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 additional document.

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 Additional Documents 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.

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 Additional Information).

STUDY 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 https://us.whales.org/2012/12/03/the-mixed-messages-of-captivity/) 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.

Are sources adequately cited? Quoted or paraphrased as appropriate?

No. Please see the Additional Comments. Many examples of mis cited or misrepresented research. This work is not in keeping with the standards of PeerJ.

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.

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.

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.

An update on captive cetacean welfare

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

An Update on Captive Cetacean Welfare

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

1. Introduction

Cetaceans (i.e., dolphins, whales, and porpoises) have long been considered challenging and ethically problematic candidates for captivity (Lott & Williamson, 2017; Rose et al., 2017 Hosey et al., 2020; Marino, 2020; Marino et al., 2020; Marino & White, 2022; McGillian, 2023;). The 2013 film *Blackfish* played a key role in changing public sentiment about captive cetaceans, particularly orcas ('killer whales') (Parsons & Rose, 2018; Boissat et al., 2021). Increasingly, the public in many parts of the world has become more concerned about the welfare of captive cetaceans and less favorable towards captivity itself (Giovos et al., 2019; Naylor & Parsons, 2019). Wasserman et al. (2018) found that, when accounting for some biases in previous surveys of visitor attitudes, support for orca shows and swim-with-dolphins programs in their survey was well below what had been reported in previous studies conducted on behalf of captive cetacean attraction operators. Clegg (2021) argued that captive cetacean facilities will need to respond to these changing social ethics to survive into the future.

This increase in public concern has led to several legislative efforts around the world to limit or eliminate keeping cetaceans for entertainment. Canadian Bill S-203 (Senate of Canada, 2025) passed in 2019, bans breeding and use of captive cetaceans for pure entertainment (S203). The U.S.-based SWIMS Act (S4740) was recently re-introduced to phase out captive cetacean entertainment in the United States. In 2021, the French government decreed a trading and breeding ban, which will end whale and dolphin captivity by 2026 (Berry, 2021). More recently. Belgium has officially become the 7th country worldwide and the 4th in Europe to enact a permanent ban on dolphinariums (The Brussels Times with Belga, 2024).

Nevertheless, captive cetacean entertainment persists in the U.S., Europe, Mexico, South America, Japan, Russia, and elsewhere. The scope of the issue of captive cetacean welfare is broad. In China, the captive cetacean entertainment industry has been growing precipitously over recent years (Chin-Ee Ong, 2017). Globally, more than 3,500 cetaceans are confined to concrete tanks or small pens in marine parks, zoos, and military facilities (Cetabase, 2024). The most abundant cetacean species in captivity are common bottlenose dolphins (*Tursiops truncatus*), beluga whales (*Delphinapterus leucas*), and orcas (*Orcinus orca*), but also includes pilot whales

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]: 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 [A3]: This language seems biased and fairly subjective.

(*Globicephala macrorhynchus*), Commerson's dolphins (*Cephalorhynchus commersonii*), white-sided dolphins (*Lagenorhynchus obliquidens*), and several other species and hybrids (Cetabase, 2025). In North America alone, there are approximately -480 bottlenose dolphins, -60 belugas, and 18 orcas in captivity (Cetabase, 2025).

Animals in zoos and marine parks in the U.S. are covered by minimal regulations set forth under the Animal Welfare Act (Animal Welfare Act and Animal Welfare Regulations, usda.gov), which are often under-enforced (Winders & Chilakamarri, 2018). Accrediting organizations (e.g., Association of Zoos and Aquariums, AZA) set welfare standards for the zoological industry. However, even under the highest standards, there remain unique challenges in meeting the essential needs of the animals (Morgan & Tromborg, 2007; Shepherdson & Carlstead, 2020). Moreover, only a relatively small number of existing zoos and aquatic parks around the world are accredited by the AZA, pointing to widespread problems in welfare standards for the majority of captive entertainment facilities.

The science of captive wild animal well-being is developing and continues to be informative about how the needs of various species held in zoos, marine parks and aquaria (Whitham & Wielebnowski, 2013; Shepherdson & Carlstead, 2020; Jacobs et al., 2021). Yet, some species, including cetaceans, still face significant challenges in captive settings (Clubb & Mason, 2003; Morgan & Tromborg, 2007; Mason, 2010; Fischer & Romero, 2018). There are numerous markers of poor welfare (e.g., stereotypies, defined as unchanging repetitive actions; Mason, 1991; Jacobs et al., 2021) and, too, ways to determine that welfare is good. Miller et al. (2020) have noted, importantly, that good welfare is not just the absence of negative welfare indicators because welfare, as a whole, must include positive aspects (Miller et al. 2020). There are several factors, e.g., diet, shelter, health, ability to express species-specific behaviors, and choice, that provide positive well-being (Vicino & Miller, 2015).

Here, we review the literature to examine how well the care of captive cetaceans around the world aligns with their needs, aiming to identify remaining challenges. This includes an overview of behavioral and clinical factors in cetacean captivity, particularly in commercial settings. Our focus is on the most recent research and representative facilities, many of which

Commented [A4]: 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.ammpa.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-Accomodation-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 [A5]: 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 [A6]: 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/10.1111/mms.12601

Commented [A7]: I would add this citation here. The cetacean welfare study provides a great wealth of information and the authors should avail themselves of it. https://doi.org/10.1371/journal.pone.0250332

Commented [A8]: I would also cite 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.

hold accreditation from professional organizations (e.g., AZA). Finally, we discuss the ethical implications of our findings.

2. Survey methodology

This review is intended for readers in the areas of animal welfare, health, and ethics. Our methodology involved conducting a scoping review of the literature (Munn et al., 2018) on captive cetacean welfare and used key words and terms such as: body condition, dietary preferences, health, stereotypies, disease, sociality, reproduction, lifespan, mortality, enrichment, performance, space, complexity, and behavioral diversity. After a review of that literature we organized the review into dimensions of the captive setting important to cetacean welfare: a) enclosures, space and exercise, b) complexity and sensory-perceptual experience, c) sociality, d) feeding and cognitive demands, and e) performances and interactions with humans, as well as specific welfare topics: brain and behavior (e.g., stereotypies, aggression) and physical health (e.g., nutrition and metabolism, skin health, dental disease, digestive and gastrointestinal disease, infections, reproduction, longevity, survival rates, and mortality rates). We examined and included data on free-living and captive cetaceans.

We conducted our primary searches using Google Scholar. We used our own papers and referenceds sources from published scientific papers as well. We selected only publications that were readable in full. Given that the field of cetacean welfare advances rapidly we did not include articles published prior to 2000 except for those we considered foundational to the field.

We used 191 substantiated sources of information in this review. These included 121 peer-reviewed papers, 28 chapters in edited books, four scientific books and one newspaper article. We used only 21 sources of gray literature (*e.g.*, conference proceedings, white papers, government documents). We gave priority to the most recently dated findings. Fourteen citations were for publications prior to the year 2000, with 131 published between 2000-2020, and 22 between 2021 - 2025. We obtained information about standards and recommended practices published by professional organizations from their websites. The objective of our review was to attain a comprehensive understanding of the factors known to be associated with health and welfare of cetaceans in captive facilities. Moreover, we did not omit findings that demonstrated

Commented [A9]: 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 [A10]: 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).

improvements in welfare or positive views of captive cetacean welfare because our aim was to generate an accurate, comprehensive and current picture of the status of captive cetaceans. To confirm that our search was comprehensive and inclusive we examined citation lists of all articles we used. Finally, findings from secondary sources (e.g., review articles, online web pages) were confirmed in primary sources whenever possible.

3. The captive environment

Captivity is the state of being confined to an artificial environment (usually designed for human benefit), which is typified by zoos, aquaria, and marine parks but also includes research laboratories and military facilities. Across these establishments, there are significant differences in terms of space allotted, quality of veterinary care, level of visitor interactions, inclusion of demonstrations/performances, and several other factors (Shepherdson & Carlstead, 2020). The captive environment is multifaceted, influencing both physical and behavioral aspects of welfare. Key factors include space and complexity, movement, sensory experiences and mental stimulation, diet, and social interactions.

3.1a Enclosures, Space, Exercise

Although some cetaceans are kept in sea pens and netted off areas in a lagoon or bay adjoining the ocean, most are kept in land-based concrete tanks. Individuals housed in enclosures continuous with the ocean tend to fare somewhat better than those in tanks (see below; Ugaz et al., 2009, 2013). In the United States, the total amount of space afforded to captive cetaceans is governed by minimum space regulations promulgated under the Animal Welfare Act (US - AWA - Subpart E. Marine Mammal Regulations I Animal Legal & Historical Center). They are also often managed by holding them in various pools for training, medical procedures, and to separate aggressive individuals. Although these pools are much smaller than the main tank, they are sometimes used for permanent housing (Couquiaud, 2005). There are also quarantine pools and maternity pools that allow for separation and enhanced control over the animals. Moreover, some tanks have lifting floors that allow the animal to be lifted out of the water to be physically restrained by trainers and veterinarians (Couquiaud, 2005).

Commented [A11]: 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 [A12]: How are these determined? The Cetacean Welfare study argues space is not a significant factor relative to trainer and conspecific social interactions.

Commented [A13]: These statements need to be contextualized with The Cetacean Welfare Study https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0250687

Commented [A14]: I know of no facility where this is true. If this is to be a modern interpretation of of the state of cetacean welfare in captivity an updated study is warranted here.

There is considerable variation in tank size across facilities. Many tanks are too small or shallow to allow natural swimming behaviors (McPhee & Carlstead, 2010). For instance, orcas are the largest cetaceans held in captivity, with adult males ranging up to 9 meters in length and weighing close to 7,000 kg (Baird, 2002). Despite this, the United States Department of Agriculture's (USDA) minimum size standard for orca enclosures is 15 m for horizontal distance and 4 m for depth, severely limiting natural movements, postures, and behaviors (Joseph & Antrim, 2010; Rose et al., 2017).

Commented [A15]: 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.

Factors other than the amount of space can also affect cetacean welfare. Miller et al. (2021) found that type and timing of enrichment can sometimes be more important than tank size for captive bottlenose dolphins. Specifically, captive dolphins on a more predictable schedule of enrichment activities were more socially interactive than those on a random schedule. These interesting findings indicate that welfare in captive dolphins (and other cetaceans) is impacted by an array of interwoven factors.

Commented [A16]: 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.

A recent study of captive dolphin movement employed wearable tags to track activity and energy expenditure across several facilities (Lauderdale et al., 2021a). Lauderdale et al (2021a) found a positive relationship between scheduled enrichment sessions and "distance traveled" by the dolphins and only a weak association of dolphin swimming behavior with certain characteristics of their tanks. (Lauderdale et al., 2021a). However, the definition of "travel" under these circumstances is unclear, as the dolphins stayed in the same tank without the change in setting that the word "travel" implies. This measure may, therefore, more accurately be labeled as "movement" instead of "travel". Based on activity levels and energy expenditure data the authors concluded that management practices (e.g., environmental enrichment schedules) were more strongly related to activity levels than habitat characteristics (e.g., size of tank, water volume availability).

Commented [A17]: Which characteristics of their tanks are the authors referring to here?

Commented [A18]: The definitions of this are outlined in the abstract and are quite clear. “Overall dynamic body acceleration (ODBA), a proxy for energy expenditure, and average distance traveled per hour (ADT) of 60 dolphins in 31 habitats were examined in relation to demographic, habitat, and management factors”. This lack of clarity on the word “travel” does not emanate from the Lauderdale study itself.

Commented [A19]: Lauderdale et al uses ODBA as a proxy for movement. So this would not be correct.

3.1.b Complexity and sensory-perceptual experience

In captivity, sensory-perceptual experiences are largely determined by the physical features of enclosures, which are relatively limited and unchanging. Most captive cetacean tanks are painted

Commented [A20]: 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.

light or bright blue and designed to maximize the ability of visitors to observe them. Underwater windows, if present, may further decrease the opportunity for captive animals to find refuge from visitor gaze. To ensure ease of maintenance and cleaning, tanks have smooth surfaces and substrates and are relatively featureless as opposed to naturalistic textures (Couquiaud, 2005; Rose & Parsons, 2019). Water clarity and cleanliness is typically achieved through filtration, ozonation, and chlorination (Couquiad, 2005). Excessive chlorination can cause skin and eye problems in marine mammals (Gage & Francis-Floyd, 2018).

The acoustic properties of concrete tanks can be problematic for cetaceans, who are highly reliant on sound to perceive and navigate their environment. Persistent, anthropogenic noise from nearby construction, traffic or amusement park rides, if not dampened sufficiently, can increase stress and negatively impact welfare, i.e., increase levels of cortisol (Yang et al., 2021). Any sharp angles in a tank can cause potentially stressful reverberations (Wright et al., 2007; Monreal-Pawlowsky et al., 2017; Huettner et al., 2021).

3.1.c Sociality

Although there is variability across cetacean species in terms of level and type of sociality, the species usually kept in captivity (e.g., common bottlenose dolphins, orcas, beluga whales) are highly social. They have extensive juvenile periods during which they learn cultural practices within a complex social network that is maintained throughout their lives in the wild (Williams & Lusseau, 2006; O'Corry-Crowe et al., 2020; Whitehead & Rendell, 2021). Bottlenose dolphins can form nested alliances within complex social networks (King et al., 2018). Free-living orcas live in nested pods within clans that are bonded by dialect and other behavioral traditions (Williams & Lusseau, 2006). In the wild, beluga whales live in small groups that join, from time to time, with larger aggregations of hundreds or thousands of individuals. Adult females are strongly bonded with their newborns as well as with older offspring. These triads stay together and join with others to form large nursery groups. Generally, group composition is fluid and underwritten by complex vocalizations and a variety of other characteristics (O'Corry-Crowe, 2009).

Commented [A21]: What are the benefits of naturalistic textures? I would imagine fake rock work would also be for the guests rather than the animals.

Commented [A22]: Can you please highlight where this is a problem? Is excessive chlorination common in modern cetacean holding facilities? What would be excessive chlorination?

Commented [A23]: 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. The authors will later endorse the use of sea pen sanctuaries (defined as "authentic"). What acoustic conditions may await these animals in such environments? Will this be an improvement or a loss in welfare, and what data support the author's positions (or are needed to make this assessment)?

In captivity, by contrast, cetaceans live in managed collections that largely forgo opportunities for choice in relationships (Waples & Gales, 2002). Clegg & Butterworth (2017) noted that social group composition in captive facilities is largely artificial and under the control of zoo management rather than the animals themselves. Animal welfare scientists have stated that "keeping animals in appropriate social groupings, and with the required space and complexity to allow individuals to choose to spend time together or apart, is likely to be the most important welfare consideration" (Brando & Buchanan-Smith, 2018, p 85). After the minimum weaning age, captive cetacean mothers and offspring living in marine parks may be separated, as are other socially bonded individuals (Rose & Parsons, 2019). Because captive cetacean groups do not resemble the multi-generational, strongly bonded social groups in the wild, there is often no assistance (and sometimes even aggression) from tank mates during and after births, with potential longstanding repercussions for the psychological well-being of the calf (Snyder-Mackler et al, 2020). The limited space available to groups of captive cetaceans may also impact their ability to use dispersal to keep intra-group aggression to a minimum, but this possibility has not been systematically studied. Finally, although keeping individual cetaceans is a violation of the U.S. Animal Welfare Act, it has occurred in some captive facilities in North America (e.g., Miami Seaquarium) and in other countries (e,g., Marineland Canada).

3.1.d Feeding and cognitive demands

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

Dietary preferences and needs vary widely across cetacean species and across communities within species. For instance, southern resident orcas in the Pacific Northwest have a diet that consists of nearly 80% chinook salmon, depending on the season. The emphasis on chinook is not just a preference; it is a vital aspect of their culture (Hanson et al., 2021). Orcas off the coast of New Zealand, on the other hand, specialize in eating sting rays, requiring delicate and intricate processing before they are ingested (Duignan et al., 2000). Orcas can also eat highly varied diets,

Commented [A24]: Zoos are moving toward using playback preferences of familiar signature whistles as a tool to ascertain preferred social partners. Also much of this is informed in America by studies of wild cetaceans in Sarasota starting with Randy Wells' dissertation. So to characterize the managed populations as ecologically irrelevant or haphazard would not be accurate. https://sarasotadolphin.org/wp-content/uploads/2023/02/1986-Wells_PhD_Dissertation.pdf, Learning from nature: bottlenose dolphin care and husbandry https://onlinelibrary.wiley.com/doi/10.1002/zoo.20252

Commented [A25]: 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 [A26]: 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 cetacean's 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 [A27]: Multi-generational populations are not a rule. Nor are preferences for kin associations (see https://www.sciencedirect.com/science/article/pii/S0376635715300930?casa_token=qqfX_wvvHzkAAAAA:g7JA198MRbRNRj5czc4Y9tNOjTtluM7cSIWkOVymp9Z9Kn3IMPyA19ZjBwwe2JALdY2WqOibOJA, https://q.bstatic.com/data/bsuitewf/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 [A28]: 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 [A29]: How ubiquitous is this practice? In the cases cited here orcas were kept in mixed species habitats. If the authors feel that is not sufficient that should be highlighted along with their reasons why they have concluded this.

Commented [A30]: This is a good addition. The authors should also consider discussing Jaakkola, 2024 here as it also speaks to opportunities for cognitive enrichment.

sometimes including mammals, sea birds, and fish (Samarra et al., 2018). Other species, like common bottlenose dolphins, also have quite diverse diets (Gannon & Waples, 2004). Yet, captive cetaceans of all species are fed a narrow selection of commercially available dead fish and occasional invertebrates (Couquiaud, 2005). Although the fish are generally of high quality, they are delivered to them (i.e., thrown directly into their mouths above water) in a manner that requires little to none of the cognitive activity relevant in natural hunting and feeding. One ~~of the~~ reason~~s~~ for providing a limited selection and uniform delivery is to maintain records of how much each individual is eating, as appetite is an important indicator of health. It should be noted that even lagoon-housed dolphins may prefer the managed diet to hunting perhaps due to the paucity of proper prey species in the lagoon, and/or the presence of other forms of stimulation, or because they never learned how to hunt for food. It must be understood that animals are evolutionarily driven to seek the most accessible and abundant food resources for survival. However, the routine consumption of readily available food sources, such as occurs in fish provisioning, ecotourism, or in the captive setting, does not satisfy the biological drive to engage complex cognitive and physical faculties inherent in foraging or hunting. These activities present gratifying opportunities and challenges that are collectively enriching and consume a large percentage of cetaceans' time budget in the wild.

3.1.e Performances and Interactions with Humans

Many captive cetaceans are trained to perform behaviors related to both husbandry and entertainment and are required to interact with humans for, sometimes, many hours a day. Training 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). Some have argued that training and performance are a form of environmental enrichment for captive cetaceans (Westlund, 2014; Melfi & Ward, 2020). Fernandez (2022) found some evidence for this assertion in published research reports, but much more research is required to understand which components of either training or performance are indeed enriching rather than just providing temporary relief from boredom.

Commented [A31]: Again, this is a fairly old study and one would look to more modern papers to discuss diets. For example does the diversity of fish species presented to the dolphin who swallows its food whole and may or may not taste it matter? Given where life expectancies are for these animals I would say there is likely less of a health consequence. It is then incumbent on the authors to describe how a lack of fish diversity here has welfare consequences that can't be ameliorated with other non-food cognitive challenges. See Jaakkola, 2024.

Commented [A32]: It is observed that when swimming fish are put into exhibits where dolphins are unfamiliar with live fish a withdrawal reaction is common. Lagoon dolphins sometimes chase wild fish and rarely catch them. In mixed species habitats where fish can encroach into dolphin exhibits one typically knows they have a fish disease issue when the dolphins start catching them (given how poor zoo-housed dolphins are in catching live fish).

Commented [A33]: 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 [A34]: These statements need citations or data.

Commented [A35]: 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

There are no specific regulations that safeguard animal well-being in interactions with visitors (e.g., dolphin assisted therapy and other swim programs, petting pools, and public feeding activities; Spradlin et al., 1999; Stewart & Marino, 2009). Although limited regulations governing swim-with-dolphins (SWD) programs exist under the U.S. Animal Welfare Act, emerging evidence indicates that these types of interactions may lead to chronic stress for the dolphins. Some studies have suggested that —several factors may play an important role in cortisol (stress hormone) levels during these interactive programs (Matsushiro et al., 2021). One study in New Zealand found that common dolphins significantly increased their use of refuge areas when exposed to the public in SWD attractions (Kyngdon et al., 2003), suggesting these sessions may be aversive or stressful. More changes in behavior have been reported during unstructured or free-style SWD sessions compared to structured sessions (Samuels & Spradlin 1995; Brensing et al. 2005). Brando (2019) found that some dolphin behaviors change during swim sessions but that these changes may be due to the presence or absence of trainers or disturbances in the pool rather than due to the swim session itself. Therefore, although there are reasons to view interactions with humans - and in particular the public - as negative for captive dolphins, it is yet to be determined which specific components of those activities (and those before or after) are important factors in how dolphins react.

4. Current Welfare Issues

The welfare of cetaceans, as with any animal, is multidimensional; each factor involved in their overall well-being is intricately linked to several others. A deep understanding of captive cetacean welfare requires appreciating that many welfare problems, particularly health challenges that present a risk to welfare (e.g., infections, parasites, etc.) occur both in captivity and in the wild. But the critical point is that there are numerous known reasons for illness, injury, and mortality in the wild, including pollution, pathogens, predators, ships, noise, nets, and so on (Avila, Kaschner & Dormann, 2018; Sanganyado & Liu, 2022). None of these have any relevancy to the captive situation and, therefore, leave open the possibility that there are other factors (e.g., stress, novel pathogen and chemical exposure, neurobiological harm) unique to or exacerbated by captivity that contribute to poor welfare and death in captive cetaceans.

Commented [A36]: Do the authors wish to refine their year 2000 cut off date or redefine what they consider a foundational research publication?

Commented [A37]: Cortisol is not necessarily a bad thing. Eustress can also lead to an increase in cortisol.

Commented [A38]: This study shows very mixed results with fairly low sample sizes. More detail here would be useful.

Commented [A39]: 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 [A40]: This is a very old paper that probably had a lot to do with the fact that there are virtually no uncontrolled swim with programs practiced amongst accredited facilities.

Commented [A41]: 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.

Commented [A42]: 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 [A43]: Except when studied in comparative health assessments the captive animals serve reliably as the control for relatively sicker wild populations. The authors should consider Greg Bossart's work here. Furthermore, the authors will have a heavy lift suggesting that captive dolphins are less healthy than their wild counterparts as a rule.https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0176202, https://pmc.ncbi.nlm.nih.gov/articles/PMC6558379/, https://fau.digital.flvc.org/islandora/object/fau%3A5935,

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

4.1. Brain and Behavior

4.1.a. Stereotypies

One of the more widespread abberations found in captive animals is stereotypic behavior (Mason & Latham, 2004; Mason & Rushen, 2008; Bacon, 2018). When present, stereotypies reflect changes in the brain. The circuitry involved in motor control and stereotypies is complex but, at the neural center of this circuitry, is the basal ganglia (or corpus striatum), which are highly conserved across mammals, including cetaceans (Grillner & Robertson, 2016; Marino, 2022). Therefore, cetacean stereotypies, like stereotypies in other mammals, are not just behavioral issues, but also represent brain function abnormalities (Jacobs et al., 2021, for review).

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) Also found in captive cetaceans are circling and repetitive swimming patterns (Jett & Ventre, 2011; Ugaz et al., 2013). However, Miller et al. (2021) did not find a high rate of route tracing behavior (a form of stereotypical swimming) in the captive bottlenose dolphins they studied but rather a high rate of behavioral diversity, suggesting an inverse relationship between behavioral diversity and stereotypies.

Commented [A44]: 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 [A45]: Not referencing this paper is a significant omission https://www.mdpi.com/2076-2615/14/6/949

Commented [A46]: 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 [A47]: I would be much more specific here, especially when arguments from other species are used to justify conclusions in cetaceans.

Commented [A48]: 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.

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. Examples include constantly rubbing their skin on hard objects, resulting in 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 (The Orca Project). Regurgitation and reingestion, which develops in response to boredom, illness, social isolation/instability, and/or stressful training interactions (Walsh et al., 1996), is another stereotypic behavior exhibited, and sometimes even socially learned, by captive cetaceans (Yeater, 2005). On the other end of the activity spectrum are symptoms which may indicate depression (e.g., spending more time logging than usual, lying 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 resting individuals who are not necessarily depressed. These various factors are best interpreted in a more holistic way, such as assessing whether many different indicators of depression are present rather than just one. Captive facilities attempt to control or diminish stereotypies primarily through reinforcement of alternative behaviors, pharmacological treatment, or environmental enrichment, but none are completely successful (Mason et al., 2007). However, one study found that cognitive foraging enrichment led to reduced stereotypies and other abnormal behaviors (Clegg et al.,2023), suggesting that more complex enrichment formats anchored in more naturalistic behaviors may be more helpful than noncognitive forms.

4.1.b. Aggression

In free-living cetaceans, serious aggression towards members of one's family or social group is rare and kept in check by dispersal and other factors (Bisther, 2002; Towers et al., 2018). But conspecific aggression is not uncommon in tanks, where space is inadequate for dispersal and is shared by individuals who are not necessarily compatible (Frohoff, 2004; Evans, 2015; Ventre & Jett, 2015). Likewise, direct attacks on humans by orcas and belugas in the wild are unknown (Pagel et al., 2017) and there is only one record of a free-living bottlenose dolphin killing a human (who was abusing him; Santos, 1997). Nevertheless, there have been hundreds of aggressive acts by captive cetaceans towards humans (Lott & Williamson, 2017) and four human deaths by captive orcas (Parsons et al., 2012). Moreover, captive bottlenose dolphins and other

Commented [A49]: There are a lot of things that aren't observed in wild cetaceans. They are hard to watch 24/7.

Commented [A50]: I assume the authors are referring to Hugo. Much of these behavioral reports come from Richard O'Barry who is an unreliable narrator at best. https://www.dolphinproject.com/blog/one-dolphins-story-hugo/

Commented [A51]: 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.

Commented [A52]: 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 [A53]: That is a sampling bias given the proximity of dolphins in captivity to humans. These should not be evaluated as apples to apples comparisons.

cetaceans, especially those in petting and feeding sessions with the public and SWD programs, also have a long record of aggression towards humans, often resulting in severe human injuries (Shane et al., 1993; Spradlin et al., 1999; Vail, 2012; Anderson et al., 2016). Maternal rejection and aggression towards calves is also not uncommon in captive cetaceans (Rose & Parsons, 2019; Marino et al., 2020).

4.2 Physical health

4.2.a. Nutrition and metabolism

Many diseases in captive cetaceans are associated with metabolic syndromes believed to be linked to the captive diet (Rosen & Worthy, 2018). Captive bottlenose dolphins, for example, are prone to developing insulin resistance and fatty liver disease, similar to type-2 diabetes in humans (Colegrove, 2018). Captive bottlenose dolphins are also 15 times more likely than free-living dolphins to express elevated iron levels (a precursor to developing hemochromatosis), which can lead to liver, heart, and reproductive problems, as well as joint pain, increased cancer risks, and death (Mazzaro et al., 2012; Venn-Watson et al., 2012, 2013). Another condition likely related to the captive diet is hypocitraturia, which is characterized by low levels of citrate urinary excretion (Zuckerman & Assimos, 2009). This disease is four times more common in captive than in free-living bottlenose dolphins and promotes the formation of kidney stones, which can lead to serious complications such as renal failure and death (Venn-Watson et al., 2010).

4.2.b. Skin Health

Skin disease is common in captive dolphins, with the most prevalent being tattoo skin disease (TSD; black or grey stippling discoloration of the skin), caused by poxvirus, and diamond skin disease (slightly raised, rhomboidal grey patches), caused by the bacterium *Erysipelothrix rhusiopathia*. Skin diseases are also found in dolphins in the wild; for example TSD is associated with poor population health (van Bressem et al., 2008). Although poxvirus is associated with TSD lesions in bottlenose dolphins, the virus typically is expressed in individuals who are immunocompromised from stress or concurrent illness. Van Bressem et al. (2008) reported that 20.6% of the 257 bottlenose dolphins held in 31 U.S. and European facilities had tattoo lesions. When left untreated, active diamond skin disease lesions can progress to a serious and life-

Commented [A54]: I am not aware of any dolphin petting programs.

Commented [A55]: 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 [A56]: cf Jaakkola et al 2020 and Dudzinski, et al., 2021)

Commented [A57]: 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.

Commented [A58]: 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.

threatening zoonotic bacterial infection (Tryland, 2018; Lacave et al., 2019). However, it is also possible for cetaceans to develop sudden illness and death in the absence of obvious skin lesions. The causative organism is found on dead fish products, the main source of infection for captive cetaceans (Lacave et al., 2019). For this reason, Erysipelas is primarily a disease of captive cetaceans (Rosen & Worthy, 2018) and numerous deaths have been reported due to peracute septicemic *Erysipelothrix* infection (Van Bonn et al, 2007).

4.2.c. Dental Disease

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

Natural tooth wear may be associated with increasing age in free-living odontocetes (Perrin & Myrick, 1980; Ramos et al., 2000; Foote et al., 2009; Loch & Simoes-Lopes, 2013); however, advanced tooth damage in free-living orcas is rare. Moreover, tooth wear in orcas in the wild is related to specific ways some orca subtypes feed. For example, when evaluating the dentition of three orca ecotypes (i.e., Offshore, Transient, and Resident), Ford et al. (2011) suggested that the abrasive skin of sleeper sharks (*Somniosus pacificus*), a frequent prey of Offshore orcas but not the other two subtypes, was implicated in their pronounced dental wear.

Commented [A59]: And that is possible in the wild. What are the authors trying to claim here about cetacean welfare in captivity?

Commented [A60]: I would recommend having Dave Rosen and Geraldine Lacave look at this section.

Commented [A61]: To give a sense of the selective interpretation of these studies, and the heavy lift that the word "May" is doing here, this is the abstract from Loch and Simoes-Lopez, 2013. Abstract
(1) Dental wear is a common phenomenon in mammals. Its occurrence is influenced by tooth anatomy, animal physiology, biomechanics and behaviour. So far, investigations of dental wear in cetaceans have been scanty and superficial. We compare the frequencies of occurrence, location and intensity of dental wear in some species of dolphins from southern Brazil, South Atlantic Ocean. (2) Teeth of ten species were evaluated using a stereoscopic microscope to identify wear facets, which were classified according to location, anatomical position and wear intensity. **(3) Frequencies of dental wear were high for all species with exception of Delphinus capensis, with less than 50% of teeth worn.** Simultaneous wear facets in the apex and lateral of teeth were more common than facets restricted to the apex or lateral faces. Wear on the dental crown was more common, but some species showed less frequent wear down to the cingulum or root level. Superficial wear seems to be the general trend for dolphins, but Stenella coeruleoalba and Pseudorca crassidens showed a higher frequency of severe wear. Only for Tursiops truncatus the frequencies of wear were significantly different between males and females. When considering the ontogeny of dental wear, only for T. truncatus and Stenella frontalis indexes of dental wear were correlated with body length. (4) Whether dental wear has implications or not in fitness and feeding behaviour, severely worn teeth may expose the pulp cavity and increase the susceptibility to local infections.

Commented [A62]: This is not true from even the study the authors cited. https://pdf.sciencedirectassets.com/271218/1-s2.0-S0003996912X00141/1-s2.0-S0003996912002610/main.pdf?X-Amz-Security-Token=IQoJb3JpZ2luX2VjEHYaCXVzLWVhc3QtMSJHMEUCIEfbKMuRwp0ttYyvHay7EpaQjCBW9dk7%2F5q5dkSnWbzxAiEAh79Hrt7UYP5xsbeXovPM3%2FILS%2BIlJIOZ9yd84vd3mXXwqvAUI%2Fv%2F%2F%2F%2F%2F%2F%2F%2F%2F%2F%2F%2FARAFGgwwNTkwMDM1NDY4NjUiDHki3P1AqWKVPtf05iqQBR1QxzPBW8WcSVbrviRhCZU0%2FexE%2BJlWJbyr%2F74ZCpf8UFQSIsBP6b8MH9bdh4v7oSxME6RBhMxkgLUOXlu955cLaVCbr3mFDuDzoI9hhQl4XSW72jYRrSH3HO3tKm7c5pDi2DcrizjDDhu1qi2IPyH0QIn3JKrmncItB9gGO0nIpenTDOlPAOhMNooblLIpjinkvo28f%2BiYDLhPYTfNzzzlFEDz1HGW9B4d7KeU9shIDmQgx1mSL8kuH0RhSBRZNi9Eza7KwMzxj%2F17eMcyoapmD6GdOzs93puQ3RwcmCXFgP0lw7cnDDFW3TLi9olo1hzY83K2vvlb%2BRs8FDCKJrxjZbesxIHY9z9BHP4Cp2un5wpO51H61Lsd5TXgVU8jwO9o1TOXc%2FizwUAbEcG1VfLb74KIf8q8NjErpF%2BFlfk5yh4K3kUrbmzwynwDqEZMRLA4khOXzNuK1loZ3CgFLw8mDd0hHx90cz%2BmMic0a63ZA9uWtD4S0pYVunJHIthGFtpDAeILcrxHH2vOJdR8k0Udjja23sVlWERSkGBuL9KSD0lEUyudUHuj6YEydeLDQm51eMh7bWKLCLUnkfy48gMB2j%2FGuCKegfwNT0Fee321eZLqYDTun2VinMsVj3HlhKg6gbBCv%2Fi647LFliM9NGu%2FOWC27dTzIEuCk%2Bcgm33G1ZgzrLSs1HP4i2 ... [1]

Commented [A63]: These studies did not suggest that tooth wear in wild orcas is rare. In fact, new studies come out frequently highlighting new forms of tooth wear- even in orcas. https://link.springer.com/article/10.1007/s10914-022-09645-1

In an effort to avoid infection and health complications, captive orcas with damaged teeth often 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 from tooth damage, captive orcas are routinely treated with antiseptics and 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

Gastritis and gastric ulceration pose significant problems for captive cetaceans. Stomach inflammation and ulceration can be caused by the administration of non-steroidal anti-inflammatory drugs as well as prolonged stress and is often associated with the bacterium *Helicobacter pylori* (Nomura et al., 1994), which has been isolated in captive bottlenose dolphins (Segawa et al., 2020). *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., 2012). Also, repetitive regurgitation and reingestion can result in chronic irritation of the delicate mucosal surfaces of the esophagus from routine exposure to acidic stomach contents, leading to inflammation, corrosion, and even death (Walsh et al., 1996). Intestinal volvulus (an abnormal rotation of the intestine) is also found in free-living and captive cetaceans and is a common cause of mortality in both (Begerman et al., 2013).

4.2.e. Infectious Disease

Viral, bacterial, and fungal infections are found in both captive and free-living cetaceans with viral and bacterial pneumonia the most common causes of fatality in captive cetaceans (Kielty, 2011; Jett & Ventre, 2012). Pulmonary mycotic infection (fungal pneumonia) is also a frequent cause of death in captive and free-living cetaceans (Reidarson et al., 2018). At least 15 of the 22 orcas who died in U.S. marine parks between 1990 and 2010 succumbed to infectious and inflammatory diseases, including pneumonia, encephalitis, bacteremia, and leptomeningitis (Kielty, 2011). Other infectious diseases in captive cetaceans are related to behavioural dysfunctions. For instance, it has been suggested that the increased time orcas spend floating on the tank surface increases vulnerability to mosquito-borne infections, such as St. Louis

Commented [A64]: 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

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

Routine preventative administration of antibiotics and antifungals often causes an imbalance of microflora and resistance to the medicines themselves (Dold, 2014; Reidarson et al., 2018; Park et al., 2020). For instance, meticillin-resistant *Staphylococcus aureus* (MRSA) was reported in captive dolphins in two Italian facilities, with one dolphin in each facility dying from MRSA-linked septicemia (Gili et al., 2017). Another recent case demonstrated the presence of resistant *Morganella morganii*, a bacterium associated with fatal sepsis in human beings, in a captive bottlenose dolphin in South Korea (Park et al., 2020). *Candidiasis*, often observed in immunocompromised individuals, is increasingly prevalent in captive cetaceans (Reidarson et al., 2018; Ohno et al., 2019). Several other opportunistic infections (e.g., *Giardia* sp. and *Cryptosporidium* spp.) have also been linked to the captive environment (Koch et al., 2018).

4.2.f. Reproduction

Most cases of neonatal death in captive facilities occur in young females giving birth for the first time (Owen, 1990; Sweeney et al., 2010), which may be due to immaturity and lack of exposure to natural mother-calf relationships (i.e., factors particularly relevant to the captive situation). Female dolphins at SeaWorld facilities are often impregnated through artificial insemination (AI), an invasive and uncomfortable procedure that requires mild sedation so that semen can be deposited inside the reproductive tract through a catheter (Robeck et al., 2005; O'Brien & Robeck, 2006). AI often involves multiple attempts. In the common bottlenose dolphin, the conception rate after AI using frozen-thawed semen is 65-70% (Robeck et al., 2009). SeaWorld also employs AI to control the sex ratio of its captive dolphin population in favor of breeding females. Out of 30 such inseminations, 28 have resulted in females (Robeck et al., 2018).

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 lactation can occasionally continue for more than two years (O'Corry Crowe, 2009). Captive beluga reproduction has been a longstanding problem because of physiological and behavioral factors

Commented [A65]: 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 [A66]: 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

Commented [A67]: How is this assessed in cetaceans? I am unsure about the use of the word "uncomfortable".

(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 as well (O'Brien et al., 2008; Robeck et al., 2010).

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 (Killer Whale I NOAA Fisheries). 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; Robeck et al., 2015). Some studies suggest that captivity can contribute to reproductive abnormalities and infertility in orca whales. For example, Robeck et al. (2004) reported that captive male orcas have smaller testes, and lower sperm counts as compared to free-living males.

Commented [A68]: Does this have any actual consequence for reproduction?

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. 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.

Estimates for free-living bottlenose dolphins suggest a mean life expectancy of ~25 years (Sergeant et al., 1973; Wells et al., 2013) and a maximum of ~50-70 years (Wells & Scott, 2009). 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). Whereas life expectancy for captive bottlenose dolphins has increased over the years, there are several reasons that data from captive groups may not be comparable to those of the free-living-populations. For instance, data collection for free-living dolphins is not nearly as complete or continuous as it is in the captive setting. Moreover, when other parameters are examined, captive dolphins fare more poorly. For instance, mean survival time in captivity (for dolphins who live

more than one year) across 67 facilities in the U.S. and Europe has been estimated to be only 12.75 years, with mortality rate twice as high in captive bottlenose dolphins compared to free-living dolphins (Long, 2018).

For orcas, the mean life expectancy for females in the Pacific Northwest is -46-50 years, with a maximum of -80 years (Olesiuk et al., 2005; Ford, 2018). Mean life expectancy for males is -30 years but they may live to -60 years (Ford, 2018). In contrast, of the more than 200 wild-caught or captive-born orcas held since the 1960s, fewer than 15% have lived to age 30 (Rose & Parsons, 2019).

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

5. Environmental Enrichment

Whether zoos and marine parks can, in principle, provide for the needs of cetaceans is a question that has received increasing attention in the domain of environmental enrichment (Jacobs et al., 2021). The marine park industry was the first to recognize the difficulties cetaceans have in coping with the incongruity between artificial and natural environments (Swaisgood & Shepherdson, 2005; Morgan & Tromborg, 2007). Over the years, enrichment practices have improved in their effectiveness in diminishing abnormal stress-related behaviors (Perlado-Campos, 2017; Matrai et al., 2020). Still, much of the enrichment for captive cetaceans remains focused on the presentation of plastic or rubber floating objects that may arouse interest initially, but are quickly habituated to (Clark, 2013). Cognitive enrichment requiring more complex natural processing behaviors are not frequently employed but some studies suggest that, when they are, these may be more effective in eliminating stress-related abnormal behaviors than simple floating objects (Clegg et al., 2023).

Commented [A69]: 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 [A70]: Again we are told we can't compare spotty wild data to complete captive data. The authors need a consistent view on this.

Commented [A71]: 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.

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Commented [A73]: Pre 2000

Commented [A74]: 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.

Commented [A75]: Can enrichment take other forms? See Heather Browning argument. Also Lauderdale LK, Miller LJ. Common bottlenose dolphin (*Tursiops truncatus*) problem solving strategies in response to a novel interactive apparatus. Behav processes. 2019 Dec 1;169:103990. pmid:31678324

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Copious scientific studies have shown that an environment that affords complexity and change allows for the highest quality of welfare across most species (Jacobs et al., 2021). Consistent with this notion are studies that suggest that dolphins in captive environments with more natural elements (e.g., sea pens or netted off areas continuous with the ocean) are less stressed and display fewer behavioral abnormalities than those living in tanks. For instance, Ugaz et al. (2009) found that the same group of bottlenose dolphins engaged in more active swimming and less logging in open sea pens (with access to ocean and a more complex environment) than when they were in closed facilities with no ocean access. As noted previously, dolphins in closed artificial environments were also found to have higher salivary cortisol (stress hormone) levels than those in open sea pens (Ugaz et al., 2013). Moreover, dolphins transferred from concrete tanks to captive ocean environments spent less time in social interactions (Ruiz et al., 2009). The authors suggested this finding could be due to the significant increase in space available (the ocean habitat was approximately five times the size of the tanks) as well as the opportunity to explore other features of the natural environment, such as fish and other organisms who may be present (Ruiz et al., 2009).

Lauderdale et al. (2021b) found that dolphins in natural ocean facilities (netted off areas continuous with the ocean) spent less time swimming in the top third of the water column than those in tanks. The authors suggested that, among other reasons, dolphins in ocean facilities may spend more time deeper in the water column because of the presence of natural flora and fauna, especially fish, who enter and exit the area (Lauderdale et al., 2021b). The above studies, while far from conclusive, strongly suggest that there are welfare benefits to dolphins (and likely other cetaceans) of living in a more natural ocean environment - even when captive.

The current literature on environmental enrichment and welfare in cetaceans indicates that much more research is needed to determine if and how specific enrichment efforts can improve welfare with the caveat that certain aspects of enrichment (e.g., space) cannot reasonably be addressed in traditional captive facilities. The effects of environmental enrichment can only be fully understood by employing well-confirmed welfare tests (Brereton & Rose, 2023). To that end, there have been several advances in developing systematic evidence-based welfare and

Commented [A77]: This study implied that captive dolphins live in impoverished environments. That just isn't quantitively or qualitatively true. See Jaakkola, 2023.

Commented [A78]: 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.

Commented [A79]: But for a dolphin moving from a pool to a sea pen the experience may be very different.

Commented [A80]: 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 [A81]: 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.

enrichment assessment methods for captive cetaceans (e.g., Hoy et al., 2010; Lauderdale et al., 2021c; Clegg et al., 2023; Baumgartner et al., 2024). These are important and necessary steps towards understanding the effects of captivity on cetaceans. However, whereas some enrichment methods may appear to contribute to improved welfare, there is no evidence to suggest that currently employed methods allow captive cetaceans to actually thrive or that positive effects are maintained over the long term (Delfour et al., 2017).

Commented [A82]: It is unclear how Delfour et al is being used to justify this opinion.

6. Discussion and Conclusion

In this review, we have underscored concerns that are vital to captive cetacean welfare. For cetaceans, there is a significant mismatch between the captive and natural environments, which contributes to their difficulties coping with life confined to concrete tanks (Mason, 2010; Hosey et al., 2020). Additionally, the natural characteristics of cetaceans (e.g., their need for space, cognitive and social complexity, etc.) predict the welfare challenges outlined above (Clubb & Mason, 2007, 2010; Pomerantz et al., 2013; Hosey et al., 2020; Mellor et al., 2021).

Much of the literature we have cited acknowledges areas where further study is needed. But there are significant (practical) limits to the extent to which land-based entertainment parks can provide larger, more complex, and variable environments that would allow cetaceans to engage in a greater range of natural behaviors. Pierce and Bekoff (2018) point out that discussions of animal welfare in zoos and marine parks often center on incremental improvements while overlooking the fundamental issue of captivity itself: they fail to acknowledge the fundamental incompatibility between captivity and life in the wild.

From an ethical standpoint, the deeper question is whether cetaceans can truly thrive in captivity, rather than merely survive. Thriving goes beyond physical health or lifespan - it encompasses overall *quality* of life and well-being. This includes factors such as the ability to exercise autonomy (as highlighted in Vicino and Miller's, 2015, emphasis on choice and control) and engage in meaningful environmental challenges. Current evidence indicates that, although marine parks and aquariums can upgrade enclosures to offer some physical and behavioral benefit, they cannot replicate the conditions of a free-living life necessary for cetaceans to truly thrive. With few exceptions, captive cetaceans cannot be released into the wild because they lack

Commented [A83]: 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 specific enrichment opportunities currently offered. This is in light of this study https://doi.org/10.1371/journal.pone.0253732 as well as related studies in the Cetacean Welfare Study that highlight that the least predictive factors in cetacean welfare are space and whether or not the animals are in a naturalistic sea pen. The authors would be wise to consider the naturism fallacy in their assessment of the current state of welfare given the work of Heather Browning. https://www.heatherbrowning.net/uploads/1/3/0/1/130104617/browning_2019_natural_behaviour_preprint.pdf

basic survival skills. Therefore, there are limited ethical alternatives. One of the most promising options is sanctuary, ocean-based captive situations where cetaceans can receive human care while experiencing more space, autonomy, and choice in a natural environment with more complexity and dynamism. Authentic sanctuaries for other wild animals, such as elephants and great apes, report improved physical and psychological health in their residents after acclimating to their new sanctuary environment (Buckley, 2009; Derby, 2009; Grow, 2020). Authentic sanctuary settings are still captive environments, but, as opposed to zoos, marine parks, and other entertainment venues (as well as military and scientific settings) they are not driven by objectives that often compete with animal well-being and autonomy (e.g., visitor experiences, ticket sales, scientific studies, breeding through AI, etc.).

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

Commented [A84]: 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 as to the difficulties in particular supporting two belugas in Iceland under the care of the Sea Life Beluga sanctuary. While the lead author may believe strongly in this form of captivity, an objective even-handed assessment of sanctuaries is in the best interest of the readers. https://doi.org/10.3390/ani14020335, https://doi.org/10.3390/jzbg6010004

Commented [A85]: How exactly do these factors (specifically ticket sales) lead to negative welfare outcomes for cetaceans?

Commented [A86]: It also seems to me that the authors are under the impression that choice and control are not possible in modern zoo settings. Jaakkola 2024 clearly outlines how this could be implemented in current existing zoos. https://pmc.ncbi.nlm.nih.gov/articles/PMC10486360/#sec5-animals-13-02707.

Commented [A87]: 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 research from Clegg and others demonstrates that good welfare outcomes can be a consequence of the same types of interactions that are listed here as potentially antithetical to good welfare. https://www.mdpi.com/2673-5636/4/1/8, https://doi.org/10.1016/j.applanim.2018.01.015,

Commented [A88]: If you are going to discus sanctuaries it would be appropriate to discuss the challenges associated with them. Animals not responding well to them, noise, veterinary access. See https://www.mdpi.com/2673-5636/6/1/4, https://www.mdpi.com/2076-2615/14/2/335

Commented [A89]: incredibilly biased language.

Commented [A90]: That is not a consensus opinion and has not been demonstrated from the selective use of primary materials present in this paper.

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