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The harmful effects of captivity and chronic stress on the well-being of orcas (*Orcinus orca*)

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ABSTRACT

Orcas are large, deep-diving cetaceans who are known for their global distribution, wide-ranging behavior, intelligence, and social complexity. They possess one of the largest and most complex brains in the mammalian kingdom. However, they are the third most common species of cetaceans kept in aquariums and marine theme parks. Most spend many years, and sometimes decades, in captivity. At the time of writing, 60 individuals are held in concrete tanks globally. The scientific data on how both wild-caught and captive-born orcas fare in captivity are increasingly robust in demonstrating that they cannot thrive under artificial circumstances in concrete tanks. In captivity, orcas exhibit a wide range of abnormal behaviors and often die at an early age from infections and other health conditions that are uncommon in a wild setting. Though numerous papers and reports describe these adverse effects, they do not offer a clear and systematic explanation for why captive orcas suffer chronic stress and how it affects their well-being. We describe likely mechanisms for the high levels of morbidity and mortality in captive orcas, including the impact of chronic stress on physiology and illness. We conclude that orcas are poor candidates for maintenance in captivity and suggest that a radical shift is required in their treatment, to meet their complex needs.

Introduction

Orcas (*Orcinus orca*, also known as killer whales) are part of the worldwide commercial trade in cetaceans and are the third most commonly confined cetacean species after bottlenose dolphins (*Tursiops truncatus*) and beluga whales (*Delphinapterus leucas*). As of January 2019, 60 orcas were held in concrete tanks globally (www.orcahome.de/orcastat, last accessed 11 January 2019). A slight majority (56.7%) were born in captivity, and a further 26 were captured at a very young age; 18 of these captured animals were recently taken from Russian waters. Most of these individuals have spent years, and sometimes decades, in captivity (www.orcahome.de/orcastat).

Despite decades of advances in veterinary care and husbandry (Gulland et al., 2018), cetaceans in captive facilities (e.g., marine theme parks, aquariums, zoos) consistently display behavioral and physiological signs of stress and frequently succumb to premature death by infection or other health conditions. The breadth of available scientific data demonstrates that, by every appropriate metric, captive orcas do not fare as well as their free-ranging counterparts (e.g., Small and DeMaster, 1995; Woodley et al., 1997; Jett and Ventre, 2015; Robeck et al., 2015).

In this study, we summarize how orcas are especially vulnerable to the negative effects of the constricted artificial environments they experience in marine theme parks, aquariums, and zoos. First, we describe the complex needs of orcas based on their evolutionary history, brain anatomy, physiology, and cognitive-behavioral characteristics. Then we describe the morbidity and mortality patterns

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seen in captivity, as well as how these patterns are associated with a failure to meet the complex needs of this species. We conclude by describing mechanisms that could explain the relationship between conditions of captivity, stress, and the high rates of morbidity and mortality observed in captive orcas.

The basis for capacities and needs of orcas

Orca evolution and phylogeny

The evolutionary history of any species, including orcas, determines the kinds of adaptations that animal possesses. Orcas are members of the order Cetacea, which contains two modern suborders: Mysticeti (baleen whales) and Odontoceti (toothed whales, dolphins, and porpoises). There are six odontocete families, comprising approximately 80-85 species (Jefferson et al, 2008). The orca is the largest member of the odontocete superfamily Delphinoidea and the only member of the genus *Orcinus* (Dahlheim and Heyning, 1999). Globally, orcas are distinguished by different ecotypes (a reproductively isolated population of orcas distinguished by cultural traditions such as prey preference, foraging techniques, vocal dialect, and group size; Ford, 2009).

Modern cetaceans evolved from terrestrial ancestors into the semiaquatic Archaeoceti (“ancient whales”) in the Tethys Sea approximately 50-55 million years ago (Gingerich and Uhen, 1998; Fordyce, 2008). The first radiation was then replaced by the Neoceti (“new whales”) at the Eocene-Oligocene boundary (~35-23 mya) (Uhen, 2010; Geisler et al., 2011), who evinced the earliest detectable changes in cetacean brain size and structure (Marino et al., 2004a).

Orca neuroanatomy

As a group, modern cetaceans, and therefore orcas, possess the neurobiological foundations of complex psychology, emotion, and behavior: 1) large relative brain size, 2) an expanded neocortex, 3) well-differentiated cortical cytoarchitecture, and 4) an elaborated limbic system. These neurobiological and sensory characteristics act as a guidepost to the kind of environment orcas need to thrive. In addition to these general characteristics, the brains of orcas (and other cetaceans) exhibit more specific characteristics relevant to intelligence, awareness, and emotionality that are expected to affect their ability to adjust to living in concrete tanks.

Encephalization

Although absolute brain size is related to intelligence, relative brain size is considered a better predictor of cognitive capacity across species (Marino et al., 2004b). Relative brain size is typically expressed as an encephalization quotient (EQ) (Jerison, 1973), which represents the average brain size of a given species in comparison with other species of the same average body weight.

Odontocetes, and in particular Delphinoidea, are the most highly encephalized nonhuman taxonomic group known, with EQs ranging from 1.8 to 5.0—significantly higher, as a group, than any other species except modern humans. Orca EQ is approximately 2.2-2.3 (Marino, 1998, 2008; Ridgway et al., 2016), compared to human EQ, which is 7.0 (Marino, 1998). The brains of adult orcas weigh on average 6621 g (Ridgway et al., 2016), compared with the approximately 1300 g average human brain (Marino, 1998).

Cerebral expansion

The orca telencephalon is characterized by three elaborated concentric tiers of limbic, paralimbic, and supralimbic tissue. One measure of the profound corticalization of orca brains is that the cerebrum constitutes an average of 81.5% of the total brain volume, compared with an average of 76.2% for humans (Wright et al., 2016). As a result, the orca brain has been described as being more corticalized than the human brain (Wright et al., 2016).

In mammals, expansion of the neocortex, which is critical for higher-order functions, occurs through folding of the surface and is, thus, indexed by surface area. The modern cetacean neocortex is among the most highly convoluted of all mammals. Orcas are the most gyrencephalic of all mammalian species, including modern humans (Manger et al., 2012). Average cortical surface area in orcas, at 14,207 cm^2, is the highest of the cetaceans (Ridgway et al., 2016) and significantly greater than in humans (i.e., 1500-2000 cm^2) (Prothero and Sundsten, 1984). The “gyrification index,” which compares neocortical surface area to total brain weight, ranges from 2.4 to 2.7 for odontocetes, exceeding the value of 1.75 for modern humans (Ridgway and Brownson, 1984).

In addition to neocortical surface area, there are a number of other dimensions of the orca brain that serve as strong predictors of complex cognitive abilities. The anterior cingulate and insular cortices, the temporal operculum, and paralimbic regions (all situated deep within the forebrain) are well developed in orcas and other cetaceans (Jacobs et al., 1979; Marino et al., 2004b; Hof and Van der Gucht, 2007). The expansion of these areas in cetaceans is arguably associated with high-level cognitive and social functions such as attention, prediction, social awareness, and empathy (Allman et al., 2005; Hof et al., 2005). It has been suggested that the elaborated opercular region of the orca brain serves a similar function to the speech-related opercular region in humans (Marino et al., 2004b). Moreover, recent studies show that the anterior cingulate and insular cortices in larger cetaceans contain a type of projection neuron, known as a spindle cell or Von Economo neuron (Hof and Van der Gucht, 2007), which may be involved in social cognition (Allman et al., 2005) and adaptive intelligent behavior (Allman et al., 2005) in mammals. Although hippocampal volume in orcas is the smallest among cetaceans relative to brain size (0.4%), the reduction of this structure was apparently accompanied by the transfer of a number of hippocampal functions (memory, learning, and navigation) to other parts of the brain, such as the highly developed entorhinal cortex or cerebellum (Wright et al., 2016).

Some authors have suggested that odontocete brain size is driven by developmental prolongation as a response to the increased learning demands of living in complex social networks (Whitehead and Mann, 2000; Connor, 2007). Overall enlargement of the orca brain is associated with protracted prenatal and postnatal developmental periods, as it is in other mammals (Whitehead and Mann, 2000; Charvet and Finlay, 2012), characterized by long periods of maternal investment in offspring care and learning, thus selecting for complex social and cognitive abilities (Whitehead and Mann, 2000). The high EQs and well-developed brains of orcas exemplify the positive correlation between relative brain size and complexity, on the one hand, and social complexity on the other hand, found in a wide range of mammals (Marino, 2002; Reader and Laland, 2002; Byrne and Corp, 2004; Marino et al., 2007; Dunbar, 2009).

Finally, improved methods of cellular visualization and analysis reveal that the cytoarchitectonic patterns in cetaceans are far more varied and complex than previously thought (Hof et al., 2005). These cytoarchitectonic patterns, in addition to encephalization and neuroanatomical complexity, are also evidence of cetacean behavioral and social complexity (Hof et al., 2005).

The limbic system and emotional regulation

Evidence for orcas’ emotional complexity stems in part from neuroanatomical data. The mammalian limbic system is a set of brain structures involved in emotions, memory, and motivation. The richly interconnected components of this system include the amygdala, cingulate, hippocampus, hypothalamus, and related structures such as the putamen, caudate, and, perhaps, the thalamus (Stephani, 2014). Recent work on orcas has shown that "limbic functions" are well integrated with other cortical functions and emotional and cognitive processing are capacities that have coevolved. Therefore, emotions and forms of cognition in realms such as reasoning, learning, and abstraction are not independent of one another (Marino et al., 2004b; Morgane et al., 2005; Pessoa and Hof, 2015).

The limbic system of orcas has been elaborated into a neighboring region, for example, the paralimbic lobe, which forms a transition to neocortical functions. Though orca brains differ from other mammalian brains by having a proportionately small hippocampus—due to a lack of olfactory structures—other limbic structures, such as the amygdala, caudate, internal capsule, and thalamus, are well developed (Marino et al., 2004b). It has been argued that the highly elaborated paralimbic lobe replaced a number of hippocampal functions involved in emotion, as there are dense connections between the paralimbic cortex and core limbic structures (Marino et al., 2004b).

Sensory regulation

All odontocetes have well-developed auditory capacities that are used in a variety of ways, including for surveillance of the environment, detection of prey, and communication. Some cetaceans do lose hearing as they age (Ketten, 2004); presbycusis is common across the class Mammalia. However, in almost all other ways, cetaceans differ significantly from other mammals in how they sense, process, and use sound. In orcas and other echolocating cetaceans, sounds are received and conducted through the lower jaw to the middle ear, inner ear, and then to primary auditory centers in the brain. A fat-filled channel in the lower jaw serves to receive and conduct the sound waves (see Cozzi et al., 2016, for a detailed discussion). Odontocetes can hear sounds across a broader frequency range than most terrestrial mammals and their ability to echolocate is an integral part of their experience of the world (Madsen and Surlykke, 2013), generating a mental representation of objects and surroundings that is processed cross-modally, that is, across hearing and vision (Pack and Herman, 1995). As sound is transmitted efficiently in water, the large proportions of the auditory nerve coincide with the need for rapid sound uptake and processing (Ridgway, 1990).

In odontocetes, there are two primary auditory cortices. One is located in the suprasylvian gyrus along the vertex of the hemispheres, lateral and adjacent to the primary visual cortex (Popov et al., 1986). The other, recently discovered, exists in the temporal lobe (Berns et al., 2015). These two primary auditory regions provide evidence for a high reliance on complex acoustic processing in odontocetes.

Vision is also well developed in orcas and acuity is preserved above and below water (Madsen and Herman, 1980). Dolphins appear to perceive similar patterns in two-dimensional forms as humans do (Tomonaga et al., 2014), and they may possess some form of color vision (Davies et al., 2012). Delphinoids use sight for a range of purposes, from prey capture to social interactions (Blois-Heulin et al., 2012).

It is unclear to what extent orcas and other odontocetes possess smell and taste. They lack a vomeronasal organ and olfactory bulbs, yet olfactory reception genes, while reduced, are not absent (Kishida et al., 2007). Although no taste buds have been found, there is some behavioral evidence for the discrimination of some tastes (Nachtigall and Hall, 1984; Kishida et al., 2015).

Finally, somatosensory perception (sense of touch, pain, body position, temperature) is important for cetaceans in a number of contexts, including social contact. Cetacean skin is well innervated and, thus, quite sensitive to touch (Tyack, 2000). Touch plays an important role in social bonding, sexual encounters, maternal care, and other affiliative—and even aggressive—contexts (Connor et al., 2000; Dudzinski et al., 2010).

Orca psychology: cognitive, emotional, and social behavior

Because psychological, behavioral, and ecological characteristics determine how well members of any species (individual differences notwithstanding) adapt to artificial settings (Mellen and MacPhee, 2001; Clubb and Mason, 2003), it is important to consider the psychological qualities of orcas, including self-awareness, emotions, social complexity, and culture.

Self-awareness

Self-awareness, the ability to conceive of and think about oneself, that is, an autobiographical "me," is part of subjective experience, also referred to as phenomenology. Orcas have demonstrated several abilities indicative of self-awareness. These abilities include imitation, which requires an understanding of the relation between one's own and another's body. Orcas have demonstrated the ability to imitate the novel actions of conspecifics (Abramson et al., 2012). Another is mirror self-recognition, that is, the ability to use a mirror to investigate one's own body. In a study of their responses to mirrors, orcas show contingency checking behavior—a correlate of self-directed responses exhibited by most individuals who demonstrate mirror self-recognition (Delfour and Marten, 2001).

Emotions

Observations of orcas reveal that they experience deep emotions and strong social attachments. These observations include reports of long-range contact calling when separated from others, grieving behaviors, and helping (epimeletic) behaviors. In addition to assisting individuals in distress, epimeletic behavior often involves adult individuals attending to a dead individual by keeping them afloat, lifting or pushing the individual, performing attempts that look like "resuscitation," and carrying them around by the mouth or on the body (Bearzi et al., 2018). These types of behaviors have been characterized by scientists as expressions of bereavement or concern about the breaking of strong social bonds (Bearzi et al., 2018).

Almost all reports of cetaceans responding to dead or injured individuals have come as opportunistic observations in the wild, as there would be no way to ethically study this behavior experimentally. The longest and best documented example of this type of bereavement behavior in a free-ranging orca was during July through August 2018 in the Salish Sea off the coast of Washington State (USA). A 20-year-old orca known as J35 or Tahlequah gave birth to a female calf who died within 30 minutes. The calf was carried on J35's back, rostrum, and in her mouth for 17 days. When the body slipped off, she retrieved it. Other members of the pod, particularly her 8-year-old son, were also observed carrying the dead calf. Members of her pod may have shared food with her during the ordeal, as she was not observed feeding on her own (Mapes, 2018; NOAA Fisheries, 2018; Figure 1, Supplemental Material).

Also in the Salish Sea, an adult male, an adult female, and two younger orcas were observed after one of the juveniles was hit by a ferry. The juvenile had visible lacerations attributed to propeller strikes and was bleeding profusely. The adults supported the injured juvenile by "cradling" this individual between them. Fifteen days later, in the vicinity of the boat strike, two orcas were observed supporting a third, presumed to be the same juvenile, although it is unclear if the juvenile survived the trauma (Ford et al., 1994a).

Epimeletic behavior in orcas is not limited to dead or injured individuals. For example, there are multiple accounts of physical support by others during entanglements, including one example in September 2014 off the coast of New Zealand when a female was supported by her two most recent offspring, with a third (her eldest, an adult male) nearby (Visser, unpublished data; Figure 2, Supplemental Material). "Standing by" has also been documented in a number of instances during strandings of orcas around the New Zealand coastline where orcas who were not stranded have remained in close proximity to those on the beach, at times risking stranding themselves (Visser, unpublished data).

Social complexity, culture, and behavioral ecology

Orcas are a cosmopolitan species and the ocean's apex predator. They feed on a large variety of aquatic species (Baird, 2002), although distinct populations tend to specialize on specific prey types (Rendell and Whitehead, 2001; Song, 2018). Orcas, when not foraging or hunting, often travel by swimming in a consistent direction at a steady pace and frequently engage in synchronized dives (Ford, 2009), suggesting an important social or ecological purpose for traveling independent of locating food. One population of orcas has been measured traveling at a rate of over 20 km/hr (Ford, 1989). Depending upon the population and hunting practices, orcas routinely swim tens of kilometers a day in a straight line (Visser, 1999b; Dahlheim et al., 2008; Durban and Pitman, 2011; Matthews et al., 2011; Fearnbach et al., 2014). Maximum daily distance has been measured at 252 km (Matthews et al., 2011) with maximum sustained distances of 160-225 km/day for up to 40 days (Durban and Pitman, 2011; Matthews et al., 2011). In addition, relatively high sustained speeds (3.7 ± 0.2 m $s-1$) for up to 30 minutes (Guinet et al., 2007) have been recorded for the species.

Although there is substantial variation in the depths to which different orca populations, ecotypes, and individuals dive, there is ample evidence for routine deep diving in the species globally. In some populations, individuals dive in excess of 750 m several times a day (Towers et al., 2018), others 200 m several times a day (Reisinger et al., 2015), while yet others dive deeper than 150 m at least once every 5 hours (Baird et al., 2005). The current maximum depth recorded is 1087 m, for a female (Reisinger et al., 2015).

Free-ranging orcas live in highly complex societies with long juvenile periods and differentiated relationships, embedded in complex social networks that rely upon learning and memory (Baird, 2000; Williams and Lusseau, 2006). Orca social life within ecotypes is strongly characterized by cultural traditions, that is, distinctive learned behaviors passed down from one generation to the next, which differ across groups and are underwritten by sophisticated social learning capacities (Whitehead, 2008). Such culture provides a way for individual whales to express their identity and benefit from the support of others in their group throughout their lives. Some orca cultural traditions are exemplified by different learned foraging strategies and other forms of cooperative behaviors (Rendell and Whitehead, 2001). Orca foraging is often accomplished through specialized, learned tactics. For example, mammal-eating orcas typically hunt in small groups and often remain silent to better detect and, possibly, surprise their prey (Barrett-Lennard et al., 1996). In the Antarctic, one population of orcas locates seals hauled out on ice floes and dislodges them by grouping together and rushing the floe, creating a wave that washes the seal into the water (Smith et al., 1981; Visser et al., 2008; Pitman and Durban, 2012). Orcas at Punta Norte, Argentina, hunt sea lion and elephant seal pups by beaching themselves and capturing the pups, typically in the surf zone (Lopez and Lopez, 1985). A similar behavior is observed in the Crozet Islands, where orcas hunt elephant seal pups (Guinet and Bouvier, 1995). In both locations, adults appear to actively teach this technique (which is dangerous as it can lead to stranding) to juveniles (Lopez and Lopez, 1985; Guinet and Bouvier, 1995).

Another component of orca culture is vocal dialects (Ford, 1991; Yurk et al., 2002; Ford, 2009), which are learned variations in the structure of vocalizations among animals who live sympatrically and come into acoustic contact. Dialects form the basis of vocal clans, developed through social learning. For instance, dialect similarity is related to group closeness; it decreases as one compares matrilineal groups within pods (extended families of closely related mothers who are daughters, sisters, or cousins, and their offspring), pods within clans (pods that share common calls), clans within communities, and communities (Deecke et al., 2000; Ford et al., 2000; Yurk et al., 2002).

Vocal learning in cetaceans reflects the same process by which human languages develop and evolve (Janik, 2014). It is based upon mimicry and requires excellent long- and short-term memory and the ability to learn from social feedback. Young orcas acquire their repertoire of sounds from their mother and other close family members, and they learn to selectively identify the calls of outside groups (Deecke et al., 2010; Crance et al., 2014). Vocal learning requires a substantial degree of social awareness and forms an important component of orcas' multiple cultural traditions, as well as their identity and sense of security and cooperation in a social group, as it does in many other highly social mammals (Cohen, 2012). In general, their acoustic capacity is central to their lives; they navigate, find prey and mates, maintain social bonds, and generally process the details of their surroundings using sound as much as, or instead of, light (Couquiaud, 2005; Parsons, 2013, for reviews on odontocete hearing and use of sound).

Morbidity and mortality of orcas living in captivity

Causes of illness and death

A 1979 review of the causes of death of 17 captive orcas in North America who had died since 1965 revealed that infectious diseases were the primary cause of death (Ridgway, 1979). This situation remains largely unchanged today. Published statements and records from the media, the US National Marine Mammal Inventory, and USDA Inspection Reports obtained under public records law demonstrate that, between 1971 and 2017, there have been 35 documented orca deaths at SeaWorld facilities alone (Kielty, 2011; Robeck et al., 2015; Aiello and Moses, 2016; Rose and Parsons, 2019). When causes of death were available, the most commonly implicated conditions were viral, bacterial and fungal infections, gastrointestinal disease, and trauma (Jett and Ventre, 2012). Despite veterinary care and therapeutic intervention, at least 15 of the 22 orcas who have died in US marine theme parks between 1990 and 2010 succumbed to infectious and inflammatory diseases, including eight who reportedly died of pneumonia; three of encephalitis; three of bacteremia; and one of leptomeningitis (Kielty, 2011).

Many of the infections captive orcas succumb to are opportunistic infections, that is, infections by pathogens that are usually harmless but can cause disease under certain unnatural, unhealthy, or compromised conditions. These include a weakened immune system (see below for the effects of stress on the immune system), chronic exposure to chemical irritants or trauma to the skin, excessive or improper use of antimicrobials, and an imbalance in the microbiota of the body or environment (which may exist in tanks) (Reidarson et al., 2018).

Jett and Ventre (2011) found that another common cause of death of captive orcas was gastrointestinal ulceration. Gastric ulceration is often caused by prolonged stress, as well as being associated with the bacterium *Helicobacter pylori* (Nomura et al., 1994). Gastric disorders such as ulcers have also been associated with behavioral stereotypies in other captive animals (Nicol et al., 2005; Moeller et al., 2008).

Although unreported (and unlikely, due to their kinetic nature and time spent below the surface) in free-ranging orca populations, mosquito-transmitted diseases have killed at least two captive orcas in marine theme parks. A 25-year-old male orca died suddenly in 1990 at SeaWorld Orlando of St. Louis encephalitis (Buck et al., 1993). And a 14-year-old male orca died without prior signs of illness in 2007 at SeaWorld San Antonio and necropsy results confirmed the presence of West Nile Virus in the brain tissue (St. Leger et al., 2011). Jett and Ventre (2012) advanced the hypothesis that frequent "logging" (hanging motionless on the surface of the water), which is commonly seen in captive orcas, left them more vulnerable to mosquito bites and increased their risk of contracting mosquito-carried viral diseases (Jett and Ventre, 2012).

Pulmonary mycotic infection (fungal pneumonia) is one of the most common causes of death in captive and free-ranging orcas and other marine mammals (Reidarson et al., 1999, 2018; Robeck and Dalton, 2002). *Candida* sp. is one of the most common organisms to cause infection in cetaceans and is on the rise (Ridgway, 1979; Reidarson et al., 1999, 2018), potentially as a result of long-term and aggressive antibiotic treatment (Dold, 2015), overtreatment of water for purity, or both (Medway, 1980). Cases of Zygomycetes infection and fatalities have also been recorded in captive orcas and other marine mammals (Robeck and Dalton, 2002; Abdo et al., 2012; Reidarson et al., 2018). The rise in fungal infections in captive marine mammals may be due to the development of resistance from increased use of antifungal medications, among other factors (Reidarson et al., 2018).

Survivorship and longevity

One set of metrics for comparing captive versus free-ranging animal well-being is life history parameters, such as survivorship and lifespan. Most of the information about the life history of orcas derives from long-term studies of resident ecotype populations in Washington state, British Columbia, and Alaska (Olesiuk et al., 1990; Ford et al., 1994b; Olesiuk et al., 2005; Ford, 2009; Matkin et al., 2014). Life history parameters for other ecotypes and populations around the globe may vary.

In natural settings, both sexes of orcas reach sexual maturity at 12-15 years of age. Females give birth approximately every 5 years and experience reproductive senescence at approximately age 40 (Ford, 2009; Foster et al., 2012a; Matkin et al., 2014; Brent et al., 2015). Females live an estimated maximum of 80 to 90 years and males an estimated maximum of 60 to 70 years. The mean life expectancy for free-ranging orcas is 46 years for females and 31 years for males (Olesiuk et al., 1990, 2005). Calves are weaned at one to two years of age, but nurse opportunistically for two to three years longer, or possibly more (Ford et al., 1994b; Newsome et al., 2009).

Before 1992, survivorship rates revealed that, despite provisioning and care, captive orcas clearly did not live as long as free-ranging orcas (Small and DeMaster, 1995; Woodley et al., 1997). Between 1992 and 2014, husbandry methods continued to evolve and a growing proportion of the captive population was captive-born. In 2015, two papers revisited survivorship and lifespan in captive orcas.

Jett and Ventre (2015) evaluated a database that comprised captive orcas held in facilities in the United States and those in foreign countries that send or receive animals to/from the United States ($N = 201$). Their primary goal was to assess changes in the captive population, rather than to compare captive and free-ranging populations. They found that orcas who entered US facilities after 1985 (primarily through captive birth) survived better than those who entered captivity before 1985, which they attributed generally to improved husbandry and the growing proportion of captive-born animals in the sample. However, while survivorship in US facilities has improved over time, they noted that survival to sexual maturity and reproductive senescence remained poor compared to free-ranging orcas.

A separate analysis by Robeck et al. (2015) focused exclusively on a subset of the captive population; whales held by SeaWorld Inc. The authors also found that annual survivorship rates had improved when compared to previous years. However, they also calculated an average life expectancy for captive-born orcas that was invalid. The equation they used to calculate the value, $-1/\text{Ln}(\text{annual survival rate})$, would only be valid if survival is constant from year to year and over all age classes (DeMaster and Drevenak, 1988). Yet they determined that annual survival rate improved over time, violating the first assumption. In addition, survivorship rates in orcas decline with age (DeMaster and Drevenak, 1988; Matkin et al., 2014) and is generally lower in calves (Olesiuk et al., 1990; Ford, 2009; Robeck et al., 2015), violating the second assumption. DeMaster and Drevenak (1988) specifically cautioned against using annual survival rate to calculate life expectancy for these and other reasons. Robeck and colleagues also lowered the maximum estimated lifespan in free-ranging orcas by excluding all whales in the Pacific Northwest populations whose exact age was unknown (i.e., those who were older than one year of age when the study began in 1973) (Robeck et al., 2015).

Abnormal behavior as a contributor to morbidity and mortality

Captive orcas exhibit a range of abnormal behaviors, *inter alia* hyperaggression, stereotypies, self-harming, rejection of offspring, and failure to nurse, which may contribute to morbidity and mortality.

Hyperaggression

Captive orcas exhibit a range of hyperaggressive abnormal behaviors (toward conspecifics and humans). Such aggression by captive orcas may be one of their most consequential social behaviors (Graham and Noonan, 2009). It has been documented since the early days of the captivity industry (Burgess, 1968; Martinez and Klinghammer, 1978) and has continued (Anonymous, 1989; Graham and Noonan, 2010; Cornell, 2011; Visser, 2012; Sánchez Hernández and Molina Borja, 2013; Ventre and Jett, 2015; Anderson et al., 2016; Visser, 2016; Visser and Lisker, 2016; Jett et al., 2017). Although free-ranging orcas do have conspecific aggressive encounters, these appear to be rare events and typically involve behavior that results in the displacement of others with limited (Visser, 1998) or no physical injury (Bisther, 2002); however, the first account of infanticide in free-ranging orca was recently documented (Towers et al. 2018). The only other recorded orca fatality from intraspecific aggression involved two females in captivity (Anonymous, 1989; Reza, 1989; Mooney, 1998).

In addition, there are no reliable reports of free-ranging orcas killing a human being, despite centuries of encounters in the wild, including decades of in-water research (Visser, 1999a, 2000, 2005b) and in-water tourism (Pagel et al., 2017). However, in the 55 years since captive display of orcas commenced, captive orcas have killed four human beings (three trainers and one member of the public) and seriously injured many more (Parsons, 2012; Wise, 2016).

In the wild, there is room for dispersal and avoidance behavior (Baird and Dill, 1995). Therefore, conflicts rarely escalate into serious or injurious attacks. In the confined space of concrete tanks, the whales are also held in artificially created "social groups," both of which stymie the natural strategies orcas use in the wild to avoid escalation of aggression.

Self-harming in free-ranging orcas is undescribed in the scientific literature, but there are numerous examples of captive orcas engaging in self-injurious behaviors, such as banging their heads against the sides of their tanks or against the separation gates (Visser and Lisker, 2016; Pollard, 2019), actively exiting the tank onto ledges for sustained periods to avoid aggression (Visser and Lisker, 2016) and refusing to eat (Hoyt, 1984; Romanov et al., 2015).

Oral stereotypies and dental disease and injury

One of the more common behavioral abnormalities found in captive animals across a wide range of species is stereotypy. Stereotypies are associated with psychological stress and generally with poor well-being (Mason and Latham, 2004). There have been numerous reports of oral stereotypies in captive orcas, including biting and chewing on hard tank surfaces, hard toys, and the steel gates used to separate the whales (Graham and Dow, 1990; Jett and Ventre, 2012; Visser, 2012; Ventre and Jett, 2015; Almunia, 2017). These behaviors lead to extensive and chronic dental pathologies (Almunia, 2017; Jett et al., 2017). In the study by Jett et al. (2017), all the subjects exhibited dental injury (N = 29), with up to 75% of their teeth showing signs of damage. Visser and Lisker (2016) reported up to 10 broken mandibular teeth on one individual (see Supplemental Material, Table 1 for details).

Much of the risk for infectious disease in captive orcas can be explained by its association with poor dental health, which provides a pathway for pathogens to enter the bloodstream (Li et al., 2000). An explanation for the link between dental wear and pathology and infectious systemic disease in orcas has been offered by Graham and Dow (1990), in their description of one ill individual. They reported that chewing on tank surfaces by the orca resulted in dental disease affecting the gingiva and pulp cavity, with necrotic, infected, or hyperplastic exposed dental pulps. The authors reported that the animal was also lethargic, was leukocytic, and suffered a risk of ensuing osteomyelitis, gingival cellulitis, and systemic infection.

Although significant dental wear is found in free-ranging orcas, it is typically isolated to those populations who have very specific feeding habits, including targeting certain prey with abrasive skin (e.g., sharks) (Ford et al., 2011) or feeding using suction (Foote et al., 2009). However, it should be noted that other populations that feed extensively on elasmobranchs (e.g., Visser, 2005a) do not have similar dental wear (Visser, 2005b). Regardless, extensive tooth deterioration in free-ranging orcas is ecotype-specific. In populations that do not have implicated feeding habits, dental wear is mild to nonexistent and dental fracture is rare (Foote et al., 2009; Ford et al., 2011; Jett et al., 2017).

In captivity, orcas are fed exclusively a diet of dead fish and squid, as well as gelatin (to minimize dehydration), often dropped directly into the back of the oral cavity and swallowed, requiring little to no contact with or manipulation by the teeth. Nevertheless, over 60% of captive orcas in the United States and Spain had fractured mandibular teeth and 24% exhibited “major” to “extreme” mandibular coronal tooth wear down to the gingiva (Jett et al., 2017).

In order to treat abscesses and drain debris and pus from the tooth cavity, most captive orcas undergo a modified pulpotomy procedure that subsequently requires daily flushing (Ventre and Jett, 2015; Jett et al., 2017). In addition, teeth may have to be extracted (Jett et al., 2017). Dental pathology in captive orcas also requires routine treatment with antiseptics and antibiotics. Chronic antibiotic use, however, may result in drug-resistant pathogens (Davies and Davies, 2010; Dold, 2015) and altered immune system function (Yang et al., 2017). Chronic antibiotic use has also been associated with disruption of intestinal flora (Kilkkinen et al., 2002; Croswell et al., 2009) and some forms of photosensitivity/toxicity (Gould et al., 1995; Karagas et al., 2007; Jett and Ventre, 2012) and ototoxicity (Grill and Maganti, 2011).

After tooth extraction, or chronic infection, or disease of the soft tissues in or around the mandibles from infections of the teeth (that can extend into the surrounding structures), remodeling of the bony architecture of the mandible may occur. One could speculate that gross changes to the structural integrity of the mandible may have an impact on how the individual can process incoming echoes during echolocation.

The association between stress, disorder, and death

Importantly, the poor health and short lifespans of captive orcas are most clearly understood as connected elements in a cycle of maladaptiveness to the conditions of captivity that involves behavioral abnormalities, physical harm and vulnerability to disease.

Defining stress

Most definitions of stress are rooted in the foundational concept of homeostasis and the ability of an organism to adapt to various circumstances (Selye, 1976). Homeostasis refers to a dynamic state of psychological and physiological equilibrium in which vital somatic and psychological parameters are maintained in a range that is optimal for well-being (McEwen, 2000; Sapolsky, 2004). All animals have evolved to be adapted to their natural environments (or, more precisely, their ancestors’ environments) (Tooby and Cosmides, 1990; Panksepp, 2010). The entire suite of dynamic homeostasis-maintaining mechanisms is termed allostasis (Sterling and Eyer, 1988; McEwen and Wingfield, 2003, 2007) and the type, duration, and magnitude of the stress response contributes to allostatic load, which has consequences for health and well-being (McEwen and Wingfield, 2007; McEwen and Rasgon, 2018). The brain is directly involved in an organism’s ability to detect deviations from homeostasis and correct them with a range of defenses, including cognitive and emotional responses (McEwen, 2002; McMillan, 2005; Wemelsfelder, 2007; Panksepp, 2010).

Many stressors are short-lived and addressed through biological adaptation. The stress responses to these acute situations may be beneficial to the organism, permitting an appropriate response to the stressor (e.g., flight from a predator) and a return to homeostasis once the stressor is no longer present. Other stressors are severe, repetitive, chronic, or outside of the adaptive capabilities of an organism. These types of stressors contribute to a constantly high allostatic load and therefore have serious consequences for health and well-being (Juster et al., 2010; McEwen, 2017).

The HPA axis

When the brain detects a threat, a coordinated physiological response involving autonomic, neuroendocrine, metabolic, immune, and behavioral factors is activated, largely dependent upon the hypothalamus-pituitary-adrenal (HPA) axis. (There are also other cellular and neural responses that are not HPA dependent but play a role in stress.) Corticotrophin releasing hormone is released from the hypothalamus, causing the release of adrenocorticotrophic hormone from the pituitary gland and the release of glucocorticoids from the adrenal gland. The main glucocorticoid involved in this response is cortisol (Lupien et al., 2009). Cortisol increases blood sugar through gluconeogenesis, suppresses the immune system, influences the metabolism of fat, protein, and carbohydrates, and affects blood pressure regulation. It also has central nervous system effects. Mineralocorticoids are also released during the stress response and these play an important role in the maintenance of electrolyte balance. Prolonged exposure to increased levels of mineralocorticoids can lead to detrimental changes in arterial pressure and other aspects of fluid retention in marine mammals (Atkinson et al., 2015). Although the HPA axis is critical to survival, its chronic activation and dysregulation can be detrimental to health and well-being (Sapolsky et al., 2000).

Chronic stress can occur if acute stressors become frequent, repetitive, or prolonged in duration or intensity, causing either desensitization to the stressor or, in many cases, sensitization so that organ systems eventually degrade. As a result, individuals become increasingly vulnerable to morbidity and mortality (Buwalda et al., 2005; McMillan, 2005; McEwen, 2017). As Atkinson et al. (2015) state, "The type, magnitude, and duration of a stress response have a cost to the animal… when stressors are chronic or severe, the accumulated costs associated with the response(s) become an allostatic overload, which can contribute to physiological dysfunction and increase the probability of disease and other pathologies" (p.464).

In addition to an overload and eventual dysregulation of the immune system, chronic stress has profound effects on brain structures, specifically the hippocampus, amygdala, and prefrontal cortex. In turn, these altered brain structures impact the HPA axis and general stress response:

> The brain is the organ that determines what is novel and possibly threatening and therefore "stressful" and it orchestrates the behavioral and physiological responses, whether health promoting or health damaging. And the brain is a biological organ that changes in its architecture and its molecular profile and its neurochemistry under acute and chronic stress and directs many systems of the body—metabolic, cardiovascular, and immune—that are involved in the short- and long-term consequences of being "stressed out" and the consequent health-damaging behaviors (McEwen, 2017, p. 2-3).

The hippocampus is involved in episodic and spatial memory and mood regulation. It is also a gateway to the way the brain responds to stressors. Substantial evidence shows that sustained glucocorticoid, for example, cortisol, release leads to shrinkage of hippocampal neurons and loss of dendritic spines (McEwen, 2016). Similarly, the amygdala is involved in fear responses and emotional regulation and is strongly affected by chronic stress, with the basolateral region responding with an increase in dendrites (Vyas et al., 2002), and the medial amygdala showing shrinkage and loss of dendrites (Bennur et al., 2007; Lau et al., 2017).

The long list of emotional, psychophysiological, and behavioral changes associated with these neurological alterations, in humans and other mammals, includes increased anxiety, posttraumatic stress, cognitive impairment, depression, and mood dysregulation (Buwalda et al., 2005; McEwen, 2006, 2017; Lupien et al., 2009). Within the prefrontal cortex, chronic stress causes debranching of medial prefrontal neurons and shrinkage of dendrites, which may be related to cognitive rigidity and loss of attentional control in humans and other animals (Liston et al., 2006). In addition, orbitofrontal cortical neurons expand dendrites that may be related to increased vigilance and sensitivity to fear-inducing stimuli (Radley et al., 2004). Moreover, both acute and chronic stressors that occur early in life have an important impact on an individual's ability to cope with stressors later in life (McEwen, 2017).

The HPA axis and its effects are highly conserved across mammals (Morgan and Tromborg, 2007; Lupien et al., 2009). Orcas and other cetaceans share brain mechanisms with other mammals, which are involved in mounting a stress response and adhere to the classic HPA model (see Atkinson et al., 2015; Atkinson and Dierauf, 2018 for reviews, Thomson and Geraci, 1986; Romano et al., 2002; Houser et al., 2011; Fair et al., 2014; Levin, 2018). Maladaptive stressors—*inter alia*: confinement; sensory overload in the form of abnormal and excessive sounds while, at the same time, sensory deprivation due to static and barren environments; abnormal social situations; loss of control and autonomy; boredom—can lead to dysregulation of the HPA axis and related health effects. Numerous factors contribute to the chronic stress experienced by orcas in concrete tanks, including the following more salient contributors.

Social stress

Sociality and social intelligence evolved as a selective advantage that confers enhanced fitness to individuals (Silk, 2007). Indeed, animals living in complex social systems may benefit from, *inter alia*, enhanced predator surveillance and avoidance, cooperative foraging and hunting, enhanced reproductive opportunities, or cooperative rearing of their young (Silk, 2007).

Furthermore, the ability to engage in social learning through complex forms of communication allows for the horizontal transmission of culture in animal societies, which may promote survival and adaptation to changing environments (Whitehead et al., 2004). Thus, the evolution of sociality and accompanying emotional complexity are intimately tied to survival, which helps explain why social animals expend tremendous energy to establish and maintain healthy social networks and why they pay such an enormous cost when denied the ability to form species-appropriate social bonds (Silk, 2007).

As highly social animals, orcas depend upon healthy and robust social relationships for proper neuroanatomical and psychological development, as well as the maintenance of mental health throughout life. As with most highly social species, the foundation to a healthy social life begins with a strong maternal bond that develops between mother and infant. Disruption of this bond results in severe, life-long consequences. Orcas have a prolonged period of maternal dependence after birth, with mothers demonstrating a long interbirth interval associated with investment in individual calf development and learning (Ward et al., 2009).

Thus, orca calves rely upon their mothers and closely related female relatives within their natal pod for protection, nourishment, and the development of essential life skills that contribute to their long-term psychological health, reproductive success, and physical fitness. In the case of the resident ecotypes of orcas in the Pacific Northwest, both male and female calves demonstrate lifelong affiliations with their natal matriline; in most cases, they never leave their maternal group (Olesiuk et al., 2005). Male orcas (including adults) experience a 3.1- to 8.3-fold increase in mortality risk in the year after their mother's death (Foster et al., 2012a). Therefore, in orcas, it appears that a healthy mother-offspring bond is not only critical to calf survival but also to that of her adult sons.

By contrast, wild-caught orcas in captive facilities have been removed from the ocean as young calves, sometimes as early as one year of age, resulting in an abrupt severing of the strong maternal and family bonds upon which they fundamentally depend for their health, well-being, and proper development. Captive-born orcas—-who account for most of the orcas in captivity in the United States today—have it no better, often experiencing insults to their social well-being from the moment they are born into an unnatural, and frequently unhealthy, social environment. In the wild, female orcas with calves would be surrounded by a support network of related females and their offspring (Foster et al., 2012b), who would participate in protecting and rearing the newborn. Captive female orcas are typically deprived of a healthy social network upon which to depend for physical or psychological support in infant rearing. In addition, captive orcas have often endured early-life social traumas themselves, which are associated with long-term compromise of social competence and maternal success later in life, as has been described for other species (Braun and Champagne, 2014; Hampson and Schwitzer, 2016). Thus, maternal neglect and incompetence are all too common phenomena in captive orca mothers (e.g., Visser and Lisker, 2016). The result is that mother-calf separation, social isolation, alienation, failure to nurse, and subsequent hand-rearing, as well as the transfer of conspecifics or calves to other facilities, are all traumatic consequences that often follow the birth of an orca calf in a marine theme park, aquarium, or zoo.

To illustrate, Loro Parque is a relatively new facility (orcas were first housed there in 2006), located in the Canary Islands, Spain. The four founding orcas (two males, two females, all captive born at various SeaWorld facilities in the United States) were separated from their mothers at very early ages (all less than 4 years, see Supplemental Material, Table 1, for details). With no mature females in the founding stock, the social structure has resulted in one of the most dysfunctional groupings of orcas ever held in captivity (Visser and Lisker, 2016). The social stressors these orcas were exposed to were not limited to separation, but included, *inter alia*, extremely unstable social networks (one orca was transferred to five facilities, with different orca hierarchies at each park). Inbreeding (uncle with niece) has occurred in two of the three calves born at Loro Parque. The mother of both inbred calves gave birth when she was under 8.5 years of age. In the wild, most (77%) female orcas produce their first viable calf between 11 and 17 years of age, but a few are primiparous as early as 9 or as late as 21 years of age (Olesiuk et al., 2005). The violations imposed on this captive female were amplified when she was impregnated only 123-135 days (4.1 to 4.5 months) after she gave birth. Her second calf was born 661 days after the first (i.e., 1.8 years). Typical (90%) intercalf interval in the wild is 3-7 years, although a few cases (3%) are as brief as 2 years (Olesiuk et al., 2005).

This same mother rejected both calves and repeatedly attacked them shortly after birth so they had to be separated from her. Furthermore, those separations occurred within hours/days of their birth and each was subsequently isolated and hand-reared. Another calf separation was forced upon a wild-born female, held at the same facility, due to an alleged lack of milk, despite a strong social bond exhibited by the mother. The mother repeatedly returned to the gate of the small (4.2 × 7.1 × 12.4 m) enclosure holding her calf, apparently in an attempt to reunite with her (Free Morgan Foundation, unpublished data). Social isolation was also imposed on the other two calves born at Loro Parque, one for over 12 months and the other from birth until the day of her death (at 10 months, 13 days old). As such, the separation issues have continued for the next generation of orcas (Supplemental Material, Table 1).

Orcas in captive display facilities are housed in artificial, man-made social groups, which exacerbates social stressors. These groups, which are frequently composed of individuals from genetically distinct populations, are also confined to concrete tanks a fraction the size of their natural home range. The result of such unnatural confinement, artificial group composition, and captive breeding is that chronically disrupted social hierarchies, social tension, and heightened aggression are fundamental to captive orca life. Similarly, free-ranging orca social networks are weakened by the loss of key individuals (Williams and Lusseau, 2006), which is relevant to the common practice of transferring captive individuals from one facility to another.

There is a large body of scientific literature showing a strong relationship among social isolation, chronic social stress, and depression in humans and many other mammals (Sandi and Haller, 2015). In captive cetaceans, social alienation, instability, and subordination can contribute to the development of illness and even death (Waples and Gales, 2002).

The stress of confinement

In humans, chimpanzees, and other animals, conditions of confinement have been associated with posttraumatic stress disorder, depression, and other mental disorders (Başoğlu, 2009; Ferdowsian et al., 2011; Aloni et al., 2018), which are in part explained by the influence of chronic stress on dysregulation of the HPA axis. Like other wide-ranging mammals (Mason, 2010), orcas are vulnerable to stress from confinement. The minimum US standards for orca enclosures of 15 m for horizontal distance and 4 m for depth clearly do not meet the physical needs of orcas, including, *inter alia*, a range of natural movements, postures, and behaviors (Joseph and Antrim, 2010; Rose et al., 2017).

Morgan and Tromborg (2007) noted that the negative impacts of enclosure size are related to the natural history of a species, including the roaming behavior of wild populations. For example, in captivity, orcas are unable to swim the distances or depths they would normally achieve. Abundant evidence shows that when a species is physiologically adapted to large home ranges, the opportunity to travel is critical to the health and well-being of its members (Clubb and Mason, 2003; Mason, 2010, McPhee and Carlstead, 2010). The confinement of naturally wide-ranging mammals causes chronic stress (Dawkins, 1998) and impairs the development of brain structures involved in sequencing behavior, thus decreasing behavioral flexibility (Robbins et al., 1996; Lewis et al., 2006). For example, Clubb and Mason (2003, 2007) found that natural home-range size predicted captive infant mortality and stereotypic pacing behavior in carnivores and that captive environments cause the most stress to naturally wide-ranging species by preventing species-typical behavior. Wide-ranging carnivores held in confined exhibits show typical physiological signs of chronic stress, such as adrenal hypertrophy (Terio et al., 2004).

Sensory deprivation and stress

Much of the sensory information orcas evolved to expect and process is either substantially altered or absent in concrete tanks. Studies have shown that these factors affect animal behavior, psychological well-being, and stress levels, as well as sensory capacities (Couquiaud, 2005; Parsons, 2013; Clegg and Butterworth, 2017, for reviews).

The natural environments of orcas contain multiple forms of auditory stimuli, but cetaceans, as all marine mammals, are adapted to the sounds they encounter in the ocean (Couquiaud, 2005; Weilgart, 2007). Anthropogenic sounds, in the ocean and in captive enclosures, may pose unique challenges to the auditory system and physiology of cetaceans. A growing body of research has found that exposure to excessive or unnatural levels or types of acoustic input can cause a number of impacts to cetaceans, including but not limited to decline in reproductive success (due to physiological and behavioral changes), accelerated aging, suppression of the immune response, as well as premature hearing loss (Romano et al., 2002; Weilgart, 2007, Wright et al., 2007). These impacts may be worsened in captivity, as cetaceans cannot evade or escape aversive noises present in tanks and their surroundings (Couquiaud, 2005). Nevertheless, the acoustic quality of tanks and performance stadiums has often been neglected in the design of captive cetacean enclosures (Couquiaud, 2005).

Processing of acoustic input by cetaceans in captive environments is affected by many aspects of concrete tanks and the surrounding stadium, particularly the tendency of these features to cause reverberation of sound and to transmit vibrations through the substrate, even over fairly long distances (Couquiaud, 2005). In addition, sources of mechanical and other human-caused sound and vibrations, for example, water pumps, nearby construction, music during performances, and even roller coasters and fireworks in some facilities, create an acoustic environment that differs greatly from the ocean (O'Neal, 1998; Couquiaud, 2005; Rose et al., 2017). Cortisol was found to be elevated up to 300-fold in bottlenose dolphins housed in a facility with nearby construction (Monreal-Pawlowsky et al., 2017). Most orcas are maintained in enclosures that are inside theme parks. Several facilities maintaining orcas have nightly fireworks displays, and construction noise and vibrations can be pervasive. As a measure to counteract the stressors construction would induce, a captive orca at Miami Seaquarium was regularly prescribed prophylactic antibiotics before even minor repair work in the stadium adjoining her tank (Visser, 2016). Captive orcas are therefore exposed to sound sources that are chronic (e.g., water pumps, filtration systems) and intermittent (e.g., fireworks, construction drilling), which are likely to affect the animals' stress and health levels over time.

Concern about acoustic stress tends to focus on underwater sound sources (e.g., see Scheifele et al., 2012). This view assumes that captive marine mammals spend most of their time below the water's surface. However, most captive marine mammals, including orcas, are at the surface much of the time, with their heads above water, stationed by their trainers and waiting for reinforcement (i.e., food) during training and shows (e.g., see Galhardo et al., 1996). Therefore, in-air noise levels are relevant to captive marine mammals (Couquiaud, 2005; Rose et al., 2017). Both indoor and outdoor stadiums with performance enclosures for orcas can have sound levels that are very loud (especially during shows), in some cases with excessive reverberation, with input from the audience, music amplifiers, and trainers' microphones.

Similarly, progressive vision deficit and even blindness are commonplace occurrences for captive cetaceans as a result of ocular disease from trauma, poor water quality, chemicals, and sun exposure (Colitz et al., 2016).

The stress of lack of control

Arguably most relevant to the issue of how well orcas adapt to living in concrete tanks is their level of self-awareness. Awareness of one's life and environment is key to how any animal responds to living in an artificial and confining setting. Self-awareness is related to the capacity for an individual to comprehend their circumstances (situational awareness), potentially leading to increased suffering and despair in deprived environments. In addition, orcas in captivity could conceivably suffer a great deal because they cannot control their ability to avoid negative stimuli (Ferdowsian and Merskin, 2012). One of the greatest stressors in the lives of captive animals is their inability to control most aspects of their surroundings and lives (Goldblatt, 1993; Sambrook and Buchanan-Smith, 1997). Morgan and Tromborg (2007) note:

> Animals in captivity generally do not have control over what individuals serve as their social partners or their mates. They have little or no control over how much space they are able to put between themselves and conspecifics, or between themselves and humans. They have little or no control over what kinds of food they are offered, nor when that food is made available. Nor are they generally able to control relevant environmental stimuli such as quantity, quality, and timing of lights, sounds, odors, or temperatures. (p. 286).

Moreover, longstanding evidence shows that unpredictable and uncontrollable experiences, especially unpleasant ones, lead to a syndrome called "learned helplessness," which results in a range of outcomes associated with chronic stress, including depression, "giving up" or lack of motivation to learn or explore, anorexia, and immune system dysfunction (Seligman, 1975; Maier and Seligman, 2016). Learned helplessness has been documented across a range of mammals in captivity (Markowitz and Eckert, 2005; Clubb and Mason, 2007; Morgan and Tromborg, 2007; Hodes et al., 2015) and a number of authors have recognized that the chronic stress associated with lack of control in captivity can have effects on health and well-being in cetaceans that are consistent with the symptoms of learned helplessness (Couquiaud, 2005; Atkinson and Dierauf, 2018).

Learned helplessness theory provides a well-reasoned mechanism underlying the psychological and physical deficits associated with lack of choice for captive cetaceans, including orcas. Extended periods of listlessness and immobility at the surface (commonly termed "logging") and catatonic-like bottom resting are behaviors reflective of such learned helplessness. An adult (wild-born) male orca at SeaWorld Florida was observed continuously (24 h/d) for a period of 7 consecutive days, to create an activity budget. The orca spent, on average, 69.6% (16.7 h) of the day inactive (Worthy et al., 2013) and as such was completely disengaged with his conspecifics, trainers, or environment. Such inactivity is unheard of in the wild, where orcas are on the move for more than 99% of their lives (e.g., see Durban and Pitman, 2011; Matthews et al., 2011; Lauriano et al., 2015).

The stress of boredom

Boredom can emerge out of circumstances where there are not enough challenges or variety in activities to keep an individual stimulated, motivated, and thriving. And while unpredictability and uncontrollability have negative consequences when they persist, there are also detriments to monotony and lack of challenges, particularly for animals like orcas who display sophisticated cognitive and psychological complexity. Orca hunting tactics, complex vocal acquisition, and dialect development are examples of social-cognitive-communicative needs found in orcas that are unavailable in concrete tanks.

Boredom is a deeply unpleasant state for humans and nonhumans alike. Chronic boredom is expressed as impaired attention, listlessness, irritability, and, when extreme, self-stimulatory behaviors (stereotypies) (Wemelsfelder, 2005). When stereotypies emerge, they increase fixation on a monotonous behavior and further reduce the behavioral range of the individual (Haskell et al., 1996; Golani et al., 1999; Mason and Rushen, 2006). The vulnerability of any animal to boredom in captivity is associated with whether their brain is adapted to dealing with complex challenges and variety. Because of their intellectual and emotional capacities, cetaceans are highly susceptible to the adverse effects of chronic boredom in captivity.

Although learning tricks and husbandry behaviors in captive facilities may be initially reinforcing, over time, the requirement for sustained vigilance during these repetitive tasks and attempts to cope with a nonchanging routine may lead to anxiety and boredom (Kiley-Worthington, 1990; Kuczaj et al., 2002; Wemelsfelder, 2005; Morgan and Tromborg, 2007; McPhee and Carlstead, 2010). Moreover, the topography and architecture of the tanks themselves contribute to boredom, as they typically lack any interesting features that invite investigation. Tanks are typically made of smoothed-concrete, regularly shaped, and have few, if any, interactive or dynamic features (Couquiaud, 2005; Rose et al., 2017). Studies comparing the behavior of captive dolphins in open facilities (allowing for ocean water flow, entry of small fish, and other natural environmental features), compared with captive dolphins in tanks, show that they are less stressed, have lower salivary cortisol levels, and are more behaviorally engaged, with less "logging" on the surface (Ugaz Ruiz et al., 2009; Ugaz et al., 2013).

Conclusion

Orcas are dolphins with large complex brains and strong social and familial ties. They routinely range widely and dive deeply. They are self-aware, cultural beings who differentiate and identify their own groups through dialect, prey preference, group size, and many other learned traditions. They have a prolonged juvenile period of social learning and the emotional bonds between mothers and calves, as well as among other relatives, are as strong as any in the animal kingdom. They also demonstrate the capacity to grieve. Although these characteristics are associated with a high degree of intelligence and social sensitivity and complexity, these characteristics also describe what natural capacities and behavior these whales need to be able to express to thrive.

The high number of calf mortalities and low survival rate of adult orcas in captive facilities are alarming and available records implicate infectious disease as the primary cause of morbidity and mortality in these animals. As with any free-ranging species of wildlife, orcas in the wild occasionally fall victim to infection and naturally experience a higher rate of mortality during the early and more vulnerable years of life. The frequency and nature of the diseases afflicting captive orcas, however, are largely distinct from their free-ranging counterparts. Furthermore, their vulnerability to infection and other diseases persists despite the relatively controlled environments to which they are confined and in which they are provided with veterinary care, sheltered from hazards and pathogens, and fed a diet that is believed to meet their basic nutritional needs.

We have provided evidence for the argument that the morbidity and mortality of orcas in captive facilities may be attributable to acute, severe, or chronic stress and its association with immune dysfunction, disease, and disorder. Access to veterinary and necropsy records, as well as biological samples from captive orcas, would add considerably to our ability to assess the strength of this hypothesis.

Cognitive, psychological, and behavioral complexity are relevant to an individual's experience in captivity because greater cognitive complexity increases the need for a complex environment and experiences. It is evident, despite the often well-intentioned efforts associated with human care, that life in concrete tanks in marine theme parks, aquariums, and zoos is failing to meet the complex needs of orcas. Yet, free-ranging orcas are still being captured in Russia for live trade and captive orcas outside of North America are still routinely being bred for public display. Confining and breeding orcas in these facilities serves to propagate stress, poor welfare, and illness in these animals. Given this evidence, the ethical ramifications of keeping orcas in captivity should be critically evaluated by society and regulators, and the industry should adapt accordingly.

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Supplementary data

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Conflict of interest

No conflicts of interest exist.

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