Behaviour Science*
1829 152:1-6.

1830 Whitehead H, Rendell L. 2021. *The Cultural Lives of Whales and Dolphins*. University of
1831 Chicago Press, Chicago, IL.

1832 Whitham JC, Wielebnowski N. 2013. New directions for zoo animal welfare science. *Applied*
1833 *Animal Behavior Science* 147: 247-260. <https://doi.org/10.1016/j.applanim.2013.02.004>

1834 Williams R, Lusseau D. 2006. A killer whale social network is vulnerable to targeted removals.
1835 *Biology Letters* 2: 497-500. <https://doi.org/10.1098/rsbl.2006.0510>

1836 Willis K. 2012. Beluga (*Delphinapterus leucas*) adult life expectancy: Wild populations vs
1837 the population in human care. Appendix F. In Georgia Aquarium (compiler),
1838 Application for a permit to import certain marine mammals for public display
1839 under the Marine Mammal Protection Act. Permit application, File No. 17324,
1840 submitted to the National Marine Fisheries Service, 77 FR 52694, 30 August 2012.

1841 Winders D & Chilakamarri V. 2018. Animal Welfare Act: Enforcement. *Animal Law* 25:249.

1842 Winship KA Jones BL. 2023. Acoustic monitoring of professionally managed marine mammals
1843 for health and welfare insights. *Animals* 13(3):2124. <https://doi.org/10.3390/ani13132124>

1844 Woodley TH, Hannah J, Lavigne DM. 1997. A comparison of survival rates for captive and free-
1845 living-ranging bottlenose dolphins (*Tursiops truncatus*); killer whales (*Orcinus orca*);
1846 and beluga whales (*Delphinapterus leucas*). Technical Report No. 97-02
1847 (Guelph; Ontario: International Marine Mammal Association; Inc.).

1848 Worthy GA, Worthy TA, Yochem PK, Dold C. 2013. Basal metabolism of an adult male killer
1849 whale (*Orcinus orca*). *Marine Mammal Science* 30:1229-1237.
1850 <https://doi.org/10.1111/mms.12091>

1851 Wright BM, Ford JKB, Ellis GM, Deecke VB, Shapiro AD, Battaile BC, Trites AW. 2017. Fine-
1852 scale foraging movements by fish-eating killer whales (*Orcinus orca*) relate to the
1853 vertical distributions and escape responses of salmonid prey (*Oncorhynchus* spp.).
1854 *Movement Ecology* 5:3. <https://doi.org/10.1186/s40462-017-0094-0>

1855 Wright AJ, Soto NA, Baldwin AL, Bateson M, Beale CM, Clark C, Deak T, Edwards E,
1856 Fernández A, Godinho A, Hatch LT, Karuschke A. Lusseau D, Martineau D, Romero
1857 LM. Weilgart LS, Wintle B, Notarbartolo di Sciara G, Martin V. 2007. Anthropogenic
1858 noise as a stressor in animals: a multidisciplinary perspective. *International Journal of*
1859 *Comparative Psychology* 20(2). <https://doi.org/10.46867/ijcp.2007.20.02.02>

1860 Yang JH, Bhargava P, McCloskey D, Mao N, Palsson BO, Collins JJ. 2017. Antibiotic-induced

1866 changes to the host metabolic environment inhibit drug efficacy and alter immune function. *Cell*
 1867 *Host and Microbe* 22:757e765.
 1868 Yang, WC, Chen CF, Chuah YC, Zhuang CR, Chen IH, Mooney TA, Stott J, Blanchard M, Jen I-
 1869 F, Chou LS. 2021. Anthropogenic sound exposure-induced stress in captive dolphins and
 1870 implications for cetacean health. *Frontiers in Marine Science* 8:606736.
 1871 Yang Z, Li J, Gui X, She X, Bao Z, Han H, Li MD. 2020. Updated review of research on the gut
 1872 microbiota and their relation to depression in animals and human beings. *Molecular*
 1873 *Psychiatry* 25:2759-2772. <https://doi.org/10.1038/s41380-020-0729-1>
 1874 Yeater DB, Dudzinski KM, Melzer D, Magee AR, Robinett M, Guerra G, Salazar K, Bolton T,
 1875 Hill HM. 2024. Training the concept of innovate in dolphins (*Tursiops truncatus*) is both
 1876 creative and cognitively stimulating. *Animals* 14(6):896.
 1877 <https://doi.org/10.3390/ani14060896>
 1878 Zuckerman JM, Assimos DG. 2009. Hypocitraturia: Pathophysiology and medical management.
 1879 *Reviews in Urology* 11:134-144. <https://doi.org/10.3909/riu0424>
 1880
 1881
 1882
 1883
 1884
 1885

Comments:

As a review paper, despite its heavy revisions, it still fails at its two ultimate goals of A) convincing the reader that, as a population, animals under managed care are experiencing uniformly poorer welfare than their wild counterparts, B) that the welfare of cetaceans in zoos and aquariums would be uniformly improved by movement into GFAS accredited sanctuaries. I fear no amount of revision can make this article successful in these endeavors. As an exercise, the authors should consider attempting to make the argument that cetaceans experience, poorer welfare in zoos and aquariums without widespread self-citation, misrepresentation of other authors, or omission from other authors. Taking Marino et al.,'s referencing of my own paper as an example, Marino et al., misleadingly implies that Bruck, 2024 believes the challenges associated with feeding, veterinary care and funding are shared equally by GFAS sanctuaries and Alliance accredited marine mammal facilities. The entire thrust of that paper highlights why those issues are exacerbated by the prescriptions of GFAS accreditation. There are issues like this throughout that render the paper unfit for publication under any pretense that these are neutral observers just calling balls and strikes. If this were an opinion commentary or philosophy paper in another journal I would be less inclined to protest; however, these authors are attempting to pass this off as a neutral and even handed evaluation of the current state of captivity for cetaceans and after reading both its original version and now this revised one I can't help but get the impression that none of these authors have set foot or much less worked with a modern accredited zoo or aquarium or their animals. Furthermore, there is a serious lack of data supporting the position that the population of animals in zoos and aquariums are in dire need of intervention and that that intervention should be sea pen sanctuaries. The authors expressed some disagreements with the cetacean welfare study's methodology but offer no competing data of their own that improves on those perceived limitations (which I explain below do not actually undercut the main theses of those papers). Surely if the animals are experiencing uniformly, poor welfare there should be a convincing case in the literature. These animals represent significant investments for the facilities that house them. One should expect at least some literature examining those issues. Rather, these authors have built a house of publications criticizing the welfare of animals in zoos and aquariums, without a foundation of data to support their conclusions. This has led to a perpetual ring of self-citations with the goal of achieving a false consensus to their conclusions. Meanwhile sleight of hand is used to both emphasize the scientific immeasurability of "quality of life" only to imply that the animals in zoos either have a poor quality of life or would have their quality of life improved by living in a GFAS sanctuary. Meanwhile no data are present to support those

conclusions because quality of life is subjective and even if you could base it on good welfare data, the authors do not present any of it to at least imply that GFAS sanctuaries would lead to at least something most cetacean welfare experts might subjectively assess to be a "quality of life" improvement. In this case the authors should identify any data they can manage from the Beluga Sea Life Sanctuary that might explain why, after 5+ years of living in a pool instead of their sea pen, Little Grey and Little White would still benefit from living in that sea pen sanctuary, despite multiple attempts to put them out there and multiple trips back to the pool. Perhaps there is a C-Well assessment that shows, despite all appearances, the belugas did have better welfare in the sea pen than the pool, and that would be a great thing to have in a paper ostensibly about the current state of captive cetacean welfare. Do the authors know how well the animals were stationing in the sanctuary? Or if they showed any signs of stress in the sanctuary like ulcers for example? Those would be good things to discuss with readers, if this paper is about the current state of captivity and why it is bad and these animals need to be in sanctuaries. While I cast no aspersions on the authors, such data would also go a long way toward showing that the lead author who happens to be president of the Whale Sanctuary Project (and, to my knowledge, still draws salary from that) is fully aware of the issues she may confront when housing her own animals in the way she elected to when writing the GFAS standards.

As far as my review, again I have chosen to directly edit the manuscript and put comments upon it as they are extensive. New comments have my name on them (old comments that weren't addressed satisfactorily or are needed for context remain with the name 'author' on them). Some of the author responses to my comments are replied to here, however, for the sake of time, I have chosen to respond to only those comments that I think the authors struggled most with or would lead to some improvement.

That being said, I must again offer that this is not the format or journal for this work. The authors do not have sufficient data, nor do they reference studies with sufficient data to make the points they are making convincingly. Much of this is opinion, and not fact. If this were to be published, I would recommend focusing not on speculation, but what is not known about cetacean welfare in zoos and how we could get at those questions honestly. To do this and to provide more captive cetacean experience to the paper, the authors should seriously consider adding an additional author or two who does not share blanket anti-captivity views to help balance out the paper. I would recommend finding a current zoo professional (someone like Lance Miller or Jessica Whitham) who works with animals/welfare and a welfare specialist (like Fabienne Delfour or Kathleen Dudzinski) to round out the author list and provide deeply needed perspective.

Reviewer 2

Basic reporting

BASIC REPORTING:

Note: Given the volume of necessary edits, I have made an editable version of this manuscript and placed comments within. Comments for how to improve a potential revision are included in that attachment.

Is the review of broad and cross-disciplinary interest and within the scope of the journal?
It seems the topic of cetacean captivity is within the scope of the journal.

I do not know exactly how broad the cross-disciplinary interest will be given cetacean captivity issues are fairly niche in scientific community. Online and in social media articles like this are used frequently to advocate for anti-captivity positions so it may have legs there.

Has the field been reviewed recently? If so, is there a good reason for this review (different point of view, accessible to a different audience, etc.)?

I think the best review of cetacean captivity (with data) is The Cetacean Welfare Study led by Lance Miller. This is a nine-paper series using the latest technology and tools to assess captive cetacean welfare across almost every accredited facility in the US and Europe.
<https://collections.plos.org/collection/cetacean-welfare/> This review barely mentions this comprehensive series of studies and seems more focused on presenting a narrative favorable to cetacean sanctuary projects. That would be fine if this took an even and comprehensive position relative to the literature. Unfortunately, this manuscript fails to do that in a meaningful way (see Attachments for line-by-line examples of these shortcomings). As such this reads very much like previous articles from these authors (Marino et al 2020 and Jacobs et al 2021) that each have comprehensive rebuttals from many groups of authors. I don't honestly know what the purpose of this paper is in terms of the scientific literature.

Although we did not originally use the term “Cetacean Welfare Study,” we did, in fact, cite four of the nine articles. In accordance with the reviewer’s comments, we have now mentioned the study and all of the articles in the introduction and incorporated more of the articles throughout the paper.

The articles may have been cited, but the information in the articles was not appropriately incorporated. For example, in the advocacy for sea pen sanctuaries no reference was made to how space and net pen vs. pool housing are the weakest predictors of welfare across that study.

Does the Introduction adequately introduce the subject and make it clear who the audience is/what the motivation is?

The Introduction does not adequately introduce the subject as the authors present a fairly biased interpretation of current captive situations (see Additional Documents for specific examples). Frankly, given the seminal nature of The Cetacean Welfare Study on this topic if the authors aren't going to frame this paper as either a rebuttal or comprehensive assessment of those conclusions then I don't know how this can either provide a reasoned different view of the state

of information for captive cetaceans or even inform a different audience about the current state of information in captive cetaceans. I don't know what the motivation for this paper is considering the author's stated goals relative to their execution of said goals though their limited evaluation of the scientific data on cetacean welfare (specifically studies that show positive welfare gains-see attachments).

We appreciate that this reviewer holds the opinion that the Cetacean Welfare Study was definitive and all-encompassing. We do not share this view. However, we do acknowledge that these were important studies that are good examples of systematic assessment of captive cetacean welfare and applaud their publication. However, our paper is intended to have a larger scope than these nine papers and, thus, we do not think it is appropriate to frame our entire paper as a direct response to the Cetacean Welfare Study. Nevertheless, as we said before, we have included and mentioned these studies throughout the paper when relevant.

The Cetacean Welfare Study (CWS) was a comprehensive data-based assessment of cetacean welfare in captive settings, but the reviewer did not hold that it was definitive and all encompassing. The reviewer only aimed to point out that aspects of that study were not mentioned in this review, especially where the findings contrasted with the authors' stated opinions on cetacean captivity. This is a review paper called "An Update on Cetacean Captive Welfare" written by a series of authors who seem not to have current direct experience working with captive cetaceans. If the authors have contrasting data, they wish to present to refute the Cetacean Welfare Study, they should present that. If the authors have methodological concerns with the CWS they should discuss those. While the authors now highlight that the CWS did not address unaccredited facilities or rough-toothed dolphins (for example), that is not a reason to omit a fulsome discussion of the welfare study. Simply, one cannot write a paper called "An Update on Cetacean Captive Welfare" and not fulsomely discuss the largest captive cetacean welfare study in history published only a few years ago. Especially where that series of studies contrasts with the author's opinions.

In our Introduction, we added:

Recently, a series of nine articles known as the Cetacean Welfare Study examined captive cetacean welfare measurements across 43 accredited zoos and aquariums in seven countries (Lauderdale et al., 2021a-c; Miller et al., 2021a-d). It was designed to identify factors related to the welfare of bottlenose dolphins (*Tursiops truncatus*), Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), beluga whales (*Delphinapterus leucas*), and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*). This project did not examine unaccredited facilities or those housing other cetaceans. Identified factors included habitat characteristics and management practices (Lauderdale et al. 2021c,d; Miller et al., 2021b), environmental enrichment (Lauderdale et al., 2021e), health reference intervals (Lauderdale et al. 2021a), biomedical markers (Lauderdale 2021a; Miller et al., 2021d) social behavior (Miller et al., 2021b), and behavioral diversity (Miller et

al., 2021a). The findings of these studies are integrated in the present review where relevant. These studies focused on which welfare factors of captive dolphins were determined to be most important, and which ones could be implemented in the future.

That being said, there are considerable methodological issues with this study. In Lauderdale et al. (2021e), for example, they say “a different individual was substituted for the second data collection”--this methodology assumes all dolphins in any given environment are interchangeable on all the selected variables. We don't know if that is true. It would not be if this study were about humans. This is a source of additional error variance. We understand why this was done, but ideally those facilities would have been excluded from the study.

Second, while the dolphins are measured, the humans who administer dolphin care, training, and enrichment are not. It seems reasonable to suspect that different humans and human teams are variable in their administration of care, training, and enrichment. Some measures of human skill, and motivation, would best be included since these would be expected to have an impact on dolphin characteristics.

Third, the paper states: “Enrichment program index. Respondents rated the frequency with which they engaged in several evaluative aspects of their enrichment programs. These included how often a team set enrichment goals, how frequently a team recorded when enrichment was provided, how often enrichment was evaluated, and how often the team adjusted the enrichment. Creating goals and setting goals were highly correlated so the creating goals question was dropped from the analysis. A principle [sic] components analysis using polychoric correlations was used to reduce the four variables into a single component that explained 56.84% of the variance.” First, it’s “principal” not “principle.” Second, these attributes are not completely operationalized in text. Over what periods of time? Are all the durations of surveyed attributes the same? If not, this confounds any analysis. Third, the use of PCA with only 56.84% of the variance captured literally means that 43.16% of the variability is missed, either showing up in the error term(s) or just being ignored. Some measure of interrater reliability could be used as a stand-in for variance in measurement at those facilities with more than one staffer. An average of some such measure would buttress the implicit assumption that all raters are identically accurate.

Thus, although the Cetacean Welfare Study represents an impressive undertaking, some fundamental questions such as rater reliability and motivations for positive care of dolphins are not addressed. An alternate and more revealing study design would have preliminary analyses that address these issues. Then utilize a variable reduction if necessary for further analysis. In the Cetacean Welfare Study, there are concerns over the

variable reduction method, but we appreciate that the goal is to support other analyses. We do not feel that the current manuscript is the place to discuss such issues.

These are not “considerable” methodological issues. None of what the authors present here justifies the exclusion of these studies. Perhaps the authors would like to explain exactly how these issues affect the interpretation of the data with regard to specifically what factors of socialization and housing are not represented correctly in the CWS? Your points about PCA do not consider the massive size and scope of the undertaking. Of course there will be variability on some of those dimensions, however, the question that needs to be asked is whether that affects the conclusions. On the variables of space, ocean vs. pool, socialization, training the size of the study washes away those interobserver effects.

Experimental design

Is the Survey Methodology consistent with a comprehensive, unbiased coverage of the subject? If not, what is missing?

No. For example. The Survey Methodology describes an arbitrary process where the authors state that papers published before 2000 would not be considered unless they were foundational papers. However, I would argue that not only are many of the pre-2000 papers not foundational, but they all seem to lean toward an anticaptivity bent. I can see Mason, 1991 but most of the others seem not to be foundational papers. The reliance on biased non-peer reviewed sources like Vail (which is not accessible) or Long 2018 <https://us.whales.org/2018/08/23/how-long-do-bottlenose-dolphins-survive-in-captivity/> is problematic because while these poorer blog sources support anti-zoo narratives they are used in place of quality peer reviewed work that shows zoos more positively. sources. Like this for lifespan data <https://royalsocietypublishing.org/doi/10.1098/rspb.2023.1895>.

We have removed the word “foundational” and now state: “Given that the field of cetacean welfare advances rapidly, we focused on articles published since 2000 with only a few exceptions.” Note that reviewer #1 requested some earlier articles to set historical markers (see above). See also response to A36, A51. We have removed the Vail citations and the Long (2018) citation. And we have already mentioned that we’ve included a very small number of non peer-reviewed papers, including at least one recommended by this reviewer.

Proie is only recommended because no peer-reviewed study has yet looked at comparative physiological markers of stress as she did it, and she specifically thanked one of the authors of this paper indicating that it is likely you all are aware of it. That being said I too wish those data were published, but I would not compare that effort to the Long or Vail references. Frankly, there is a big difference between the author's intended citations and the citation of a MSc

However, we thank the reviewer for calling our attention to Tidiere et al (2023) and we have incorporated their results in our paper, along with others suggested by all four reviewers.

There have also been several articles that have been published since the original manuscript was written—those have now been incorporated.

Note in this regard, the reviewer asked us in A78 to include a non-peer-reviewed master's thesis (Proci, 2013), which we have done.

Are sources adequately cited? Quoted or paraphrased as appropriate?

No. Please see the attachments. Many examples of misrepresented research. This work is not in keeping with the standards of PeerJ.

We have addressed these issues in responding to all of the reviewers' comments.

Is the review organized logically into coherent paragraphs/subsections?

There is a great deal of repetition where concepts like stereotypical behaviors are brought up throughout with little organization.

Stereotypies are introduced and defined in the introduction, mentioned as a key word in methodologies. Apart from section 4.1.a on stereotypies, they are again mentioned (1) with regard to dental issues, which seem appropriate because oral stereotypies result in dental problems, and (2) with regards to enrichment, as stereotypies are a welfare issue that enrichment is supposed to alleviate. As such, this does not seem repetitive or disorganized to us. Note also that Reviewer #1 stated: "... the way the author structured the review is good." Moreover, Reviewer #3 notes: "This review is incredibly well written and conceived."

I appreciate the perspectives of Reviewers 1 and 3 and I'm glad they had a better time with the paper than I did, however, I disagree.

Validity of the findings

Is there a well developed and supported argument that meets the goals set out in the Introduction?

Not with this level of bias, no. This is not an assessment of the current state of cetacean captivity (that would be The Cetacean Welfare Study). This is a remix of Marino et al, 2020 and Jacobs, et al., 2021 and it lacks a fulsome review of the literature, both in terms of challenges for zoos as well as the challenges zoos have overcome.

As we have explained elsewhere, this paper goes beyond Marino et al. (2020) and Jacobs et al. (2021). We incorporated 191 substantiated sources of information in the initially submitted review— and have incorporated ~90 new articles in the revision to address the

concerns of the four reviewers—most of these, as was the case in the original manuscript, point out problems that exist for captive cetaceans. We thus believe we have provided a comprehensive overview regarding the well-being of cetaceans. We believe the bulk of the literature does indeed suggest that there continue to be significant issues with regard to housing cetaceans in captivity, particularly for larger cetaceans such as orcas. We note that the Cetacean Welfare Study provides an assessment of certain welfare factors, but it does so only for dolphins and only in accredited facilities. Moreover, it does not really address the overall **well-being** of captive cetaceans. As we note in our conclusion now, the nine papers in question only use the word “well-being” one time, and then only in a direct quote.

In terms of bias, we realize there are arguments both for and against housing cetaceans in captivity (as partially outlined, for example, in Corkeron, Marine Mammal Captivity, an Evolving Issue, 2022). There is also a wealth of research on welfare measures in cetaceans, and some evidence of positive benefits (e.g., longer lifespans of dolphins in captivity). However, the accusation of bias would suggest we have ignored literature demonstrating that cetaceans are thriving in captivity. If we have missed papers that, in fact, demonstrate that cetaceans are **thriving** in captivity (not just that there are welfare measures that have been explored, or perceived incremental improvements), we would certainly be open to including those.

Does the Conclusion identify unresolved questions / gaps / future directions?

The conclusions and ideas for moving forward are also not well organized and seem muddled in focus. There should be specifically a section that considers paths moving forward, especially in the assessment of if sanctuaries would be effective for improving welfare. Instead of discussing the challenges associated with a sanctuary, something the lead author should be familiar with, sanctuaries are offered as a panacea, unchallenged. It gives the appearance of self-interested bias, and is a missed opportunity to highlight the sober knowledge the WSP has gained since it began its efforts in 2016.

In contrast to this, we note that reviewer #1 says the following: “Additionally, I would like to point out that I personally appreciate that the authors end the paper with statements that highlight the direction for improving cetacean welfare, which questions the need for continuing to hold captive cetaceans, the consideration of moving towards the development of sanctuaries, and the need for building a list of species that are for sure should not be held captive anymore.” We have expanded the conclusion to provide a broader perspective regarding sanctuaries, including possible welfare issues that will require continued monitoring. We have stated from the beginning that sanctuaries are indeed a form of captivity. We never claimed they were a panacea. This is now spelled out more clearly in the conclusion.

Regarding bias and the Whale Sanctuary Project, we fail to see how this is a bias or a conflict of interest insofar as the ultimate goal of any sanctuary is to become unnecessary (because there are no longer any animals requiring sanctuary). Sanctuaries are non-profit; as such none of the authors of this manuscript benefit if the paper is published. We would like to point out that conflict of interest is also a two-way street. If an author or reviewer works with captive cetaceans, that should also be disclosed as anyone who works with captive cetaceans is, in fact, directly affected by decisions about captivity as their career depends on having captive cetaceans. Several of the articles suggested by this reviewer are written by individuals in such a situation. We ask that the editor keep this in mind when considering reviewer comments.

note The reviewer has attached an annotated manuscript to this review.

COMMENTS ON LINE EDITS IN ATTACHMENT

Section 1.

- A1. This does not seem like a controversial statement. Moreover, we are simply opening the paper with a general framing statement here. This is an appropriate way in which to bring the reader into the issue, which is then treated more deeply later on in the paper.

The comment stands. The framing is controversial, however, not seemingly to the authors who rely mostly on self-citation to make said argument. Truth is there is not a strong body of evidence outside of the non-data/review papers of a select few authors (mostly the authors of this paper) that claim that the current conditions/welfare of cetaceans in accredited zoos and aquariums is poor. The online and popular press dialogue on this issue does not match the actual science discourse of this topic.

- A2. We thank the reviewer for his or her point and have added: The changes mentioned above all require there to be an alternative for the animals in these facilities that improve their welfare (see our discussion of sanctuaries).
- A3. We have changed “confined to” to “housed in”.
- A4. We have added other accredited agencies in this section, and have rewritten the section.
- A5. We have removed the Jacobs citation here. Note, however, there is only one rebuttal that we know of, not multiple in the literature, and the one is questionable at best (see Section 5 comments). The rebuttal simply states that dolphin captive environments are not impoverished, but says nothing about captive environments for larger cetacea. Moreover, the rebuttal does not question the basic tenet of

Jacobs et al. (2021), namely that impoverished environments are neurobiologically harmful, which has been established with decades of experimental work on a wide range of species.

- A6. We have incorporated the general findings of the Cetacean Welfare Study in this introductory section, and explore it further in the appropriate subsections of the paper.
- A7. We have now cited the Lauderdale et al. (2021) paper.
- A8. We don't think the recommended paper fits here; but we have cited it elsewhere. See our comment on A75-78.

Section 2.

- A9. We have rephrased this to be clearer. Note, we have removed the word "foundational" and now state: "Given that the field of cetacean welfare advances rapidly we focused on articles published since 2000 with only a few exceptions." See response to A36, A51.
- A10. We believe the revised paper is more comprehensive than the original paper with the inclusion of additional articles, as suggested by the reviewers.

Section 3.

- A11. We have provided citations for the term captivity, and, later on in the paper, we have noted that authentic sanctuaries are a form of captivity and provided a definition.
- A12. We appreciate that the Cetacean Welfare Study argues that amount of space is not as important as other factors for bottlenose dolphins and smaller cetaceans, but it would be problematic to use the conclusions of one study on a limited range of species (within a limited range of enclosure spaces and no consideration of a possible floor effect in data interpretation) to omit an important factor that continues to be a focus of discussion about the welfare of larger animals who swim long distances and dive deep, such as orcas. The Cetacean Welfare Study did not include orcas, nor did it consider non-accredited facilities. Therefore, it is limited in scope.

It is more problematic to use no data and speculation to argue against data. What you call a floor effect is still a twofold difference in maximum depth across the study. None of the criticisms here preclude a discussion of the contrasting findings of that study. You are bringing "no data" to a "data" fight. I don't know how you can adequately discuss the current state of captive welfare without citing these nine papers more fulsomely,

including when they contrast with your beliefs or assumptions. While you may want to compare greater depths and think the CWS would be improved by such data, right now your discounting of their findings is speculative. You need data to confront data.

A13. We have significantly revised this section of the paper to incorporate more findings from the Cetacean Welfare Study

A14. We have removed this statement.

A15. We have expanded Section 3.1a considerably, as requested by Reviewer#4 to provide more context, including the sizes of actual enclosures (vis-a-vis the size of natural habitats).

A16-18. As noted above, we have significantly expanded this section and include research from the Cetacean Welfare Study.

A19. We have removed this section, as it was confusing and not critical to our analysis.

A20. Although there is some variation in tank size across facilities, the point is that they are all very similar in one respect - that they are not very complex or interesting environments nor do they change much. So we contend that our statement still stands.

OK. but what are the welfare consequences of a stable vs. unstable environment? As you know predictability tends to lead to better welfare outcomes in managed populations. It should be your goal to have a paper that makes its points whether people believe you or not. Too often you are asking me to just believe you about what is good welfare with no data to support it.

A21. The reviewer asks an interesting question about whether naturalistic objects in the tanks are beneficial. Certainly, it is the case that, in zoos and aquariums, these features can be more important for visitors than the animals on display. However, Miller et al. (2021) found that the total number of habitats available to captive dolphins is positively related to behavioral diversity (an indicator of positive welfare). Although “number of habitats” is not the same as “tank features” per se, this finding suggests that access to a wider range of physical environments (and features) are important for dolphin welfare. Moreover, dolphins in natural settings (e.g., lagoons) tend to have less stress than those in tanks (Ugaz, 2013).

Given some facilities have recently added rockwork to their pools I asked a relevant party what the thought behind that was, they said it is for the guests, not for the dolphins. So these transitive leaps are a bit too speculative given there are actual assessments out there on these features. While the dolphins do not care much about the rockwork, facilities have started adding things like sand pits in the bottom of their enclosures for the dolphins to root around in and find stuff. Brookfield Zoo has just done this for example. The dolphins do respond very well to that. I would consider asking Lance Miller about it and cite the personal communication, better yet maybe entice some folks who work with these animals to co-author with you so you can be brought up to date on modern welfare practices.

A22. We have removed this statement about excessive chlorination.

A23. We have expanded this section to address acoustical issues in more depth, and have cited Stevens et al. (2021) along with several additional sources.

Please reread Stevens et al., to more accurately cite what that paper is saying.

A24. We are encouraged by the reviewer's statements about zoos moving towards using playback and other methods to assess social preferences in captive cetaceans. However, we would ask how those preferences, once ascertained, would be honored given that there is a very limited amount of space in marine parks. We are not implying that a captive managed dolphin does not have social preferences within the constraints of the opportunities available. We are saying that the breadth of opportunity for social preference and association is highly restricted, which we can expect to have an undeniable negative welfare impact in a species with a highly dynamic social life.

In bottlenose, the animals are moved to their preferred social partner (we are working to identify the signature signals in belugas so once could perform the same assessment with them). I'm not sure why you think this is as restrictive as it is. Bottlenose are moved quite frequently with an eye toward social partner preference. I would not have been able to do the memory study if they weren't. And on that topic, they aren't moving young animals anymore as implied in your paper. The standard is toward keeping calves with mom until she rejects them. For females that likely means they stay with mom, while males are identified based on compatible male pair bonds. In all of my playbacks the strongest responses were for MPB, dolphins rarely show strong responses to mothers or calves. Laela may have published data on this in the wild and we will have a paper out on this soon.

A25. The reviewer is correct in pointing out that the Cetacean Welfare Study found that space may not be the most important welfare factor for dolphins and belugas (although there is a potential floor effect as a confound). However, the statement by Brando & Buchanan-Smith mentions other factors, such as complexity, choice, and appropriate social groupings, which are still issues. These remain important factors and are not completely unrelated to space.

A26. The reviewer takes issue with the claim that "pre-weaned animals" are separated from their mothers. But we never said this. We actually say: "After the minimum weaning age, captive cetacean mothers and offspring living in marine parks may be separated." We do not claim that mothers and calves are routinely separated but only that it does happen.

See above. I will caveat that I am talking about the standards for accredited facilities. If you have examples of bad actors elsewhere feel free to name and shame as appropriate.

A27. We thank the reviewer for the information on social groups and have replaced the original statement with: Because captive cetacean groups do not resemble social groups in the wild there may be longstanding repercussions for the psychosocial well-being of calves.

That's an open question isn't it? Does the amount of movement between facilities in the Atlantic Bottlenose Dolphin Breeding Consortium, for example, sufficiently simulate fission fusion dynamics? That could be a great area for future study.

A28. We have added more information about Clegg et al (2023).

A29. The reviewer's point is well-taken and we have removed this statement from our paper.

A30. We added Jaakkola (2024) in Section 5, which we expanded to say more about cognitive enrichment. We have also added: Remarking on the lack of complexity in captive environments Jaakkola (2024, p.2) stated: "in contrast to the situation in the wild, these animals live in highly predictable and structured environments."

See comments above.

A31. We have replaced (Couquiaud, 2005) with a more recent paper on captive cetacean diets. We have replaced the word "narrow" with "narrower". We have also added: Rosen and Worthy (2018, p. 719) note, "both a lack of diet diversity and the reliance on frozen foods present potential nutritional challenges."

But the facilities have mitigations for these issues which you should highlight. As an example, for frozen fish and water loss, hydration is applied.

We do not necessarily claim that a narrower diet is detrimental from the cognitive viewpoint as we focus more on the delivery method. We refer to the manner of food delivery as potentially problematic in the statement: "they are delivered to them in a manner (i.e., thrown directly into their mouths above water) that requires little to none of the cognitive activity relevant in natural hunting and feeding." And, in accordance with the reviewer's request, we have added that: "the lack of stimulation from the way food is delivered must be countered by the implementation of other methods of cognitive enrichment."

Better yet you could also discuss the use of food puzzles where managed animals must work through enrichment devices to access food. I'm pretty sure these are highlighted in Isabella Clegg's enrichment catalogue.

A32. We thank the reviewer for his/her remarks and added: It should be noted that dolphins kept in lagoons will sometimes chase wild fish but they rarely catch them, presumably due to their lack of hunting skills.

Even in the wild dolphins rarely catch fish one on one. This is much of the basis of dolphin sociality. Fish are very well tuned to avoid being eaten and can turn on a dime. Dolphins are like a semi-truck with almost none of the turning radius of a high bodied fish. Hence you see cooperation around the formation of bait balls, strand feeding, lob feeding, etc. It has little to do with captivity except that motivation is much reduced when one is provisioned and schooling fish in sufficient quantities for a bait ball likely do not exist in lagoons. Although I would agree that advanced hunting tactics are not part of the repertoire of behaviors passed from mom to calf in managed facilities. There should be plenty of papers to cite on hunting strategies.

A33. We also thank the reviewer for mentioning the many highly specific ways in which free-living cetaceans engage in feeding.

A34. We have included three references regarding time budgets: Neumann, 2001; Stockin et al., 2009; Noren & Hauser, 2016.

See comment on paper itself. I was referring to a citation demonstrating that, for example, provisioning does not satisfy biological drives, etc. I can see a scenario where dolphins master the art of getting people to give them fish and they find that cognitively enriching (both in the wild and in zoos). Watch the diversity of attention seeking behaviors from dolphins before a feed session. These are engaged animals. A question worthy of study, but it is important not to make assumptions here.

A35. We have incorporated three of the suggested papers from the reviewer in this section. Ramirez (1999) is a dated reference and, while training undoubtedly increases compliance of the animals and facilitates the captive management of wildlife, this is an alternate purpose to enhancing welfare. Enhanced compliance cannot be assumed to automatically correlate with enhanced welfare. Thus, we do not feel that this reference fits within the scope of the paper.

I think anyone who has a pet whom they train can easily understand what benefits training and engagement have on welfare. Training by itself does not lead to compliance, and Ken has never said that it did. Training is about the formation of a relationship between the trained and the trainer. I encourage you to study this more closely, in person, because you are missing a lot here. The only thing that can guarantee "compliance" is the nature of the relationship that trainer has with that animal. In your parlance enhanced compliance is indicative of a positive relationship which is indicative of good welfare (in a positive reinforcement model of training).

A36. We have previously addressed this issue in our responses.

Section 4.

A37. We thank the reviewer for pointing out that cortisol is not always a bad thing. It becomes harmful when it becomes dysregulated during chronic stress. We have added this point to our paper.

A38. We added: Much more research is needed in this area as the study conducted by Matsushiro et al. (2021) involved only five dolphins and revealed the possibility of - but not the definitive presence of - chronic stress with SWD programs during seasons when the number of visitors to the park was high.

A39. We added: "...with a small sample size of three dolphins..." and "However, they found no overall decrease in welfare due to SWD activities."

- A40. The reviewer points out that Samuels and Spradlin (1995) is an old paper. In order to comply with the reviewer's views we have omitted that paper. However, the reviewer goes on to say that there are virtually no uncontrolled swim programs at accredited facilities. That may be true but in this paper we are considering both accredited and unaccredited facilities.

That wasn't my view. That was you selectively enforcing your own criteria for the benefit of your anti-zoo position. I think the age of the publication is less important as a specific number or date than having a handle on the way the topic is evolving over the years. For example, I think 2006 is too old a citation for talking about captive lifespans because that has so materially evolved over the last twenty years, whereas mirrored affiliative behavior in zoos and the wild is less likely to have such profound shifts (or at least indicate worse welfare in 2025 than in 1995). As for your distinction on accredited and unaccredited facilities make that distinction in the paper. Stop painting with this overtly broad brush. Not all facilities are the same, but too often in this paper you seem to want to make the worst of them the example for all of them. That doesn't paint an honest assessment of current practices.

- A41. The reviewer suggests: "I wouldn't focus on unstructured SWD as it isn't practiced commonly in accredited facilities." That is the case, but we did not exclude unaccredited facilities in our review, therefore the same cannot be said of them.

See above.

- A42. We thank the reviewer for this suggestion and have added: More research on important physiological and behavioral factors, i.e., oxytocin levels, more precise cortisol levels, etc. may elucidate the nature of the dolphin-trainer relationship and how it impacts dolphin welfare.

- A43. We are familiar with Dr. Bossart's work since one of us has worked alongside him in the field on health assessments of the IRL dolphins. Dr. Bossart's research referenced by the reviewer includes studies in which captive dolphins with no sign of recent illness (healthy individuals) are compared to wild populations, especially those in the Indian River Lagoon in Florida, whose population health is compromised, primarily by heavy pollution and human interaction. We have never claimed that there are no healthy individuals in captivity who can reliably be used as controls for sick individuals in the wild, as the reviewer seems to be suggesting. The increased rate and/or differential etiology of disease in captive populations, as our research suggests, does not preclude the existence of a good number of healthy individuals at any given period of time. We have included the work of Bossart et al. (2003, 2017) and of Fair et al. (2017) into the paper.

- A44. Marino et al (2020) is a peer-reviewed scientific paper which has not been substantively critiqued. The reviewer is referring to two biased opinion pieces. The problems with these critiques are extensive. To cite just one example, Dudzinski et al. (2020) tried to dismiss Marino's et al's argument that

orcas under human care suffer from chronic stress by saying Marino *et al.*, misrepresented the conclusions of Atkinson *et al.* (2015), who found physiological mediator differences between terrestrial mammals and marine mammals. And yet, they failed to see that Atkinson *et al.* (2015) states the following; “Overall, the neuroendocrine system in marine mammals appears to respond largely in a manner similar to that of terrestrial mammals” (p. 469); “In response to a challenge or stimulation with ACTH, marine mammals appear to respond similarly to terrestrial mammals...” (p. 469); “...diurnal variations of GCs exist in marine mammals, similar to that observed in terrestrial mammals” (p. 470); “...the expression of glucocorticoids, particularly cortisol, appears to be a maintained characteristic of the stress response across marine and terrestrial mammals” (p. 476); and, in the conclusion: “Physiological indices of stress commonly measured in terrestrial mammals, such as GC or ACTH, have been measured in many marine mammal species and in general indicate that the HPA axis functions similarly to terrestrial mammals” (p. 477). In other words, despite some variations in marine mammals when compared to terrestrial mammals, the stress mechanisms are remarkably similar. The other article, Jaakkola *et al.* (2020), makes the same mistake, and is written by individuals with a conflict of interest insofar as they work with captive dolphins and thus have an inherent interest in maintaining the status quo when it comes to cetacean captivity (despite them claiming no conflict of interest). In this, and in other ways, the critiques offered by the opinion papers cited by this reviewer are problematic. The current manuscript does not seem to be the place to debate these issues.

It's not a conflict of interest when people disagree with you. You can be wrong, and in this case, you can be wrong because of bias and misrepresentation. Because we are literally confronting the same issues now, I only have to point to how you have misrepresented my work here to highlight that this is a pattern. What I am referring to two are also peer-reviewed papers (not opinion pieces- another misrepresentation) some of whom had authors with anti-captivity views who were so offended by the misrepresentation and bias that they chose to respond in the literature to maintain the integrity of scientific discourse on this issue. This is the problem with using an activist approach of advocacy, but from the framing of a neutral scientist. Even in your response you are highlighting the problem that got two sets of authors to both write peer-reviewed papers responding to that paper. Using your example, you selectively cited Atkinson where on top level things he argued that there were some similarities, but you glazed over the differences. Selective citing and interpretation of citations are not appropriate in scientific discourse. Period.

Just so we are all clear, while many of the basic systems of cetacean stress like the HPA axis for example are conserved, marine mammals tend to have higher basal cortisol levels and more variability than their terrestrial counterparts. Furthermore, marine mammals generally are thought to modulate their sensitivity to glucocorticoids at the tissue level to avoid chronic damage from persistently elevated levels. These would have been important differences I would have recommended you add had I peer reviewed that paper, and it highlights the importance of a good peer review process so we can eliminate this ugliness.

Commented Which you should have discussed in your 2020 paper fulsomely. With implications for what these differences mean both for absolute cortisol measurements and the effects of elevated blood cortisol on bodies that can mitigate that effect at the tissue level. You did not adequately discuss these crucial differences and a lot of authors pointed that out.

Commented LIKE?

Commented Perhaps their work with captive dolphins have given them a perspective you would benefit from. Unless you are impugning their integrity. I know you are sensitive to the idea that you are doing this because of your salary from the WSP. Do you think that people who disagree with you only do so for money while when you disagree with other's it is principled? That would be a problematic viewpoint.

- A45. This paper is discussed in Section 5 with regards to cognitive enrichment.
- A46. Again, the mentioned rebuttal has significant flaws, including a severe conflict of interest. Moreover, the article does not dispute that stereotypes represent neural issues, which is the claim of this sentence.

I'm sorry. you can be criticized and be magnanimous about it. That's how science is supposed to work. Marino, 2020 should read (Marino 2020, c.f. Jaakkola et. al., 2021; Dudzinski et al, 2021) and Jacobs et al., 2021 should read (Jacobs et al., 2021, c.f. Jaakkola, 2023). Two reasons: 1) if you think these critiques are unfair you have had plenty of time to respond in peer review. 2) Your job in this paper is to present a state of the art in cetacean captivity, denying the acknowledgement of these papers denies your readers the chance to make up their minds for themselves. Which is exactly the problem.

Section 5.

- A47. We are not sure what the issue is here: we say that stereotypes are found in other captive species, and then provide citations for that statement. We subsequently provide citations specific to cetaceans, and go into more detail on this issue.
- A48. None of the Cetacean Welfare Study papers mention Gyax (1993); note that we did mention Miller et al. (2021) later in the paragraph, and their finding of an inverse relationship between behavioral diversity and route tracing.
- A49. We have added the caveat that it is difficult to make definitive observations of free-living cetaceans.
- A50. We have removed the current reference and replaced it with Ringelstein (2021).
- A51. Again, we have removed the term foundational; we have kept Walsh et al. (1996) and have added Calle (2005).
- A52. The central point of Mason et al. (2007) is to show that, to date, there are no ways to completely eliminate ARBs in captive wild animals. That is also the point we are making. It may be that, in the future, more successful methods will be devised and used.
- A53. The reviewer makes a good point about the fact that there may be many more recorded attacks of cetaceans on humans in captivity than in the wild because of sampling. Nevertheless, we searched for reports of cetacean attacks on humans in the wild and found only the one dolphin case. While orcas, belugas, and other cetaceans do not come into contact with humans in the wild as much as in captivity, there is certainly some opportunity for interaction and one would think there would be more cases if the aggression issue occurred in the wild.
- A54. We have replaced the word "petting" with "interaction".

- A55. The reviewer provides two links in this comment. The first is Anderson et al. (2016), which is a peer-reviewed paper, and the one we cite in the manuscript. We have kept this citation. The second is the opinion piece (i.e., Anderson, 2016), which is not the one we cited. As such, we're not sure what the objection is about.
- A56. We addressed this in A44.
- A57. We have added references to the fact that infanticide does occur in the wild. We have already addressed the fact that there is high first-time infant mortality in the wild in our section on Reproduction.
- A58. We have adjusted the language to address the reviewer's concern about phrasing of the statistics related to iron levels between captive managed and free-ranging populations.
- A59. The reviewer's comment here is answered in the sentence following: "The causative organism is found on dead fish products, the main source of infection for captive cetaceans (Laacave et al., 2019). For this reason, Erysipelas is primarily a disease of captive cetaceans..."
- A60. This comment does not require any edits.
- A61. We see no need for edits here. If the reviewer had looked beyond the cited paper's abstract, they would have found the following content: "Dental wear is a consequence of a multifactorial process involving three synergistic components...and normally is related to age progression... More recently, Foote et al. (2025) observed distinct dental wear rates in different haplotypes of killer whales from the North Atlantic, suggesting that genetic and ecological divergence of populations may be reflected in dietary specializations and dental wear. The same idea was corroborated by Ford et al. (2011) relating the extreme wear of offshore killer whales with a diet based on sharks, prey that can be extremely abrasive on teeth... For most of the species analysed, although general prevalence of wear was high, wear was mostly superficial and affected enamel and outer dentine...superficial wear would have limited or negligible implications for the fitness of individuals, moderate and severe wear could have the potential to expose the pulp cavity and lead to tissue necrosis and increase the susceptibility to infections... **In general, the occurrence of dental wear is related to progression of age.**" Although the paper finds that the frequency of dental wear in free-ranging cetaceans is high (something that we have never disputed) it specifically qualifies that wear as superficial and age-related for the vast majority of species other than those with specific life history characteristics that precipitate more aggressive patterns of dental wear.
- A62. The link provided by the reviewer in this comment is not accessible in the pdf format we received. However, we believe the reviewer's concern is addressed in response to comment A61 above.
- A63. The paper the reviewer is citing is not in contradiction to our statements. We have never stated that superficial and slowly progressive forms of wear are rare in orcas. However, we do specifically refer to "advanced" tooth damage as rare in

orca. We have added the term “traumatic” to the text to further characterize the type of tooth damage we are referring to in captive cetaceans. The two new forms of dental wear being described in the referenced paper are both superficial in nature, gradual in process, and do not precipitate dental injuries that can be characterized as “advanced” and “traumatic”. The point of this section is not to debate whether or not free-ranging cetaceans experience dental wear; of course they do. The purpose is to highlight the differential processes that lead to tooth wear and damage in captive vs. free ranging populations. As with other tissues in the body, the teeth have healing mechanisms designed to protect the sensitive pulp chamber from infection, a condition which can be life-threatening. However, these mechanisms (i.e. tertiary dentin formation) can only occur in situations where damage to the integrity of the tooth is gradual and subtle, such as with progressive age-related wear. By contrast, in captive situations, cetaceans are prone to sudden traumatic injuries, such as complex crown fractures. Such fractures by definition extend into the pulp chamber and often fail to heal, leaving the tooth vulnerable to infection without invasive pulpotomy procedures and routine, daily antiseptic flushing. Thus, these differences in the cause and nature of dental injuries are the reason why there is a greater health risk associated with dental disease in captive populations. Content and references have been added to clarify this point.

- A64. Citation and elaboration has been added to address reviewer’s concern about a lack of recent literature supporting the presence of gastric ulceration in captive cetaceans. As with dental disease, the purpose of this section is not to suggest that this disease is not also a problem for free-ranging cetaceans, but simply to highlight that it exists as a common challenge for captive populations and that, in some cases, factors associated with the captive environment or husbandry have contributed to the development of the disease.
- A65. The reviewer correctly points out that this is intended to be a review of literature related to the state of captive cetacean health and welfare. Nowhere in this paragraph does it state that free-ranging cetaceans fail to succumb to illness, nor do we feel this is relevant to the discussion. In fact, there are several places within the text of this paragraph that explicitly acknowledge that the diseases discussed do in fact also affect free-ranging cetaceans. Dr. Bossart’s research referenced by the reviewer includes studies in which captive dolphins with no sign of recent illness (healthy individuals) are compared to wild populations in the Indian River Lagoon in Florida whose population health is understood to be compromised, primarily by heavy pollution and human interactions. We have never claimed that there are no healthy individuals in captivity who can reliably be used as controlled for sick individuals in the wild, as the reviewer seems to be suggesting. We fail to see the relevance of this to our arguments and therefore have chosen not to contextualize it, as the reviewer has requested. Finally, publications detailing the cause of morbidity and mortality of captive cetaceans are limited due to the paucity of literature that emerges from the industry that holds these data (see Rally et al., 2018. Looking behind the Curtain: Achieving Disclosure of Medical

and Scientific Information for Cetaceans in Captivity through Voluntary Compliance and Federal Enforcement).

- A66. We do not believe that a “comprehensive review of birth control” in captive cetaceans is relevant to this section, which is intended to discuss the reproductive health consequences of captive environments on cetaceans.
- A67. We have deleted the word “uncomfortable”.
- A68. We have deleted this sentence altogether.
- A69. In the interest of clarity, we deleted that statement.
- A70. Same.
- A71. Yes, before 2000—we address this above noting that we removed the term “foundational” in our methodology and that we did include some citations that were before 2000.
- A72. Yes, but see our comments on this issue and in A73 below.
- A73. Yes, before 2000—we address this above noting that we removed the term “foundational” in our methodology and that we did include some citations that were before 2000.
- A74. In agreement with the reviewer, we explicitly state that much more research on different populations of belugas is necessary at this point.
- A75. Of course, enrichment can take a variety of forms, and this should be clear from the revision of Section 5. Environmental Enrichment.
- A76 - 77. This reviewer says that we should include a study by Jaakkola (2023), which claims that accredited captive environments for dolphins are not impoverished. We have now cited this publication, but we note briefly there are problems with its conclusions because of an oversimplified understanding of the environmental enrichment paradigm. Moreover, the paper does not discuss facilities that are not accredited, nor does it discuss facilities housing larger cetaceans. There are other issues with the study that we do not mention in the manuscript. Specifically, there appears to be bias and conflict of interest insofar as the author’s career relies on captive dolphins (she is the director of the Dolphin Research Center) and this piece was published in a special issue of *Animals* that was sponsored by Dolphin Quest, SeaWorld, and Loro Parque—all facilities that support dolphin captivity. The same is true for another article recommended by this reviewer, namely Bruck (2024).
- A78. We have added Proie (2013), although it should be noted this is not a peer-reviewed article but rather a master’s thesis.
- A79. Referring to Ugaz (2009), the reviewer states: But for a dolphin moving from a pool to a sea pen the experience may be very different. We agree that it may be or, perhaps not. We don’t know at this point and the reviewer’s statement is conjecture.

- A80. This issue is discussed above with regards to space.
- A81. The reviewer is implying that the fact that captive dolphins are known to require encouragement to leave lagoon-based captive facilities and enter the ocean may be an indication that larger spaces are not inherently enriching. It is well known that captive wild animals have enhanced fear-responses to changes in their daily routines or environments. Introduction to a new environment is inherently stressful for any animal. For this reason, it is not uncommon for captive animals to seek familiar spaces and display behavioral indications of stress when asked to enter an unfamiliar space and require encouragement to do so. However, offering an occasional opportunity to explore a vast and unknown environment is quite a different situation to providing a primary enclosure that is spatially enriching. In no way would we consider any studies involving the former scenario to be an accurate reflection of the “effectiveness of space in improving welfare.”
- A82. We have deleted this statement.

Section 6.

- A83. We have significantly expanded this section, including information about sanctuaries. Although Browning (2020) makes some interesting points regarding natural behavior, we do not accept many of the arguments put forth, especially when it comes to ignoring the fundamental evolutionary history of a species. Captivity inherently constrains any animal, and our contention all along is that some species (including cetaceans) are more negatively affected by captivity than others. One goal of the AZA and other accrediting agencies is, in fact, to stimulate “natural behavior.” Numerous studies over the years by Georgia Mason and others have shown that the effects of captivity are largely dependent upon how well the captive situation fits with the natural adaptive characteristics of a given species. Moreover, the reviewer has an inaccurate view of the “naturalistic fallacy”. He or she implies that it has to do with the appropriateness of an environment for a given species. In fact, the fallacy has more to do with assuming a positive moral or ethical valence to nature. Our stance is about the evidence for how well cetacean evolved characteristics fit with the captive environment and not whether nature - in and of itself - is “good or bad.”

The definition I am operating under is: The naturalistic fallacy is an informal logical fallacy which argues that if something is ‘natural’ it must be good (which is a very common definition- the authors are free to look it up). In this case sanctuaries would fall under that because the assumption is it is more natural than a concrete tank, therefore it is better. The mistake here is assuming that the animal, who maybe has never known nature, will somehow react positively to it because they evolved for it. The more likely scenario is that the animal, who is argued by these authors to be cognitively complex, will not see real nature as natural because it has no experience with it, and potentially react to nature as if it is unnatural (i.e. stress responses, etc.). One of many differences between

terrestrial sanctuaries and cetacean sanctuaries is the animal's perception of its world. An elephant can see over its zoo exhibit and know there is a world out there he/she might inhabit. For a dolphin in a pool who has never lived elsewhere (although it would be interesting to see how zoo to zoo movement over lifespan affects this) the only world it knows is the pool it's in. So if you put it in a 100-acre sanctuary I think you have to ask is that really fundamentally the same thing for the dolphin as it would be for the elephant released to a 100-acre preserve? Given how many fish it takes to get dolphins to swim out of their pools into connected outer ocean habitats I question that it is. I definitely do not think it can be assumed that it is (see Little White and Little Grey).

A84. We have included two references here that raise questions about sanctuaries (e.g., Bruck, 2024; Almunia & Canchal, 2025). It should be noted that both of these have severe conflicts of interest insofar as the authors of both articles work with captive cetaceans in traditional settings and thus are critical of sanctuaries, which offer more natural environments. We do not feel it is appropriate in the conclusion to have an in depth discussion on the issue of sanctuaries. Moreover, many of the objections in Bruck (2024) have already been addressed elsewhere (Marino et al., 2025). We also now note in this section that accreditation standards for cetacean sanctuaries have been adopted by the Global Federation of Animal Sanctuaries.

I'm critical of sanctuaries because they are an untested idea that has seen two belugas stress out in Iceland (over 5 years of repeated attempts to put them in that sea pen) and has seen no progress from the WSP side since inception in 2016 (with a similar timeline for Baltimore Aquarium). If you are going to present sanctuaries as the panacea for the issues you have highlighted then you better have a discussion about their potential issues. The authors cannot just fundamentally ignore any papers that are critical of their views or opinions, especially when these authors come to the debate with so little data.

Bruck, 2024 went through a peer review process with a pro-sanctuary reviewer who made the paper better for their thoughts and suggestions. The same is true here. Not everyone who disagrees with you is doing so because they are on the take. People legitimately disagree with your ideas because you have failed to support them and have used "trust me" arguments where they are not warranted. Go collect data as described in my comments on the paper and assess whether cetaceans would prefer this form of captivity, but do not assume that sanctuaries are a welfare improvement without meaningful data to support it.

As for Marino, 2025. Here is comprehensive list of omitted materials from that paper (which was a commentary). Note there is no reference to Bruck, 2024 or Almunia, & Canchal, 2025 in that paper. If you are going to write a rebuttal to the points made in those papers then you probably would have cited them.

A85. We have removed the term "ticket sales" from this sentence.

- A86. The reviewer may be correct in stating that choice and control “...could be implemented in current existing zoos” and we do cite this paper in the following statement:

The question thus remains: how can one definitively determine which welfare assessments actually provide quality of life? For example, researchers would probably agree that having autonomy (i.e., choice and control over the environment) should improve well-being (Jaakkola, 2023) by providing captive animals with the opportunity to thrive (Vincino & Miller, 2015; Miller et al., 2020).

However, we contend that significant questions remain about autonomy for captive cetaceans—choice issues mentioned in the conclusion section. Moreover, the reviewer again points to Jaakkola (2023) but we already noted the problems in this paper and in the author’s conclusion.

- A87. We have made this same point in our section on Interactions with humans. And we have added another citation.
- A88. Please see A84 above.
- A89. We have rephrased this sentence.
- A90. The reviewer states that this is not a consensus opinion. We do not claim it to be. It is our conclusion based on the evidence we have presented.
- A91. It is unclear what the issue is with regards to the author’s affiliation (there is no stated basis for conflict of interest). The article was published in a peer-reviewed journal, the same journal containing other articles that this reviewer has repeatedly suggested we cite, namely, *Animals*. It is unclear how this article is any different than, say, Bruck (2024—where there is a stated conflict of interest). Why is this article an “opinion” piece, but Bruck (2024) is not?

It's not a conflict of interest issue it's a qualifications and quality of the information issue. Forget the fact that you agree with the author and ask yourself to what standard do you hold this information if you were neutral on it. Its not a proper review paper, its not a data paper, it's just a narrative more appropriate for some short personal book. It is by no means a causal study as the name implies. I don't care what journal published it; I wouldn't cite it as a matter of professionalism. It is up the authors to evaluate sources of evidence beyond what journal they come from. I invite the editor to read Bruck 2024 and Anderson 2016 as it is fairly obvious the difference in scope and support for each papers conclusions.