Developing Standards of Care for Marine Mammals in Captivity and Recommendations Regarding How Best to Ensure the Most Humane Treatment of Captive Cetaceans

A report prepared for the Ontario
Ministry of Community Safety and Correctional Services

Final Report: May 30, 2014

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Report Overview

Purpose

This Committee was convened by the Government of Ontario's Ministry of Community Safety and Correctional Services in October 2013 to (1) evaluate Ontario's current regulations pertaining to the care of marine mammals in captivity for public display, (2) consider whether current regulations are sufficient to ensure the care of these marine mammals, and, if not, to (3) suggest how existing regulations could be improved. Additionally, the Committee was asked to (4) give special consideration to the welfare of cetaceans in public display facilities.

The mandate of the Committee was to address the first three aims concerning regulations for the care of marine mammals in display facilities using documents in the public domain, their professional expertise, and consultations with animal care specialists, and to evaluate the broader aim concerning the welfare of captive cetaceans using their interpretation of the best scientific data available, assisted by consultations with the scientific community. As a result, this report represents the scientific perspective of the Committee and does not include other viewpoints such as those concerned with social, ethical, political, and economic factors. In addition, this report does not make a determination as to whether cetaceans should be kept in captivity; that issue is beyond the purview of the Committee.

Report Structure

The report is divided into two main sections. The first section (Part 1) addresses the aims related to Standards of Care for captive marine mammals. To do so, the Committee reviews current animal care regulations pertaining to marine mammals in Ontario, discusses potential problems associated with the interpretation and enforcement of current regulations, and provides specific recommendations and supporting information to improve regulations concerning the welfare of marine mammals in public display facilities.

The second section of this report (Part 2) is a summary of available scientific (peer-reviewed and published) information concerning the welfare of cetaceans in captivity. Here, the Committee describes potential sources of stress for captive marine mammals and evaluates metrics of stress and health for captive cetaceans. The Committee has also including an Appendix that summarizes cognitive considerations specific to cetaceans that may be relevant to their captive welfare. The material provided in Part 2 of the report provides much of the scientific basis used to support the recommendations and conclusions offered in Part 1.

Committee Members

Dr. David Rosen chaired this Committee. Dr. Rosen is an expert in the physiological and behavioural ecology of marine mammals, with a BSc in Marine Biology and MSc and PhD degrees in Biopsychology. Dr. Rosen has published more than 60 studies of captive and wild marine mammals, including those related to bioenergetics, nutrition, behaviour, and stress. Dr. Rosen is presently a Research Associate with the Marine Mammal Research Unit at the University of British Columbia (Vancouver, Canada), and heads the Marine Mammal Energetics and Nutrition Laboratory. He is an Associate Editor for the scientific journals *Aquatic Mammals* and *Frontiers in Aquatic Physiology*, and is the past President of the Comparative Nutrition Society.

Dr. Rosen was assisted by two colleagues that served as members of this Committee: Dr. Heather Koopman, a marine mammal physiologist and Dr. Colleen Reichmuth, a marine mammal behaviourist.

Dr. Koopman presently serves as Associate Professor in the Department of Biology and Marine Biology at the University of North Carolina Wilmington (USA) and Senior Scientist with the Grand Manan Whale and Seabird Research Station (New Brunswick, Canada). Dr. Koopman is trained as an animal physiologist with particular expertise in cetaceans, seabirds, and sharks. She has a BSc in Marine Biology and Biochemistry, an MSc in Zoology, and a PhD in Environment. Dr. Koopman presently serves as the Secretary for the Society for Marine Mammalogy and has published more than 25 scientific articles concerning the physiology and ecology of marine mammals.

Dr. Reichmuth is a Research Scientist in the Institute of Marine Sciences at the University of California Santa Cruz (USA) where she directs the Cognitive and Sensory Systems Research Program at Long Marine Laboratory. She has a BSc in Biology and MSc and PhD degrees in Ocean Sciences. Dr. Reichmuth has particular expertise in the cognitive, sensory, and behavioural biology of pinnipeds and other marine mammals. She has been directly involved in the training and care of captive marine mammals for more than 20 years. She conducts research with both captive and wild individuals and has published over 40 scientific articles describing this work.

Explanation of Key Terms

For the purposes of this report, the general term **marine mammal** includes odontocete cetaceans (dolphins and porpoises), pinnipeds (seals, sea lions, and walruses), sea otters, and sirenians (manatees and dugongs). Baleen whales are also marine mammals, but they are rarely referenced in this report because these species are not kept in long-term captivity anywhere in the world. While polar bears are generally considered marine mammals, they are not included in this report because their captive care is more appropriately addressed by animal care considerations for terrestrial wildlife, including other ursid carnivores.

The use of the term **captivity** in this report refers to the holding of animals primarily for the purpose of public display in zoological facilities including aquariums. While marine mammals are sometimes held in captivity primarily for the purposes of rehabilitation and research, these activities are not explicitly considered herein. The use of the term by no means denotes any *a priori* judgement.

Executive Summary

A review of the current scientific literature on the well-being of captive cetaceans highlighted several areas of concern. There are several aspects specific to the aquarium environment that can potentially cause stress in captive cetaceans, although none are unique to this group, and most can be mitigated through proper husbandry and habitat design. The most critical issues identified are the need for adequate pool space and design, appropriate social groups, and environmental enrichment. Additional concerns relate to suitable light and sound exposure in the habitat.

The relative survival rates of captive cetaceans in comparison to their wild counterparts seem to vary by species. However, there is an overall trend for wild-caught individuals to suffer higher rates of mortality during the capture process and upon the initial acclimation period in the facility. While survival of captive cetaceans has generally improved over the years, there are still differences between individual facilities worldwide. Bacterial pneumonia is the most common cause of mortality among both wild and captive cetaceans. Most diseases reported for captive cetaceans are also common in their wild counterparts, although there are no data to directly compare rates of infection or resulting mortalities.

Studies have demonstrated that cetaceans show physiological responses to stress that are typical of other mammals, although the nature of the stress response varies considerably by species. Studies show that transport, arrival at a new facility, and the introduction of new “pool mates” can cause acute stress in several species. Unfortunately, obtaining samples to monitor the health status of individual captive cetaceans can also lead to stress responses, although adequate training can reduce these negative effects. Behavioural observations can be used as an alternate, inexpensive means to assess some aspects of animal well-being. A reliable observer program by husbandry staff can identify several indicators of medical and psychological issues early in their development. Lack of appetite and lethargy are behavioural indicators of physical or psychological concerns, as are stereotyped and self-harm behaviours. Acoustic signals may also be employed for monitoring cetacean well-being. Perhaps the most recognizable behavioural indicator of social issues within the habitat is aggression directed at social partners. Aggression can be minimized by appropriate social groupings and pool design.

These findings suggest that ensuring the welfare of captive cetaceans presents unique challenges due to the psychological and physiological needs of these animals. While we have given special consideration to the welfare of captive cetaceans according to the objectives set forth for the Committee, we have considered all marine mammals in our review of existing regulations. It is our

opinion that the present Standards of Care that apply to marine mammals in public display facilities are insufficient under the current *Ontario Society for the Prevention of Cruelty to Animals Act*. It is our opinion, based upon our review of the regulations and the available scientific evidence, that adequate care in captivity requires the adoption of an additional set of Standards of Care to address needs specific to this group of animals.

Part 1: Recommendations for Standards of Care for Captive Marine Mammals in Ontario

1.1. Overview

Part 1 of this report describes existing animal care regulations pertaining to marine mammals in Ontario, discusses recognized concerns with current regulations, and provides specific recommendations and supporting information to improve regulations to ensure the care of marine mammals in captivity.

1.2 Approach

The Committee worked to determine whether existing regulations pertaining to the care of captive of marine mammals in Ontario were sufficient and, if not, to recommend appropriate changes to the Standards of Care that would best ensure the welfare of marine mammals in public display facilities.

To address this objective, we reviewed existing regulations pertaining to the care of captive marine mammals in Ontario and a variety of publically available documents commenting on these regulations. We also consulted with the Ontario Ministry of Community Safety and Correctional Services to ensure a clear understanding of existing Provincial regulations and how they are applied and enforced.

To evaluate existing regulations and comment on whether we believe they are adequate or should be modified, and to make informed recommendations for any modifications, we relied on several resources. These included our own professional expertise, consultations with veterinarians and other animal care specialists and marine mammal scientists, documents in the public domain, professional standards and regulations used elsewhere, and scientific and veterinary sources. Ultimately, we used this information to formulate a series of recommendations to the Ontario Ministry of Community Safety and Correctional Services.

1.3 Current regulations for the care of marine mammals in Ontario

The *Ontario Society for the Prevention of Cruelty to Animals (OSPCA) Act*[1] (1955) – amended by the *Provincial Animal Welfare Act*[2] (2009) – is the primary provincial legislation governing the welfare of marine mammals in public display facilities in Ontario. The OSPCA Act provides basic Standards of Care for animals,[3] including requirements related to the availability of food and water, general care and medical care associated with welfare considerations, safe transportation, environmental and social living conditions, protection from harm, and humane treatment including methods of killing that minimize pain and distress. While these Standards apply to most animals in human care,[4] the OSPCA Act also includes special provisions for dogs that live primarily outdoors, and wildlife and primates living in captivity.

In addition to establishing minimum Standards of Care for animals, the OSPCA Act establishes mandates concerning the personal responsibility of individuals that cause or allow animals to be in distress,[5] and the professional responsibility of veterinarians that suspect animal abuse or neglect. Like the basic Standards of Care included in the OSPCA Act, these responsibilities are applicable to all animals covered by the regulations.

The animal care regulations currently included in the OSPCA Act are intentionally broad as to cover a range of animal species and situations. However, the OSPCA Act also stipulates that Standards of Care should be "*adequate and appropriate or necessary to the specific animal, having regard to its species, breed and other relevant factors*."[6] For marine mammals in public display facilities in Ontario, the relevant regulations presently include the basic Standards of Care applicable to all captive animals,[7] as well as those pertaining to wildlife kept in captivity, which provide additional requirements for the care for non-domestic animals.[8] There are no additional specific provisions in the OSPCA Act for the care of marine mammals in captivity.

The Standards of Care specified by the OSPCA Act are presently enacted by a system of public reporting of animal welfare concerns to the OSPCA. The OSPCA is an independent, non-profit organization that receives funding from both government and private donors. Complaints concerning animal welfare are directed to and investigated by OSPCA–trained and approved inspectors and agents, who have the authority to enforce any law in Ontario that pertain to animal welfare. These individuals are granted police powers of inspection, assessment, and enforcement by the *Act.*[9]

In addition to the Provincial regulations for the treatment of animals specified in the OSPCA Act, there are additional protective measures for animals granted under Ontario's *Veterinarians Act*[10]*,* which ensures professional standards of practice for those providing veterinary treatment to individual animals. Marine mammals in Ontario are also subject to Federal regulations under Canada's *Criminal Code*,[11] the *Animals for Research Act,*[12] and the *Fisheries Act.*[13] Of these, only the *Fisheries Act* includes specific provisions for living marine mammals that pertain in any way to their use in public display facilities. These relate to the capture or release of wild marine mammals in Canadian waters, and the transport of captive marine mammals across Canadian borders.[14] There are no regulations in the *Fisheries Act* associated with the care of marine mammals in captivity. Internationally, there are limited restrictions on the import of certain marine mammal species into Canada through Canada's membership in the *Convention on International Trade in Endangered Species* (CITES).[15] There is no international oversight of marine mammals once they are in Canada.

1.4 Recognized concerns associated with current regulations for the care of marine mammals in Ontario

Several Federal[16] and Provincial[17] assessments, professional institutions,[18] and advocacy groups[19] have recognized that current regulations for marine mammals in captivity may be inadequate to ensure the welfare of some or all of these animals, and may be difficult to apply and enforce. There has also been considerable media attention and public debate on this issue in Ontario, and concern from stakeholders on all sides. Some of the issues raised include the following:

1. Regulations established by the OSPCA Act provide general Standards of Care for captive animals in Ontario. However, the application of these Standards to marine mammals may be challenging. Reasonable and appropriate translation of existing Standards may require knowledge of species not commonly encountered in human care.
2. When responding to complaints about the welfare of marine mammals in public display facilities, inspectors and agents of the OSPCA may, in some cases, lack specialized training or zoological expertise to support reasonable and appropriate translation of existing Standards. However, the OSPCA Act[20] does empower OSPCA inspectors and agents to enlist professional assistance in interpreting these regulations for marine mammals.[21]
3. Given the general nature of the existing Standards that apply to marine mammals in Ontario, it may be unclear to public facilities how these regulations will be translated and enforced for captive marine mammals, making it difficult for owner/operators of public display facilities to ensure compliance with existing regulations.
4. There is concern for whether the Standards of Care that presently apply to marine mammals in Ontario are sufficient to ensure the welfare of these animals in captivity, or whether special provisions are required to account for their specific needs. There is also concern for how marine mammals (particularly cetaceans) are acquired for public display.
5. There is public debate over whether all or some marine mammals should be kept in public display facilities at all, regardless of the Standards of Care that are (or that may be) established through regulation. This concern is based on the premise that the needs of all or some marine mammals are so complex that they cannot be reasonably accommodated in any captive environment.

These five concerns regarding the adequacy of the existing regulations for the welfare of captive marine mammals in Ontario suggest that a review of the current Standards of Care in Ontario for marine mammals is warranted. Much of this report is dedicated to a science-based evaluation of whether the Standards of Care specified under the OSPCA Act are sufficient to ensure the welfare of marine mammals in captivity, or whether special Standards for marine mammals should or can be implemented that provide sufficient Standards to ensure the welfare of this group of animals.

1.5 Summary of Committee opinion and recommendations for regulations for the care of marine mammals in Ontario

It is our opinion that the current Standards of Care for marine mammals in display facilities are insufficient under the current regulatory structure in Ontario. As previously noted, regulations governing the care and treatment of marine mammals fall primarily under the *Ontario Society for the Prevention of Cruelty to Animals Act*. This legislation defines basic Standards of Care that are applicable to all animals in human care (Section 2), and provides special provisions for several groups of animals. In addition to the regulations of Section 2, marine mammals fall under regulations pertaining to the Standards of Care for wildlife (Sections 4 and 5). It is our opinion, based upon our review of the regulations and the available scientific evidence, that adequate care in captivity requires the adoption of an additional set of regulations specific to this group of animals.

While the requirements of marine mammals in captivity are complex, it is our opinion that three regulatory changes to the OSPCA Act's Standards of Care would address many of the concerns identified in Section 1.4 of this Report. We suggest that these special provisions for marine mammals be used to supplement the applicable Standards of Care currently in place. In the following section (Section 1.6), we provide background material and rationale for the recommendations we offer here. A separate scientific review of the concerns and challenges related to keeping cetaceans in captivity is provided in Part 2 of this Report.

Specific Recommendations

1) **We recommend additional regulation(s) to supplement the OSPCA Act that are specifically tailored to meet the needs of marine mammals that are not currently covered by other relevant sections of the *Act*.[22] These recommendations for Standards of Care apply to all facilities that hold marine mammals primarily for public display. These can be broadly grouped into three over-arching goals, each with a specific set of recommendations:**

    i. ***Facilities must demonstrate responsibility to the long-term well-being of marine mammals in their care.***

        a. **Each facility must have an established Animal Welfare Committee.**
        b. **Each facility must have a written Animal Management Plan that provides justification for all marine mammals housed in the facility.**
        c. **Each facility is required to help maintain a provincial inventory of marine mammals housed in display facilities.**
        d. **Each facility must have access to a qualified veterinarian with expertise in marine mammal medicine, who oversees a program of preventive veterinary medicine and clinical care for all marine**

mammals held in the facility, in accordance with professional standards of practice in Ontario.

e. Each facility must have a written Veterinary Care Program. This should be developed by a veterinarian in collaboration with other experts (biologists, trainers, curators, etc.), and should include an annual physical examination of each marine mammal.

ii. Facilities that hold marine mammals must meet their physical and psychological environmental needs.

f. Consideration must be given to the three-dimensional environment in which marine mammals live and the need to provide sufficient space for species-appropriate activities both in and out of the water. Therefore, it is recommended that each facility adopt a set of minimum space requirements that are based upon established, internationally recognized codes.

g. Marine mammals must be protected from exposure to noise that could cause auditory discomfort or distress and lead to injury.

h. The water supply must be reliable and contribute to the good health and well-being of the marine mammals.

i. Provisions must be made for appropriate light exposure, including consideration of the type, level, and cycle of exposure.

j. Each facility must provide suitable social and environmental enrichment programs.

iii. Facilities must ensure that marine mammals are not harmed in their contact with the general public.

k. Facilities with public contact programs must ensure the programs are adequately designed and outfitted to minimize potential risks to the health and safety of the marine mammals and humans.

l. Facilities with a public contact program must have a written policy that clearly identifies and addresses the safety issues and concerns for all participants in the program, including the marine mammals, and specifies the qualifications of those conducting the public contact session.

2) We recommend additional regulation(s) through the OSPCA Act for facilities acquiring new wild-born animals. These regulations are designed to protect the welfare of cetaceans destined for public display, either through foreign or domestic acquisitions, with particular emphasis on safeguarding the health of wild populations.

3) We recommend the timely adoption of the *Guidelines On: The Care and Maintenance of Marine Mammals* established by the Canadian Council on Animal Care (CCAC)[23] as a specific Standard of Care for marine mammals under the OSPCA Act.

1.6 Supporting information for the Committee's recommendations

The Committee carefully considered each of the three main recommendations provided in the previous section. In this section, we explain each recommendation, in more detail, highlight some of the most relevant supportive material, and summarize why we feel these changes to the OSPCA Act are important for ensuring the welfare of marine mammals in display facilities.

Supporting information for Recommendation 1*:*

We recommend additional regulation(s) to supplement the OSPCA Act that are specifically tailored to meet the needs of marine mammals that are not currently covered by other relevant sections of the Act. These recommendations for Standards of Care apply to all facilities that hold marine mammals primarily for the purposes of public display.

i. ***Facilities must demonstrate responsibility to the long-term well–being of marine mammals in their care.***

a. **Each facility must have an established Animal Welfare Committee.**

It is essential that proper oversight on animal care and use be provided in the form of an Animal Welfare Committee (or equivalent). In brief, a facility's Animal Welfare Committee is responsible for overseeing all aspects of animal care and use within its facility (including display, education, and research). It must hold regular meetings, and its work must be clearly documented.

Animal Welfare Committees are often associated with research facilities or academic institutions. However, we suggest that such a Committee is equally important for facilities that primarily display marine mammals, and that they can be instrumental in carrying out many of the other specific recommendations that the Committee has proposed. We also have specific recommendations to ensure a required level of independence and professional input for the Committee. Specifically, we recommend that a facility's Animal Welfare Committee consist of (but not be limited to) a research investigator and/or interpreter/educational specialist, the facility's supervising veterinarian, a non-animal user within the facility, a community representative, and a member of the husbandry staff. Facilities that cannot fill the positions internally should seek qualified external members. We recommend that an external expert in marine mammals (either a qualified veterinarian or scientist) sit on the Committee. We further recommend that, while the Animal Welfare Committee should report directly to the senior administrator of the facility, this Committee should operate independently of this individual.

As part of its duties to ensure the proper care and use of animals in the facility, the Animal Welfare Committee should also be responsible for ensuring that concerns over animal care raised by staff are addressed and properly recorded. This can be facilitated by a written and posted "whistle blower" policy.

b. Each facility must have a written Animal Management Plan that provides justification for all marine mammals housed in the facility.

A written Animal Management Plan is important to ensure that facilities do not develop into mere collections of individual marine mammals. This Plan will help guarantee that the number of individuals does not exceed the facility's capacity for proper care, including the arrangement of appropriate social groups. Conversely, it is important to have approved plans to care for individuals whose social group may be smaller than optimum. By developing an Animal Management Plan, the Animal Welfare Committee will oversee that the facility's collection (both in regard to the numbers and species of marine mammals) is appropriate for the stated scientific and educational goals and the size and condition of the facility (including staffing capacity). This is particularly important when there are plans for transferring animals between facilities, and for any facility that allows breeding. The Animal Management Plan is also a valuable tool to anticipate the needs of animals as they age.

c. Each facility is required to help maintain a provincial inventory of marine mammals housed in display facilities.

There is a perception that a lack of transparency exists in the way that marine mammals are managed within display facilities, which contributes to concern for their well-being. We suggest that this can be partly alleviated through a provincial inventory of the marine mammals that are maintained in display facilities. Individual facilities would be responsible for ensuring this registry is up to date by providing timely information on acquisitions, births, and mortalities. Additional information on lineages (when known), and causes of mortality (when known) would also be beneficial for ensuring the long-term health of marine mammals in human care (see discussion of *Life History Characteristics* and *Diseases and Sources of Mortality* in Part 2).

d. Each facility must have access to a qualified veterinarian with expertise in marine mammal medicine, who oversees a program of preventive veterinary medicine and clinical care for all marine mammals held in the facility, in accordance with professional standards of practice in Ontario.

This recommendation recognizes that marine mammals have specific physiological and behavioural requirements that necessitate a degree of specialization in their care. This does not mean that facilities must employ a specialized veterinarian, but it must have reasonable access to one to assist with the animal's care in a timely fashion.

e. Each facility must have a written Veterinary Care Program. This should be developed by a veterinarian in collaboration with other experts (biologists, trainers, curators, etc.), and should include an annual physical examination of each marine mammal.

In conjunction with the previous recommendation, this Veterinary Care Program should be developed with the assistance of a veterinarian with recognized expertise in marine mammal care. The work of the veterinary team can be facilitated through appropriate animal training, in order to increase the range of potential diagnostics that can be undertaken without additional stress to the animals (see discussion in *Interactions with aquarium staff* in Part 2). Annual physical examinations must be appropriately documented, including a written plan for any required follow-up treatments.

ii. Facilities that hold marine mammals must meet their physical and psychological environmental needs.

f. Consideration must be given to the three-dimensional environment in which marine mammals live and the need to provide sufficient space for species-appropriate activities both in and out of the water. Therefore, it is recommended that each facility adopt a set of minimum space requirements that are based upon established, internationally recognized codes.

Adequate and appropriate habitat space is a primary concern for all captive marine mammals (see discussion on *Restricted movement* in Part 2). We recognize that smaller pools are sometimes required for specialized care or temporary holding (including shows), but these should only be used on a short-term, defined basis. The intention of primary pools is to provide sufficient living space, both horizontally and vertically, so that the animal can make normal postural and social adjustments with adequate freedom of movement in or out of the water. This suggests that primary pools must meet certain dimensions on surface area and depth. Additionally, pinnipeds and sea otters must also be provided with adequate haul out space.

There are no current Canadian regulations defining explicit pool sizes and dry haul out space for marine mammals. There are, however, several internationally recognized standards and guidelines including regulations set out for the United States[24], the United Kingdom[25], Brazil[26], the Bahamas[27], Argentina[28], and the European Association of Aquatic Mammals (specifically for *Tursiops*)[29]. Each of these represents an attempt at best practices, and there is no substantial scientific basis for adoption of one set of criteria over another. However, barring any adoption of a particular set of legislative regulations within either Canada or Ontario, it is recommended that each facility adopt a set of minimum space requirements based upon one of these established, internationally recognized codes. The guidelines a facility chooses to adopt for minimum quantitative space requirements must be explicitly included in their written Animal Management Plans that provide justification for all marine mammals housed in the facility, and must be approved by the facility’s Animal Welfare Committee. These guidelines should include details and limits on holding animals outside of their primary habitats (except in the cases of medical requirements). In cases where the adherence to the guidelines is not possible at the time of adoption, the Animal Management Plan must detail a strategy for compliance within a reasonable timeline[30]. Any new primary holding areas within a facility must meet these new requirements.

g. Marine mammals must be protected from exposure to noise that could cause auditory discomfort or distress and lead to injury.

Given the importance of sound to cetaceans, and that many marine mammals have auditory sensitivities outside of normal human hearing, it is important that facilities ensure that ambient noise levels do not cause stress to the animals or contribute to hearing loss. This is the basis for the recommendation that an auditory monitoring program be instituted for cetaceans kept in aquariums, which includes annual or regular testing (as defined in a Standard Operating Procedure) of both in-air and underwater sound levels. Particular attention should be paid to intermittent sources, such as those due to construction, public address systems, or new water treatment equipment (see *Sound levels* in Part 2). Sound level readings should be taken and interpreted by appropriately qualified personnel (including knowledge of marine mammal auditory profiles).

h. The water supply must be reliable and contribute to the good health and well-being of the marine mammals.

The quality of the water in the habitat is obviously of critical importance to marine mammals. Therefore, we recommend that each facility should implement a Standard Operating Procedure (approved by the Animal Welfare Committee) for the monitoring of their water supply. This includes defined standards for important parameters (examples include chlorine concentrations, faecal coliform levels, etc.)[31], a schedule of regular testing, an appropriate reporting mechanism, and a defined method of external review and/or testing.

i. Provisions must be made for appropriate light exposure, including consideration of the type, level, and cycle of exposure.

Appropriate light conditions are important for the well-being of marine mammals (for a full discussion see *Light conditions* in Part 2) to the extent that it should be recognized as an environmental health issue. Lighting considerations include the quality and intensity of the light, as well as its distribution and duration (photoperiod). Adequate lighting levels are required for the health of individual animals, as well to provide sufficient illumination for routine health and hygiene checks and for cleaning. As far as possible, sunlight should be used as the primary light source, and artificial light should be spectrally similar to sunlight. The pattern of lighting must also be considered. Some marine mammals require exposure to natural or simulated annual photoperiods to regulate annual cycles related to reproduction and moult. Therefore, the photoperiod conditions provided to marine mammals that live indoors should be carefully considered, and physiological cycles (such as patterns of moult in pinnipeds) should be used as an indication of the efficacy of the lighting environment. Care should also be taken that animals are not over-exposed to certain types of light, most notably (but not exclusively) ultraviolet radiation. Glare from surfaces should also be taken into account when determining appropriate light levels for a given enclosure.

j. **Each facility must provide suitable social and environmental enrichment programs.**

We recommend that structured enrichment programs must take a central role in ensuring the well-being of marine mammals in captivity. The primary aim of enrichment efforts is to enhance animal welfare by providing opportunities that facilitate the expression of species-typical behaviours and promote psychological well-being through physical exercise, manipulative activities, and cognitive challenges according to species-specific characteristics.[32] Environmental enrichment is a term used to refer to provision of stimulating and responsive environments above the basic conditions that meet the animal's physical, physiological, and psychological needs[33]. We further note that the thoughtful application of enrichment can reduce stereotypic behaviour and stress, and increase the expression of more flexible, positive behaviour (see *Stereotyped behaviour* in Part 2). Given the cognitive capabilities of cetaceans (Appendix A) and other marine mammals,[34] a meaningful enrichment program, developed with regular consultation with the Animal Welfare Committee to ensure efficacy and safety, should be required for marine mammals in captivity. Enrichment can be provided in various forms that may be interactive (involving other animals or human caretakers) or indirect, giving the animal the choice of whether to engage in the enrichment or not. The enrichment program should include an ongoing evaluation of the individual animals' responses to any forms of enrichment offered.

iii. Facilities must ensure that marine mammals are not harmed in their contact with the general public.

k. **Facilities with public contact programs must ensure the programs are adequately designed and outfitted to minimize potential risks to the health and safety of the marine mammals and humans.**

l. **Facilities with a public contact program must have a written policy that clearly identifies and addresses the safety issues and concerns for all participants in the program, including the marine mammals, and specifies the qualifications of those conducting the public contact session.**

There is a concern for adequate control and oversight for programs that rely upon contact between captive marine mammals and the public. This can take the form of direct physical contact or special access that the public is not usually permitted and for which issues of animal care and safety (for both animals and humans) may not be adequately considered. We feel that such interactions must meet a high standard of preparation and oversight. This can be accommodated by having a written Standard Operating Policy (approved by the Animal Welfare Committee) that details the conditions and aims of such encounters, with opportunity for regular evaluation of its efficacy.

Supporting information for Recommendation 2:

We recommend additional regulation(s) through the OSPCA Act for facilities acquiring new wild-born animals. These regulations are designed to protect the welfare of cetaceans destined for public display, either through foreign or domestic acquisitions, with particular emphasis on safeguarding the health of wild populations.

There is apprehension among scientists, stakeholders, and the general public regarding the acquisition of marine mammals from wild stocks. This is particularly true for cetaceans. The acquisition of wild-born cetaceans is a valid concern in regard to animal welfare, as it impacts the welfare of the individuals being imported as well as their source populations. The Committee holds the opinion that ensuring the welfare of cetaceans destined for facilities in Ontario should not be limited to the daily needs of individuals once they are in those facilities. Consideration must also be given to how they were acquired as well as the potential impact of wild–captures on source populations.

Many of the concerns expressed in regard to the welfare of cetaceans in captivity relate to a perceived lack of regulation over the international import and trade of cetaceans, and whether removals of individual cetaceans is negatively impacting the health of wild populations. In Canada, the Department of Fisheries and Oceans (DFO) is responsible for the import/export of marine mammals into or out of Canadian waters through the Marine Mammal Protection Regulations under the *Fisheries Act*[35]. The *Species At Risk Act* (SARA) prohibits the capturing of any listed species or designatable units of a species in Canadian waters.[36] However, these federal regulations only apply to the capture/import of marine mammals from Canadian waters. Canada has not issued a capture permit for cetaceans from Canadian waters in decades.

The issue is more of a concern regarding the import of cetaceans from other countries. Such imports are governed by CITES (Convention on the International Trade in Endangered Species of Wild Fauna and Flora), of which Canada is a signatory via Bill C-42 (1992). This international agreement imposes restrictions on the import and export of certain marine mammal species, largely based upon the status of their stocks in the wild. CITES import permits are the responsibility of the Canadian Wildlife Service, but only in cases where a CITES import permit is required. Almost all species of cetaceans are listed as Appendix II species[37], which states that an export permit or re-export certificate issued by the Management Authority of the State of export or re-export is required (but not an import permit from the receiving nation). An export permit may be issued only if the specimen was legally obtained, and if the export will not be detrimental to the survival of the species due to its removal from the wild population.

A panel of international experts convened by the World Conservation Union (IUCN) has summarized the concern over the impact of removals of individual cetaceans on the health of wild populations.[38] As the panel pointed out, “removal of live cetaceans from the wild, for captive display and/or research, is equivalent to incidental or deliberate killing, as the animals brought into captivity (or killed during capture operations) are no longer available to help maintain their natural populations." In theory, CITES regulations were established to prevent removals that threaten the viability of source populations from occurring.

However, the IUCN panel noted that targeted captures often take advantage of "lax, or non-existent" regulations in smaller, remote, or undeveloped nations without adequate assessment of population status. Subsequently, that panel made several suggestions about the removal of cetaceans from the wild for the purposes of live display, some of which have been incorporated into this report.

A subsequent review of the regulation of the trade of cetaceans under CITES found the process fraught with problems.[39] These included inaccurate and fraudulent reporting, false use of importation of cetaceans under education or breeding exemptions when the objective is clearly commercial in nature, and the lack of scientific rigour in the preparation, review, and evaluation of "non-detrimental findings" which allow for the export of live cetaceans for commercial purposes. Given the uncertainty related to the scientific validity of the population impact statements issued by some exporting countries, the Committee has recommended that the importing facilities in Ontario must take measures to ensure that the removal of wild-born cetaceans destined for import (either directly or via another facility) do not negatively impact their native populations (specifics given below).

While such conservation concerns emphasize the potential impact of removals on population numbers, there are additional scientific concerns associated with removals of cetaceans from the wild. A review of the literature has suggested that, for many common species, wild-born cetaceans have a lower initial survival rate than their captive-born conspecifics (summarized in *Life history*). Capturing individual whales from hierarchical social organizations in the wild can also have long-term consequences on the remaining animals in the wild population. For example, a study that simulated "captures" of individuals among resident killer whale pods found that removal of juvenile females (mimicking the trend of live captures for aquariums) had a particularly detrimental effect on group cohesion, and were likely to break the existing social network into isolated groups.[40] There are also concerns regarding the physiological impact of the methods used to capture cetaceans in the wild. Obviously, if captures of wild stock are to be permitted, they should only be designed to be humane, to have minimal physical and psychological impact on all animals involved, be planned and conducted by experts, and be supervised by a knowledgeable veterinarian. Even in the most humanely planned and executed operations, the capture session is likely to result in significant levels of stress for both the target individuals and their conspecifics. Therefore, the Committee wants to make it clear that cetaceans should never be acquired from drive fisheries or from other similar sources.

This last point highlights another concern regarding the source of imported cetaceans. There have been suggestions that the origin of some cetaceans is being deliberately obscured. This is of particular concern for wild-caught cetaceans being imported from aquariums that are effectively holding facilities for animals destined for export to other countries. For this reason, the recommendations of the Committee extend to cetaceans that are wild–born but are being imported from other facilities (again, specifics given below).

Given these scientific facts, we recommend that removals from the wild should be undertaken only under limited, well-defined, sustainable, justified, and well-documented circumstances. Barring any implementation of stricter federal regulation, the aim of the recommendations made by the Committee is to enable the Province of Ontario take steps to ensure the welfare of cetaceans being imported into the province and the viability of their source stocks in the wild.

We therefore make the following specific recommendations:

i. *Requirement to demonstrate a need for wild captures*: When considering new acquisitions, display facilities should do everything they can to obtain new or additional cetaceans from existing captive populations. Obtaining animals from the wild should be a last resort in order to attend to the welfare of existing individual cetaceans, and must be supported by a sound scientific population assessment (detailed below). The requirement for such individuals must be clearly justified in the facility's Animal Management Planned, as authorized by its Animal Welfare Committee. This justification must not only include the welfare basis for requiring the animal, but must also detail the reasons why this need cannot be met through either importing individuals already in captivity or exporting individuals from the host facility.

ii. *Conditions for obtaining cetaceans from the wild:* Before facilities import cetaceans acquired from the wild they must be able to demonstrate to the Government of Ontario that (i) there exists a genuine welfare concern that can only be remedied by such an action (as detailed above), and (ii) such removal will not compromise the sustainability of the wild stock or wild population from which the animals were taken, or compromise the ecosystem. This ecological evaluation should take the form of an independent report reviewed by a panel of external scientists that is prepared by the requesting facility. Consideration of status assessments made by CITES, IUCN, and relevant scientific assessments made in foreign nations or in Canada should be part of the report. For many cetacean populations, sufficient data with which to assess status is lacking, due to an absence of long-term monitoring programs to identify trends. If the population is data-deficient, such that a determination of healthy status cannot be made, no animals should be removed from that population.

iii. *Conditions for obtaining wild-born cetaceans from other facilities:* Before facilities acquire cetaceans from any source which were captured from the wild after 1996[41], the facility must be able to similarly demonstrate that such removals did not compromise the sustainability of the wild stock or wild population from which the animals were taken at that time using the criteria previously described. This will ensure that recently captured animals held by other facilities meet the same standards of scientific population assessment as animals acquired directly from the wild.

These proposed limits on the acquisition of cetaceans from wild populations are not intended to limit the introduction of animals under the following circumstances:

i. Cetaceans that were born in a zoo or aquarium at any time.
ii. Cetaceans that were rescued from the wild and rehabilitated but deemed non-releasable by the appropriate government authorities. In the case of animals held in foreign facilities, an independent review of the criteria and circumstances of this classification must be undertaken by recognized scientific or veterinary experts in Canada.
iii. Cetaceans where the Provincial or Federal government has requested a facility to step in and hold the animals.

Supporting information for Recommendation 3

We recommend a regulation that adopts the Guidelines on: The Care and Maintenance of Marine Mammals developed by the Canadian Council on Animal Care (CCAC) as a specific Standard of Care for marine mammals under the *OSPCA Act*.

The Canadian Council on Animal Care (CCAC) has been actively developing a set of guidelines for the Standards of Care of marine mammals in human care using input from scientists, managers, stakeholders, and animal care experts. These guidelines are comprehensive, and are the product of an extensive consultation and review process. While these guidelines do not take the needs of particular species into account, they do offer a detailed inventory of the most important Standards of Care for marine mammals

The *CCAC Guidelines on the Care and Maintenance of Marine Mammals* proposes a number of guidelines that can be designated as either “must” or “should”. The term “must” is used for cases that are obligatory while the term “should” is used to indicate a defeasible obligation. The Guidelines also provide supporting information that will be helpful to animal custodians as well as to OSPCA inspectors. Hence, we are recommending the adoption of the *CCAC Guidelines on the Care and Maintenance of Marine Mammals* as a single specific Standard of Care for marine mammals under the OSPCA Act, with the understanding that the “must” provisions be absolute minimum requirements while any exceptions to implementation of the “should” guidelines must be justified to, and approved by, an Animal Welfare Committee. While the CCAC guidelines are appropriate for the general needs of marine mammals, it is important to note that they still, in many cases, require subjective review and interpretation, as do other Standards of Care defined in the OSPCA Act.

The Committee notes that the *CCAC Guidelines on the Care and Maintenance of Marine Mammals* are not yet publically available, but are expected to be released in the near future. However, we felt it was important to utilize this product, after carefully reviewing each recommended guideline and determining whether it was appropriate or sufficient for our own purposes. Some of these guidelines are already covered under existing aspects of the OSPCA Act, including those related to adequate nutrition, general care and medical care, safe transportation, environmental and social living conditions, protection from harm, and humane treatment. Some of the proposed guidelines are also contained within parts of Recommendation 1 of this Report. However, we feel adoption of this document can only serve to strengthen the care given to marine mammals in captivity.

Notes and References Cited in Part 1

1 Ontario Regulation 60/09

2 Provincial Animal Welfare Act, 2008, SO 2008, c. 16- Bill 50.

3 Ontario Regulation 60/09: Standards of Care, Section 2(1-8).

4 Animals involved in activities associated with agriculture are exempt from some provisions of the OSPCA Act.

5 The OSPCA Act defines “distress” as the state of being in need of proper care, water, food or shelter or being injured, sick or in pain or suffering or being abused or subject to undue or unnecessary hardship, privation or neglect.

6 Ontario Regulation 60/09: Standards of Care, Section 1(4).

7 Ontario Regulation 60/09: Standards of Care, section 2.

8 Ontario Regulation 60/09: Standards of Care, sections 4 and 5.

9 OSPCA Act: section 11(1-3).

10 Veterinarians Act, RSO 1990, c V.3.

11 Criminal Code, RSC 1985, c C-46, sections 444-447.

12 Animals for Research Act, RSO 1990, c A-22.

13 Fisheries Act, RSC 1985, c F-14.

14 Fisheries Act, RSC 1985, c F-14, Marine Mammal Regulations (SOR/93-56).

15 Convention on International Trade in Endangered Species of Wild Fauna and Flora, www.cites.org.

16 Lien, J. 1999. Lien report: A review of live-capture and captivity of marine mammals in Canada. Department of Fisheries and Oceans, Ottawa, Ontario.

17 Ontario Community Safety Minister Madeleine Meilleur, October 25, 2013.

18 CAZA Accreditation Report on Marineland, 2013.

19 OSPCA Act: A Better Way Forward. Animal Justice Canada. A. Hamp-Gonsalves, N. Novakovic, E. Schoales, Z. Husrevoglu and N. dePencier Wright. December 2013.

20 OSPCA Act, Section 11(5.1).

21 There was public concern over an announcement by the OSPCA Chair that individual animals under veterinary care were exempt from the requirements of the OSPCA Act. However, this misinterpretation has since been clarified by the Minister as well as the OSPCA, and the Committee has determined that this issue does not require further consideration.

22 Many of the specifics on Recommendation #1 have been based on the work of the CCAC during the development of the CCAC “G*uidelines On: The Care and Maintenance of Marine Mammals*”.

23 CCAC Guidelines on: The Care and Maintenance of Marine Mammals – pending public release.

24 Code of Federal Regulations, US Government. Title 9 – Animals And Animal Products, Chapter I – Animal And Plant Health Inspection Service, Department Of Agriculture. Part 3 – Standards. Subpart E – Specifications for the Humane Handling, Care, Treatment, and Transportation of Marine Mammals under the Animal Welfare Act (AWA). Revised as of January 3, 2001.

25 Annex G: Supplement to the Secretary of State’s Standards of Modern Zoo

Practice: Additional Standards for UK Cetacean Keeping.

26 Ministry of The Environment, Brazilian Institute For The Environment And Natural Renewable Resources (Ibama), Regulation No 3 Of 8 February 2002. English translation.

27 Ministry of Agriculture, Fisheries And Local Government. The Marine Mammal Protection Act, 2005 (No. 12 Of 2005). The Marine Mammal (Captive Dolphin Facilities) Regulations, 2005. The Bahamas, 3rd October, 2005.

28 National Ministry of Natural Resources and Human Environment (SRNyHA) (Argentina). Resolution 351/95. Regulations governing oceanariums. Buenos Aires 18 September 1995. English translation.

29 www.eaam.org/jdownloads/Documents and Guidelines/eaam_standards_and_guidelines_for_the_management_of_bottlenose_dolphins_un der_human_care_sept_2009.pdf

30 The European Association of Aquatic Mammals recommended a 10-year timeline for the adoption of their guidelines.

31 For example, Marine Mammal Water Quality: Proceedings of a Symposium. 1998. U.S. Dept. of Agriculture, Animal and Plant Health Inspection Service, Technical Bulletin No 1868.

32 National Research Council (2008) Guide for the Care and Use of Laboratory Animals, Eighth Edition. National Academies Press, Washington DC.

33 Shepherdson DJ, Mellen JD, Hutchins M (1998) Second nature: environmental enrichment for captive animals. Washington, DC: Smithsonian Institution Press. 350 p.

34 Schusterman, R.J., Reichmuth Kastak, C., and Kastak, D. (2002) The cognitive sea lion: meaning and memory in the lab and in nature. In: The Cognitive Animal: Empirical and Theoretical Perspectives on Animal Cognition, M. Bekoff, C. Allen, G. Burghardt (Eds), MIT Press, pp 217-228.

35 http://laws-lois.justice.gc.ca/eng/regulations/SOR-93-56/index.html.

36 http://laws-lois.justice.gc.ca/eng/acts/s-15.3/.

37 Some species of cetaceans are listed in Appendix I of CITES (www.cites.org/eng/app/reserve.php). Such species are not eligible for import for commercial purposes such as display in aquariums.

38 Reeves RR, Smith BD, Crespo EA, Notarbartolo di Sciara G (2003) Dolphins, whales and porpoises: 2002-2010 conservation action plan for the world's cetaceans. IUCN/SSC Cetacean Specialist Group. Gland, Switzerland and Cambridge, UK. ix + 139 p.

39 Fisher SJ, Reeves RR (2005) The global trade in live cetaceans: implications for conservation. Journal of International Wildlife Law and Policy 8: 315-340.

40 Williams R, Lusseau D (2006) A killer whale social network is vulnerable to targeted removals. Biology Letters 2: 497-500.

41 This date is somewhat arbitrary but has already been implemented in the bylaws governing procurement of cetaceans for the Vancouver Aquarium.

Part 2: Scientific Review of the Welfare of Cetaceans Held in Public Display Facilities

Summary

This section provides a review of the welfare of cetaceans in public display facilities based on current scientific knowledge. This section examines the potential causes of stress for cetaceans living in public display facilities, evaluates the efficacy of a series of metrics in terms of their ability to provide information on the welfare of cetaceans held in these facilities, and summarizes what these measures tell us about the well-being of cetaceans held primarily for public display.

Managing the artificial environment to minimize stress and optimize well-being for captive animals requires an understanding of the environmental factors that are potentially stressful. There are several aspects of the aquarium environment that can potentially cause stress in captive cetaceans, although none are unique to this group, and most can be mitigated through proper husbandry and habitat design. Cetaceans have highly organized and complex social structures and attention must be paid to interactions among individuals. One of the most critical issues is to provide habitats that have adequate space and are arranged or shaped to allow individuals visual escapes from conspecifics to minimize negative interactions. Animals should be maintained in appropriate social groups, although these may not necessarily mimic those found in nature. An appropriate and varied enrichment program should be in place to prevent repetitive behaviours and stress associated with lack of stimulation. Given the reliance that cetaceans have on sound production and hearing, sound levels within the environment can detrimentally affect these animals and should therefore be carefully monitored over the full hearing range of the species. The nature and pattern of lighting can affect the physiological cycles of individual animals. Particularly, constant lighting in indoor enclosures can disrupt natural biological rhythms, and measures should be taken to limit natural UV exposure. An appropriate thermal environment is also essential to maintaining the health of individual animals. Finally, interactions with humans – both husbandry staff and the public – must be undertaken in a manner that ensures a positive, healthy experience for the individual cetaceans.

Many traditional life history measures (including reproductive rates and age structures) used to quantify the health of wild populations may be inappropriate to use with groups of captive cetaceans. Annual survival rates (ASRs) may provide a more robust measure to compare life history parameters among wild and captive cetacean populations or between groups of captive cetaceans. The relative survival rates of captive cetaceans in comparison to their wild counterparts seem to vary by species. There is evidence that cetaceans brought into captivity from the wild suffer a quantifiable level of mortality during the capture process. There are also data showing that wild-caught animals suffer higher mortality rates during their initial acclimation to captive environments, although their post-acclimation survival is approximately equivalent to that of captive-born individuals. There is

also evidence that ASRs have historically improved among facilities for many commonly held species of cetaceans. In addition, ASRs have been found to differ between facilities, providing a possible metric with which to identify specific animal care issues at these facilities.

Bacterial pneumonia is the most common identified cause of mortality among both wild and captive cetaceans. Historical mortality rates for captive killer whales due to pneumonia appear to be particularly high; however advances in veterinary treatment have lowered this frequency in captive individuals. Most diseases reported for captive cetaceans are also common in their wild counterparts, although there are no data to directly compare rates of infection or resulting mortalities. One notable exception is the higher prevalence of “droop fin” among captive male killer whales (although the health impact of this phenomenon is unclear). Conversely, captive cetaceans are known to have a lower parasite load, which should contribute to lower morbidity and mortality.

Studies have demonstrated that cetaceans show physiological responses to stress that are typical of other mammals, although the nature of the stress response varies considerably by species. Studies show that transport, arrival at a new facility, and the introduction of new “pool mates” can lead to stress in several species. Short-term stress responses have been demonstrated to occur in animals that are captured and handled for sampling (e.g., blood, heart rate, etc.), even if these individuals have been frequently handled for other procedures in the past. Unfortunately, this rapid onset of the stress response during the sampling process can disguise other physiological changes of interest, including pre-existing stressors. Training of individual captive animals for voluntary participation in sampling procedures can reduce handling-associated stress and enable husbandry staff to more accurately monitor stress signals in individual cetaceans in their care. In cases where the animals are well trained, individuals do not display hormonal changes that would indicate heightened physiological stress compared to their wild counterparts. However, this type of voluntary sampling is not universal, thereby restricting the number of meaningful comparisons between groups of animals. The development and testing of alternate sampling methods will improve our ability to monitor individual animals in captivity and make direct comparisons to their wild counterparts.

Behavioural observations can be used as an inexpensive means to assess animal well-being. A reliable observer program by husbandry staff can identify several indicators of medical and psychological issues early in their development. Lack of appetite and lethargy are strong behavioural indicators of physical or psychological concerns. Incidents of stereotyped behaviour (e.g., body rubbing, repetitive body motions) and self-harm behaviours (cribbing, vomiting) are also strong indicators of suboptimal holding conditions or other sources of stress (including lack of appropriate enrichment). The frequency of reports of such incidents has decreased through the years, although it is unclear whether this is due to improvements in husbandry practices or trends in journal publishing. Seemingly repetitive swimming patterns should be classified with caution, as they may be the natural result of physical restrictions of the habitat rather than stereotyped behaviour *per se*. Perhaps the most recognizable behavioural indicator of social issues within the habitat is aggression. While wild animals also exhibit aggressive behaviour, behaviours due to natural inter-animal aggression can become exaggerated in captive individuals due to the inability of other animals to escape as they might in the wild or because of the creation of “artificial” social groups. This can also result in “nervous” animals. Occurrence and effects of aggressive behaviour can be minimized by appropriate social groupings and pool design that allows visual separation of individuals in potential conflict. Changes in the production of acoustic signals can be used as possible measures of stress and conflict in some cetacean species, although monitoring and interpretation may require a degree of specialized equipment and skills.

2.1 Framework and Overview

1. Goal of the review:

This section provides a review of the welfare of cetaceans in public display facilities based on current scientific knowledge. Specifically, the report undertakes the following tasks:

i. Identify and discuss potential sources of stress in cetaceans held in public display facilities.
ii. Identify and evaluate potential metrics for measuring stress in cetaceans.
iii. Review published scientific information regarding the well–being of cetaceans using these measures.

This review will provide a scientific basis for the recommendations forwarded in Part 1 of this report (facilities, monitoring, and training) that ensure the welfare of cetaceans and other marine mammals held in display facilities.

2. Cetaceans being evaluated

This review only considers the welfare of cetaceans in facilities in which the primary goal is public display, regardless of whether facilities undertake a degree of research or are involved in the rescue and rehabilitation of wild animals. By extension, this review partially excludes facilities for which the primary objective is research. However, it does use the scientific results of the research that is conducted at these types of facilities.

3. Ethics of managed animal populations

This review is undertaken upon the premise that it is generally acceptable for animals to be kept in facilities such as zoos and aquariums. While there is an arena of ethical debate on this point, this discussion is outside of the goals of this review. Rather, the aim of this review is to assess the scientific evidence regarding the well-being of cetaceans held in display facilities. Given the premise that it is acceptable to keep animals in display facilities, the question then becomes whether there are specific issues or concerns associated with the welfare of cetaceans in particular, compared to other captive animals.

4. Justification of managed animal populations

Facilities that hold cetaceans for public display often cite the value of their animals for scientific advances, conservation, rehabilitation, captive breeding, and public education. While this is a valuable discussion to undertake, these justifications for maintaining marine mammals in captivity are outside of the mandate of this report. Additional information on some of these topics can be found in a variety of publications and books.

Some resources discussing the value of zoos and aquaria on public conservation education include:

Balmford A, Leader-Williams N, Mace GM, Manica A, Walter O, West C, Zimmermann A (2007) Message received? Quantifying the impact of informal conservation education on adults visiting UK zoos. Conservation Biology Series-Cambridge 15: 120-136.

Barney EC, Mintzes JJ, Yen C-F (2005) Assessing knowledge, attitudes, and behavior toward charismatic megafauna: The case of dolphins. The Journal of Environmental Education 36: 41-55.

Frost W (2010) Zoos and tourism: conservation, education, entertainment? Channel View Publications.

Marino, L., Lilienfeld, S. O., Malamud, R., Nobis, N. and Broglio, R. 2010. Do zoos and aquariums promote attitude change in visitors? A critical evaluation of the American Zoo and Aquarium study. Society and Animals, 18: 126-138.

Miller L, Zeigler-Hill V, Mellen J, Koeppel J, Greer T, *et al.* (2013) Dolphin shows and interaction programs: benefits for conservation education? Zoo Biology 32: 45-53.

Skibins JC, Powell RB (2013) Conservation caring: Measuring the influence of zoo visitors' connection to wildlife on pro-conservation behaviors. Zoo Biology 32: 528-540.

Some discussion on the value of captive marine mammal breeding programs can be found in the following:

Ames MH (1991) Saving some cetaceans may require breeding in captivity. Bioscience: 746-749.

Ding W, Yujiang H, Kexiong W, Quingzhong Z, Daoquang C, Zhuo W, Zhang X (2005) Aquatic Resource Conservation. The first Yangtze finless porpoise successfully born in captivity. Environmental Science and Pollution Research 12: 247-250.

Seddon PJ, Armstrong DP, Maloney RF (2007) Developing the science of reintroduction biology. Conservation Biology 21: 303-312.

One aspect of this discussion that the Committee feels does warrant brief mention is the value of scientific studies conducted with captive marine mammals. There have been suggestions that there is little (further) scientific value to be gained from studying cetaceans in aquariums [1] [2]. However, several published reviews have highlighted the scientific information pertaining to animal care and conservation that have been obtained from managed cetacean populations [3] [4], including additional reviews encompassing two issues of the *International Journal of Comparative Psychology* (2010; issues 23.3 and 23.4). While Rose *et al.* [5] calculated that only 5% of scientific studies concerning cetaceans derived from work conducted with captive individuals, a more comprehensive review estimated this figure to be closer to 30% [4].

5. Types of information considered

Any assessment of the relative well-being of captive cetaceans obviously requires some form of comparison between groups of animals. One comparison would be to examine the well-being of cetaceans in captive environments with other (equivalent) groups of animals also held in zoos and aquaria. This would perhaps supply the most direct answer to the question of whether being maintained in public display facilities is particularly detrimental to cetaceans. However, it should be noted that inevitable difficulties arise regarding the validity and nature of cross-species comparisons, even in choosing the appropriate species (or groups of species) with which to compare cetaceans.

Alternately, comparisons can be made between captive populations of cetaceans and their wild counterparts. This approach has the benefit of providing the most direct comparisons across conspecifics that differ in their “habitat” (i.e., wild vs. artificial). However, this approach cannot directly address the issue of whether there are specific issues pertaining to the well-being of cetaceans (i.e., it cannot determine whether any observed differences are unique to this group). In addition, these comparisons can be handicapped by a lack of suitable data from wild cetaceans, natural variation in key characteristics between different wild populations at different times, and small sample sizes within captive and wild populations that make statistical tests inappropriate.

6. Information sources:

The goal of this review is to provide an overview of the current state of scientific knowledge. Hence, we have largely limited our review to scientific results published in the primary literature (i.e., scientific journals), as these have undergone extensive peer review. Exceptions have been made in cases where we feel that data available from other sources is both reliable and too valuable not to include.

The primary tool for this review was a thorough search of the primary (peer-reviewed and published) scientific literature. This was accomplished by using recognized electronic databases, supplemented with non-electronic reviews, including a literature review by Hill and Lackups [4].

We also put out a public request for information on the MARMAM listserve (https://lists.uvic.ca/mailman/listinfo/marmam), which is the primary public communication tool for marine mammal scientists, conservationists, educators, and advocates. There are approximately 8,500 individuals that receiving postings to this list. This action served to invite any interested party to submit information on areas of research that would be valuable to this Committee in its review. A list of the individuals and organizations that responded to this inquiry is provided in Appendix B.

In addition, we explicitly contacted several individuals who had previously expressed interest in any potential changes in the regulatory structure of captive cetaceans in Ontario. Some of those contacted chose to provide submissions to the Committee.

We also consulted several “grey-literature” reports (i.e., these have not been vetted by the scientific peer-review process). However, we felt that these documents were important pieces of work that would help the Committee by ensuring that we had not missed significant publications in the primary literature, and that we had addressed the relevant areas of concern raised by these reports. These reports included (but were not limited to):

Rose NA, Parsons ECM, Garinato R (2009). The case against marine mammals in captivity (4th edition). The Humane Society of the United States and the World Society for the Protection of Animals.

Mayer S (1998) A review of the scientific justifications for maintaining cetaceans in captivity. Whale and Dolphin Conservation Society.

Lien Report: A review of live-capture and captivity of marine mammals in Canada. Prepared for the Dept. of Fisheries and Oceans Canada, 31 March 1999.

Throughout all aspects of the review process, the Committee used an extensive network of professional marine mammal scientists for a number of tasks. In the case of apparent gaps or discrepancies in the scientific literature, we consulted recognized scientific or veterinary experts for additional sources of information, to confirm that published data was not available, or to assist the Committee in understanding the sources of the scientific debate. Experts were also contacted to assist with the writing of or review of specific areas of research that the Committee members felt required outside expertise. Experts also provided unpublished data when the Committee deemed that this information was central to a specific topic area.

2.2 Potential Environmental Sources of Stress

In any discussion of the welfare of cetaceans held in display facilities it is important to identify which aspects of those facilities may be most important for the well-being of this group of animals. Understanding which environmental factors are potentially stressful allows management of the artificial environment in such a way as to minimize stress and optimize the well-being of individual animals. Hence, the identification of potential stressors to cetaceans held for public display, and understanding means of mitigating them, is key to evaluating and ensuring the welfare of these individuals, regardless of any ultimate discussion of whether they should continue to be held for this purpose.

In the context of this report, a review of the potential sources of stress should serve as an aid to facilities for maximizing the well-being of cetaceans in their care. Within each section, we have provided information on how these factors might affect individual cetaceans, and made suggestions where possible regarding how to mitigate any negative effects. In addition, this review serves to provide scientific justification for many of the specific recommendations provided in Part 1 of the report. When appropriate, we have provided cross-references to the specific recommendations forwarded in Part 1.

In their general review on the subject of stressors experienced by animals in captivity, Morgan and Tromborg [6] divide stimuli into “abiotic stressors” and “confinement-specific stressors”. The former category encompasses environmental stimuli that are present in some form in every environment (e.g., light, sound, physical substrate, etc.) but may be altered in their nature within a display environment. The latter category includes stimuli that are largely unique to display situations and over which the animal has little or no control. For the purposes of this review, we adopt these two primary divisions and include many of the secondary divisions of this original framework, with modifications and emphasis as appropriate to a discussion focused on cetaceans.

Abiotic Environmental Stressors

Increased concern for the well-being of animals held in public display facilities has led to specific advancements in the quality of their physical habitat. This includes incorporation of features that increase animals’ behavioural opportunities, as well as altering the physical environment to make it healthier (e.g., controlling disease vectors) and more suitable to the specific physiology of target species (e.g., light and sound levels). Many of the changes have been implemented using a “common sense” approach, but there has also been an increased effort to incorporate scientific information in the design of these changes and to quantify and test the effect of these changes on animal well-being. The aim of all of these efforts has been to produce an artificial habitat that minimizes the negative aspects of that artificiality by mimicking or incorporating physical aspects of the animals’ natural environment as much as possible given the physical realities of a display facility.

The following sections describe aspects of the physical environment of cetaceans in aquariums that, while also present in their natural habitat, may differ in their quality or variation within their artificial holding area.

Sound levels

One of the earliest lines of scientific research with cetaceans focused on their sound production capabilities, given their reliance on sound to navigate, communicate, and find resources in the wild [7]. By extension, the field of bioacoustics also started to flourish with studies on the specific auditory capabilities of cetaceans.

Historically, auditory tests have utilized behavioural responses to determine whether animals are able to hear a given tone (sound frequency) at a given volume (signal amplitude). Advances in computer technology and neurobiology have also permitted scientists to carry out physiological studies where they can record the 'detection response' of the animal by measuring neural responses to sound stimulation. Such behavioural and physiological hearing tests result in species-specific audiograms, which - simply put - describe an animal's hearing range and sensitivity. Using these methods, there have been a number of high quality audiograms measured for individuals from a number of cetacean species that, among other things, can be used to describe the types of sounds that these animals can hear and are most sensitive to.

Ironically, because of the way that sensory systems are studied, we understand best the hearing range for those species that are kept in captivity. In general, species of odontocete whales such as bottlenose dolphins, killer whales and belugas have extremely sensitive hearing that is especially tuned to high frequencies in excess of 20 KHz [8]. This high-frequency hearing sensitivity exists in part because of the need for these species to use high frequency echolocation [9] as part of their natural hunting and orientation behaviours. In addition, because they have evolved in an aquatic environment where vision, smell, and taste have limited range, sound becomes the dominant sensory modality [10]; thus, cetaceans likely depend on sound to the same extent that humans depend upon vision to assess their environment. Captive studies have also provided information about the ability cetaceans to hear signals within masking noise, the directionality of detection, and the abilities to discriminate sound frequencies and temporal patterns [9]. In brief, cetaceans have demonstrated extraordinary auditory capabilities compared to many other mammalian species. One caveat to note, however, is that auditory data obtained from captive individuals are constrained by individual variation, and may not necessarily represent the hearing range or capabilities of the species as a whole.

The detrimental effect of loud sounds on mammalian physiology is also an area of ongoing scientific investigation [8,11]. This includes the potential effects of both periodic and constant noise sources. In general, excessive sound exposure causes elevated levels of arousal, producing both short- and long-term changes in behaviour and physiology [12]. There is an accumulating body of knowledge on the effects of anthropogenic noise sources (e.g., military and industrial activities) on the behaviour and physiology of wild cetaceans [recent examples include 13,14-16]. In instances of low acoustic impact, cetaceans can habituate to noise. However, in the most serious cases, exposure to sound could cause pain, temporary or permanent deafness, tissue rupture, and bone damage [8,17,18,19,20], as observed in other mammals.

Given the importance of sound and the enhanced sensitivity of many cetaceans species [7], and the scientific recognition that sound exposure can be particularly detrimental to this group of mammals [21], it is surprising that there are few studies examining the effects of different sound sources in aquaria on cetacean behaviour or physiology, or even cataloguing these auditory sources. A few studies that have examined noise levels within aquariums have primarily focussed on the concern of the effects of noise on fish [e.g., 22]. A recent study conducted at the Georgia Aquarium specifically (although not exclusively) examined noise levels within the marine mammal habitats [23]. In general, these studies note that the most significant levels of background noise (at least those produced within the potential hearing range of cetaceans) are produced by the pumps and motors associated with the water circulation and cleaning (life support) systems. The received level of the direct noise produced by these mechanics is dependent upon both the distance of the machinery from the habitat and the acoustic design of the pool (shape, depth, and materials).

It is also important to consider that the potential effects of noise on cetaceans may not be limited to their auditory range, but that disturbances may also be caused by their ability to detect low-frequency vibrotactile signals transmitted through the water [9]. In fact, it has been suggested that such signals may present the most significant acoustic challenge to cetaceans in captive facilities [23].

The acoustic profile of the machinery associated with the production of noise in aquaria can be significantly altered through seemingly minor modifications to the mechanical operations. For example, loose metallic parts can cause significant “banging”, while slight changes in pump efficiency can cause major changes in transmitted vibrations. Hence, any acoustic evaluation of the acoustic environment of cetaceans should include an on-going monitoring program to detect significant changes over time.

Another important aspect of the auditory landscape in aquaria is the noises contributed by the general public and the facility’s “shows”. Crowd noises can be loud and unpredictable, and there have been reports of increased vigilance behaviour with increased crowd sizes in harbour seals [Suarez and Morgan, quoted in 6]. However, it is not clear whether sound levels are the affecting agent *per se*, and there have been no published studies on any potential effect of crowd noise on cetaceans. Of greater concern are the sounds generated by a facility’s sound system, which can include vocal interpretation and/or music. These sounds can take the form of either in-air disturbances or – depending on the arrangement of the sound amplification system – can contribute to the aquatic acoustic profile. This is particularly true if the public address systems are placed over the water, since sound pressure transmission is particularly effective in the vertical plane [23].

Another source of acoustic disturbance is construction in or near the facility. This can represent a significant source of unpredictable noises in the cetaceans' habitat. Quite often, the exact effect is difficult to predict, and careful monitoring is therefore essential. For example, the Vancouver Aquarium implemented a sound-monitoring system in one of their cetacean pools during recent renovations that not only keeps a cumulative record of sound exposure, but also sends an automatic alert to curatorial staff if pre-set acoustic thresholds are exceeded.

It is important to keep in mind that the acoustic range of cetaceans is significantly different than humans, particularly in their capacity to hear ultrasonic (>20 kHz) sounds. Hence, periodic assessments are important in monitoring these frequencies, in the underwater environment, given that increases in ultrasonic anthropogenic sound sources will not be readily apparent to curatorial staff.

All of the previous discussion is related to concerns regarding whether there is "too much" noise in the acoustic environment of an aquarium tank. However, Dr. Paul Spong, a Canadian cetacean researcher (Director, OrcaLab, British Columbia) argues that it is lack of appropriate acoustic stimulation is also an important concern. He suggests that, in comparison to the "rich acoustic world to which cetaceans are naturally exposed to" an artificial aquarium setting, with its lack of relevant acoustic enrichment, presents a form of sensory deprivation. Given this statement, sound is an important aspect of the aquarium environment that should be carefully considered when addressing means of designing and enriching the overall environment of the captive whale's habitat.

The available scientific knowledge supports the recommendation that marine mammals in display facilities must be protected from exposure to noise that could cause auditory discomfort or distress and lead to injury. This includes the recommendation that an auditory monitoring program be instituted for cetaceans kept in aquariums. Additional details of this recommendation are presented in Part 1 of this report.

Light conditions

It is well-known that the amount and structure of the light available in a captive habitat must be considered in order to maximize animal welfare [24]. There are three areas of special concern regarding illumination in habitats that can potentially affect the well-being of cetaceans: type of lighting, light cycles, and intensity. Concerns with the type of light sources and the photoperiod the animals experience in captivity are largely minimized if the animals are held in an outdoor enclosure. However, light intensity may still be an issue, even with a natural light source.

There has been some research on the visual pigments that define the visible spectrum of cetaceans [e.g., 25,26,27]. Different light sources have a different spectral composition in that they give off different wavelengths from natural light. For example, fluorescent lighting is frequently used in display facilities given its low cost and maintenance requirements. While "flickering" of such lights may cause problems for cetaceans, there are no studies that have investigated whether the differences in emitted light frequency have any affect on cetacean behaviour or physiology.

In contrast, there is a large body of evidence that artificial photoperiods can have pronounced physiological effects on mammals. In general, exposure to continuous or extended light cycles can alter melatonin and serotonin levels, with significant effects on the functioning on the central nervous system [28]. In addition, disruption of the animal's natural circadian activity affects hormonal control of a number of biological systems, most notably those governing sleep, reproduction and food intake [29]. Even short-term exposure to continuous photoperiod has been associated with increased plasma corticosterone levels in rats [30]. While most display facilities do not keep their main lights on continuously, the presence of lighting for security and/or in underwater viewing areas will also have an effect on perceived photoperiod.

When animals are housed in facilities that are out of their natural geographic range, the changes in photoperiod and the intensity of light may be problematic. The intensity of light, on its own, can have a significant effect on the behaviour and health of cetaceans. Intense, uneven lighting can cause high contrast shadow areas that may elicit fear or other behavioural reactions in some species. Conversely, shaded areas may provide areas of refuge or from relief from UV exposure. The reactions and requirements of individuals are likely both species and age-specific.

The topic of UV exposure is one that has been studied in captive cetaceans. There is evidence that increased UV exposure results in increased prevalence of epidermal and visual health issues [31,32,33]. It has been suggested that these issues are more prevalent in display animals due to the clarity of the water, animals spending more time at the surface (e.g., interacting with trainers), and animals having minimal opportunity to escape intense exposure by increasing their preferred depth in the water column. Some facilities have installed shaded areas to alleviate the effects of UV exposure, and pool colour and reflectivity also plays a role in mitigating or exacerbating this factor.

Given this scientific information, we recommend that provisions must be made for appropriate light exposure, including consideration of the type, level, and cycle of exposure. This includes the recommendation that display facilities take measures to limit the exposure of cetaceans and other marine mammals to UV radiation and that the photoperiod conditions provided to marine mammals that live indoors should be carefully considered.

Thermal environment

Thermal conditions constitute one of the primary factors for delineating a species' geographic distribution [34]. When endotherms are outside of their thermoneutral zone (i.e., conditions are too warm or too cold) they must expend additional energy to maintain their core body temperatures within a narrow, optimal physiological range. In addition to the energetic cost of thermal compensation when animals are outside of this optimal range, inappropriate thermal environments will alter behaviour and appetite, and can result in increases in circulating stress hormones. In the wild, animals can often move to find a more suitable thermal location when environmental changes occur, an option that is obviously curtailed in captivity.

In many countries, there are specific thermal criteria for holding specific types of animals (although these are almost exclusively aimed at research laboratory facilities). The goal of these recommendations is to ensure that animals are housed in enclosures that provide environmental temperature and humidity ranges appropriate for the species. In the US, Dept. of Agriculture (APHIS) regulations governing marine mammals held in indoor pools state that "*the air and water temperatures in indoor facilities shall be sufficiently regulated by heating or cooling to protect the marine mammals from extremes of temperature, to provide for their good health and well-being and to prevent discomfort, in accordance with the currently accepted practices as cited in appropriate professional journals or reference guides, depending upon the species housed therein. Rapid changes in air and water temperatures shall be avoided*."

While these regulations use the phrase "*in accordance with the currently accepted practices as cited in appropriate professional journals or reference guides*", in truth there are no empirical studies measuring the thermoneutral zone of cetaceans, except for the bottlenose dolphin [35,36].

As previously noted, quite often animals are kept in facilities far from their natural geographic location. Their preferred thermal environment is largely innate, although the specificity of the required thermal environment can be mitigated by an inherent physiological flexibility and adaptability to suitable water temperatures. However, this physiological capacity is limited, and the opportunity for behavioural adaptations (e.g., moving between microclimates including changes in depth) is almost non-existent. Therefore, it is imperative that these animals are kept in pools with appropriate water temperatures. These temperature ranges may be specific to subpopulations, particularly for species with extensive total distributions.

Importance of maintaining an adequate thermal environment is most critical when animals are moved from one extreme climate to another (e.g., moving polar animals to a tropical climate). For cetaceans, keeping warm tends to be less of a physiological issue than staying cool, except perhaps for physically smaller species. Within aquaria, maintaining water that is cool enough is usually more of an issue than the reverse for logistical reasons. In an aquarium, inadequate water turnover and circulation can cause surface water temperatures to become elevated beyond that which is possible in local oceans. In addition, cetaceans in aquaria have no access to (and thus cannot utilize) cooler, deeper waters for thermoregulatory control.

This concern is specifically addressed in US Dept. of Agriculture (APHIS) regulations for outdoor enclosures, which require that "*No … warm water dwelling species of … cetaceans shall be housed in outdoor pools where water temperature cannot be maintained within the temperature range to meet their needs*."

Many facilities use chilling units to generate water temperatures appropriate for display cetaceans. Care must be taken, however, that the machinery required for this task does not contribute to environmental noise issues (discussed in *Sound levels*). It is also important to note that shading put in place to minimize UV exposure (see *Light conditions*) will also serve to decrease heat absorption by pool water.

Confinement-specific Stressors

The previously described environmental stimuli are those that a cetacean may normally encounter in the wild, but a captive individual is unable to exert the same level of behavioural exposure control within the confines of display facilities. For example, cetaceans in the wild may be able to move from areas with high ambient sound levels to quieter areas, thereby mitigating any potential stress from these sources. This next section describes those environmental stimuli that are unique to the aquarium environment and where the individual cetacean has no ability to modify its level of exposure to these potential stressors.

Restricted movement (pool size)

On first consideration, it would seem fundamental that small enclosures and their inherent limitation on movement would be a prime determinant of the level of stress in captive animals. Certainly, early studies on animal abnormal behaviour supported this hypothesis [e.g., 37 and others]. However, a more complete examination of the scientific data suggests that there is a significant difference between the concepts of "larger" and "optimal" enclosure sizes.

For many mammals, there is a body of scientific evidence that excessively small enclosures are related to a variety of negative characteristics in a range of terrestrial vertebrates [partially reviewed in 6]. Reported effects of small cages include increases in agonistic behaviour, reductions in overall activity, decreased growth rate (often interpreted as an indicator of chronic stress response), and diminished reproductive behaviour and capacity.

Moving individuals out of excessively small cages almost always has beneficial effects on behaviour and physiology. Yet, there is competing evidence that moving animals into larger and "more natural" zoo environments can also increase stress levels. This seems intuitive for animals that are hunted in open spaces, such as small rodents. However, several studies have found no change or an increase in abnormal behaviour patterns when primates were moved to larger, more naturalistic exhibits [38,39,40].

Cetaceans in the wild have individual home ranges that far exceed the pool size capacity of any aquarium. The same may be said of most, if not all, large mammals held in zoos and aquaria. There is an underlying assumption in pool size design and regulations that larger, deeper pools will be beneficial to cetacean well-being. This generalization is not wholly unwarranted, although it should be noted that some cetacean species naturally inhabit relatively shallow waters, and that some studies (discussed below) suggest behavioural preferences may not necessarily be for the largest available pool.

There have been suggestions that "open" holding pools are better for cetacean welfare than typical closed aquarium pools. Open pools are constructed using netting or fencing (either to form a complete enclosure or to section off a portion of a natural inlet) and are situated within larger natural bodies of water. A comparative study of aquaria using open and closed holding systems found that a greater proportion of time was spent swimming in open enclosures (unfortunately, it is unclear whether there were differences in pool size), but that cortisol levels were not different between animals in the two types of habitat, suggesting no differences in physiological stress levels [41]. A review of several metrics of individual animal and population health indicated that bottlenose dolphins in the US Navy program (which are housed in open sea pens) was equal to or better than those of other captive populations [42]. Unfortunately, it is not known the degree to which any single metric was dependent on the habitat type or other management or environmental variables.

As previously noted, it is generally accepted that pool sizes that are "too small" will be detrimental to cetacean well-being. However, the exact measure of "too small" remains undefined. It may come as a surprise that Canada currently has no regulations concerning minimal pool size requirements for any marine mammals, including cetacean species.

While there is little international consensus on what constitutes adequate space for any particular species, in the United States the criteria for cetacean space requirements were established by the US Dept. of Agriculture in 1979. For cetaceans, the minimum space required in a primary pool must address four factors: minimal horizontal dimension (MHD), depth, volume, and surface area. Exact dimensions are further differentiated according to the "type" of cetacean (essentially a classification into 2 groups). These minimal values are further modified by group sizes. While the regulations are very detailed, there is still debate over their exact interpretation, such as whether space is determined as a total or as a continuous measure. This is exemplified in recent debate over whether orca habitats with an internal "island" meet government regulations.

These legal requirements are formulated on a concept of reasonable practices. For example, required pool sizes logically increase for physically larger species and for larger group sizes. However, assuring adequate habitat size may require more specific adjustments to suit the specific needs of different species. For example, it has been hypothesized that species that are migratory or naturally roam over greater home ranges will have more difficulty thriving in constrained environments than more 'resident' species. This hypothesis was supported by a comparative study among mammalian carnivores [43,44], although no such inter-specific study of cetaceans has been undertaken. There is a similarly untested hypothesis that shallow water species will fare better in aquaria than deep diving species, given the inherent restrictions on dive depth in such facilities [45].

While the adequacy of pool sizes may be the most frequently cited concern for holding cetaceans in aquaria, there are few studies that can be used to evaluate the impact of pool size or physical features on cetacean behaviour or welfare. There is some older observational information demonstrating increases in head-rubbing behaviour by bottlenose dolphins upon moving to smaller pools, although other simultaneous environmental changes (including social arrangements, health of conspecifics, and show requirements) raise questions regarding the actual trigger for this behaviour [46]. Other older studies have reported that confining bottlenose dolphins to smaller pools have, in some cases, resulted in increased aggression [47,48]. Bassos and Wells [49] reported that dolphins swam (in circles) more frequently in larger pools, while they remained floating motionless more often when confined to small pools. There is anecdotal evidence that some dolphins, given an option, choose to stay in a larger pool by resisting gating into their smaller holding pools after a performance [48]. However, a study on tank size preference came to the somewhat surprising conclusion that bottlenose dolphins preferred intermediate sized pools (whether measured as depth, surface area, or volume) [50].

Pool shape may also play a role in cetacean well-being. There is a report that pools which are more oblong than circular may be more conducive to successful nursing in killer whales, apparently by allowing greater manoeuvrability [51]. The potential impact of pool shape (particularly in relation to social aggression) is explored separately (see *Absence of retreat space*).

One of the more detailed behavioural analyses of the effects of pool size and configuration on behaviour was conducted not in a public aquarium but at the research pools of the Long Marine Lab, at the University of California, Santa Cruz. Bassos and Wells [49] examined the effect of pool features on the behaviour of two bottlenose dolphins housed in either a 54-ft diameter pool (which was larger in both horizontal and vertical dimensions,) and a 30-ft diameter pool. However, it is important to note that the pools also differed in other aspects: the larger pool had sloping walls and bottom, while the smaller pool had a flat bottom and vertical wall. This demonstrates problems with *in situ* experiments where multiple factors could be affecting performance measures.

The Bassos and Wells study reported that both dolphins travelled more in the larger pool, and rested more frequently in the smaller pool (these behaviours were mutually exclusive). The authors suggested that the behavioural parameters for which significant differences were found were those that would be limited more by horizontal dimensions than by any of the other physical attributes of the pools.

Following, the pool with the greatest horizontal space was used more for swimming and less for resting. However it should be noted that the depths of the two pools were very similar (2.4 m vs. 1.8-2.1 m) and thus depth preferences could not be assessed. The authors also suggested that in both pools the dolphins spent significantly less time swimming than wild conspecific from the same population. Bassos and Wells further hypothesized that increasing pool size enhances energetic opportunities for the captive cetaceans and may decrease aggressive encounters, although no such changes were reported in their study.

Thus, while pool size appears to be an important criterion for behaviour and stress, the quality of the habitat is also important. Habitat quality not only pertains to the physical aspects, but also the opportunities for appropriate social interaction and behavioural opportunities.

Given that the available science highlights the importance of pool size to cetacean well-being, we recommend that consideration must be given to the three-dimensional environment in which marine mammals live and the need to provide sufficient space for species-appropriate activities both in and out of the water. As such, pools must provide sufficient space, both horizontally and vertically, so that the animal can make normal postural and social adjustments with adequate freedom of movement. We recommend that facilities that hold cetaceans must formally adopt a written code for minimum size requirements, based on internationally-recognized standards. Additional details of this recommendation are presented in Part 1 of this report.

Absence of retreat space (pool shape)

In addition to the consideration of absolute pool size, the configuration and shape of a pool can affect the well-being of a cetacean. This is primarily important in the opportunity for individuals to “escape” (or break visual contact) with other members of their social group. Secondarily, these features can contribute to aspects of environmental enrichment.

As discussed later in the section *Behaviours related to aggression*, agonistic interactions are the most commonly documented behavioural indicators of welfare concerns among display cetaceans. While aggressive social interactions may be more prevalent as a result of “abnormal” or novel social groupings (see *Abnormal social groups*), they also occur as part of normal cetacean life history in natural environments, particularly in relation to breeding cycles. Many of the documented instances of aggressive behaviours between cetaceans held in the same pool have been attributed to a lack of opportunity for the target individual to visually escape from the aggressing individual. It is assumed that the target individual moving away from the aggressor, an option that is obviously limited in captive facilities mitigates such social dynamics in the wild. Pool geometry should therefore be a design consideration, in order to provide appropriate “retreat spaces” to lessen the incidence and intensity of agonistic interactions. In pre-existing pools, consideration should be made for opening connections between pools to allow ‘escape’ behaviours during agonistic encounters.

Proximity to humans

There have been several well-known examples of cetaceans having an apparent interest in interacting with humans in the wild. In some cases the animals clearly benefit from supplemental feeding that occurs during these interactions, while the tangible benefit to them in other types of encounters is more open to debate (although frequently they are labelled as positive social interactions for both species). However, most cetaceans do not freely interact with humans, and even the most "social" groups in the wild avail themselves of the opportunity to voluntarily break off encounters with human contact.

In an aquarium, there is much less opportunity for cetaceans to avoid both the public and the caretaking staff. Hence, the (constant) proximity to humans may be greater than is comfortable for some species or individuals. The degree to which forced proximity potentially negatively impacts the welfare of cetaceans depends largely on the nature of the interactions and the ability for individuals to escape or avoid such contact. However, the nature of the relationship between the individual cetaceans and these two groups of humans obviously differs, and must be considered somewhat separately.

Interactions with aquarium staff

The "comfort level" of human contact for different types of animals or even individual members of the same species is a complex, and dynamic value. In general terms, species differ in their flight distances from humans [reviewed in 52]. These natural tendencies are decreased when individual animals are exposed to human interactions under positive conditions, such as through good caretaking (and appropriate training) in zoos and aquaria. Most professional marine mammal trainers would argue that there is not a species currently held that has not proven to be amenable to a close relationship with its husbandry staff, when the latter act with the best interests of the animal in mind. Opponents of holding cetaceans in captivity would characterize the relationship less favourably. However, there is ample evidence that consistent positive and/or gentle interactions between animals and their human handlers results in decreased flight behaviours and physiological stress, and increased reproductive rates [reviewed in 6]. There is also evidence that frequent close contact with humans can serve as a form of environmental enrichment, particularly for social animals.

In general, cetaceans are provided with food reinforcement for successfully undertaking specific tasks, which can vary from cooperative husbandry behaviours to show performances. How these interactions affect animal welfare likely depends on the options available to individual animals if they do not wish to take part in human-initiated tasks. Actions that may cause concern are the withholding of food to force the animal to interact (as discussed in *Restricted feeding and foraging opportunities*), and restricting the space where the animal can retreat to remove itself from the interaction.

The latter action occurs when animals that do not wish to interact with humans (staff or the public) are restricted from moving to parts of the habitat where they may feel more secure. This often takes the form of “gating”, whereby an animal is physically restricted from moving into a pool that is either smaller or further away from the stimulus it is avoiding (whether a crowd, conspecifics, or some other environmental condition). To some extent this behavioural management is essential, particularly for skittish individuals in new environments that may remain isolated in small sections of the habitat if left entirely alone. Well-trained staff will find a balance between the need for gradual exposure to novel environments and the security of known spaces for individual animals.

Regular husbandry activities performed by staff in public display facilities include such items as cleaning of the pool and maintenance of the habitat. However, it should be noted that these types of husbandry behaviours that caretakers may view as “routine”, might not be viewed as such by the animals in their care, depending on the frequency and regularity of the task. Another type of interaction with staff relates to issues of health assessment and treatment. The health of marine mammals is difficult, if not impossible, to ascertain without close inspection that often relies upon direct physical contact. Regular physical contact with caretakers can be facilitated by training. Behavioural indicators of poor health of a captive cetacean (decreased activity or appetite) are often only apparent when the physiological condition has deteriorated extensively. Therefore, the contact required to diagnose and treat illnesses may, if not anticipated, result in increased stress levels, with the associated further consequences to animal health (see Section 2.3.2).

Captive cetaceans can be trained to perform behaviours that are used to closely monitor health, and that will assist in any future treatment [53]. This includes training the animals to be familiar with tasks such as extensive physical touching (for daily examinations and administration of treatments), proximity of veterinary staff and specialized equipment (e.g., ultrasounds, stethoscopes, x-rays), obtaining biological samples (e.g., blood, expectorant from blows, saliva, urine), and remaining comfortable in a smaller medical pool. Some facilities have also trained their cetaceans for daily weights and to remain calm when removed from the water (either via slings or on dry “slide out” areas). Such training should include exposure to personnel that are not the regular handlers (preferably veterinary staff that are likely to come into contact with the individual) given that an animal’s ability to distinguish between individuals can lead to stress if it is not habituated to a variety of humans.

There are numerous benefits to training captive cetaceans. Proactive training for evaluation, handling, and sampling clearly facilitates early detection of problems and maximizes treatment options. Training of novel behaviours under a variety of changing conditions also serves to mentally stimulate individuals, thereby providing additional enrichment. Also, such husbandry protocols can be used to collect important physiological data on the welfare of individuals to different environments, to try to make quantitative decisions on factors that affect the welfare of cetaceans in aquaria. It is important to consider that wild cetaceans must always engage in certain behaviours in order to acquire fish. The ability to acquire fish from the captive environment through participation in an appropriate operant conditioning training program is necessary to enrich the captive care of cetaceans and provide dynamic opportunities for learning.

Interactions with the public

There is no general trend in the available data to suggest whether human visitors enhance or are detrimental to the well-being of mammals. For some mammalian species, "active" zoo audiences result in higher levels of activity (including positive play interactions within the group and with audience members) in the display animals; in other species, large crowds can decrease overall activity levels. Some studies have documented an increase in aggressive behaviours in captive mammals exposed to viewing by the public. The negative effects of large crowds have been correlated to negative physiological indicators of health, including increased cortisol levels and even increased mortality in some species [reviewed in 6]. However, it should be emphasized that these studies are few in number and inconsistent in their conclusions.

There have been no studies that have specifically been conducted to evaluate the effects of crowds on cetaceans. One study that documented changes in dolphin behaviour during swim-with-a-dolphin encounters [54] reported an increase in use of refuge areas, and a decrease in aggressive, submissive, and play behaviour during these sessions. Given that the nature of the interaction is quite different from the experiences in most aquaria, and the contradictory nature of the findings, it is not possible to draw any firm conclusions on the effect of crowds on the well-being of aquarium cetaceans.

A potential risk associated with crowds is an increased likelihood of harmful foreign objects being (accidentally or deliberately) introduced into the animal's habitat. For cetaceans, this risk is relatively minor, as they are not, in general, prone to ingestion of foreign objects (including food items). This risk can obviously be mitigated by careful habitat design and close supervision of captive cetaceans.

A recent development in aquaria programs may present a special challenge to managing the effects of interactions with the public. More facilities are initiating special "behind-the-scene" tours to small groups as an added experience. These interactions obviously present additional concerns regarding the increased proximity and potential increase in the extent of physical contact with the animals. In addition, there may be addition pressures on staff to "ensure" interaction given the special circumstance of these tours. Again, a positive operant training program with regular evaluation of animal behaviour is needed to provide adequate monitoring of cetaceans in these situations.

Given these concerns, we recommend that facilities with public contact programs must ensure the programs are adequately designed and outfitted to minimize potential risks to the health and safety of the marine mammals and humans. This includes having a written policy that clearly identifies and addresses the safety issues and concerns for all participants in the program, including the marine mammals, and specifies the qualifications of those conducting the public contact session. Additional details of this recommendation are presented in Part 1 of this report.

Restricted feeding and foraging opportunities

Cetaceans in the wild often spend a significant proportion of their day engaged in foraging behaviours, although this differs tremendously between species (as well as time of year and age). In an aquarium, food is provided by humans, but that is not the only difference between wild and display animals. Food scheduling, quality, physical characteristics, and variety are all aspects that are limited by logistics. However, they do not all have an equal potential impact on the well-being of cetaceans.

In general, the quality of food consumed by cetaceans in aquaria is very high. Fish are usually “human grade”, with most animals known to reject substandard offerings even within that category. While cetaceans are typically fed previously frozen fish, specialized commercially available supplements (e.g., Mazuri VitaZoo) have been shown to be sufficient to counter the long-recognized potential for vitamin loss from freezing [55].

Aside from prey quality, the variety of prey may be a concern. Many cetaceans consume a broad array of prey items in the natural environment. Aquarium staff have increasingly realized that such variety has both nutritional and psychological benefits that cannot be satisfied from more uniform diets. For piscivores, it is often not possible to obtain prey items that are identical to species consumed in the wild, but suitable replacements are usually used. An extreme exception would be for mammal-eating killer whales that must be acclimated to consuming fish. Given that the dietary preference of these animals for marine mammals appears to be behavioural rather than physiological, there is no *a priori* reason to suspect that these diet changes do not fulfil their nutritional requirements.

Food is generally provided as a primary positive reinforcer for most cetaceans in aquaria. The withholding of food is often used to motivate animals to perform expected behaviours. In this context, trainers use food restriction as a way of motivating an animal, and actually making the desired behaviour more positive (given the eventuality of associated rewards). However, there is a danger of food withholding turning into a negative reinforcement (which should in no way be interpreted as “punishment”). Depending on the circumstances, the withholding of food when an animal is not undertaking a desired task can cause internal conflicts between their desire for food and their aversion to certain behaviours. Properly trained husbandry staff will not ask animals to undertake behaviours they will refuse, but even so, conflicts can arise.

One significant difference between food acquisition in the wild and in the aquarium is that animals do not have to actively forage for their prey. This eliminates the “challenges” of search, pursuit, and capture that may serve as mental stimulation for these animals. Many studies have shown that animals will work to obtain food, even when that food is freely available to them [reviewed in 6]. This “contrafreeloading” behaviour suggests that foraging is an inherently rewarding behaviour.

There may even be a requirement to forage in some terrestrial species, particularly among carnivores for whom food handling times represent a minor portion of the entire food acquisition process (i.e., compared to herbivores or frugivores that still must devote significant time to feeding even when items are readily available). For many terrestrial species in zoos, having animals work for their food – via food hiding or embedding into a “puzzle” device – seems to increase overall activity, but also decreases stereotypic and aggressive behaviour. This form of enrichment is becoming more prevalent in its use among marine mammals, although it has yet to become employed with any frequency for cetaceans.

Another aspect of feeding in facilities is the predictable timing of the event. Among different zoo and laboratory animals, the consequences of such anticipation are contradictory; in some species, regular feedings result in increases in abnormal or repetitive behaviour (such as pacing), while in other species instituting irregular feeding schedules increases aggressive interactions. It should be noted that many species that demonstrate anticipatory feeding behaviour also exhibit physiological changes, such as increased heart rates and breathing rates; however, it is usually impossible to differentiate whether these physiological changes are part of a normal preparatory response or are indicators of stress.

Marine mammals demonstrate temporal predictability, i.e., have a noted ability to predict feeding events by husbandry staff. Among cetaceans, only a single study has examined changes in behaviour immediately prior to scheduled interaction times (either husbandry or show events) [56]. This study found that there was a decrease in overall activity (and associated space use), and an increase in vigilance behaviour as a group of bottlenose dolphins appeared to “wait” and look for husbandry staff. However, there was no indication of any increase stereotypic or aggressive behaviour, and no changes in breathing rates.

Abnormal social groups

Appropriate social groupings are generally considered important for the well-being of mammals. On one extreme, social isolation has been demonstrated to result in adverse behavioural and physiological consequences (as demonstrated in the extensive body of work by researchers such as Mason and Harlow). For many species, social isolation is clearly a stressful condition [reviewed in 6]. Most curators have recognized that social groupings can improve the well-being of animals in their care. However, animals kept in facilities are maintained in social groupings that would not typically occur in nature.

Many consider cetaceans to be, as a group, particularly social animals, although there is certainly a tremendous variation in the social organization between and within individual species. In many cetacean species in the wild, the pods are centred on stable social hierarchies. However, even within a species, these natural organizations can differ widely between local populations, season, genders, and (in the case of killer whales) ecotype.

In the wild, group size of bottlenose dolphins varies tremendously. Bottlenose dolphins are considered to live in a fission-fusion society where smaller groups might merge for some activity (e.g., socializing or foraging) and then separate and reform, not necessarily with the same membership. The group composition of wild bottlenose dolphins is based largely on age, sex, reproductive condition, relationships, and association histories. Basic group types include nursery groups (mothers and their most recent offspring), juveniles (both males and females), and adult males (alone or in pairs). Mother-calf bonds are long-lasting, and can for the basis of a multigenerational group. While associations between males and females are short-lived, adult males can form strong, long-lasting pair bonds.

Beluga whales in the wild are usually found in pods of ~10 individuals of mixed age and gender (usually led by a large male), although several individual pods may come together to form substantially larger groups, particularly during the breeding season. Social hierarchies are considered relatively fluid compared to other cetaceans. In addition to the mixed composition pods, females with young may form separate pods during the calving season, and some pods may consist exclusively of both mature and immature males.

Killer whales are also categorized as social animals that occur primarily in relatively stable social groups that range in size from 2 to 15 animals. Larger groups can often be observed as temporary groupings of smaller social units. Single whales, usually adult males, also occur in many populations. Specific variations in social organization are associated with different subpopulations, age groups, and ecotypes.

Social groupings are important when considering marine mammals in aquaria where social dynamics will clearly occur but where, due to the logistics of the environment, certain aspects of the normal social dynamics are impeded. Individual animals in captive settings will be housed with others that they might not necessarily form positive social bonds with. The social groupings of cetaceans in aquaria are partly dictated by the age and gender profile of animals in the collection, as well as the pool space available for maintaining separate groups, and therefore may not reflect the types of groups found in the wild. In the case of the latter, atypical social situations can result from having too many individuals (i.e., forced sociality in addition to the issues of overcrowding which can themselves lead to aggression). Ironically, high reproductive success – usually considered a measure of a healthy aquarium population – can result in such overcrowding situations in the absence of a proper animal management plan.

In many aquarium conditions, the individuals in the habitat establish steady social hierarchies that do not mirror those that naturally occur in the wild, but which serve to maintain social stability and minimize unwanted social interactions. However, within the aquarium environment, there is also a threat of changes in social groupings due to moves between exhibits or facilities, which can disrupt these established social hierarchies. Introducing single or multiple individuals (either from other facilities or from the wild) and placing them in the new environment together creates problems, as individuals were likely each removed from separate social groups and thus are faced with establishing their own social order in their new environment, which can cause stress (see Section 2.3.2).

It may not be surprising that social relationships have been identified as a proximate cause of many cases of aggression in display cetaceans. However, it should be noted that stable dominance hierarchies will not preclude aggressive behaviour in many cetacean species, either in the wild or an aquarium environment. Some of these negative social interactions have been associated with aggressive attacks by mature males on younger individuals, particularly during mating periods. In captive bottlenose dolphins, it has been proposed that this aggression arises because the situation of adult males interacting permanently within the social group is a basic alteration to the normal dolphin social structure. Frequently this interaction results in the establishment of a dominant male individual and is often the source of many social and behavioural problems especially related to juveniles within the social group [53]. An early report on bottlenose dolphins noted that males in the habitat were aggressive to the birth of a calf, despite the fact that a stable dominance order had been established within the group (suggesting that the behaviour was not due to pre-existing abnormal social structure *per se*) [57]. The dominant male was so persistently aggressive (although the authors note it was obvious that he did not attempt to kill the calf), that it was necessary to medicate him for two days. However, both the other adult females stayed close to the calf and appeared to assist the mother in intercepting the dominant male.

Aggressive interactions can obviously result in overt physical injuries (e.g. rake marks, etc.). It has even been proposed to be the explanation for mortality in several cases of bottlenose dolphins held in aquaria [58]. However, stress resulting from social instability can be a subtler, but serious, concern. There can be a certain amount of ongoing, psychological intimidation from the dominant animal from which the juvenile has no reasonable means of escape. It has been suggested that captive juvenile dolphins are frequently poorly prepared to tolerate this interaction and, thus, it represents a very real psychological stress resulting in many medical problems [53]. These resulting medical problems can include gastric ulcerations, loss of immunity and consequently an increased incidence of incidental and potentially life-threatening infections [53].

Aggressive dominance interactions are often assumed to be the result of aggressive males. However, in one of the earliest studies of captive bottlenose dolphin behaviour, an adult female (the only mature animal in the holding group) repeatedly attacked two younger animals introduced into the tank, which reportedly eventually led to their deaths [57].

Not all of the negative effects of inappropriate social groupings are due to aggression *per se*. For example, it has been shown that proximity of other females interrupted nursing in a group of bottlenose dolphins [59]. The practice of having "aunts" is common in many aquariums, and is often invoked in aquariums as it is thought to mimic the natural social groupings observed in the wild [60]. However, it appears that companion females are not necessarily beneficial, and that the lack of space and privacy may limit nursing opportunities for the calf, particularly in the early postpartum period.

The negative effects of abnormal or imposed social hierarchies can be minimized in several ways. Careful animal management is often used to separate collection animals into balanced, defined social groups. For example, separate pools may be used to establish maternity groups, breeding groups, and groups of non-breeding males. Obviously, the design of these groupings is somewhat dependent on the natural social groupings of the species, but also constrained by the size and number of available habitats for separation. Hence, it is important that the concept of social groupings be incorporated into a facility's animal management (and breeding) plan. Management plans can be facilitated by incorporating transfers within or between facilities, but due care must be taken to minimize the resulting disruptions to established social hierarchies. Finally, as previously mentioned, the effects of negative social interactions can be mitigated by appropriate pool design so that target animals can safely retreat, thereby diffusing the aggressive situation before it becomes a detriment to well-being.

Given these scientific facts, we have recommended that all facilities holding cetaceans must have a written Animal Management Plan that takes into account the need for appropriate social groupings. Additional details of this recommendation are presented in Part 1 of this report.

Lack of Control (and other mediating solutions)

Many of the potential stressors previously discussed have the common characteristic that the individual animal retains little or no control over these conditions within its habitat. As such, captive animals are unable to mitigate any potential negative effects by changes in their own behaviour. Therefore, particular care must be taken in designing and monitoring these aspects of the cetacean's environment. While it is also important to monitor the individual animals for signs of stress, such symptoms (even when readily apparent) typically cannot identify the source of the stress on their own. Rather, facilities must be proactive in their evaluation of the effects of different aspects of the habitat, informed by additional scientific studies of aquariums and a fuller understanding of the animal's natural history.

Some would suggest that the lack of control that animals experience over their habitat is detrimental to the well-being of display cetaceans. There is evidence among some laboratory species that animals who are deprived of control over (strenuously) negative influences in their environment, develop “learned helplessness” [61]. This is characterized by a cessation of attempts to mitigate the negative effect as well a number of other physical changes associated with chronic stress (e.g. lack of appetite, lack of activity, increased circulating stress hormones).

However, these experiments represent extreme cases of both stressors and lack of control. The importance of controllability in animal welfare is a subject of considerable debate, not least because of the range of responses among species and the difficulty in conducting empirical studies. However, this is not to say that efforts should not be undertaken to provide display cetaceans with a greater level of control over certain aspects of their environment. While the objective is certainly worthwhile, the trick is to identify aspects that can be altered by the individual animal that do not inadvertently jeopardize its welfare (or those of its colleagues). This includes keeping in mind that predictability can be a positive influence on the well-being of cetaceans. In that respect, it is also important try to find an optimal balance between predictability and variability (either external or via animal control) that is ideal for each species.

2.3 Potential Indicators of Health and Well-Being of Cetaceans in Captivity

The purpose of this section is to 1) evaluate potential metrics to quantitatively evaluate the effects of long-term captivity on individual cetaceans and 2) summarize the scientific evidence to date regarding the well-being of cetaceans using these parameters.

We have chosen to investigate the following categories in our efforts to evaluate both their effectiveness as monitoring tools and to determine the level of information they can provide regarding the well-being of cetaceans held in display facilities:

i. Life history parameters
  - Including comparative survival, longevity, and reproduction

ii. Physiological measures of stress levels
  - Primarily focussed on stress hormones

iii. Behavioural measures of stress
  - Including vocalizations, aggressive and stereotyped behaviours

iv. Prevalence of disease and sources of mortality

We also have provided a summary of our overall evaluation, including future data requirements and suggestions for on-going monitoring.

2.3.1 Life History Characteristics as an Indicator of Cetacean Welfare

One of the common concerns regarding keeping cetaceans in captivity is that the apparent lifespan and reproductive success (number of surviving offspring) of these animals is substantially less than that of their wild counterparts. This would superficially seem a simple hypothesis to test through the statistical comparison of appropriate measures of longevity and reproduction between cetaceans kept for display and those in the wild. However, this simple concept is burdened by debate over precisely what that appropriate metric may be, and the acquisition of the necessary data with which to assess longevity and reproduction.

Unfortunately, life history data are surprisingly sparse for wild populations of many common species of cetaceans, and reporting for cetaceans held in aquaria is inconsistent. It may be surprising to learn that maintaining accurate records of life history data from cetaceans held in public facilities is a relatively new concept. It was not until the implementation of the Marine Mammal Protection Act (1972) that facilities in the United States were required to keep such data. Even so, the data were often difficult to obtain by outside scientists (either because of institutional inertia or a lack of centralized record keeping), and some types of data were not kept at all. This is one of the reasons that we have recommended the formation of a centralized database for information on cetaceans held in facilities in Ontario.

Even when data are available, statistical analyses become problematic for species that are less commonly held in display facilities as the results of such comparisons become less reliable due to the issue of low sample sizes reducing statistical power.

It can also be argued that a simple comparison using data from all facilities over their entire history reduces the usefulness of the exercise. In theory, comparisons of life history data from display facilities can identify changes in animal welfare over time and across different facilities. Ignoring the influence of these factors not only reduces the value of the analysis in regard to understanding what gains (if any) have been made in cetacean husbandry and medicine, but also adds confusion to the interpretation and discussion of any quantitative results.

Despite these limitations, there are a number of important evaluations that can be undertaken. While a primary concern is relative reproduction and survival rates of cetaceans in aquariums, but it is important to differentiate between different groups of cetaceans (e.g., captive vs. wild-born, calves vs. non-calves). Specifically, identifying the initial survival rates of animals brought into facilities from the wild, the reproductive rates of females, the survival rates of calves born in facilities, and the long-term longevity of non-calf cetaceans in facilities all answer different, but significant questions.

Longevity, age structure, and survival ages

There is much debate regarding the “longevity” of cetaceans held in display facilities, with opponents contending individuals have significantly shorter lifespans when held under such conditions compared to their wild counterparts. When comparing the well-being of cetaceans in facilities to their wild counterparts it is important to apply appropriate data sets and calculate appropriate metrics. Several metrics are commonly used to measure the health of wild marine mammal populations, including population age structures, median survival ages, and annual survival rates. However, some of these metrics are likely inappropriate for comparisons between display and wild cetacean populations, due to the fact that aquarium populations are not self-supporting, but are "managed". Hence, such measures may be less useful indicators of health for populations that have controlled breeding programs, animal transfers, or include animals that were wild caught due to the biases that these actions introduce. Adding confusion to the debate is that the terms used are sometimes misused or undefined.

Longevity is defined as the average life span of individuals within a defined population, an expression of the number of days or years survived. However, as DeMaster and Drevenak [62] point out, calculating longevity for groups of managed animals may be inappropriate for several reasons:

i. When applied to small populations (such as those held by a single facility) over a short time period, this metric is exceedingly biased.
ii. It is very sensitive to the proportion of animals that have been recently acquired and the age structure of the population.
iii. Point estimates of survival can be misleading when it is assumed that survival rates have not changed over the extended study periods required for long-lived species such as cetaceans.
iv. Estimates of survival in aquaria that include stillborn or short-lived calves will bias estimates downwards in comparison to wild populations where such events are rarely quantified.
v. Perhaps the most critical drawback to the use of longevity is that it can only give an accurate measurement when the majority of animals in the study population have died.
vi. An example of the bias due to animal acquisitions can be seen in the study of Venn-Watson *et al.,* [42] who examined several of these population parameters in an evaluation of the health of bottlenose dolphins in the U.S. Navy's Marine Mammal Program. These authors found that estimates of population age structure were heavily influenced by the collection of a large number of young dolphins between 1987 and 1989. Similarly, estimates of median survival age – which appeared to increase from 14.3 to 26.1 years between 1997 and 2007 – were also affected by these collection changes.

Failing to account for "surviving" individuals when calculating longevity can be illustrated by the following, simplified example. If a facility obtains 3 cetaceans, and one dies at 1 year of age, a second dies when 5 years old, and the third is still alive at 20 years of age, the calculated longevity will be 3 years (the average of 1 and 5 years). In other words, the calculation does not take into account the long life of the surviving individual (since there is no "age at death" at the time of estimation). Such a calculation was the basis of Greenwood and Taylor's [63] estimated survival of 2.21 years for 9 killer whales introduced from the wild, which did not take into account the 15 animals still alive in aquaria. A similar omission was the basis for Best and Ross' [64] low estimate for survival of captured bottlenose dolphins. In addition, including the apparent survival times for stillborn individuals (effectively 0 years) will not only disproportionately skew the results [see 65], but the resulting numbers are not comparable to values derived for wild populations. Given these considerations, DeMaster and Drevenak [62] suggested that researchers discontinue the practice of publishing the mean survival time of animals that have died in captivity.

However, this is not to say that mean survival time is not a valuable metric if used appropriately, such as on relatively large populations over a sufficient time period. Specifically, sufficient numbers of Atlantic bottlenose dolphins have been maintained in human care such that calculated lifespan should be an accurate measure of survivability. Several studies of managed populations suggest that the estimated median lifespan of dolphins in human care (34.3 years) [42,66] is nearly double the value for wild dolphins (17.4 years) [67].

Annual Survival Rates (ASRs)

DeMaster and Drevenak [62] suggest that Annual Survival Rates (ASR) are the most unbiased measure of the tendency for individuals to survive in a specific set of circumstances (whether in the wild, in display facilities, or in a specific institution). An ASR is the probability of an individual surviving over an entire year, and is based upon the total number of days that individuals in the study population have survived to date. As such, it can account for individuals that have not yet died. ASRs are also beneficial as they can be generated with relatively sparse data. However, the metric is sensitive to the number of data points (number of individuals and total number of "whale-days") which limit their resulting statistical power, and can also be biased by inclusion/omission of (in)appropriate data [e.g., 64,65]. Most ASR studies to date have concentrated on the three species of cetaceans most commonly found in display facilities: bottlenose dolphins, beluga whales and killer whales. The commonality of these species allows for a range of comparisons, including examinations of changes across time and between facilities.

Changes in survival across time

The ability of ASRs to highlight differences in survival through time allows an analysis of potential improvements in husbandry and veterinary practices on this parameter. For example, DeMaster and Drevenak [62] estimated the mean post-capture ASR for bottlenose dolphins held in North American facilities from 1975 to 1987 was 0.93 (95% CI= 0.92-0.94, n = 864). These authors found that the survival of dolphins in captivity significantly improved between the periods 1975-1979 and 1980-1984. A later, larger study (n=1707) reported a further significant increase in ASR for captive bottlenose dolphins during the period 1988 -1992 (0.951) [68]. Similarly, a report by Klinowska and Brown (unpublished manuscript prepared for the Dept. of the Environment, UK., 1986) also reported that ASR for some cetacean species had increased since 1980 [quoted in 68].

Similar trends of improved ASRs were demonstrated for dolphins held as part of the Navy's Marine Mammal Program. Venn-Watson *et al.* [42] found that survival rates for bottlenose dolphin calves less than three years old (excluding those that died at less than 30 days) in the Marine Mammal Program (1988-2007) ranged from 0.92 to 0.99, and that the mean annual survival rates of all dolphins ranged from 0.97 to 0.99. In addition, the calculated mortality rate of the entire population decreased from 4.7% in 2003 to 2.4% in 2007. The authors note that these apparent improvements in mortality rates come despite an increasingly mature population, which the authors suggest resulted from improved management and treatment of chronic problems associated with aging cetaceans.

DeMaster and Drevenak [62] also estimated the ASR for killer whales held in aquaria between 1975 to 1987 at 0.93 (0.90-0.96 CI, n = 40), and 0.94 ± 0.04 for beluga whales (n = 48) over the same period. Unlike their findings for bottlenose dolphins, these authors found no differences between the ASRs for killer whales and beluga whales between two timeframes, 1975-1979 and 1980-1984. However, the authors were unable to differentiate whether the significant improvements only noted for bottlenose dolphins were due to species-specific improvements, or whether the larger sample size for bottlenose dolphins provided additional statistical power to detect differences for this species.

In a recent presentation to the Society for Marine Mammalogy (special panel discussion on "Scientific Studies of Captive and Free-living Killer Whales" at the Biennial Conference on the Biology of Marine Mammals, Dunedin, NZ, December 2013), data was produced that suggested the ASRs of captive killer whales had steadily improved each decade, from a low of 0.917 in the period 1965-74, to a high of 0.983 during the period 2005-13 (Wilhelmina Innes, unpublished data). These values were calculated following the same methods (and extending the original database) used by DeMaster and Drevenak [62]. This trend was confirmed by an additional treatment of the dataset by another researcher presented as part of the same panel discussion (Patterson, unpubl. data). These data are in direct conflict with the contention by Rose [69] that the ASR for non-calf killer whales in captivity was lower in 2011 than in 1995 (0.927 vs. 0.937).

Differences in survival between facilities

ASRs can also provide a standard measure of the survival of a specific cetacean species in different facilities, particularly for commonly held species. This can potentially be used to focus attention on differences in husbandry practices that can ultimately lead to increased well-being for all members of the species kept in aquariums.

For example, DeMaster and Drevanak [62] report that the ASR for bottlenose dolphins differed significantly between the 57 facilities studied, whereby 6 facilities had significantly lower ASRs and 1 facility had a significantly higher ASR than the others. In a further analysis of the data, these authors suggest that the differences in acclimation processes (i.e., that recently captured animals are infrequently acclimated to captivity at the facility that will permanently hold them) may explain some of the differences between facility-specific rates of survival.

Comparisons of ASRs can also assist in pinpointing specific issues that might differentiate the well-being of different species within facilities. For example, Reeves *et al.* [70], examined the ASR of five different species (based on data from 139 individual cetaceans), from 1974 through 1983 at Ocean Park, Hong Kong. They found very low ASRs for short-finned pilot whales (effectively 0.0), false killer whales (0.58) and Pacific white-sided dolphins (0.59). ASR for bottlenose dolphins differed widely depending on subspecies (either 0.25 or 0.83). In comparison, the annual survival rate for two killer whales was quite high (0.94). In addition to providing ASRs for species less commonly held in aquarium collections, this analysis also highlighted species-specific differences in survival, which the authors suggested was likely due to the procurement of species poorly suited for survival in Hong Kong's climate. The generally low ASRs also served to highlight serious problems encountered during the Parks' first decade of operation that likely led directly to low rates of survival, such as periodic overstocking, inadequate water quality (filtration, purification and chilling systems), and outbreaks of bacterial infections.

Differences in survival between wild and managed populations

A central question regarding the well-being of managed cetaceans is whether survival of cetaceans in display facilities is significantly different than for individuals in the wild. With increased data from both managed and wild populations, scientists are beginning to quantitatively address this question, although the results are far from conclusive. This broad question can actually be broken down into two more specific comparisons: first, whether there are overall differences in survival between captive (regardless of origin) and wild populations of cetaceans and, second, whether animals brought into captivity from the wild have the same survival as captive-born animals.

Although DeMaster and Drevenak [62] suggested that ASRs in captivity may be better than or equal to survival in the wild for many species of cetaceans (although see below), such a comparison is often hampered by a lack of compatible data between wild and captive populations which are required to make valid comparisons. Specifically, life history parameters are often dissimilar between different populations (e.g., British Columbia and Icelandic killer whales), subpopulations (e.g., northern and southern resident killer whales in British Columbia and Washington) ecotypes (e.g., resident vs. transient vs. offshore killer whales), and study periods. Captive and wild populations are rarely matched for age structures, which are known to affect survival rates.

Overall, there is a critical lack of studies comparing the survival of captive and wild cetacean populations. The resulting lack of consensus on whether the survival of captive-born cetaceans is significantly different than for populations in the wild is also hampered by species-specific differences and differences in Some reports have suggested that the mortality rate of oceanarium dolphins was 7% [71]. More recent analyses clearly show that survival in aquaria is much higher than this for this species [42,68,72].

In contrast, DeMaster and Drevenak [62] note that the survival for captive killer whales in their study (0.93-0.94) was lower than that reported during the same era for killer whales off Vancouver Island [73]. The most recent analyses of the survival of captive-born killer whales estimated a mean ASR of 0.979. In comparison, a recent study on the ASR of resident killer whales in southern Alaska ranged from 0.945 for calves up to 1.5 yr, to 0.997 for calves 1.5 to 2.5 yr, and between 0.989 and 0.992 for adults up to 14.5 yr [74].

Survival of cetaceans introduced from the wild.

One of the specific concerns regarding having cetaceans in aquaria relates to the “success” of acquiring whales from the wild. Specifically, there are concerns that a significant number of whales are killed in the capture process, and that the survival of those brought into facilities is very low during their initial acclimation period. These concerns are in addition to the potential impact on wild populations of such removals (discussed in Part 1). Greenwood and Taylor [63] reviewed the data available at the time and reported that between 1962 and 1973, 263 killer whales were taken from the waters off of Vancouver Island (BC and WA). Of these 263 animals, 50 (19%) were distributed to aquaria, while 12 (5%) died during the capture process; the remainder (201; 76%) were returned to the wild or escaped during the capture process. These net captures were suspended in American waters after 1973 on implementation of the Marine Mammal Protection Act, and only two additional whales were captured in these waters through 1978. For both the North American and the European market, captures of whales switched to Iceland, first as incidental to fishing entanglement, and then commercially by 1976. To our knowledge, there are no other published reports on mortality rates for cetaceans during targeted capture activities.

Greenwood and Taylor [63] also examined the survival of those killer whales once they were brought into display facilities. At the time of their review, 24 killer whales had been permanently exhibited in European facilities since 1968, although only 8 remained in European facilities at the time of their analysis. Of the remaining 16 individuals, 9 had died and 7 had been transferred to other non-European facilities.

For the 9 animals that died, they lived between 0.42 and 5.75 yr after their date of capture (with a mean survival time of 2.21 yr). Greenwood and Taylor also recalculated the survival times of killer whales in North American facilities from a review by Ridgeway [75]. These authors concluded that initial survival rates for killer whales brought into captive settings from the wild were similarly low for both European and North American facilities, suggesting that these animals are particularly vulnerable during their initial holding period. These authors found that younger animals generally adjusted better to their novel situation and that, within two years of capture, survival for all age groups was greatly improved. The authors concluded that killer whales in captivity are clearly capable of living for long periods in display facilities, provided that they survive the first two years. A subsequent review of the survival of bottlenose dolphins, killer whales, and beluga whales, suggested that acclimation occurs somewhere in the first 90 days, after which they appear to become more resilient as time passes [62]. Similarly, a review of mortality among Amazon river dolphins found that, among wild-born animals, mortality was highest in the first 2 months immediately post-capture and transport, accounting for 32 of 123 deaths [76].

A more thorough subsequent review specifically examined early survival of the two most common species of marine mammal in captivity, the bottlenose dolphin (1,256 individuals) and the California sea lion (1,624 individuals) [72]. The study divided the animals into wild-born and >1 yr old or captive-born and < 1 yr old (the authors excluded records for animals with deaths associated with birth such as stillbirths, premature animals). The authors observed that the number of mortalities for wild-born bottlenose dolphins (and California sea lions) was relatively higher during the first 25-30 days of captivity compared to days 31-90.

Based on this analysis, the authors of the study initially estimated that acclimation occurred sometime within the first 90 d of captivity. Hence, survival during days 91-365 was considered to represent survival of animals acclimated to captivity. Based on these assumptions, they calculated the (post-acclimation) ASR of captive bottlenose dolphins as being 0.943. This allowed the authors to then go back and perform a more detailed test to better refine the acclimation period. The authors tested each 5-day interval from an individual's introduction from the wild (day 0) to determine whether the survival rate was significantly different from the "acclimated" (normal) survival rate. This analysis suggested that survival rate first reached the acclimated rate after approximately 35-40 days in captivity for wild-born bottlenose dolphins, while captive-born bottlenose dolphins acclimated to captivity in no more than 50 d. Hence, the authors suggested that, based on survival, acclimation to captivity appears to occur in approximately 35-50 days for bottlenose dolphins transferred from the wild or transferred between facilities.

Due to these known initial periods of high mortalities, most studies of survival in aquaria (and comparisons to wild populations) exclude this initial period of acclimation. However, the central question as to the well-being of cetaceans brought into aquaria from the wild is whether this initial period of lower survival is a result of bringing whales into these facilities, or whether this is just a natural consequence of the inherent lower ASR of the young animals, which are that are frequently the age class that is introduced from the wild. For a specific example, we can re-examine the data from the study by Small and DeMaster [72] which reported that the ASR of captive-born bottlenose dolphins does not exceed 0.70 until about 50 days after birth. While wild-born dolphins in this study also had a low initial ASR (0.826) these were all >1 yr old (at which point captive-born animals had reached their steady ASR of 0.948), suggesting that the initial acclimation period was prone to higher mortality rates than could be explained solely by the animals' age. In other words, the initial lower survival of wild-born animals during this initial acclimation period was due to a change in their environment, rather than an age effect. It is also important to note that this acclimation period (and concurrent decrease in survival) seemed to reoccur for wild-born bottlenose dolphins when they were transferred to a second facility.

It is also interesting to investigate the relative survival of captive-born and wild-born cetaceans past this initial period of acclimation. Small and DeMaster [72] found that captive-born bottlenose dolphins actually had a slightly lower ASR than wild-born animals that survived their first year [0.894 vs 0.904, 72], while the ASR for captive-born non-calf bottlenose dolphins was only slightly higher than for wild-born dolphins (0.970 vs. 0.951; a difference that was not statistically meaningful). In a subsequent, larger study, this difference in survival between captive-born and wild-born non-calf dolphins was even smaller (0.948 vs. 0.944) [68]. In comparison, an unpublished analysis suggested the ASR of captive-born killer whales was significantly higher than wild-caught individuals (0.979 vs. 0.952), once differences in early mortality/acclimation were taken into account (although this comparison did not account for potential age effects; Wilhelmina Innes, unpublished data, presented to a special panel at the Biennial Conference on the Biology of Marine Mammals, Dunedin, NZ, December 2013).

Reproductive rates in display facilities

Most biologists would agree that reproductive rates can function as an indicator of the health of individuals within a population. This is particularly true for marine mammals, for which certain aspects of health and body condition may naturally control annual reproductive cycles. Key reproductive parameters that may be indicative of animal health are birth rates (also considering stillbirths), immediate post-partum survival, and survival within the calf's/pup's first year.

Birth rate is considered a metric of mammalian health, as the females of many species are known to control their reproductive cycles in response to environmental signals and their own physical condition. This may be particularly true for species that are annual breeders, and for those (such as many species of marine mammals) in which delayed implantation is used as a reproductive strategy. Unfortunately, there are few comprehensive studies of birth rates within captive cetacean populations. Estimates of birth rates in captivity have become increasingly biased due to a rising reliance on artificial insemination in some common species (such as bottlenose dolphins). In addition, the rate of stillbirths and those living for only short periods is biased against captive animals, as these events are essentially impossible to observe in the wild.

Survivorship during the first year of life (or portions thereof) has also been proposed to provide a qualitative means of evaluating the overall well-being of different cetacean populations, including comparisons between different individuals, groups of facilities, and to examine changes across time. This is due to the fact that individual calves are relatively susceptible to stress and disease during this period, and that they are also dependent on their mother for nursing (whose condition will also contribute to the well-being of her calf).

Sweeney *et al.*, [77] performed a comparison of the survival of bottlenose dolphin neonates from three US facilities: Dolphin Quest, Sea World Parks, and the U.S. Navy Marine Mammal program. These authors examined both survivorship in the first 30 days of life and through the first year. The extensive dataset also allowed them to make comparisons between the periods 1990-1999 and 2000-2009 to evaluate any potential changes in these estimates over time. Measures of survivorship up through 1 yr of age may be particularly important for comparisons, as this is the point at which wild animals are generally included with in the overall population database in long-term studies [78].

Overall, Sweeney *et al.* found that survival to the first 30 days of life averaged 85.1% of total live births, while survival through one year of age was 80.7% of total live births. The most significant finding was that neonatal losses in the first 30 days decreased from 21.8% in the first decade (1990's) to 9.4% in the later decade (2000's). Further, this improvement occurred after the first 48 hr period, the time frame in which the potential of successful medical and husbandry management are most likely to occur and also are best implemented. These authors suggest that the *Tursiops* Neonate Survivability Workshop has likely contributed to the increasing survivability of neonates by establishing means of determining if a neonate is beginning to fail, the best means of intervention, and outlining how managers can anticipate threats to neonates and take measures to mitigate these risks. Unfortunately, there are few published data on neonate losses in wild populations, although long-term research projects [such as those in Sarasota Bay; 78] are producing some estimates. Unfortunately, much of the research on cetacean population demographics is necessarily concentrated on subpopulations of conservation concern that likely do not represent healthy populations.

2.3.2 Diseases and Sources of Mortality in Captive Cetaceans

One way of evaluating the well-being of cetaceans in aquaria is to determine whether these animals are prone to unusual disease events or sources of mortality.

Given the statutory requirements to report mortalities of cetaceans in human care in the United States, it would seem that a survey of the U.S. Marine Mammal Inventory Report (maintained by the National Marine Fisheries Service, an agency within the U.S. Department of Commerce) would yield a wealth of knowledge regarding the source of fatalities in these animals. Unfortunately, this is not the case. In Canada, there is no centralized reporting database. This is one of the reasons this Committee has recommended that each facility is required to help maintain a provincial inventory of marine mammals maintained in display facilities, including details on mortality events.

In the late 1970's, Sam Ridgway [75] conducted the first systematic survey of the causes of death of killer whales captured from the wild since 1965 and introduced into 6 North American display facilities. Of the 16 individuals, there appears to be a higher mortality rate among females (13) than males (3). At least one of the deaths was directly associated with the whale having been shot prior to the capture event. There were few trends among the remaining data; among the females, 3 were diagnosed with disorders of the urogenital system. One female (pregnant upon capture) died after a stillbirth, while another died of pyometra and septicaemia while pregnant. Two of the older, larger females died from haemorrhages associated with the vascular system, although it must be noted that atherosclerosis has also been reported in wild killer whales [79]. Pneumonia is listed as the cause of death in 5 of the cases, but it is unclear whether this is a secondary condition resulting from other primary causes.

A later survey [63] reported on the cause of death in 9 killer whales (out of a total of 24) that had been primarily displayed only in Europe. They reported that 8 of the 9 whales that died were males (compared to 15 of 24 in the entire sample), and that the majority had died from infectious disease. One male died from severe trauma inflicted by another conspecific.

This high incidence of death by pneumonia and bacterial infections is cause for concern. Unfortunately, the lack of modern data makes it impossible to ascertain whether developments in veterinary medicine have altered this statistic. Clearly, this would be a fruitful analysis to undertake. One other review of note detailed the causes of mortality among the relatively rare Amazon and Orinoco river dolphin (*Inia geoffrensis*) in captivity, and found that pneumonia and skin lesions (cutaneous and subcutaneous ulcerations and abscesses) were the most common findings from 105 necropsies [76].

While the rate of pneumonia in these early mortalities may have been high, it is not surprising that this was one of the most common causes of death. Bacterial pneumonia seems also to be the most common cause of mortality among wild cetaceans [80,81,82]. Similarly, systemic mycotic infections have been recorded in both captive and free-living cetaceans (although they occur much less frequently than bacterial infection), although candidiasis has been suggested to be a particular problem for captive cetaceans [80].

There are, of course, a host of diseases and conditions that both wild and captive cetaceans may contract. Some of these have led to surveys of specific diseases [e.g., 83,84,85,86]. More central to the present discussion, the range of potential afflictions have been summarized in several reviews [87,88]. In general, veterinarians divide potential diseases into 7 categories: viral, bacterial, mycotic (fungal), parasitic, nutritional, metabolic, and neoplastic (cancers) diseases. Separate from this list of diseases, the aforementioned reviews also discuss a broad range of physical injuries. However, the published reviews tend to be for clinical diagnosis and treatment, and do not endeavour to rank or enumerate the frequency of occurrence of each affliction. In fact, an informal survey of practicing marine mammal veterinarians revealed that it was virtually impossible to produce a list of “most common” diseases among any single group of cetaceans. Certainly, there has been no complete analysis of whether captive cetaceans are more or less likely to suffer illness than their wild counterparts. Partly, this is due to the fact that most of our information on the latter comes from stranded individuals.

Two differences are recognized between captive and wild populations. "Droop fin" is the common name given for collapsed dorsal fins seen almost exclusively among male orcas, and apparently at a higher prevalence among captive animals [89]. Although the phenomenon has become the focus of animal welfare concerns, there is no firm evidence that this morphological feature has direct a correlation to the health or well-being of an individual animal. Another clear difference between disease in captive and wild cetaceans is in the incidence of parasites. Parasite burdens (both endo- and ectoparasites) are common and can be substantial in wild cetaceans [90]. However, heavy parasite loads do not develop in captive born cetaceans and are quickly purged (either naturally through changes in diet or through a course of medication) in animals introduced from the wild. Although parasitic infections will not inevitably cause disease on their own, they are known to contribute to morbidity and mortality [91].

2.3.3 Physiological Indicators of Stress in Cetaceans

Definitions

"Physiological stress" in animals has been defined in many ways. Selye [92] defined it as "the non-specific response of the body to any demand made upon it". Later, Moberg [93] proposed that the stress response is divided into three phases: i) recognition of a threat to homeostasis; ii) the stress response; iii) consequences of stress and the response. Moberg [94] also pointed out that, unlike other diseases, stress has no defined aetiology or prognosis, making it difficult to strictly define and measure. Moberg [94] used the following terms, for animals in general:

> *Stress* – biological response elicited when an animal perceives a threat to homeostasis;
> *Stressor* – the threat
> *Distress* – when the stress response threatens the animal's well-being.

Dierauf [95] pointed out that marine mammals have evolved many anatomical, morphological, and physiological adaptations for life in an aquatic environment, and whether classical definitions of stress apply to these species is not known. Dierauf [95] did, however, define a series of stressors experienced by marine mammals in captive settings, including the following: capture stress, transport, separation, social isolation, inadequate nutrition, overcrowding, poorly designed enclosures, noise, excessive light, and sharing a pen with aggressive individuals (many of these topics are discussed in detail in other sections of this report).

Stress, and the stress response, can be deleterious for individuals, negatively impacting survival, or having sub-lethal effects such as decreased immunity, poor health, impaired growth and metabolism, and adverse impacts on reproduction. It is important to recognize that stress (and the stress response) can occur over the short term (“acute” stress; minutes to days) or over much longer periods (“chronic” stress; days to weeks or years).

Common physiological indicators of stress in cetaceans

This section of the review will focus on stress indicators that can be measured physiologically, either in tissue samples (e.g. blood, fecal material) or physical measurements (heart rate, respiration rate) collected from individuals. The most commonly used indicators of stress in marine mammals fall into two general categories: changes in white blood cell parameters, and changes in the glucocorticoid hormones that are used broadly as measures of stress in many animals (cortisol). There is considerable evidence that stressful stimuli appear to elicit distinctive adrenocortical responses in cetaceans [96,97]; cortisol release is one of the main effects. Typically, physiological changes have been measured using blood samples; however there is now a growing body of literature validating the use of fecal material to measure stress and reproductive hormones [e.g., 98,99]. We will also report data on other physiological parameters where appropriate.

As reviewed by Dierauf [95] and Curry [100], these are some of the major physiological indicators of stress that have been observed in marine mammals:

Indicator	Definition
Neutrophilia	Increased levels of neutrophils (white blood cells that respond to bacterial infection or inflammation)
Eosinopenia	Decreased levels of eosinophils (white blood cells that combat infection and parasite loads)
Leukocytosis	Overall increased (or decreased) levels of white blood cells
Increase in serum cortisol	Increase in circulating levels of cortisol, the stress hormone produced by the adrenal glands; responds to stress and low blood sugar levels. Cortisol can also be measured in fecal material.
Increase in serum aldosterone	Steroid hormone produced by the adrenal glands that regulates blood pressure
Decreased serum iron levels	Iron deficiency; can lead to anaemia
Decreased plasma T3 and T4	Thyroid hormones; T4 (inactive) is converted to T3 (active); T3 regulates all aspects of metabolism
Increased prostaglandins	Family of physiological regulators; control muscle contraction, hormone regulation, cell growth, response to inflammation
Increased erythrocyte sedimentation rates	Common non-specific measure of inflammation; decrease in rate at which red blood cells fall in a collected sample.
Hyperthermia	Increased body temperature above the range in which it can be regulated by the animal
Capture myopathy	Damage to muscles associated with capture and handling

Comparative data from wild and captive animals

The large majority of studies on stress in captive cetaceans have been carried out on a single species, the bottlenose dolphin. There are also some data on beluga whales and a small amount of information on the harbour porpoise. It is important to note that many health and stress indicators will exhibit intra-specific variation with sex, age, and season [e.g., 101].

Stress associated with capture and handling

Several experiments with bottlenose dolphins and belugas have demonstrated that the process of capturing does elicit a stress response. Thomson and Geraci [102] examined changes in blood stress hormones and white blood cells in three captive bottlenose dolphins that were subjected to two different "capture" conditions: "calm-capture", in which dolphins were surrounded by a net and captured as quickly as possible; and "chase-capture", in which the dolphin was repeatedly chased, captured and released for 3 hours prior to each blood sampling. In both cases, dolphins were held out of the water for 6 hours post-capture. Blood samples were collected repeatedly, starting at 10 minutes and up to 6 hours post-capture. Cortisol levels in the calm-capture group increased from ~30-40 nmol/L immediately post-capture to ~80-120 nmol/L within the first hour out of the water and remained in this range for the duration of the experiment. In the chase-capture group, cortisol values immediately post-capture were much higher (~60-80 nmol/L) and remained in the 70-110 nmol/L range for the duration of the experiment. Previous work had shown cortisol levels in captive bottlenose dolphins to be ~90 nmol/L [103,104]. For aldosterone, the calm-capture group showed a large increase with time out of water, from 280 pmol/L to 650-1880 pmol/L at the 3 hr mark, after which levels decreased to 290-750 pmol/L. In the chase-capture group, aldosterone levels remained steady with time out of water in the range 300-700 pmol/L. In both capture scenarios, eosinophils declined over the six-hour holding period, with "gradual recovery" by the following day. Thus, both capture methods yielded a stress response (although different biochemically) even though all three dolphins had been in captivity for three years, during which they had been routinely handled for other studies, indicating that a stress response was invoked even under the calmest possible conditions.

Using a different approach, St. Aubin and Geraci [97] captured 24 wild juvenile beluga whales in Hudson Bay, and measured their stress responses (specifically in terms of T3 and T4 thyroid hormone levels) under a number of different conditions. Seventeen whales were captured, blood sampled, and released immediately; one whale was held for 15 hours and then released; and six were kept under captive conditions for 10 weeks. The group of 17 animals was used as the control with which to compare short and long term holding and handling. The one animal held for 15 hours had serial blood samples collected at 1-6 hour intervals. The 10-week group was sampled during the first few days post-capture and then during the last five weeks of the capture period. In the short-term holding period (15 hours), T3 levels decreased over time, down to 50% of initial levels by the 12 hour holding point; T4 levels did not show a clear pattern. In the long-term holding group, T3 declined considerably (up to 80%) during the first 2-4 days of capture; T4 levels decreased 35-65%. By the end of the captivity period, both hormones started to show some recovery but were still “significantly depressed” compared to the control values. The two studies above suggest that i) handling of toothed whales induces a significant stress response, and ii) animals in captivity for >2 months still exhibit signs of a stress response.

In contrast, work by St. Aubin *et al.* [96] comparing stress in wild and “semi-domesticated” (the latter held in open sea pens for multiple years and trained to present their tail flukes for blood sampling) bottlenose dolphins after capture and brief restraint showed different trends. Cortisol (2.6 vs. 1.9 ug/dL; 71 vs. 52 nmol/L) and aldosterone (116 vs. 28 pg/mL) levels were higher in the wild dolphins; thyroid hormones showed significant age and sex effects, making comparisons more complicated between the two groups. Most of the variation in thyroid hormone values was attributed to the reproductive status of females. These authors suggested that removal from the wild does not lead to systematic changes in thyroid function in bottlenose dolphins. Ortiz and Worthy [105] also measured cortisol levels in wild bottlenose dolphins what had been captured as part of a health assessment protocol in the waters off of Beaufort, North Carolina (n=31) and found mean cortisol levels to be similar (77.3 nmol/L) to the values reported by St. Aubin *et al.* [96]. Ugaz *et al.* [106] used a novel approach, that of quantifying salivary cortisol, to assess stress levels in captive bottlenose dolphins in open and closed pen/pool facilities. These authors found higher cortisol levels (means per pool 0.65 to 1.4 nmol/L) in saliva of dolphins in closed pools compared to their conspecifics in open pens (means per pen 0.09 to 0.3 nmol/L); open pen animals were also more active.

There are few data on harbour porpoises, a species that has been kept in captivity in a few countries (e.g. Denmark), and under rehabilitation circumstances in others (the United States and the Netherlands). However, the release of wild animals from open pen fishing structures (herring weirs in the Bay of Fundy, Canada) have provided opportunities to evaluate the effects of handling time on stress levels in this species. Porpoises that were handled for longer time periods (30 min to 1 hour for attachment of electronic tags) had significantly higher levels of serum cortisol (315 nmol/L) than those handled only briefly (< 30 min; time required to remove from the weir, attach a plastic rototag, and release; 224 nmol/L) [107]. These values are much higher than values from captured wild (see above) or chased and captured *Tursiops* [102], which underscores the points made by Mason [45; see below] about high variability in response to stress across different species. In addition, there is considerable evidence that response to stress also varies with the individual animal, and the conditions the animal is experiencing. Harbour porpoises kept in captivity in Denmark exhibited large individual variability in cortisol levels (individual Coefficients of Variation values for mean serum cortisol in four porpoises ranged from 41-85%) [108]. The authors of that study also compared stress levels, measured as cortisol levels, in these porpoises under two handling regimes for blood sampling: animals removed from the water (OWR) and those sampled poolside while undergoing Voluntary Husbandry Behaviours (VHB). Cortisol levels were significantly higher (2-3 fold) in porpoises sampled via the OWR method (range 135 – 179 nmol/L) compared with the VHB method (range 44-55 nmol/L). Such data have led to the conclusion that cortisol is a good indicator of stress in this species. Eskensen *et al.* [109] report cortisol levels in wild harbour porpoises removed from pound nets (a similar type of fishing gear to herring weirs; handling time <1 hour) between 171-932 nmol/L (mean 455; n=42), values which are far higher than any other value reported for this, or any, species. Desportes *et al.* [108] also concluded that even though the VHB sampling regime for harbour porpoises led to lower cortisol levels, it still induced a stress response, and that regular and frequent handling over several years did not suppress the significant stress response in their animals. This is similar to the results obtained for dolphins by Thomson and Geraci [102], and for belugas by St. Aubin and Geraci [97], pointing to the high sensitivity these odontocetes have to handling in captivity.

Stress associated with holding and captivity

There are few published data on physiological stress indicators in animals being held in captivity. Suzuki *et al.* [110] measured cortisol in three killer whales and two bottlenose dolphins from the Kamogawa Sea World facility, as part of a study to validate the use of radio immunoassay to measure cortisol. These authors reported serum cortisol values between 1.5 and 3.8 ng/mL (4 to 11 nmol/L), which are lower than the wild (26; 71 nmol/L) and semi-domesticated (19 ng/mL; 52 nmol/L) values from St. Aubin *et al.* [96].

Spoon and Romano [111] had the opportunity to observe the stress response of belugas as they were moved from one facility to another (“transport” group) compared to the “resident” belugas in the destination facility. Both groups exhibited significant increases in norepinephrine and in epinephrine at the point of arrival of the transport group to the new facility (~2.5 fold increases in both), with subsequent decreases back to baseline over several months. In the transport group, cortisol increased ~3-fold (from 1 µg/dl to > 6 µg/dl) at the arrival to the facility, and then declined after 5-6 months. The two groups of animals displayed very different responses in their phagocyte function, which suggests that transport and the introduction of new individuals leads to different responses in the immune system of captive cetaceans. These authors suggested that the hypothalamo-pituitary adrenal (HPA; release of cortisol and other glucocorticoids) and sympatho-adrenal medullary (SAM; release of epinephrine and norepinephrine) axes of the stress response in belugas (and likely other cetaceans) have complex regulatory roles in immune function that will vary with stressor type and intensity. Nonetheless, it does appear that both transport, arrival at a new facility, and the introduction of new “pool mates” can lead to stress in belugas and perhaps in other toothed whales.

Noda *et al*. [112] measured stress responses associated with transport in captive bottlenose dolphins moved from one facility to another (6 hour trip). Serum cortisol levels during pre-transport handling (154 nmol/L) and transport (171 nmol/L) were significantly higher than “resting” pre-handling values (33 nmol/L). In addition, significant changes in leukograms (decreased white blood cell counts and eosinophils) were noted and ascribed to stress-related immunosuppression induced by release of corticosteroids.

More recently, Trana [113] demonstrated that cortisol can be reliably measured in the blubber of beluga whales, and showed that animals trapped in ice for several months had higher blubber cortisol concentrations than those killed in a native subsistence hunt. Trapped whales had blubber values seven times higher (1.76 ng/g) than the hunted animals (0.25 ng/g). Blubber cortisol reflects slower turnover than blood values, potentially on the order of 1-4+ days, and therefore indicates stress over a longer time period.

Mason [45] compiled a general review of the variation across species (including data on several orders of mammals and birds) in terms of response to captivity and found that many species do very poorly in captivity, being susceptible to reproductive problems, chronic stress, and stress-related illnesses. This seemed particularly true for species with large home ranges or migration patterns, and those with complex social organization. Mason does point out that this pattern is not consistent, with other species faring better in captivity, with higher survival and reproductive rates, and less incidence of illness.

Evidence of stress associated with anthropogenic perturbation

Recent investigations have focused on the potential stress associated with exposure to anthropogenic impacts, such as noise, on cetaceans. Rolland *et al.* [98] showed that steroid hormones and glucocorticoids could be reliably measured non-invasively in endangered north Atlantic right whales, and these authors used concentrations as indicators of pregnancy. Several years later, Rolland *et al.* [114] had the opportunity to retrospectively measure fecal cortisol levels before and after a major decrease in underwater noise. Directly after the tragic events of September 11, 2001, there was an abrupt decline in ship traffic in the Bay of Fundy, Canada, which is one of the main summer feeding grounds of this species. Overall, there was a 6 dB decrease in ocean sounds in the 50 Hz-20 kHz range after 9/11, with a concurrent significant decline in fecal glucocorticoid metabolite levels in the whales. These authors noted that terrestrial species show increases in glucocorticoid levels in response to natural stressors (social aggression, predators, starvation) but also anthropogenic sources [tourism traffic, road noise; see 114 for references]. Although right whales are not kept in captivity (nor are any other mysticetes on a regular basis), these data do show that increased habitat noise, at least in the form of ship traffic, can increase stress levels in right whales.

Long term effects of elevated stress hormones

Short-term elevations of glucocorticoids can lead to mobilization of energy reserves and behavioural alterations. In contrast, chronic exposure to high circulating cortisol levels from repeated or continuous stressors can have deleterious effects at both individual and population levels. In their review of the endocrinology of stress, Romero and Butler [115] provide ample evidence that over various time frames, glucocorticoids have five major effects:

1. raising blood glucose levels,
2. altering behaviour,
3. inhibiting growth,
4. negatively impacting reproduction,
5. altering immune function.

In addition, the compounding effects of stress and exposure to pathogens can compromise immune defenses, and elevated cortisol can also compromise immunity to tumour and virus-infected cells. While the immediate increase in blood glucose levels can be beneficial in the short term by providing resources to tissues and organs, the long term or chronic presence of these hormones in circulation will likely have negative impacts. Thus, physiological responses to acute stress can enhance fitness, but longer term exposures to stressors and associated stress hormones can lead to a decline in fitness.

2.3.4 Behavioural Measures of the Well-being of Cetaceans.

Determining the effect of an aquarium environment on individual cetaceans and managing the captive environment to minimize stress and optimize well-being for individual animals requires the development of appropriate measures that reflect the well-being of the individual, as well as a program for regular monitoring [e.g., 116]. Symptoms of stress in cetaceans are typically disguised, and stressors, or even diseases, often are not detected until the condition is quite advanced [53].

In many cases, a behavioural response may be the first indicator that there is something wrong, and may provide a clue to its underlying causes. Hence, there is good reason to believe that behavioural observations can be used to assess animal well-being. The advantages of this method are that behavioural measures are non-invasive and can be carried out with minimal cost under a range of conditions, although they do require proper training and experienced observers. The challenges are defining meaningful behavioural indicators, ascertaining the strength and nature of the relationship between observed behaviour and physical or mental condition, and quantifying the behavioural indicator in a useful, comparative manner. This requires the systematic collection of quantitative behavioural data to elucidate both immediate and long-term manifestations of stress.

In this section we detail different types of behaviour that might be used as practical indicators in maintaining the health and well-being of captive cetaceans. This includes a review of the available empirical data that has been collected to date and an evaluation of what these studies can tell us about the past and current welfare of cetaceans in captivity. Each potential behavioural indicator will be addressed separately, although they may be implemented in tandem as part of an ongoing behavioural monitoring programs for cetaceans held in display facilities.

Food intake behaviours

Inappetence

A lack of appetite was recognized early in the development of marine mammal medicine as a standard sign of disease in cetaceans [117]. It is still one of the primary cues used by veterinary and husbandry staff to identify the occurrence of potential medical problems. Unfortunately, as with many behavioural indicators of illness in marine mammals, inappetence may only manifest under extreme conditions and/or very late in the disease process (although the response is likely species and individual specific).

Inappetence may also be a symptom of stress [53]. Again, the evidence suggests that if such behaviour develops as a response to environmental stress, the situation has persisted for a significant period of time, and may be difficult to identify and correct. For example, Castellote and Fossa [118] noted that the appetite of captive beluga whales remained unchanged despite being subject to apparent stressors that were sufficient to significantly alter their vocal behaviour for several weeks, suggesting that vocalization was a stronger indicator of well-being than food intake (see *Acoustic activity*). This is not to say that inappetence should be discounted as a behavioural indicator. It likely reflects significant underlying conditions, and the consequences of improper nutrition is, in itself, serious and can complicate underlying medical issues. However, although it may only provide a strong signal, lack of appetite cannot generally differentiate between environmental stress and disease causes, nor can it be used as a more specific indictor within either of these categories.

Vomiting

Another food intake disorder that can manifest as a behavioural indicator of well-being is vomiting. This behaviour usually results from behavioural or psychological causes, and can subsequently become solidly ingrained within the animal’s behavioural repertoire. Vomiting can also develop due to satiation and possibly boredom, and can be the result of unintentional behavioural conditioning where the vomiting was mistakenly reinforced during the training of other behaviours. Once established, the vomiting behaviour can be very difficult to eliminate. This can cause problems of caloric intake and fluid loss.

Vomiting can obviously be initiated solely due to medical conditions, usually related to gastrointestinal issues. Conversely, vomiting that begins as a behavioural response can induce medical issues (tracheal damage or stomach ulcers due to frequent regurgitations) that further promote this response. Hence, if not observed and treated rapidly, the behavioural and medical issues can become intertwined and proportionally difficult to resolve.

Foreign body consumption

While the ingestion of foreign (non-food) bodies is primarily viewed as a problem with captive animals, it is a behaviour that is also seen in wild individuals [119]. There is no known causative factor in the consumption of foreign materials by marine mammals. Certain individuals are more likely to consume objects particularly if they are nervous due to social conditions or animals that are undergoing illness. However, some individual, healthy marine mammals in aquariums will readily play with or swallow foreign objects dropped into their habitat (usually due to their novelty) while their conspecifics show no interest in them.

Symptoms associated with foreign body consumption are often extremely vague, if existent at all. It largely depends on the composition, size and shape of the object. Objects can remain in the animal's stomach for months before any symptoms of gastric inflammation of obstruction or intoxication occur.

Although foreign body ingestion can be classified as an aberrant behaviour, it cannot, by itself, be used as a sign of stress in captive cetaceans.

Self-inflicted trauma

Reports of behaviours that cause physical damage to the individual cetacean are extremely rare. Some potential self-harm behaviours can be described as stereotypical behaviours (these are addressed separately). The two most common self-harm behaviours – rubbing and cribbing (tooth wear) – also vary widely in their manifestations and the resulting degree of physical damage to the individual whale. Many of the resulting types of physical damage are similar to injuries seen in wild individuals, but it is unknown whether the proximate causes are the same or whether it is more prevalent in the aquarium environment.

Rubbing

This behaviour is usually characterized by repeated rubbing of specific areas of an individuals' body against a specific area of its habitat. This behaviour can originate as attempts to alleviate minor physical discomfort, often associated with natural physical changes such as moulting of the epidermis in cetaceans. This behaviour can become self-reinforcing if the original behaviour results in irritation that the animal attempts to resolve by further rubbing. This behaviour can also originate as (or develop into) an attempt at self-stimulation, usually considered to be associated with "boredom". For either origin, the behaviour can develop into stereotyped behaviour, particularly if the individual is inadvertently reinforced for performing the action as part of an attempt to extinguish it (*see Stereotyped behaviour*). Fortunately, in cetaceans, rubbing against the environment rarely results in significant trauma. This problem can be prevented by early treatment of any underlying medical condition, the provision of adequately-sized environments allowing for a wider range of behavioural activities, and by ensuring that all pool surfaces are free of rough textures and protrusions.

Cribbing (tooth wear)

In many cetacean species, animals may be observed biting on various fixtures within their enclosures. When this becomes obsessive and when the objects are unyielding, an undue amount of tooth wear results. Since cetacean teeth do not grow significantly past infancy, tooth wear is permanent. This can also cause abscesses and other forms of gingival inflammation. This is usually caused by boredom and usually resolved by creating a more simulating and interactive environment. However, it may also be a sign of underlying medical issues (*see Rubbing*) that should be investigated and treated as quickly as possible to minimize any long-term impact.

Stereotyped behaviour

Definition of stereotyped behaviour in animals

There is some concern expressed that cetaceans in aquariums have a tendency to display stereotyped behaviours that are indicative of boredom and/or poor well-being. Stereotypy is a behavioural pattern that is repetitive, invariant and has no obvious goal [120]. Its prevalence has commonly been suggested to indicate welfare problems in a variety of animals [121,122,123]. The most commonly cited examples include incessant pacing, body movements, or body rubbing.

It has been suggested that the development of stereotyped behaviours is most frequent in wild-born animals introduced into captivity. The hypothesized causes for the development of such behaviours are a lack of appropriate social interactions and confinement to small unstructured cages [45,124] (see *Environmental Considerations*). There are several broad groups of behaviours exhibited by animals in captivity that may qualify as stereotyped behaviour patterns.

1. Behavioural patterns may be observed that are repeatedly shown in a rigid way and do not correspond to behaviour observed in the wild.
2. The animals might show very rigid spatial movement patterns. An oft-cited example for marine mammals is a report by Lorenz [1969; cited in 125] of spatial movement patterns in a sea lion consisting of swimming in circles on fixed routes and turning at predictable locations. Such observations seem to qualify as stereotyped behaviour and could be used to assess stereotyped behaviour patterns in cetaceans.
3. Stereotyped behaviour patterns increase in frequency and speed in expectation of food [126,127].

In this section we will provide a survey of the types of stereotyped behaviours seen in cetaceans in aquaria that have been reported in the scientific literature, followed by a discussion of the potential use of these measures as indicators of the well-being of cetaceans kept in display facilities.

Potential stereotyped behaviours seen in captive cetaceans

The most commonly reported potential stereotypic behaviour for cetaceans is that of continuous swimming patterns. Ridgway [128] reports that swimming in circles is very commonly observed in recently captured dolphins. This author claims that this is an initial panic-like reaction, and that the amount of stereotypy decreases with the length of time in captivity (unfortunately, he does not specify the rate or extent of the decrease). Gygax [125] examined the spatial movement patterns and behaviour of two female long-term display bottlenose dolphins for evidence of stereotyped behaviour, and found that both of the dolphins showed quite rigid swimming routes (complete clockwise circles). Similar results (including a complete preference for clockwise swimming) were reported for a pair of male bottlenose dolphins [129]. In a larger study, Sobel *et al.* [130] found consistent swimming directions (e.g., 85% of the swimming was in counterclockwise circles) among a group of 13 recently captured bottlenose dolphins.

However, it is possible that the continuous swimming patterns observed in dolphins do not represent true stereotyped behaviour. First, such swimming patterns are observed even when the animals are in large groups, which typically extinguish or diminish stereotypic behaviour. Second, such swimming patterns tend to cover the entire pool area; repetitive movements which do not cover the whole area (which would be a stronger indication of stereotyped behaviour) are rarely seen [131]. Alternate hypotheses suggest that the consistent movement patterns are simply a result of the physical characteristics of the pool. In addition, the direction of rotation may have a sensory [e.g., eye dominance; 128] or neurophysiological basis [130].

An alternate (and somewhat contradictory) report of possible stereotypic behaviour was provided by Galhardo *et al.* [132] who found that bottlenose dolphins in aquaria spent a large proportion of their time engaged in "head movements above the water", far more often than seen in their wild counterparts. Although this behaviour was exaggerated in frequency compared to their wild behavioural repertoire, they recognized that this behaviour was a direct result of the enrichment interactions at the water surface (i.e. toys, staff). While such behaviour is thus unlikely to induce concerns related to stereotyped behaviour, it has been subsequently recognized as a potential concern regarding the effects of increased UV exposure on cetacean vision (see *Light conditions*).

Greenwood [46] reports on a different, specific stereotypic behaviour in cetaceans - head pressing – that would certainly seem to fit the definition of aberrant, non-functional behaviour. The paper describes two separate case studies involving 3 Atlantic bottlenose dolphins (all long-term aquarium residents) that developed a similar head-pressing behaviour. The behaviour is described as the individual repeatedly (but gently) placing its melon (the fatty portion on the top of the cranium) against a vertical wall of the pool, such that it did not result in any physical damage to the animal. It must be emphasized that this behaviour is different than (the previously described) "self-harming" or incessant rubbing behaviours that have been of concern for other groups of mammals [133].

In both of these case studies, the behaviour developed when an animal was moved into a smaller pool. In the first case, a male developed this behaviour after being placed into a smaller (40,000 L) pool with another dolphin as part of a show. The behaviour was extinguished immediately when returned into the larger pool. In the second case, a male and female pair was moved to a smaller (60,000 L) tank in order to treat the ill male. Upon moving to the smaller tank, both animals immediately appeared distressed, swimming violently and vocalizing loudly. After a few hours, the male developed consistent head-pressing behaviour. While the female only occasionally exhibited this behaviour when with the male, the rate of display increased dramatically following the male's death (of unrelated causes).

Upon her return to the larger pool, the head-pressing behaviour stopped immediately, although other distress behaviours continued for 24 hr (e.g., tail slapping, vocalizing, food refusal).

The head-pressing by these 3 animals was hypothesised to be a reaction to a restricted, monotonous environment, although the reaction of the female is probably more indicative of stress rather than monotony. In these cases the containment in the smaller tank was either for unusually long periods of time, or the animals were introduced to a smaller pool to which they had not previously been exposed.

Curiously, this head-pressing behaviour has not been reported in any other cetaceans, with the possible the exception of a similar head-pressing behaviour reported for harbour porpoises [i.e., head pressing against the pool bottom while swimming; 134]. This lack of reporting is despite several studies that extensively monitored cetacean behaviour in pools [e.g., 125,135]. Also of interest is the observation that all of the published reports of stereotyped behaviour in display cetaceans are relatively old. It is unclear whether this reflects a trend in publication or study interest, or whether it reflects changes in management that have resulted in true decreases in stereotyped behaviour [particularly through changes in enrichment; 136].

Finally, mention should be made regarding the possible manifestation of excessive sexual activity as a form of stereotyped behaviour. In many cetaceans, particularly bottlenose dolphins and other small delphinids, sexual activity is a common occurrence and sexual behaviour is not necessarily reproductive. However, excessive sexual behaviour can become a stereotypic behaviour and may be considered a manifestation of boredom.

Stereotypic behaviours as indicators of well-being

Stereotyped behaviours frequently develop in wild animals introduced into captivity, and can develop in long-term captive situations [120,121,137]. Stereotypies are often interpreted as indicators of poor welfare (almost by definition), although the manner of quantifying and interpreting this relationship is varied. For example, increasing levels of stereotypic behaviour can be seen to reflect increasingly poor welfare, or the mere presence of any level of stereotypic behaviour might be interpreted as an indication of welfare issue, or there may be a critical (yet arbitrary) threshold percentage of the time budget that must be devoted to stereotypic behaviours to be considered indicative of poor welfare.

All of these approaches make the common assumption that there is a simple relationship between the prevalence of stereotypic behaviour and animal welfare. Certainly, a broad review of the literature suggests that environments that induce or increase stereotypy are indeed typically worse than those that do not [137]. For this reason, reducing stereotypy is the most common aim of environmental enrichment programs in zoos and aquaria [138]. Some facilities attempt to extinguish stereotypy by making the target behaviour unpleasant or physically difficult, or through pharmaceutical intervention. While there is undoubtedly a role in quantifying stereotypic behaviour in animal welfare assessments, there are significant pitfalls to relying on such behaviour to be a true indicator of poor welfare and, conversely, that the absence of such behaviour is an accurate indicator of good welfare. This is due to three general facts regarding the relationship between stereotypies and welfare:

1. Stereotypic behaviour is a poor indicator of welfare.
2. Extinguishing the target behaviour does not necessarily improve animal welfare.
3. Improvements in animal welfare will not necessarily result in decreases in stereotypic behaviour.

The overall lack of relationship between the frequency of stereotypic behaviour and other measures of animal welfare was clearly documented in a literature review conducted by Mason and Latham [137], and many of the following observations are based on their review. While that review demonstrated that there was no overall, simple relationship, it does not mean that the two factors are independent. Specifically, Mason and Latham's survey shows that -where data are available - environments that elicit or enhance stereotypies are typically sub-optimal. However, in contrast, within a stereotypy-inducing environment, the most stereotypic animals are likely to be the least welfare-compromised individuals. But even those statements are over-simplifications. That same review shows that stereotypies can appear or increase in situations that seem neutral, or even beneficial, with respect to welfare, and other studies reveal that some aversive environments do not elicit stereotypies.

To recognize why stereotypies are not a clear indication of welfare (in the words of Mason and Latham, "are not a faithful signal of suffering"), one needs to understand the four potential motivations for stereotypic behaviour. First, stereotypies can serve as "do-it-yourself enrichments". This occurs when captive animals devise their own ways of performing natural behaviours. Since these obviously occur in an artificial environment, they may be distorted or curtailed in their expression due to physical or social limitations, and therefore be difficult to recognize. In such circumstances, stereotypies would result in an apparent benefit to the individual and concern should be focused on the welfare of the least stereotypic animals.

Second, stereotypies may serve a positive function as a general coping mechanism, by increasing or decreasing arousal to external or internal stimuli [reviewed in 120], in what Mason and Latham [137] termed "The Mantra Effect". This is another example where, within any population of stereotypy-susceptible individuals, the welfare of non-stereotyping animals may be of greater concern.

Third, stereotypies may persist as habits that are disconnected from their root source. In other words, with repetition, behaviour may shift into a form of automatic processing known as central control [139]. This type of automatic behavioural control allows preferred, regularly occurring physical movements to become faster, with minimal cognitive processing or need for sensory feedback [139]. However, the same processes of ‘body memory’ means that stereotypic behaviours may become dissociated from welfare (good or bad). Behaviourally, this means that stereotypies that have reached this developmental stage should occur more often and for longer periods, in a more diverse set of situations, and also should be harder to interrupt or modulate with changes in the environment. However, this also means that there is an increased disassociation between the expression of stereotypy and welfare [121]. By the same token, a failure to alleviate stereotypy should not automatically be interpreted as a failure to improve welfare. There is only one circumstance in which reduced stereotypy means improved welfare, and that is when the motivation to perform the source-behaviour is diminished.

Finally, stereotypic behaviours can be the result of perseverative behaviour. ‘Perseveration’ is defined as ‘the continuation or recurrence of an activity without the appropriate stimulus’ [140]. In this context, stereotypies are a symptom of altered behavioural control, such that *all* of an animal’s behaviour becomes less appropriately coupled to internal state and external circumstance. In these circumstances, the relationship between perseveration and welfare is complex, but in many ways resembles that of central control. Like central control, perseveration is also a factor largely neutral with respect to welfare (although welfare can nevertheless influence stereotypy levels), and resulting stereotypies may similarly be hard to cure with enrichments (although this does not mean that welfare has been unaffected). The most important aspect of perseverance is that stereotypy can be linked with reduced abilities to respond appropriately to novel stimuli, and even with tendencies to find environmental change stressful. This would suggest that the use of environmental enrichments to alleviate such behaviours must be more gradual, as the novelty of enrichments may themselves cause stress and fear [138].

Behaviours related to aggression

A range of behaviours related to aggressive expression of social interactions can be a source of, and a potential measure of stress. Behaviours due to natural inter-animal aggression can become exaggerated and problematic due to the inability of other animals to escape as they might in the wild. Aggression is a problem when secondary animals do not have the space to withdraw from aggressive confrontations such as from a dominant male. In addition to the physical trauma, these animals can be forced into corners of the exhibit and presented with nearly constant psychological intimidation from the dominant individual. It appears most commonly in the form of intimidation with infliction of rake-bite lacerations to the secondary animal. This results in cutaneous pathology and the intimidated animal is frequently rendered vulnerable to the onset of subsequent diseases.

Aggression is also occasionally seen directed towards trainers. This may be due to some previous mistreatment of the animal or may be a manifestation of the aberrant behavioural state of the individual. Aggression expressed by killer whales towards their trainers is a matter of grave concern, given that water behaviours with trainers have become more prevalent in recent years. There has obviously been great interest in understanding the causes of the well-publicized, tragic occasions when Orca-human interactions have led to injury or even death. Unfortunately, there are rarely any conclusive answers. In a few cases of aggression, the behaviour has been attributed to disease or to the presence of frustrating or confusing situations but in other cases there has been no clear causal factor. There is also the concern that certain individual whales are more susceptible to this behaviour than others.

Some individuals exhibit what might be more accurately classified as “destructive behaviour” which, in some cases, can be mistaken for social aggression. Destructive behaviour can manifest as aggression to other conspecifics, killing or harassment of other aquatic species, or destruction of the habitat itself. Unlike social aggression, destructive behaviour within the habitat can often be attributed to boredom. Hence, efforts to prevent destructive behaviour differ from those for social aggression, including the design of interesting and stimulating devices for the animals’ recreation.

The opposite side of the interaction are behavioural changes observed in the individual animal that is the target of the aggression. Submissive behaviour due to another animal’s aggressive behaviour results in the state of constant psychological stress, and can render the animal vulnerable to a variety of disease episodes. Resolution is possible by the removal of the aggressive animal or allowing the target animal to get out of the line of sight of the aggressor.

Nervous behaviour can be observed in animals that are the target of social aggression, or are maladapted to their social group or to their environment. It is manifested by general hyperactivity and excessive behaviour [53]. It is most common among infant and juvenile individuals, although it can persist throughout an animal’s life, sometimes even when the original trigger is removed.

The expression of nervous behaviour can be complicated by exaggerated behaviours of other animals within the enclosure that tend to further promote the nervous episodes. Nervous animals frequently exhibit additional symptoms such as vomiting, foreign body consumption, and self-inflicted trauma (see previous portions of this section). Such animals frequently suffer repeated disease problems until the source of their nervousness is resolved [53].

Acoustic activity as a method to evaluate welfare

Most physiological metrics for stress response require handling the subject, a process that may confer additional stress [e.g., see 108]. Vocalization patterns have been suggested as a potential non-invasive metric of animal well-being. A number of vocalization parameters have been found to vary with stress in terrestrial animals, including vocal rate intensity, frequency, range, maximum frequency, minimum frequency, number of harmonics and duration.

The acoustic repertoire of cetaceans is likely the most heavily studied aspects of their physiology and behaviour. Cetaceans have a number of different acoustic signals, both for communication and those associated with sonar capabilities.

However, despite their wide acoustic repertoire and the apparent importance of sound production in their lives, acoustic activity is rarely included among those behaviours monitored to evaluate the suitability of housing or handling in zoos and aquaria. This is despite the fact that there is an extensive body of literature documenting that vocalization rate, types of vocalization, and acoustic structure within a call type may vary with stressful contexts such as aggression, panic, social separation, and levels of stress hormones among terrestrial animals. This raises the question of whether acoustic behaviour could be exploited as a useful monitor of psychological well-being in captive colonies of cetaceans, particularly if it can be demonstrated that they are associated with stereotypical behaviours, stressful environmental conditions, or aversive social situations.

The utility of using vocalizations as a metric for the well-being of cetaceans in aquariums is dependent upon how logistically easy and inexpensive these measures are to implement. Some acoustic studies require expensive, calibrated equipment and detailed knowledge of vocal repertoire. However, some studies – such as that by Castellote and Fossa [118] – have tried to demonstrate that simpler metrics (such as total vocalization rate) may be a useful tool for measuring acoustic activity in relation to welfare in captive environments. Such measures have the benefit of requiring no expensive equipment or detailed analysis/interpretation. Similarly, acoustic profiles may also be useful in evaluating environmental enrichment protocols. However, in order to be a valid metric of well-being, it must first be demonstrated that specific types of acoustic activity quantitatively relate to the well being or mental state of cetaceans in display facilities. On the whole, acoustic signals would seem to hold promise as an alternate measure of stress and conflict in some cetacean species, although monitoring and interpretation may require a degree of specialized equipment and skills.

Dolphin signature whistles

Most studies on dolphin communication have focused on whistles [141]. This type of vocalization is thought to serve as “signature whistles” for individuals through specific, recognizable changes in their acoustic characteristics [142,143]. Whistles are omnidirectional and hence have the capacity to convey information to all members of a dolphin school about identity and relative position [144]. Overall, signature whistles tend to be highly stable; this makes them ideal signals that may vary among contexts [145]. It has therefore been suggested that these whistle types can provide rudimentary information regarding the “emotional state” of the whistler [143] and that they may provide a vocal indicator of short-term stress in bottlenose dolphins.

McBride and Hebb [57] published one of the first reports of context-specific whistling in bottlenose dolphins. When the animals were first introduced into the tank, the whistling was heard constantly for the first week or two, at the same time that excitement or "nervous behaviour" was evident. On later occasions, whenever a strange object was introduced into the tank the same combination of whistling and excitement reappeared, and lasted for an hour or so (although an unexcited avoidance of the object might continue much longer).

Lilly [146] was the first to propose that dolphins produced a specific “distress whistle”, that serves as an explicit indicator of stress to the extent that other dolphins respond to these cues by offering aid. However, a more rigorous study of 100 managed dolphins found no evidence of such distress whistles [143]. While certain parameters of signature whistles did appear to be closely related to the level of arousal of an individual dolphin, these were not consistent across individuals. Another study found changes in signature whistle frequency and time parameters between dolphins when taking part in interactive programs compared to when they were maintained in isolation [147].

Changes in signature whistle characteristics were also examined in what might be considered an acute stress encounter in wild bottlenose dolphins, specifically during brief capture and release events in Sarasota, Florida [148]. In this study, signature whistle rates increased by 1 to 2 orders of magnitude during capture events (number of loops also increased) compared to undisturbed conditions, with the effect diminishing over the duration of a capture session. A similar study of the same Sarasota Bay population also measured higher production of signature whistles by bottlenose dolphins that were temporarily restrained versus free swimming [149]. However, these differences were restricted to only male pairs, who rarely used whistles when not restrained. The authors concluded that wild and managed bottlenose dolphins used signature whistles as contact calls, and although there was a relationship to behavioural state, it was not a direct measure of well-being *per se*.

Certainly, evidence from such studies must be interpreted with care. Some of the increase in whistle production may have been caused or augmented by the increased vicinity of the research boats, as has been demonstrated in separate studies on the same dolphin population [150]. Alternately, increasing signature vocalizations could reflect an increased motivation to communicate rather than an increased stress level, and decreases over the course of a capture session could result from fatigue rather than any decrease in stress levels.

Dolphin pulsed vocalizations

Traditionally, burst-pulse sounds have primarily been investigated as part of the dolphin’s echolocation capabilities. However, some researchers have investigated the role of these sounds in communication, particularly in social situations. Hence, there is the potential for these sounds to be an indicator of aggressive interactions between individual dolphins.

Dawson [151] reported a significantly greater abundance of high-repetition-rate burst-pulse sounds, labeled “cries,” during aerial and aggressive behaviour situations than during feeding in wild Hector’s dolphins. Amundin [152] reported the use of burst-pulsed sounds in agonistic and distress situations in the (non-whistling) harbour porpoise. Connor and Smolker [153] reported that a pulsed “pop” sound was correlated with courtship and/or dominance behaviour in wild bottlenose dolphins. In this study, the pulses (which were audible to researchers at the water surface) were only produced by males in the presence of “female consorts". Since the vocalization was also always accompanied by "head-jerks" (an assumed aggressive behaviour) the sounds were interpreted to be a threat vocalization that induces the female to remain close to the popping male during consortships.

As with most areas of research, much of the acoustic research with cetaceans in aquariums has been carried out on bottlenose dolphins. Overstrom [154] reported the production of pulsed sounds correlated with aggressive behaviours in this species. The primary component of agonistic displays between 5 dolphins was an open-mouthed posture accompanied by violent vertical head motions and the emission of pulse-type vocalizations. These pulsed sounds were the only type directly associated with the open-mouthed interactions. Further, it was found that the level of aggressive response between the participants of the interactions increased with the production and subsequent duration of burst-pulse sounds.

Blomqvist and Amundin [155] also found that burst-pulse sounds were associated with aggressive interactions in captive bottlenose dolphins. These authors studied dolphins while either free-swimming in tanks (using data from a previous study by Karlsson 1997) or when temporarily separated into two subgroups by means of a net barrier. Aggressive interactions took the form of two animals in a face-to-face position (in the latter study while on opposite sides of the net barrier). Acoustic bursts (i.e., emission of burst-pulse sounds) were only observed in situations containing aggressive behaviour elements [including violent head jerks, pectoral fin jerks, S-shaped body postures, and jaw claps; cf. 154,156].

These acoustic displays were thought to be highly directional, seemingly aimed at the target animals (as demonstrated by the fact that animals pointed their rostrum in the general direction of the other). On a few occasions, a target dolphin was seen to hide behind a corner of the pool, perhaps not just trying to keep out of sight but also out of the direction of sound emission of the other animal. It should be emphasized that these acoustic signals may provide a benefit to the animals by serving as social cues. Blomqvist and Amundin [155] suggest that the sounds as well as the visual behaviour patterns may be part of a ritualized behaviour sequence, with the purpose of settling rank conflicts or other disagreements between herd members with a minimum of physical fighting. They cite the prevalence of "avoidance behaviours" ("open mouth threat" or "tail blow") in response the aggressive burst pulses, a behaviour also demonstrated by wild harbour porpoises [152]. This is supported by the observation that, while some of the encounters between pairs of bottlenose dolphins climaxed in both animals charging toward each other (apparently trying to bite and/or hit each other with rostrum and/or tail fin) these physical encounters were very short and did not result in any injuries. Further, similar behaviours have been observed in wild Atlantic spotted dolphins [157], suggesting that this behaviour may represent a sample of the normal, species-specific behavioural repertoire.

The concept that vocal warnings serve to diffuse or limit aggressive encounters was further demonstrated in a study of play-fighting in captive bottlenose dolphins

[158]. The study found that play-fighting subadult dolphins emitted a characteristic sound -a short pulse burst followed by a whistle – which was never observed in aggressive interactions. The burst component was indistinguishable from adult aggressive signals, and only the whistle component seemed to differentiate the signal intent. This corresponds with the observation in other species that play-fighting is often accompanied by distinct acoustic and/or visual appeasement behaviours to prevent escalation into a potentially dangerous agonistic encounter.

The use of appeasement qualifiers raises questions about the usefulness of acoustic signalling rate as an indicator of well-being, particularly given that play behaviour should increase with well-being. The same might be argued for the frequency of vocal signals among mature individuals; care should be taken to differentiate aggressive signalling induced by stress and signalling normally associated with mating behaviours.

Beluga and Orca vocalizations

In contrast to the proposed relationship between vocalizations and stress in dolphins, there is evidence of a decrease or even a cessation in the acoustic activity of both wild and captive beluga whales in the presence of natural predators (i.e., killer whales) or environmental disturbance [reviewed in 118], a trait also observed in free-ranging narwhals [159].

Castellote and Fossa [118] investigated the acoustic response of two beluga whales to two different (presumed) disturbances: transportation (by air to facility) and an environmental disturbance (introduction of harbour seals into the habitat). Both of these disturbances drastically reduced the acoustic activity of the beluga whales. After transportation, the vocalization rate dropped dramatically, remained very low during the next 4 weeks, and did not reach the same level as before the transport until the 5th week. Similarly, exposure to seals (even though partly exposed beforehand) caused decreased vocalizations for 2 weeks.

A study of a mating pair of killer whales in an aquarium revealed a strong relationship between acoustic and agonistic behaviours [160]. Specifically, the researchers found that vocalization rates were about 3 times higher during aggressive chase episodes than during control periods (although the incidents were relatively rare – about 8 times in 5 months). Further, a subset of specific call types were observed almost exclusively during these agonistic interactions, suggesting that they could be used as acoustic indicators of increased aggression in this species. It is also interesting to note that the incidence of aggressive behaviour is much lower than in captive bottlenose dolphins, and confirms similar comparisons among wild counterparts.

References Cited in Part 2

1. Marino L, Frohoff T (2011) Towards a new paradigm of non–captive research on cetacean cognition. PloS one 6: e24121.
2. Mayer S (1998) A review of the scientific justifications for maintaining cetaceans in captivity: Whale and Dolphin Conservation Society. 44 p.
3. Houser DS, Finneran JJ, Ridgway SH (2010) Research with navy marine mammals benefits animal care, conservation and biology. International Journal of Comparative Psychology 23: 249–268.
4. Hill H, Lackups M (2010) Journal publication trends regarding cetaceans found in both wild and captive environments: What do we study and where do we publish? International Journal of Comparative Psychology 23: 414–534.
5. Rose NA, Parsons ECM, Garinato R (2009) The case against marine mammals in captivity (4th edition). The Humane Society of the United States and the World Society for the Protection of Animals.
6. Morgan KN, Tromborg CT (2007) Sources of stress in captivity. Applied Animal Behaviour Science 102: 262-302.
7. Au WW, Popper AN, Fay RR (2000) Hearing by whales and dolphins. New York: Springer-Verlag. 485 p.
8. Richardson WJ, Greene Jr CR, Malme CI, Thomson DH (1995) Marine mammals and noise. San Diego, CA: Academic Press. 576 p.
9. Au WWL (1993) The sonar of dolphins. New York: Springer-Verlag. 277 p.
10. Watkins WA, Wartzok D (1985) Sensory biophysics of marine mammals.
11. Marine Mammal Science 1: 219-260.

Gamble MR (1982) Sound and its significance for laboratory animals. Biological Reviews 57: 395-421.

12. Kight CR, Swaddle JP (2011) How and why environmental noise impacts animals: an integrative, mechanistic review. Ecology Letters 14: 1052-1061.
13. Nowacek DP, Thorne LH, Johnston DW, Tyack PL (2007) Responses of cetaceans to anthropogenic noise. Mammal Review 37: 81-115.
14. Moore SE, Reeves RR, Southall BL, Ragen TJ, Suydam RS*, et al.* (2012) A new framework for assessing the effects of anthropogenic sound on marine mammals in a rapidly changing Arctic. BioScience 62: 289-295.
15. Zirbel K, Balint P, Parsons E (2011) Navy sonar, cetaceans and the US Supreme Court: A review of cetacean mitigation and litigation in the US. Marine Pollution Bulletin 63: 40-48.
16. Weilgart LS (2007) A brief review of known effects of noise on marine mammals. International Journal of Comparative Psychology 20: 159-168.
17. Todd S, Stevick P, Lien J, Marques F, Ketten D (1996) Behavioural effects of exposure to underwater explosions in humpback whales (*Megaptera novaeangliae*). Canadian Journal of Zoology 74: 1661-1672.
18. Gordon J, Gillespie D, Potter J, Frantzis A, Simmonds MP*, et al.* (2003) A review of the effects of seismic surveys on marine mammals. Marine Technology Society Journal 37: 16-34.
19. Parsons E, Dolman SJ, Wright AJ, Rose NA, Burns W (2008) Navy sonar and

cetaceans: Just how much does the gun need to smoke before we act? Marine Pollution Bulletin 56: 1248-1257.

20. Ketten DR (2012) Marine mammal auditory system noise impacts: Evidence and incidence. In: Popper AN, Hawkins A, editors. The Effects of noise on aquatic life. New York: Springer-Verlag. pp. 207-212.

21. Southall BL, Bowles AE, Ellison WT, Finneran JJ, Gentry RL, *et al.* (2007) Marine mammal noise exposure criteria: Initial scientific recommendations. Aquatic Mammals 33: 1-521.

22. O'Neal DM (1998) Comparison of the underwater ambient noise measured in three large exhibits at the Monterey Bay Aquarium and in the inner Monterey Bay [M.Sc. thesis]. Monterey, CA: Naval Postgraduate School.

23. Scheifele P, Johnson M, Kretschmer L, Clark J, Kemper D, *et al.* (2012) Ambient habitat noise and vibration at the Georgia Aquarium. The Journal of the Acoustical Society of America 132: EL88-EL94.

24. Bellhorn R (1980) Lighting in the animal environment. Laboratory Animal Science 30: 440-450.

25. Yokoyama S (2000) Molecular evolution of vertebrate visual pigments. Progress in Retinal and Eye Research 19: 385-419.

26. Meredith RW, Gatesy J, Emerling CA, York VM, Springer MS (2013) Rod monochromacy and the coevolution of cetacean retinal opsins. PLoS genetics 9: e1003432.

27. Griebel U, Peichl L (2003) Colour vision in aquatic mammals—facts and open questions. Aquatic Mammals 29: 18-30.

28. Navara KJ, Nelson RJ (2007) The dark side of light at night: physiological, epidemiological, and ecological consequences. Journal of Pineal Research 43: 215-224.

29. Dobson CM (2014) Dynamics and timekeeping in biological systems. Annual Review of Biochemistry 83: 15.11-15.16.

30. Van der Meer E, Van Loo P, Baumans V (2004) Short-term effects of a disturbed light–dark cycle and environmental enrichment on aggression and stress-related parameters in male mice. Laboratory Animals 38: 376-383.

31. Wilson B, Arnold H, Bearzi G, Fortuna C, Gaspar R, *et al.* (1999) Epidermal diseases in bottlenose dolphins: impacts of natural and anthropogenic factors. Proceedings of the Royal Society of London Series B: Biological Sciences 266: 1077-1083.

32. Bowman A, Martinez–Levasseur LM, Acevedo–Whitehouse K, Gendron D, Birch-Machin MA (2013) The simultaneous detection of mitochondrial DNA damage from sun–exposed skin of three whale species and its association with UV–induced microscopic lesions and apoptosis. Mitochondrion 13: 342–349.33.

33. Martinez-Levasseur LM, Birch-Machin MA, Bowman A, Gendron D, Weatherhead E, *et al.* (2013) Whales use distinct strategies to counteract solar ultraviolet radiation. Scientific Reports 3: 1-6.

34. Angilletta Jr. MJ (2009) Thermal adaptation: A theoretical and empirical synthesis. New York: Oxford University Press. 289 p.

35. Yeates LC, Houser DS (2008) Thermal tolerance in bottlenose dolphins

(*Tursiops truncatus*). Journal of Experimental Biology 211: 3249-3257.

36. Williams TM, Estes JA, Doak DF, Springer AM (2004) Killer appetites: Assessing the role of predators in ecological communities. Ecology 85: 3373-3384.

37. Levy DM (1944) On the problem of movement restraint: Tics, stereotyped movements, hyperactivity. American Journal of Orthopsychiatry 14: 644.

38. Goerke B, Fleming L, Creel M (1987) Behavioral changes of a juvenile gorilla after a transfer to a more naturalistic environment. Zoo Biology 6: 283-295.

39. Line SW, Morgan KN, Markowitz H, Strong S (1990) Increased cage size does not alter heart rate or behavior in female rhesus monkeys. American Journal of Primatology 20: 107-113.

40. Morgan KN, Mondesir FL, Buell K, Guy P, Carmella V*, et al.* (2002) Changes in chimp behavior, visitor behavior, and visitor attitude with a change in habitat. Animal Behavior Society Annual Meeting. Bloomington, IN.

41. Luna Blasio A, Valdez Pérez R, Romano Pardo M, Galindo Maldonado F (2012) Maintenance behaviour and cortisol levels in bottlenose dolphins (*Tursiops truncatu*s) in closed and open facilities. Veterinaria México 43: 103-112.

42. Venn-Watson SK, Jensen ED, Ridgway SH (2011) Evaluation of population health among bottlenose dolphins (*Tursiops truncatus*) at the United States Navy Marine Mammal Program. Journal of the American Veterinary Medical Association 238: 356-360.

43. Clubb R, Mason GJ (2007) Natural behavioural biology as a risk factor in carnivore welfare: How analysing species differences could help zoos improve enclosures. Applied Animal Behaviour Science 102: 303-328.

44. Clubb R, Mason G (2003) Animal welfare: captivity effects on wide-ranging carnivores. Nature 425: 473-474.

45. Mason GJ (2010) Species differences in responses to captivity: stress, welfare and the comparative method. Trends in Ecology and Evolution 25: 713-721.

46. Greenwood A (1977) A stereotyped behaviour pattern in dolphins. Aquatic Mammals 5: 15-17.

47. Caldwell M, Caldwell D, Townsend B. (1968) Social behavior as a husbandry factor in captive odontocete cetaceans; Proceedings of the 2nd Symposium on Disease and Husbandry of Aquatic Mammals.

48. Myers WA, Overstrom NA (1978) The role of daily observation in the husbandry of captive dolphins (*Tursiops truncatus)*: Biological Systems.

49. Bassos MK, Wells RS (1996) Effect of pool features on the behavior of two bottlenose dolphins. Marine mammal science 12: 321-324.

50. Shyan MR, Merritt D, Kohlmeier NM, Barton K, Tenge J (2002) Effects of pool size on free-choice selections by Atlantic bottlenosed dolphins at one zoo facility. Journal of Applied Animal Welfare Science 5: 215-225.

51. Asper ED, Young WG, Walsh MT (1988) Observations on the birth and development of a captive-born Killer whale *Orcinus orc*a. International Zoo Yearbook 27: 295-304.

52. Tarlow EM, Blumstein DT (2007) Evaluating methods to quantify anthropogenic stressors on wild animals. Applied Animal Behaviour Science 102: 429-451.

53. Sweeney J (1990) Marine mammal behavioral diagnostics. CRC Handbook

of Marine Mammal Medicine. Baco Raton, FL: CRC Press.

54. Kyngdon D, Minot E, Stafford K (2003) Behavioural responses of captive common dolphins *Delphinus delphis* to a 'Swim-with-Dolphin' programme. Applied Animal Behaviour Science 81: 163-170.

55. Geraci JR (1975) Pinniped nutrition. Rapports et Proces-verbaux des Reunion Conseil International pour l'Exploration de la Mer 169: 312-323.

56. Jensen ALM, Delfour F, Carter T (2013) Anticipatory behavior in captive bottlenose dolphins (*Tursiops truncatus*): A preliminary study. Zoo Biology 32: 436-444.

57. McBride AF, Hebb DO (1948) Behavior of the captive bottle-nose dolphin, *Tursiops truncatus*. Journal of Comparative and Physiological Psychology 41: 111-123.

58. Waples KA, Gales NJ (2002) Evaluating and minimising social stress in the care of captive bottlenose dolphins (*Tursiops aduncus*). Zoo Biology 21: 5-26.

59. Mello I, Nordensten L, Amundin M (2005) Reactions of three bottlenose dolphin dams with calves to other members of the group in connection with nursing. Zoo Biology 24: 543-555.

60. Mann J, Smuts BB (1998) Natal attraction: allomaternal care and mother–infant separations in wild bottlenose dolphins. Animal Behaviour 55: 1097-1113.

61. Maier SF, Seligman ME (1976) Learned helplessness: Theory and evidence. Journal of Experimental Psychology: General 105: 3-46.

62. DeMaster DP, Drevenak JK (1988) Survivorship patterns in three species of captive cetaceans. Marine Mammal Science 4: 297-311.

63. Greenwood A, Taylor D (1985) Captive killer whales in Europe. Aquatic Mammals 1: 10-12.

64. Best P, Ross G (1984) Live-capture fishery for small cetaceans in South African waters. Reports of the International Whaling Commission 34: 615-618.

65. Hui C, Ridgway S (1978) Survivorship patterns in captive killer whales (*Orcinus orca*). Bulletin of the Southern California Academy of Sciences 77: 45-51.

66. Innes WS (2005) Survival rates of Marine Mammals in Captivity: Temporal Trends and Institutional Analysis. [M.Sc. thesis]. Durham, NC: Duke University.

67. Wells RS, Scott MD (1990) Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. Report of the International Whaling Commission 12: 497-415.

68. Small RJ, Demaster DP (1995) Survival of five species of captive marine mammals. Marine Mammal Science 11: 209-226.

69. Rose NA (2011) Killer Controversy: Why Orcas Should No Longer Be Kept in Captivity. Washington, D.C.: Humane Society International and The Humane Society of the United States. 16 p.

70. Reeves RR, DeMaster DP, Hill CL, Leatherwood S (1994) Survivorship of odontocete cetaceans at Ocean Park, Hong Kong, 1974-1994. Asian Marine Biology 11: 107-124.

71. Asper ED, Duffield DA, Dimeo-Ediger N, Shell D (1990) Marine mammals in zoos, aquaria and marine zoological parks in North America: 1990 census report. International Zoo Yearbook 29: 179-187.

72. Small RJ, Demaster DP (1995) Acclimation to captivity: a quantitative estimate based on survival of bottlenose dolphins and California sea lions. Marine Mammal Science 11: 510-519.

73. Bigg M (1982) An assessment of killer whale (Orcinus orca) stocks off Vancouver Island, British Columbia. Report of the International Whaling Commission 32: 5-666.

74. Matkin CO, Ward Testa J, Ellis GM, Saulitis EL (2013) Life history and population dynamics of southern Alaska resident killer whales (*Orcinus orca*). Marine Mammal Science 30: 460-479.

75. Ridgway SH (1979) Reported causes of death of captive killer whales (*Orcinus orca*). Journal of Wildlife Diseases 15: 99-104.

76. Bonar CJ, Boede EO, Hartmann MG, Lowenstein-Whaley J, Mujica-Jorquera E*, et al.* (2007) A retrospective study of pathologic findings in the Amazon and Orinoco river dolphin (*Inia geoffrensis*) in captivity. Journal of Zoo and Wildlife Medicine 38: 177-191.

77. Sweeney JC, Stone R, Campbell M, McBain J, Leger JS*, et al.* (2010) Comparative survivability of *Tursiops* neonates from three US institutions for the decades 1990-1999 and 2000-2009. Aquatic Mammals 36.

78. Wells RS (2003) Dolphin social complexity: lessons from long-term study and life history. In: de Waal FBM, Tyack PL, editors. Animal social complexity: Intelligence, culture, and individualized societies. Cambridge, MA: Harvard University Press. pp. 32-56.

79. Roberts Jr J, Boice R, Brownell Jr R, Brown D (1965) Spontaneous atherosclerosis in Pacific toothed and baleen whales. Comparative atherosclerosis: the morphology of spontaneous and induced atherosclerotic lesions in animals and its relation to human disease Harper and Row, New York, New York: 151-155.

80. Dunn JL (1990) Bacterial and mycotic diseases of cetaceans and pinnipeds. In: Dierauf LA, editor. CRC handbook of marine mammal medicine: health, disease, and rehabilitation. Boca Raton, Florida: CRC Press, Inc. pp. 73-87.

81. Siebert U, Wünschmann A, Weiss R, Frank H, Benke H*, et al.* (2001) Post-mortem Findings in Harbour Porpoises (*Phocoena phocoena*) from the German North and Baltic Seas. Journal of Comparative Pathology 124: 102-114.

82. Venn-Watson S, Daniels R, Smith C (2012) Thirty year retrospective evaluation of pneumonia in a bottlenose dolphin *Tursiops truncatus* population. Diseases of aquatic organisms 99: 237-242.

83. Garner MM, Shwetz C, Ramer JC, Rasmussen JM, Petrini K*, et al.* (2002) Congenital diffuse hyperplastic goiter associated with perinatal mortality in 11 captive-born bottlenose dolphins (*Tursiops truncatus*). Journal of Zoo and Wildlife Medicine 33: 350-355.

84. Van Bressem M-F, Van Waerebeek K, Flach L, Reyes JC, de Oliveira MC*, et al.* Skin diseases in cetaceans. International Whaling Commission SC/60/DW8 1-11.

85. Palmer CJ, Schroeder JP, Fujioka RS, Douglas JT (1991) *Staphylococcus aureus* infection in newly captured Pacific bottlenose dolphins (*Tursiops truncatus*

gilli). Journal of Zoo and Wildlife Medicine 22: 330-338.
86. Maggi RG, Raverty SA, Lester SJ, Huff DG, Haulena M*, et al.* (2008) Bartonella henselae in captive and hunter-harvested beluga (*Delphinapterus leucas*). Journal of Wildlife Diseases 44: 871-877.
87. Sweeney J, Ridgway S (1975) Common diseases of small cetaceans. Journal of the American Veterinary Medical Associaion 167: 533-540.
88. Dierauf L, Gulland FM (2001) CRC handbook of marine mammal medicine: health, disease, and rehabilitation. Baco Raton, FL: CRC Press.
89. Ford JKB, Ellis GM, Balcomb KC (2000) Killer whales: The natural history and genealogy of *Orcinus orca* in British Columbia and Washington State: University of British Columbia Press, Vancouver, BC, Canada. 108 p.
90. Daily MD (2001) Parasitic diseases. In: Dierauf LA, Gulland F, editors. CRC handbook of marine mammal medicine: health, disease, and rehabilitation. Boca Raton, FL: CRC Press. pp. 357-382.
91. Baker J, Martin A (1992) Causes of mortality and parasites and incidental lesions in harbour porpoises (*Phocoena phocoena*) from British waters. Veterinary Record 130: 554-558.
92. Selye H (1973) The evolution of the stress concept. American Scientist 61: 692-699.
93. Moberg G (1987) Problems in defining stress and distress in animals. Journal of the American Veterinary Medical Association 191: 1207-1211.
94. Moberg G (2000) Biological response to stress: implications for animal welfare. In: Moberg GP, Mench JA, editors. The biology of animal stress: basic principles and implications for animal welfare. Wallingford, U.K. : CABI Publishing. pp. 1-21.
95. Dierauf LA (1990) Stress in marine mammals. CRC handbook of marine mammal medicine. Boca Raton, FL: CRC Press. pp. 295-301.
96. St Aubin D, Ridgway SH, Wells R, Rhinehart H (1996) Dolphin thyroid and adrenal hormones: circulating levels in wild and semidomesticated *Tursiops truncatus*, and influence of sex, age, and season. Marine Mammal Science 12: 1-13.
97. St. Aubin D, Geraci J (1988) Capture and handling stress suppresses circulating levels of thyroxine (T4) and triiodothyronine (T3) in beluga whales *Delphinapterus leucas*. Physiological Zoology 61: 170-175.
98. Rolland RM, Hunt KE, Kraus SD, Wasser SK (2005) Assessing reproductive status of right whales (*Eubalaena glacialis*) using fecal hormone metabolites. General and Comparative Endocrinology 142: 308-317.
99. Hunt KE, Rolland RM, Kraus SD, Wasser SK (2006) Analysis of fecal glucocorticoids in the North Atlantic right whale (*Eubalaena glacialis*). General and Comparative Endocrinology 148: 260-272.
100. Curry BE (1999) Stress in mammals: the potential influence of fishery-induced stress on dolphins in the eastern tropical Pacific Ocean. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Science Center. NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-260 NOAA Technical Memorandum

NOAA-TM-NMFS-SWFSC-260.

101. St Aubin DJ, Deguise S, Richard PR, Smith TG, Geraci JR (2001) Hematology and plasma chemistry as indicators of health and ecological status in beluga whales, *Delphinapterus leucas*. Arctic 54: 317-331.

102. Thomson CA, Geraci JR (1986) Cortisol, aldersterone, and leucocytes in the stress response of bottlenose dolphins, *Tursiops truncatus*. Canadian Journal of Fisheries and Aquatic Sciences 43: 1010-1016.

103. Orlov MV, Mukhlya AM, Kulikov NA (1988) Hormonal indices in the bottle-nosed dolphin *Tursiops truncatus* in the norm and in the dynamics of experimental stress. Journal of Evolutionary Biochemistry and Physiology 24: 431-436.

104. Copland MD, Needham DJ. (1992) Hematological and biochemical changes associated with transport of dolphins (*Tursiops truncatus*); Proceedings of the 23rd Annual International Association for Animal Medicine Conference, Hong Kong. pp. 25-28

105. Ortiz RM, Worthy GAJ (2000) Effects of capture on adrenal steroid and vasopressin concentrations in free-ranging bottlenose dolphins (*Tursiops truncatus*). Comparative Biochemistry and Physiology a-Molecular and Integrative Physiology 125: 317-324.

106. Ugaz C, Valdez RA, Romano MC, Galindo F (2013) Behavior and salivary cortisol of captive dolphins (*Tursiops truncatus*) kept in open and closed facilities. Journal of Veterinary Behavior: Clinical Applications and Research 8: 285-290.

107. Koopman HN, Westgate AJ, Read AJ, Gaskin DE (1995) Blood chemistry of wild harbor porpoises *Phocoena phocoena* (L). Marine Mammal Science 11: 123-135.

108. Desportes G, Buholzer L, Anderson-Hansen K, Blanchet M, Acquarone M*, et al.* (2007) Decrease stress; train your animals: The effect of handling methods on cortisol levels in harbour porpoises (*Phocoena phocoena*) under human care. Aquatic Mammals 33: 286-292.

109. Eskesen IG, Teilmann J, Geertsen B, Desportes G, Riget F*, et al.* (2009) Stress level in wild harbour porpoises (*Phocoena phocoena*) during satellite tagging measured by respiration, heart rate and cortisol. Journal of the Marine Biological Association of the United Kingdom 89: 885-892.

110. Suzuki M, Tobayama T, Katsumata E, Yoshioka M, Aida K (1998) Serum cortisol levels in captive Killer whale and bottlenose dolphin. Fisheries Science 64: 643-647.

111. Spoon TR, Romano TA (2012) Neuroimmunological response of beluga whales (*Delphinapterus leucas*) to translocation and a novel social environment. Brain, Behavior, and Immunity 26: 122-131.

112. Noda K, Akiyoshi H, Aoki M, Shimada T, Ohashi F (2007) Relationship between transportation stress and polymorphonuclear cell functions of bottlenose dolphins, *Tursiops truncatus*. The Journal of Veterinary Medical Science/The Japanese Society of Veterinary Science 69: 379-383.

113. Trana MR (2014) Variation in blubber cortisol as a measure of stress in beluga whales of the Canadian Arctic [M.Sc. thesis]. Winnipeg, MB: University of Manitoba.

114. Rolland RM, Parks SE, Hunt KE, Castellote M, Corkeron PJ*, et al.* (2012) Evidence that ship noise increases stress in right whales. Proceedings of the Royal Society B: Biological Sciences 279: 2363-2368.
115. Romero LM, Butler LK (2007) Endocrinology of stress. International Journal of Comparative Psychology 20: 89-95.
116. Owen MA, Swaisgood RR, Czekala NM, Steinman K, Lindburg DG (2004) Monitoring stress in captive giant pandas (*Ailuropoda melanoleuca*): behavioral and hormonal responses to ambient noise. Zoo Biology 23: 147-164.
117. Sweeney JC, Ridgway SH (1975) Procedures for clinical management of small cetaceans. Journal of the American Veterinary Medical Association 167: 540-545.
118. Castellote M, Fossa F (2006) Measuring acoustic activity as a method to evaluate welfare in captive beluga whales (*Delphinapterus leucas*). Aquatic Mammals 32: 325-333.
119. Kastelein R, Lavaleije M (1992) Foreign bodies in the stomach of a female harbour porpoise (*Phocoena phocoena*) from the North Sea. Aquatic Mammals 18: 40-46.
120. Mason GJ (1991) Stereotypies: a critical review. Animal behaviour 41: 1015-1037.
121. Mason GJ (1991) Stereotypies and suffering. Behavioural Processes 25: 103-115.
122. Appleby MC (1999) What should we do about animal welfare? Oxford: Blackwell Science. 192 p.
123. Shepherdson D, Lewis KD, Carlstead K, Bauman J, Perrin N (2013) Individual and environmental factors associated with stereotypic behavior and fecal glucocorticoid metabolite levels in zoo housed polar bears. Applied Animal Behaviour Science 147: 268-277.
124. Dawkins MS (2003) Behaviour as a tool in the assessment of animal welfare. Zoology 106: 383-387.
125. Gygax L (1993) Spatial movement patterns and behaviour of two captive bottlenose dolphins (*Tursiops truncatus*): absence of stereotyped behaviour or lack of definition? Applied Animal Behaviour Science 38: 337-344.
126. Waitt C, Buchanan-Smith HM (2001) What time is feeding?: How delays and anticipation of feeding schedules affect stump-tailed macaque behavior. Applied Animal Behaviour Science 75: 75-85.
127. Bassett L, Buchanan-Smith HM (2007) Effects of predictability on the welfare of captive animals. Applied Animal Behaviour Science 102: 223-245.
128. Ridgway SH (1990) The central nervous system of the bottlenose dolphin. In: Leatherwood S, Reeves R, editors. The bottlenose dolphin. San Diego: Academic Press. pp. 69-97.
129. Marino L, Stowe J (1997) Lateralized behavior in two captive bottlenose dolphins (*Tursiops truncatus*). Zoo Biology 16: 173-177.
130. Sobel N, Supin AY, Myslobodsky M (1994) Rotational swimming tendencies in the dolphin (*Tursiops truncatus*). Behavioural Brain Research 65: 41-45.
131. Clubb R, Vickery S (2006) Locomotory stereotypies in carnivores: does pacing

stem from hunting, ranging, or frustrated escape. In: Mason G, Rushen J, editors. Stereotypic animal behaviour: fundamentals and applications to welfare. Oxfordshire, UK: CABI. pp. 58-85.

132. Galhardo L, Appleby M, Waran N, Dos Santos M (1996) Spontaneous activities of captive performing bottlenose dolphins (*Tursiops truncatus*). Animal Welfare 5: 373-389.

133. Dellinge-Ness LA, Handler L (2006) Self-injurious behavior in human and non-human primates. Clinical Psychology Review 26: 503-514.

134. Amundin M (1974) Occupational therapy for harbour porpoises (Phocoena phocoena). Aquatic Mammals 2: 6-10.

135. Holobinko A, Waring GH (2010) Conflict and reconciliation behavior trends of the bottlenose dolphin (*Tursiops truncatus*). Zoo Biology 29: 567-585.

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

137. Mason G, Latham N (2004) Can't stop, won't stop: is stereotypy a reliable animal welfare indicator? Animal Welfare 13: S57-69.

138. Young RJ (2008) Environmental enrichment for captive animals. Oxford: John Wiley & Sons. 228 p.

139. Fentress JC (1976) Dynamic boundaries of patterned behaviour: Interaction and self-organization. In: Bateson PPG, Hinde RA, editors. Growing points in ethology. Oxford: Cambridge Univ Press. pp. 135-169.

140. Sandson J, Albert ML (1987) Perseveration in behavioral neurology. Neurology 37: 1736-1736.

141. Janik VM, Sayigh LS (2013) Communication in bottlenose dolphins: 50 years of signature whistle research. Journal of Comparative Physiology A 199: 479-489.

142. Tyack PL (1997) Development and social functions of signature whistles in bottlenose dolphins *Tursiops truncatus*. Bioacoustics 8: 21-46.

143. Caldwell M, Caldwell D, Tyack PL (1990) Review of the signature-whistle hypothesis for the Atlantic bottlenose dolphin. In: Leatherwood S, Reeves RR, editors. The bottlenose dolphin. San Diego, CA: Academic Press. pp. 199-234.

144. Kershenbaum A, Sayigh LS, Janik VM (2013) The encoding of individual identity in dolphin signature whistles: how much information is needed? PloS one 8: e77671.

145. Gridley T, Cockcroft VG, Hawkins ER, Blewitt ML, Morisaka T*, et al.* (2014) Signature whistles in free-ranging populations of Indo-Pacific bottlenose dolphins, *Tursiops aduncus*. Marine Mammal Science 30: 512-527.

146. Lilly JC (1963) Distress call of the bottlenose dolphin: stimuli and evoked behavioral responses. Science 139: 116-118.

147. Janik VM, Todt D, Dehnhardt G (1994) Signature whistle variations in a bottlenosed dolphin, Tursiops truncatus. Behavioral Ecology and Sociobiology 35: 243-248.

148. Esch HC, Sayigh LS, Blum JE, Wells RS (2009) Whistles as potential indicators of stress in bottlenose dolphins (*Tursiops truncatus*). Journal of Mammalogy 90: 638-650.

149. Watwood SL, Owen EC, Tyack PL, Wells RS (2005) Signature whistle use by temporarily restrained and free-swimming bottlenose dolphins, *Tursiops truncatus*. Animal Behaviour 69: 1373-1386.
150. Buckstaff KC (2004) Effects of watercraft noise on the acoustic behavior of bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. Marine Mammal Science 20: 709-725.
151. Dawson SM (1991) Clicks and communication: the behavioural and social contexts of Hector's dolphin vocalizations. Ethology 88: 265-276.
152. Amundin M (1991) Sound production in odontocetes with emphasis on the harbour porpoise (*Phocoena phocoena*) [Ph.D. thesis]. Stockholm, Sweden: University of Stockholm. 128 p.
153. Connor RC, Smolker RA (1996) 'Pop' goes the dolphin: A vocalization male bottlenose dolphins produce during consorthips. Behaviour 133: 643-662.
154. Overstrom NA (1983) Association between burst-pulse sounds and aggressive behavior in captive Atlantic bottlenosed dolphins (*Tursiops truncatus*). Zoo Biology 2: 93-103.
155. Blomqvist C, Amundin M (2004) High-frequency burst-pulse sounds in agonistic/aggressive interactions in bottlenose dolphins, *Tursiops truncatus*. In: Thomas JA, Moss CF, Vater M, editors. Echolocation in bats and dolphins. Chicago: The University of Chicago Press. pp. 425-431.
156. Defran RH, Pryor K (1980) The behavior and training of cetaceans in captivity. In: Herman LM, editor. Cetacean behavior: Mechanisms and functions. New York: J. Wiley & Sons. pp. 319-362.
157. Dudzinski KM (1998) Contact behavior and signal exchange in Atlantic spotted dolphins (*Stenella frontalis*). Aquatic Mammals 24: 129-142.
158. Blomqvist C, Mello I, Amundin M (2005) An acoustic play-fight signal in bottlenose dolphins (*Tursiops truncatus*) in human care. Aquatic Mammals 31: 187-194.
159. Finley K, Miller G, Davis R, Greene C (1990) Reactions of belugas, *Delphinapterus leucas*, and narwhals, Monodon monoceros, to ice–breaking ships in the Canadian High Arctic. Canadian Bulletin of Fisheries and Aquatic Sciences 224: 97-117.
160. Graham MA, Noonan M (2010) Call types and acoustic features associated with aggressive chase in the killer whale (*Orcinus orca*). Aquatic Mammals 36: 9-18.
161. Ashwell-Erickson S, Elsner R (1981), The energy cost of free existence for Bering Sea harbor and spotted seals. In: Hood DW, Calder JA, editors. The eastern Bering Sea shelf: Oceanography and resources. Seattle: University of Washington Press. pp. 869-899.

Appendix A: Review of Cetacean cognitive abilities

Background and context

One of the common arguments for not holding cetaceans in display facilities is that these animals possess extraordinary cognitive abilities. The mental capacity of cetaceans is a primary focus of discussions of the welfare of this group in aquaria, and even has extended into legal arguments that cetaceans should be granted legal status of “non-human persons” (as has been done in India, and proposed in Rumania).

In this section we will review the scientific evidence for cetacean cognitive abilities. First, it is important to note that we will be using the term “cognitive abilities” in lieu of “intelligence”. The study of human intelligence is a field of investigation that, among other avenues of inquiry, develops tools to make quantitative measures of cognitive abilities to facilitate comparisons between human individuals, or more commonly between an individual and the rest of human society. By definition, these measures of intelligence test for skills that are viewed as particularly important for the function of individual humans within a human society. To test animals on the same tasks as humans would be inappropriate, as well as logistically impossible. For example, testing the abilities of cetaceans to put a series of pictures into a logical story sequence would be as unfair as asking humans to determine whether objects are solid or hollow from their acoustic profile.

Therefore, most scientists who study the mental capabilities of animals prefer to use the term “cognitive abilities”. This term allows comparison of species across a range of more relevant tasks and measurements without additional anthrocentric bias.

Second, it is important to realize that, for most discussions of cetacean cognitive abilities, the data are largely limited to a small subset of dolphin species, and within that group the vast majority of scientific studies have been conducted on bottlenose dolphins. Extrapolation of the results of studies from this species to other species of cetaceans should be considered tenuous.

Interest in cetacean intelligence began with John Lilly’s neuroscience and subsequent behavioural work with captive bottlenose dolphins in the 1960’s and 1970’s [1]. His books introduced a variety of concepts central to the modern debate on cetacean cognition, including the attributes of high intelligence (likely surpassing humans) and large brain size, as well as more less quantifiable characteristics such as the assertions cetaceans are “sensitive, compassionate, ethical, philosophical”, and have “extraordinary language abilities” [2].

The following review presents a non-exhaustive synopsis of the scientific research into the cognitive abilities of cetaceans. The area of cetacean cognition continues to be a highly active field of research. Not surprisingly, there is considerable, often passionate, debate regarding the interpretation of specific scientific experiments, and what the body of scientific knowledge says regarding the abilities of cetaceans compared to other groups of animals. The difficulty of interpreting the results of specific tasks was highlighted early in the field of animal cognition by McBride and Hebb[3] who suggested that scientists tend to design the test in light of their subject's known capabilities, and that whenever the experimental results do not conform to our *a priori* expectation regarding "higher" and "lower" species, the results tend to be explained in terms of training differences or experimental procedure error. A fervent debate continues over the cognitive abilities of cetaceans, how their abilities "rank" relative to other groups of animals [4] [5] [6], and how this relates to the welfare (and ethics) of cetaceans held in display facilities[7] [8].

Main points

To summarize the extensive scientific material pertaining to the cognitive abilities of cetaceans, we have chosen to address the following series of questions.

1. Do cetaceans demonstrate "special" cognitive abilities?

   Yes, cetaceans can perform certain cognitive tasks – most notably in the area of communication learning – that have rarely been demonstrated in other groups of animals e.g. see 9.

2. Do cetaceans have "unique" cognitive abilities?

   No, there is no clear evidence that cetaceans can perform tasks that no other group of animals can perform. In addition, in some areas of cognitive tasks the performance of cetaceans falls short of the demonstrated abilities of other groups of animals e.g., see 10 11.

3. Does the body of scientific evidence show that the cognitive abilities of cetaceans make it impossible to properly attend to their well-being in display facilities?

   No, there is no conclusive evidence one way or the other that the cognitive abilities of cetaceans constitute an inherent barrier to maintaining physically healthy individuals in aquaria. However, because of certain aspects of their cognitive abilities, it is important for facilities to ensure that their psychological needs are being met (see previous discussion on *Enrichment*).

Overview of the Science of Dolphin Cognition

Introduction

This brief overview of the study of cognition in delphinids covers the following topics: brain size and structure; self-knowledge and social cognition; symbol and concept comprehension; memory, planning, and problem solving; emotion and subjective experience; tool use and culture; and language in dolphins. The majority of research – both in the lab and in the wild – has been conducted on bottlenose dolphins (*Tursiops* sp.); consequently, the results of the studies reported herein focus heavily on *Tursiops*. The study of dolphin cognition has flourished over the past 50 years, and scientists have learned much about the nature of dolphin minds. This review highlights the current debates in the scientific literature as to what dolphins might be thinking (and why), and attempts to provide a snapshot of the current state of our knowledge.

Brain Size and Structure

Bottlenose dolphins (*Tursiops truncatus*) have brains that are larger on average than the human brain. The bottlenose brain weighs 1,824 grams[12], whereas estimates of human average brain weight are about 1,500 grams.[13] Brain size in delphinids (like most animals) typically scales with body size,[14] leading to smaller delphinids with smaller body size like the tucuxi (*Sotalia fluvitalis*) having smaller brains (i.e., 688 grams) than larger species like the killer whale (*Orcinus orca*; brain weight 5059 grams). Attempts to account for the body/brain scaling relationship have led to a number of methods for estimating the 'relative' size of dolphin brains, including brain weight as a percentage of body weight; brain weight in relation to brain stem weight, and the Encephalization Quotient (EQ). EQ is the measure of an animal's brain size in comparison to what might be expected for an animal of that size, and was first developed by Harry Jersion.[15]

According to some studies, delphinids have an EQ between 1.55 and 4.56, suggesting that their brains can be up to 4.5 times larger than expected for their body size. [16] Species like tucuxi and the Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) have EQs close to 4.5; bottlenose dolphins come in at 4.14; and killer whales have an EQ of about 2.57. [17] With humans having an EQ of 7, this puts many delphinind species just below humans on the EQ scale.

Some studies have found correlations between large EQs and complex behaviour. Larger EQ sizes correspond to larger behavioural repertoires for some mammals,[18] and the ability to cope with novel environmental situations.[19] Larger EQs are correlated with larger pod size in some delphinids, [20] possibly indicating a relationship between social complexity and brain size/power. Whether or not EQ is a reliable indicator of cognitive complexity is still being debated. Different data and methods of calculation can lead to huge variation in EQ ratings[21] with human EQ ranging from 1.16 to 12.6 depending on the method used.[22] Correlations between cognition in general and EQ are not always clear, with some species with similar EQs performing quite differently on the same cognitive tests (e.g., mirror self-recognition).[23] [24] [25] [26] [27] [28] At present, the nature of the relationship between brain size, EQ, and cognition in the animal kingdom is poorly understood, although dolphin brain size appears to be related to their form of social cognition.

In addition to overall brain size, the dolphin cerebral cortex is larger (in terms of surface area) than the human brain (3745 cm^2 vs. 2275 cm^2),[29] although it is far less dense with fewer overall neurons.[30] [31] A number of hypotheses exist to explain the large encephalization (i.e., large brain and cortical size) found in delphinids. It was originally assumed that large brain size was necessary for audio-processing – a likely result of the dolphin echolocation system.[32] The auditory nerve and other mid-brain and cortical structures involved in sound processing are quite large in echolocating cetaceans. It is still unclear, however, as to whether large cortical areas in dolphins – including the *association cortex* whose function is unknown – is related to echolocation processing.[33] A controversial hypothesis[34] from recent years posited that the dolphin brain grew larger as a response to global cooling of ocean water, with larger brains helping to generate heat to keep dolphins warm.[35] The leading hypothesis as to why dolphins evolved large brains is the increased need to keep track of tricky social relationships: the social brain hypothesis. [36] [37] From the fission-fusion societies of bottlenose dolphins to the matrilineal groups of killer whales, the dolphin brain – much like the brains of the great apes – might needed to have evolved extra processing power in order to keep track of ever-changing relationships in large, complex social groups. The exact evolutionary pressures that led to the evolution of large brains in delphinids are, however, still being debated.

Individual structures within the dolphin brain have been correlated with complex cognition. Scientists have found Von Economo neurons (VENs) in the areas of the dolphin brain assumed to be involved in social cognition (the anterior cingulate, anterior insular, and frontopolar cortices), and it is thought that these neurons are evidence of complex emotional and social cognition. [38] [39] [40] It is still now known, however, what the exact function of VENs are, or whether they are involved in emotional or social cognition in delphinids or other species in which they've been found.[41] [42] [43] [44] [45] [46] Dolphins lack a frontal (cortical) lobe, which is an area of the brain that, in primates, is known to be responsible for cognitive skills involving self-awareness.[47] A lack of a frontal lobe does not, however, seem to be related to dolphins' success at the mirror self-recognition task. Dolphins have a relatively large cerebellum, although it is unknown how this relates to their behaviour (e.g., the cerebellum might be related to delphinid tool-use). [48] While some mid-brain hippocampal structures in delphinids are reduced in size, the cortical areas of the delphinid limbic system (e.g., the paralimbic cortex, cingulate and insular cortex) are relatively large (compared to primates), leading some to speculate that dolphins might have access to or experience their emotions more deeply than primates, or that these areas are responsible for complex emotions like empathy.[49] [50] [51] [52] [53] [54]

However, the exact function of these limbic areas is, at present, unknown.

Self-Knowledge and Social Cognition

Research conducted in both the lab and the wild have revealed that dolphins (particularly bottlenose dolphins) display fairly complex forms of self-knowledge. A bottlenose dolphin at the Kewalo Basin Marine Mammal Laboratory leaned to associate symbols with nine different body parts, suggesting she was able to name/label parts of her own body.[55] Other bottlenose dolphins at various facilities displayed skill in the ability to imitate/mimic the movements of both other dolphins and human trainers, including the ability to both repeat and invent novel behaviours.[56] [57] [58] [59] [60] [61] This suggests an ability to monitor, remember, and self-imitate one's own behaviour as well as the behaviour of others. Killer whales have displayed similar abilities.[62] A number of dolphin species display the ability to mimic a variety of sounds in their environment; a skill they retain throughout their lives.[63] [64] [65] [66] [67] [68] [69] The ability for motor imitation could be a result of higher level cognitive processing involving an animal not only mapping its body plan onto that of another, but making a guess as to the intended body movements of another agent. It might therefore imply knowledge of the minds and internal thoughts of other agents. Although dolphins are skilled at both motor and vocal imitation, it is not known how complex the underlying metal abilities are driving their imitative skills.

Bottlenose dolphins are one of only a handful of species (including the great apes, elephants, and magpies) that have passed the mirror self-recognition test, [70] suggesting that they have some ability to recognize an image of themselves in a mirror. [71] [72] [73] [74] Early tests revealed self-knowledge behaviour in front of a mirror for delphinids including contingency checking, which critics suggested are not true indicators of self-recognition.[75] [76] [77] [78] [79] This was observed in killer whales as well as bottlenose dolphins. A 2001 test of mirror self-recognition using the "mark test" was generally accepted as revealing self-recognition in the bottlenose dolphin.[80] For this test, an animal was marked with either a sham (fake) dye or real dye on its skin, and is scored to see if it engaged in behaviours indicating that it used the mirror to inspect the mark (if present) on its body. In the 2001 experiment, the dolphins appeared to use the mirror to inspect their bodies when marked, leading most researchers to accept that they had passed this test for self-recognition. A debate continues in the scientific literature as to if the mirror self-recognition test is capable of revealing "higher" levels of self-awareness or consciousness in non-human animals that might be similar to that found in humans (*Home sapiens*).[81] [82] [83] [84] [85] [86] [87] [88] [89] [90] [91] [92] [93] [94] [95] [96] [97] [98] [99] [100] [101] Definitions of s*elf-awareness* or *consciousness* (or related terms) tend to vary in the literature, with any number of cognitive processes being implicated in self-recognition behaviour where mirrors are concerned.

It is possible that signature whistles – which dolphins use to identify themselves, and might also label each other – are evidence of self-knowledge or self-awareness.[102] [103] If dolphins use these labels to "call out" to each other, it might suggest that they have some knowledge of each other's minds or mental/ attentional states. Studies of metacognition in the bottlenose dolphin suggest that might have an awareness of their own cognition to the extent that they can inform researchers as to how confident they are about their own levels of knowledge (i.e., being asked to differentiate between two tones that are difficult to distinguish and choosing to answer the question as "unsure").[104] [105] Monitoring one's own thought processes and decision making in this manner is a form of self-knowledge. A debate continues in the literature as to whether these metacognition tests are a result of true mind/self-knowledge or lower level associative learning.[106] [107]

Dolphins display a number of skills that suggests that they have knowledge about the minds of other individuals, leading to complex forms of social cognition which help explain the nature/structure of their social groupings. Bottlenose dolphins are one of the few species able to follow the direction of a human's gaze toward an object or event.[108] [109] It is possible that this can be interpreted as the dolphins understanding that the other individual (e.g., a human researcher) can "see" or "perceive" something. Similarly, dolphins are able to follow the human pointing gesture to an object or event, and can incorporate pointing gestures into their language/symbol comprehension systems.[110] [111] [112] [113] [114] [115] Bottlenose dolphins also produce pointing-like gestures (using body and rostrum alignment) seemingly for the benefit of human researchers (and possibly to manipulate the humans' focus of attention) by indicating the direction of an object or event.[116] [117] There is some evidence to suggest that dolphins might both produce and comprehend (spontaneously) pointing gestures in the wild. [118] [119] Whether or not dolphins attribute more complex mental states to other agents (e.g., "believing" or "knowing" as opposed to just "seeing" or "perceiving") is still not known. The most common tests of these complex forms of mental state attribution included tests of deception skill (which are unknown in delphinids) and the *false belief* task. Early tests suggested that dolphins might pass the false belief task (i.e., an indication that they understand that another individual can possesses false/incorrect information), although these are preliminary results that are not generally accepted as hard evidence.[120]

It is possible/likely that the skills dolphins display in areas of social cognition can be directly related to the nature of their social systems. Many species live in a fission-fusion society, with groups changing in composition throughout the day, and friendships/alliances changing in strength over time.[121] Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Australia display complex social groupings involving long-term male alliances that occasionally join forces with other male alliances forming second- a third-order alliances.[122] [123] [124] [125] These groupings are non-random, and indicate that individuals and groups are able to keep track of and maintain alliances based on who might owe whom a favor, and the strength of individual social bonds within a larger, complex social network.[126] These alliances are also an example of cooperative behaviour, with alliance males benefiting from their association with other individuals with similar goals (e.g., desiring access to females).[127] Similar cooperative behaviour in delphinids can be observed in dusky (*Lagenorhynchus obscurus*) and spinner dolphins (*Stenella longirostris*) that cooperate to hunt fish,[128] [129] and bottlenose dolphins that cooperatively create mud plumes or coordinate their stranding behaviour to ensnare fish/prey.[130] [131]

Cooperative behaviour is also witnessed in the bottlenose dolphins that hunt together with human fishermen in South America,[132] Australia,[133] India,[134] and Africa,[135] as well as killer whales that coordinated to capture their prey.[136] [137] [138] [139] In addition, false killer whales (*Pseudorca crassidens*) and rough-toothed dolphins (*Steno bredanensis*) have been observed feeding prey to their young.[140]

Dolphins have been observed engaging in altruistic behaviour involving providing care to their young, or to sick and injured conspecifics.[141] [142] [143] [144] [145] [146] [147] [148] [149] [150] Killer whales often remain within their family group for life, cooperating with conspecifics in all aspects of their social life,[151] [152] and young bottlenose dolphins have a protracted period of juvenile development whereby they remain close to their mothers for years.[153] [154] [155] Whether or not these altruistic and seemingly empathic cooperative social traits are a product of a deep understanding of the minds of others, or are behaviours that occur without the need for knowledge of other minds is still a matter of debate in the scientific literature.

Symbol and Concept Comprehension

A symbol is a stimulus -usually visual or auditory -that represents a concrete or abstract idea/concept.[156] [157] Dolphins – particularly bottlenose dolphins – have been tested extensively for their ability to both comprehend and produce symbols. Work at Kewalo Basin with language trained dolphins revealed their ability to do the following: follow instructions using symbols to stand in for a number of abstract concepts (e.g., left/right, up/down) as well as concrete objects, some of which were presented after a delay;[158] [159] report on the presence/absence of objects in their pool;[160] follow commands given in their symbol-system that were up to five "words" long and occurred in random/never before seen symbol combinations including formulating correct responses to anomalous/wrong symbol combinations;[161] [162] [163] [164] and understand that symbols can represent a class of object/concept (e.g., balls in general as opposed to one specific ball).[165] [166] Dolphins at Kewalo Basin learned up to 60 different word-symbols.[167] As an example, the dolphin Akeakamai, who was taught a gestural-based symbol system, could follow the following command that indicated that she needed to take the hoop to the ball: *ball hoop fetch*. By reversing the word order for the two objects in her symbol system, Akeakamai would know to take the ball to the hoop. By varying word order as a means of testing the dolphins' comprehension and by presenting novel symbol order, the researchers could be sure that the dolphins were not just associating symbols with behaviour via rote learning, but by using mental representations of the meaning of the concepts in question. Only a handful of species (including the great apes and parrots) are able to comprehend and work with symbols and symbol combinations to this extent and thus might form complex mental representations of mental concepts.[168] These results also suggests that dolphins can comprehend a rudimentary form of "syntax," as well as recursive properties,[169] although this is likely not similar to "syntax" in the sense of human language.[170]

Further research into dolphins' abilities to work with mental representations and concepts at various facilities have revealed the following skills: dolphins can classify objects as being either the same/different as well as being less/fewer and larger/smaller;[171] [172] [173] [174] they can classify tone series as either descending or ascending in frequencies and can easily discriminate between different kinds of artificial or natural (i.e., dolphin originated) whistle sounds;[175] [176] [177] and dolphins understand that an object continues to exists even after it is hidden from view (i.e., object permanence).[178] Dolphins, however, do not pass the final stage of object permanence testing involving tracking the displacement/movement of an object that is hidden from view.[179]

Dolphins have shown the ability to recognize images presented to them on a (distorted) television screen, [180] following commands given in their gestural symbol systems via a 2D television image. They are able to solve a number of match-to-sample tasks involving determining the visual match to an object they are presented with visually (e.g., when shown a hoop they can find the corresponding hoop from a series of different objects).[181] They are able to do this with objects presented to them where they must first inspect them with echolocation, and can transfer the object information gained between the modes of echolocation and vision (e.g., they can find the hoop visually after having previously only perceived the hoop via echolocation). [182] [183] [184] [185] [186] This suggests that they have created a mental representation of the object and/or its features that transfers easily across modalities. It is unknown if this cross-modal recognition skill is something arising from aspects of the dolphin cortex as far as the adjacency of visual and auditory structures are concerned,[187] [188] or if this is more similar to the kind of cross-modal skill seen in most other species.[189]

Memory, Planning, and Problem Solving

Dolphins' working/short-term memory is revealed via their ability to perform well on symbol comprehension tasks (e.g., recalling the action that needs to be performed for a sentence involving up to five symbols).[190] They are able to remember objects presented in a match-to-sample task for up to 80 seconds,[191] and can remember up to four items when presented with serial lists and asked to recall object order.[192] Dolphins' long-term memory is revealed via their ability to recall arbitrary associations between objects and their symbols as well as trained behaviour and their symbols for decades. One study found that dolphins can remember the signature whistle of their former tank-mates that they had not encountered in over 20 years.[193] Dolphins also display a form of "episodic" memory, allowing them to recall past events by placing themselves as the center of the memory's narrative. This type of memory encodes personal information within the memory, as opposed to just semantic information, and is thus considered to be a more complex form off memory.[194] It is unknown the extent to which this form of memory might rely on cognitive skills possibly unique to humans, or whether non-human animals truly possesses episodic or episodic-like memory. It has been argue that the ability to repeat both learned and novel behaviours they've just performed in dolphins is suggestive of episodic memory.[195] [196]

Memory skills, and in particular the kind of personal memory that is encoded in episodic memory, are essential for problem solving – an ability that dolphins display in both experimental and observational contexts.[197] Examples include Indo-Pacific bottlenose dolphins working together to herd females of the same species;[198] killer whales working in unison to wash prey species off of ice floes;[199] Indo-Pacific bottlenose dolphins using sea sponges as tools when foraging in the sand for prey;[200] and bottlenose dolphins use air bubbles for prey capture[201] as well as stranding themselves in unison in shallow water in pursuit of fish.[202] Captive killer whales occasionally lure seagulls into their pool by brandishing pieces of fish, [203] and rough-toothed dolphin use objects to prop open gates and manipulate human-made infrastructure in/near their pools.[204] A wild Indo-Pacific bottlenose dolphin has been observed deboning a cuttlefish using a protracted and complicated series of behaviours – possibly a result of insight problem solving.[205]

Problem solving skills in a laboratory setting are evident in a series of experiments conducted at Disney's The Living Seas. Two bottlenose dolphins appeared to devise a solution to a weight-box experiment via insight problem solving by collecting a series of weights at the same time as opposed to picking them up one by one – and then dropping them in a box to release a fish reward.[206] [207] [208] The dolphins had previously witnessed a human solve this task, but had not observed the method of picking up multiple weights in order to save time. This behaviour might then have been a product of insight if the dolphins were able to envision a (better) solution to the problem without first engaging in trial and error learning.

It has been argued that the language-trained dolphins also displayed problem solving skill in their correct responses to anomalous symbol commands,[209] and by rounding up objects in their pool in one go (as opposed to one by one) when given the command to clean up their pool.[210] These problem solving skills are also mirrored in the various games that dolphins have invented as a means of play. This includes surfing, aerial displays, erratic swimming, social play, and object play.[211] Object play involves dolphins playing with other animals in their environments, as well as games like "seaweed keep away" and "ball toss" which they play in natural settings with conspecifics as well as human researchers.[212] [213] [214] Dolphins have been observed towing each other around their enclosures using a hula hoop, and plucking feathers from unsuspecting birds that land on the surface of their pools.[215] [216]

Bubble play in dolphins likely involves a form of problem solving. Bubble play has been observed in Amazon river dolphins (*Inia geoffrensis*), beluga whales (*Delphinapterus leucas*), and bottlenose dolphins. It involves creating bubble curtains, vortices, or bubble rings released either from their mouths or their blowholes.[217] [218] [219] [220] [221] [222] They manipulate these bubbles and invent games involving sending smaller bubbles up through larger bubbles. Interestingly, the dolphins involved in these games appear to actively monitor the size, shape, and stability of their bubbles, and only continue with their game if the bubbles are sufficiently well formed, which suggests a complex understanding of both the objects they are manipulating and the nature of the game itself.[223] They have also been observed purposefully making the games more difficult for themselves.

Emotion and Subjective Experience

Considerable controversy exists in the scientific literature as to the extent to which dolphins and other non-human animals have and/or experience their emotions or other subjective internal states. It is generally accepted that species with a limbic system (i.e., most vertebrates) possess basic emotions and/or similar arousal systems.[224] [225] [226] Whether or not delphinids or other species have subjective or conscious access to their emotions is difficult to assess given the current literature and experimental paradigms. There is plenty of observational evidence that dolphins behave in ways that suggest that they have rich emotional experiences, including grieving for their dead or displaying empathy.[227] [228] [229] [230] [231] [232] [233] [234] [235] [236] [237] [238] [239] [240] This type of behaviour involves mothers carrying the body of their dead calves for extended periods of time, and sick/injured dolphins being supported in the water by conspecifics. There are also reports of dolphins providing this kind of aid to other species, including humans. It remains controversial, however, as to if this can be used as empirical evidence of rich inner lives for dolphins and other animal, and the extent to which providing caregiving or altruistic behaviour is the result of something akin to human-like empathy.[241] [242] [243] [244] [245] [246] It remains possible that this type of behaviour can exist in dolphins without subjective experience of emotion,[247] although arguments exist that these examples of altruistic behaviour[248] [249] could be seen as direct evidence of the subjective experience of emotion in dolphins.[250] [251] Some evidence exists from neurobiology that dolphins and other vertebrates surely experience their emotions, although this too is controversial. [252] [253] [254] [255]

Tool Use and Culture

Indo-Pacific bottlenose dolphins have been observed using marine sponges as tools, a behaviour referred to as "sponging."[256] [257] [258] [259] [260] Around 55 animals – mostly female – hold the sponges on the tips of their rostrums ostensibly to protect themselves while digging in the sand for prey species. This behaviour appears to be passed down from mother to daughter, and is contained to a small group within the overall population of dolphins in Shark Bay, Australia.[261] [262] It is possible and/or likely that this behaviour first arose around 180 years ago (possible in two distinct groups/populations) via a flash of insight, having been transmitted to others within the group via social leaning. [263] Once a sponge has lost its use as a protective tool, the dolphins will snap off a new sponge from the seafloor. They will also occasionally abandon a sponge when chasing/consuming prey only to pick it up again soon after to continue foraging. Although there was some controversy in the literature as to whether this behaviour was a product of either genetics or local conditions, research appears to indicate that cultural transmission is the most likely explanation.

The transmission of tool use skill via social learning is one of a handful or traits in delphinids that is accepted to be a result of "cultural" leaning. Culture in animals refers is sometimes defined as the "information or behaviour acquired from conspecifics through some form of social learning"[264] and was summarized as it perhaps to delphinids in 2001.[265] Aside from the tool use described for Shark Bay, the vocal dialects of killer whales are cited as an example of culture transmission in dolphins. So too is the pod-specific greeting ceremonies seen in killer whales, as well as the variety of different hunting techniques that are possibly acquired via social transmission for killer whales and bottlenose dolphins around the word. Bottlenose dolphins have also been observed cooperatively hunting with human fishermen as well as accepting handouts from humans – both possibly a result of cultural transmission. [266] [267] [268] Young Atlantic spotted dolphins (*Stenella frontalis*) have also been observed teaching their young to hunt. [269] This form of teaching – which is related to the idea of cultural transmission – is often cited as an example of complex cognition in delphinids. Controversy exists in the scientific literature as to whether all of these behaviours (including tool use) are truly an example of culture and/or teaching in delphinids, although most scientists accept that, at least for the dialects in killer whales, cultural transmission is the most likely explanation. [270] [271] [272] [273] [274] [275] [276] [277] [278] [279] [280] [281] [282] [283] [284] [285]

Language in Dolphins

Generations of scientists have searched for language and language-like properties within the vocal structures of both wild and captive delphinids. Early research from the 1960s tested their ability to transmit complex, arbitrary semantic information via their natural vocalizations, with results suggesting that dolphins' natural communication systems lacked this ability. [286] [287] [288] [289] [290] Soviet scientists published on the possible ability of dolphins to transmit this type of information via their communication systems in the 1980s, although these results are inconclusive.[291] [292] Information theory was used as early as the 1960s to search for information and "words" within the natural communication systems of dolphins, with results being inconclusive.[293] [294] [295] [296] Recent use of information theory as applied to dolphin vocalizations has revealed that their vocal systems might contain both structure and complexity. This is based on their signals confirming to Zipf's statistic (suggesting redundancy in signals reminiscent of the structure in human language), and entropic slope (suggesting a non-random order to whistle/click production). [297] [298] [299] However, the use of information theory to study animal communication systems has received criticism, [300] and the publications on the subject cannot confirm the presence of either structure or complexity in dolphin vocalizations. The 1960s saw many experiments cataloging dolphin vocalizations in attempt to uncover a "vocabulary" of meaningful utterances, with little success.[301] [302] Scientists continue to catalog vocalizations (whistles, click, and burst-pulse sounds) and match them with behaviour to this day,[303] [304] [305] [306] [307] although little evidence of a language-system in delphinid vocalizations has been found.[308]

Some aspects of dolphin communication, however, remain both intriguing and unique. Dolphins are the only animal other than humans that produce a label for themselves – called a signature whistle – that is based solely on the contours (as opposed to vocal quality) of the whistle itself. [309] [310] The unique whistles are learned by dolphins (of a number of different species) during the first year of life, and are likely used as contact calls to identify themselves to members of the group. It is also possible/likely that dolphins imitate the signature whistles of their associates, possibly as a means of calling out to them or getting their attention.[311] This might be an indication that they have some knowledge of the mental states of other individuals.[312]

Delphinids retain the ability to acquired and imitate sounds in their environment throughout their lives.[313] [314] [315] [316] Calves make use of this ability when learning signature whistles and other shared contact calls within their social group, and young killer whales acquire the group-specific vocal dialect of their family group, as well as imitate the calls of neighbouring social groups. [317] [318] [319] [320] [321] [322] Dolphins are able to use the ability to mimic/imitate sounds in symbol use experiments, learning to imitate whistles that are associated with different objects and actions. [323]

A number of experiments have been conducted to attempt to teach dolphins to produce/use symbols in order to communicate with human researchers. Experiments from the 1960s attempted to teach dolphins to “speak” English,[324] with a number of research attempts throughout the 80s and 90s intended to inspire dolphins to use artificial symbols.[325] [326] [327] [328] [329] [330] [331] [332] [333] [334] Some of these experiments used keyboards (as was seen in the artificial symbol work involving the great apes), whereas other involve auditory symbols. In general, these experiments have had limited success (when compared to similar experiments with great apes) in inspiring dolphins to engage in symbol/language production with humans.

Summary

In many respects, dolphins show cognitive skills that are typically only seen in the great apes, corvids, and elephants. This includes skill in language and symbol use, social cognition, and complex social groupings. This is somewhat unexpected considering how distantly related to primates (in particular) dolphins are. While it is still unknown just how the large dolphin brain or specific brain areas/features contribute to dolphin cognition in a global sense, it seems likely at present that the nature of dolphin cognition (and their large brains) are a result of the way their minds evolved to cope with the complex and fluid social groupings they find themselves in. Thus, their skill with symbols, pointing, gaze comprehension, mental state comprehension, tool use, problem solving, play, etc. are likely a result of a mind that evolved to handle complex and novel problems arising from social constraints. In this sense, the dolphin mind is more similar to the kind of mind seen in primate, elephants, corvids, and other animals facing similar social challenges. However, there is much that scientists do not know about the dolphin mind, or about the minds and cognitive abilities of understudied species, which makes it difficult to draw concrete conclusions about the nature of the dolphin mind and how it compares to the minds of other animals. A review of the current body of literature on dolphin cognition reveals much discussion and debate in terms of what the science has to say about what is going on inside the dolphin mind.

Literature Cited in Review

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[1] Lilly JC (1967) The mind of the dolphin: Doubleday.

[2] Lilly JC (1978) Communication between man and dolphin. Crown, New York, NY.

[3] McBride AF, Hebb DO (1948) Behavior of the captive bottle-nose dolphin, *Tursiops truncatus*. Journal of Comparative and Physiological Psychology 41: 111.

[4] Güntürkün O (2014) Is dolphin cognition special? Brain, Behavior and Evolution Published online DOI:10.1159/000357551.

5 Manger P (2013) Questioning the interpretations of behavioral observations of cetaceans: Is there really support for a special intellectual status for this mammalian order? Neuroscience 250: 664-696.
6 Barrett L, Würsig B (2014) Why dolphins are not aquatic apes. Animal Behavior and Cognition 1: 1-18.
7 Marino L, Frohoff T (2011) Towards a new paradigm of non-captive research on cetacean cognition. PloS one 6: e24121.
8 Grimm D (2011) Animal cognition. Are dolphins too smart for captivity? Science (New York, NY) 332: 526
9 Herman LM (2012) Body and self in dolphins. Consciousness and Cognition 21: 526-545.
10 Güntürkün O (2014) Is dolphin cognition special? Brain, Behavior and Evolution Published online DOI:10.1159/000357551
11 Gregg J (2013) Are dolphins really smart?: The mammal behind the myth: Oxford University Press.
12 Marino, L. (2002). Brain size evolution. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (pp. 158-162). Academic Press.
13 Nelson, G.E. (1982). *Fundamental Concepts of Biology*. New York: Wiley, 262
14 Byrne, R. W. (1996). Machiavellian intelligence. *Evolutionary Anthropology: Issues, News and Reviews*, *5*(5), 172-180.
15 Jerison, H. J. (1977). The theory of encephalization. *Annals Of The New York Academy Of Sciences*, *299*, 146-160
16 Marino, L. (2002). Brain size evolution. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (pp. 158-162). Academic Press.
17 Marino, L. (2002). Brain size evolution. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (pp. 158-162). Academic Press.
18 Changizi, M.A. (2003). The relationship between number of muscles, behavioral repertoire size, and encephalization in mammals. *Journal of Theoretical Biology, 220*, 157-168.
19 Sol, D, Bacher, S., Reader, S. M., Lefebvre, L. (2008). Brain size predicts the success of mammal species introduced into novel environments. *American Naturalist, 172*, S63.S71
20 Marino, L. (1998) A comparison of encephalization between odontocete cetaceans and anthropoid primates. *Brain, Behavior and Evolution,* 51, 230–238.
21 See the discussion in the section Brain and Body Scaling: The Traditional View in Herculano-Houzel, S. (2009). The Human Brain in Numbers: A Linearly Scaled-up Primate Brain. *Frontiers in human neuroscience*, *3*(November), 11. doi: 10.3389/neuro.09.031.2009
22 Boddy, A. M., McGowen, M. R., Sherwood, C. C., Grossman, L. I., Goodman, M., & Wildman, D. E. (2012). Comparative analysis of encephalization in mammals reveals relaxed constraints on anthropoid primate and cetacean brain scaling. *Journal of Evolutionary Biology*, *25*, 981-994.

23 Shoshani, J., Kupsky, W. J., & Marchant, G. H. (2006). Elephant brain. Part I: gross morphology, functions, comparative anatomy, and evolution. *Brain Research Bulletin*, *70*(2), 124-157.

24 Roth, G., & Dicke, U. (2005). Evolution of the brain and intelligence. *Trends in Cognitive Sciences*, *9*(5), 250-257.

25 Martin, R.D. (1984). Body size, brain size and feeding strategies. In D. J. Chivers, B. Wood & A. Bilsborough, (Eds.), *Food Acquisition and Processing in Primates* (pp. 733103). Plenum Press, New York.

26 Anderson, J. R. (1983). Responses to mirror image stimulation and assessment of self-recognition in mirror- and peer-reared stumptail macaques. *The Quarterly journal of experimental psychology B Comparative and physiological psychology*, *35*(3), 201-212.

27 Plotnik, J. M., De Waal, F. B. M., Moore, D., & Reiss, D. (2010). Self-recognition in the Asian elephant and future directions for cognitive research with elephants in zoological settings. *Zoo Biology*, *29*(2), 179-191

28 Rajala, A. Z., Reininger, K. R., Lancaster, K. M., & Populin, L. C. (2010). Rhesus Monkeys (*Macaca mulatta*) Do Recognize Themselves in the Mirror: Implications for the Evolution of Self-Recognition. (J. Lauwereyns, Ed.)*PLoS ONE*, *5*(9), 8.

29 Ridgway, S.H. (1990). The central nervous system of the bottlenose dolphin. In S. Leatherwood, & R. R. Reeves, (Eds.), *The Bottlenose Dolphin* (pp. 69—97). Academic Press.

30 Oelschläger, H.H.A., Oelschläger, J.S. (2009). Brain. In Perrin, W.F. Würsig, B., & Thewissen, J.G.M. (Eds*), Encyclopedia of Marine Mammals* (pp. 134-149). Academic Press.

31 Roth, G. (2000). The evolution and ontogeny of consciousness. In T. Metzinger (Ed.), *Neural correlates of consciousness: Empirical and conceptual questions* (pp. 77-97). Massachusetts: MIT Press.

32 See Ridgway, S. H. (1990). The central nervous system of the bottlenose dolphin. In S. Leatherwood & R. R. Reeves (Eds.)*The Bottlenose Dolphin*, pp. 69-97. Academic Press*. And Ridgway, S.H., & Au, W.W.L. (1999). Hearing and echolocation: Dolphin, In G. Adelman & B. Smith (Eds.), Elsevier's Encyclopedia of Neuroscience (858-862). New York: Elsevier Science.*

33 Marino, L. (2007). Cetacean brains: how aquatic are they? *Anatomical record Hoboken NJ 2007*, *290*(6), 694-700.

34 Marino, L., Butti, C., Connor, R. C., Fordyce, R. E., Herman, L. M., Hof, P. R., Lefebvre, L., et al. (2008). A claim in search of evidence: reply to Manger's thermogenesis hypothesis of cetacean brain structure. *Biological Reviews of the Cambridge Philosophical Society, 83*(4), 417-40.

35 Manger, P. R. (2006). An examination of cetacean brain structure with a novel hypothesis correlating thermogenesis to the evolution of a big brain. *Biological Reviews of the Cambridge Philosophical Society, 81*(2), 293-338.

36 For a discussion see Pearson, H.C., & Shelton, D.E. (2010). A large-brained social animal. In Würsig, B., and Würsig, M., (Eds.), The Dusky Dolphin: Master Acrobat off Different Shores (pp. 333-353). San Diego, CA: Elsevier, Inc.

37 Connor, R.C. (2007). Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. *Philosophical Transactions of the Royal Society B Biological Sciences*, *362*(1480), 587-602.

38 Lamm, C., & Singer, T. (2010). The role of anterior insular cortex in social emotions. *Brain Structure & Function, 241*(5–6), 579-951

39 Butti, C., Santos, M., Uppal, N., Hof, P.R. (2011). Von Economo neurons: Clinical and evolutionary perspectives. Cortex. doi:10.1016/j.cortex.2011.10.004.

40 Hof, P. R., & Van Der Gucht, E. (2007). Structure of the cerebral cortex of the humpback whale,Megaptera novaeangliae (Cetacea, Mysticeti, Balaenopteridae). *The Anatomical Record Part A Discoveries in Molecular Cellular and Evolutionary Biology, 31*, 1-31.

41 Philippi, C.L., Feinstein, J.S., Khalsa, S.S., Damasio, A., Tranel, D., *et al.* (2012) Preserved self-awareness following extensive bilateral brain damage to the insula, anterior cingulate, and medial prefrontal cortices. *PLoS ONE, 7*,8, e38413. doi:10.1371/journal.pone.0038413

42 Van Essen, D. (1997). *A tension-based theory of morphogenesis* and compact wiring in the central nervous system. *Nature, 385*, 313–318

43 Sherwood, C. C., Bauernfeind, A. L., Bianchi, S., Raghanti, M. A., & Hof, P. R. (2012). Human brain evolution writ large and small. (M. Hofman & D. Falk, Eds.)*Progress in Brain Research*, *195*, 237-54.

44 Hof, P. R., & Van Der Gucht, E. (2007). Structure of the cerebral cortex of the humpback whale, *Megaptera novaeangliae* (Cetacea, Mysticeti, Balaenopteridae). *The Anatomical Record Part A Discoveries in Molecular Cellular and Evolutionary Biology, 31*, 1-31.

45 Hakeem, A.Y., Sherwood, C.C., Bonar, C.J., Butti, C., Hof, P.R., & Allman, J.M. (2009). Von Economo neurons in the elephant brain. *Anatomical Record, 292*(2),242-248.

46 Thanks to Patrick Hof for this insight.

47 Manger, P. R. (2006). An examination of cetacean brain structure with a novel hypothesis correlating thermogenesis to the evolution of a big brain. *Biological Reviews of the Cambridge Philosophical Society, 81*(2), 293-338.

48 Tamada, T., Miyauchi, S., Imamizu, H., Yoshioka, T., & Kawato, M. (1999). Cerebro-cerebellar functional connectivity revealed by the laterality index in tool-use learning. *NeuroReport, 10*(2), 325-331

49 Marino, L. (2004). Cetacean brain evolution: Multiplication generates complexity. *International Journal of Comparative Psychology, 17*, 1-16.

50 Marino, L. (2011). Brain structure and intelligence in cetaceans In Brakes, P., & Simmonds, M. (Eds.), *Whales and Dolphins: Cognition, Culture, Conservation and Human Perceptions,* (pp. 113-128). Earthscan: London, 125.

51 Jerison, H.J. (1986). The perceptual worlds of dolphins. In Schusterman, R.J., Thomas, J., & Wood, F.G. (Eds.) *Dolphin cognition and behavior: a comparative approach*, (pp. 141-166). Hillsdale, N.J., Erlbaum.

52 Herzing, D.L. & White, T. (1999). Dolphins and the question of personhood. *Etica Animali, 9(*98), 64-84. p. 74

53 White, T. (2007). *In Defense of Dolphins: The New Moral Frontier*. Malden, MA: Blackwell Publishing ,42.

54 Kuczaj, S., Tranel, K., Trone, M., & Hill, H. (2001). Are animals capable of deception or empathy? Implications for animal consciousness and animal welfare. *Animal Welfare, 10*(1), S161-S173.

55 Herman, L. M., Matus, D.S., Herman, E. Y., Ivancic, M., & Pack, A. A. (2001). The bottlenosed dolphin's (*Tursiops truncatus*) understanding of gestures as symbol representations of its body parts. *Animal Learning & Behavior 29*, 250-264.

56 Herman, L. M. (2002). Vocal, social, and self-imitation by bottlenosed dolphins. In K. Dautenhahn & C. Nehaniv (Eds.), *Imitation in animals and* artifacts (pp. 63-108). Cambridge: MIT Press.

57 Mercado, E., Murray, S. O., Uyeyama, R. K., Pack, A. A., & Herman, L. M. (1998) Memory for recent actions in the bottlenosed dolphin (*Tursiops truncatus*): Repetition of arbitrary behaviors using an abstract rule. *Animal Learning Behavior*, *26*(2), 210-218.

58 Zentall, T. R., (2008). Representing past and future even ts. In E. Dere, A. Easton, L. Nadel, & J. P. Huston (Eds.), *Handbook of Episodic Memory Research,* (pp.217-234). Oxford, UK: Elsevier, 230.

59 Herman, L. M., Morrel-Samuels, P., & Pack, A. A. (1990). Bottlenosed dolphin and human recognition of veridical and degraded video displays of an artificial gestural language. *Journal of experimental psychology General*, *119*(2), 215-230

60 Bauer, G. B., & Johnson, C. M. (1994). Trained motor imitation by bottlenose dolphins (*Tursiops truncatus*). *Perceptual and Motor Skills, 79*, 1307-1315.

61 Jaakkola, Kelly; Guarino, Emily; & Rodriguez, Mandy. (2010). Blindfolded Imitation in a Bottlenose Dolphin (*Tursiops truncatus*). *International Journal of Comparative Psychology*, 23(4)

62 Abramson, J.Z., Hernández-Lloreda, V., Call, J., Colmenares, F. (2012). Experimental evidence for action imitation in killer whales (*Orcinus orca*). Animal Cognition, Aug 9 [Epub ahead of print]

63 Richards, D.G., Wolz, J.P., Herman, L.M. (1984.) Vocal mimicry of computer-generated sounds and vocal labeling of objects by a bottlenosed dolphin, *Tursiops truncatus*. *Journal of Comparative Psychology, 1*, 10-28.

64 Reiss, D., McCowan, B. J. (1993). Spontaneous vocal mimicry and production by bottlenose dolphins (*Tursiops truncatus*): evidence for vocal learning. *Journal of Comparative Psychology, 107*(3), 301-12.

65 Janik, V. M. (2000). Whistle matching in wild bottlenose dolphins (*Tursiops* truncatus). Science, 289, 1355 e 1357.

66 Ford, J. K. B. (1991). Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Canadian Journal Of Zoology*, *69*(6), 1454-1483.

67 Foote, A. D., Griffin, R. M., Howitt, D., Larsson, L., Miller, P. J. O., & Rus Hoelzel, A. (2006). Killer whales are capable of vocal learning. *Biology Letters*, *2*(4), 509-512.

68 Kremers, D., Jaramillo, M. B., Böye, M., Lemasson, A., & Hausberger, M.

(2011). Do dolphins rehearse show-stimuli when at rest? Delayed matching of auditory memory. *Frontiers in psychology*, *2*(December), 386. doi: 10.3389/fpsyg.2011.00386

69 May-Collado, L. J. (2010). Changes in whistle structure of two dolphin species during interspecific associations. *Ethology, 116*, 1065–1074.

70 Gallup, G.G. Jr. (1970). Chimpanzees: Self recognition. *Science, 167*(3914), 86–87.

71 For an overview of these events, see Reiss, D. (2011). *The Dolphin in the Mirror: Exploring Dolphin Minds and Saving Dolphin Lives*. Houghton Mifflin Harcourt.

72 Marino, L.; Reiss, D.; Gallup, G. (1993). Self-Recognition in the Bottlenose Dolphin: A Methodological Test Case for the Study of Extraterrestrial Intelligence. In G.S. Shostak, (Ed.), *Third Decennial US-USSR Conference on SETI. ASP Conference Series*, *47*, 393.

73 For details on these kinds of behaviors see Sarko, D., Marino, L., & Reiss, D. (2003). A bottlenose dolphin's (*Tursiops truncatus*) responses to its mirror image: further analysis. *International Journal of Comparative Psychology, 15*, 69 -76.

74 Marten, K. & Psarakos, S. (1995). Evidence of self-awareness in the bottlenose dolphin (*Tursiops truncatus*). In Parker, S.T., Mitchell, R. & Boccia, M. Self-awareness in Animals and Humans: Developmental Perspectives, (pp. 361–379). Cambridge: Cambridge University Press.

75 Sarko, D., Marino, L., & Reiss, D. (2003). A bottlenose dolphin's (*Tursiops truncatus*) responses to its mirror image: further analysis. *International Journal of Comparative Psychology, 15*, 69 -76. p. 70

76 Delfour, F., & Marten, K. (2001). Mirror image processing in three marine mammal species: Killer whales (*Orcinus orca*), false killer whales (*Pseudorca crassidens*) and California sea lions (*Zalophus californianus*). *Behavioural Processes, 53*, 181-190.

77 Anderson, J. R. (1995). Self-recognition in dolphins: Credible cetaceans, compromised criteria, controls, and conclusions. *Consciousness and Cognition, 4*, 239–243.

78 Mitchell, R. W. (1995). Evidence of dolphin self-recognition and the difficulties of interpretation. *Consciousness and Cognition*, *4*(2), 229-234.

79 Hart, D., & Whitlow Jr., J. W. (1995). The experience of self in the bottlenose dolphin. *Consciousness and Cognition*, *4*(2), 244-247.

80 Reiss, D., & Marino, L. (2001). Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(10), 5937-5942.

81 Gallup, G. G. Jr., (1994). Self-recognition: Research strategies and experimental design. In S. T. Parker, R. W. Mitchell, & M. L. Boccia (Eds.), *Self-awareness in animals and humans: Developmental perspectives,* (pp. 35–50). Cambridge, UK: Cambridge University Press, 48.

82 Reiss, D., & Marino, L. (2001). Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(10), 5937-5942. p. 5942

83 Note that the key difference between this study and other MSR studies is that the pigeons had been trained to use the mirror, as opposed to spontaneously using the mirror. Epstein, R., Lanza, R. P., & Skinner, B. F. (1981). "Self-awareness" in the pigeon. Science, 212, 695-696.

84 Rajala, A. Z., Reininger, K. R., Lancaster, K. M., & Populin, L. C. (2010). Rhesus monkeys (*Macaca mulatta*) do recognize themselves in the mirror: Implications for the evolution of self-recognition. *PLoS ONE*, *5*(9), 8.

85 Ikeda, Y. (2009). A perspective on the study of cognition and sociality of cephalopod mollusks, a group of intelligent marine invertebrates. *Japanese Psychological Research*, *51*(3), 146-153.

86 Broesch, T., Callaghan, T., Henrich, J., Murphy, C., & Rochat, P. (2010). Cultural variations in children's mirror self-recognition. *Journal of CrossCultural Psychology*, *42*(6), 1018-1029.

87 Lurz, R. (2011). Mindreading Animals: The Debate over What Animals Know about Other Minds. Cambridge, MA: MIT Press.

88 Reiss, D. (2011). The Dolphin in the Mirror: Exploring Dolphin Minds and Saving Dolphin Lives. Houghton Mifflin Harcourt.

89 Bekoff, M. (2001). Observations of scent-marking and discriminating self from others by a domestic dog (*Canis familiaris*): tales of displaced yellow snow *Behavioural Processes, 55*(2), 75-79. doi: 10.1016/S0376-6357(01)00142-5

90 Lockwood, J.A. & Rentz, D.C.F. (1996). Nest construction and recognition in a gryllacridid: The discovery of pheromonally mediated autorecognition in an insect. *Australian Journal of Zoology, 44*, 129–141.

91 Mitchell, R.W. (1997). Kinesthetic-visual matching and the self-concept as explanations of mirror-self-recognition. *Journal for the Theory of Social Behavior, 27*(1), 17–39.

92 Heyes, C. M. (1994). Reflections on self–recognition in primates. *Animal Behaviour, 47*, 909–919.

93 Rochat, P., & Zahavi, D. (2011). The uncanny mirror: A reframing of mirror self-experience. *Consciousness and Cognition, 20*, 204–213.

94 Morin, A. (2011). Self-recognition, theory-of-mind, and self-awareness: what side are you on? *Laterality*, *16*(3), 367-383.

95 Mitchell, R.W. (1993). Mental models of mirror self-recognition: two theories. *New Ideas in Psychology, 11*,295–325.

96 Carruthers, P. (2009). How we know our own minds: the relationship between mindreading and metacognition. *Behavioral and Brain Sciences*, *32*(2), 121-138

97 Humphrey, N. (1976). The social function of intellect. In P. P. G. Bateson & R. A. Hinde (Eds.), *Growing Points in Ethology*, (pp. 303- 317). Cambridge: Cambridge University Press.

98 Marino, L. (2011). Brain structure and intelligence in cetaceans In Brakes, P., & Simmonds, M. (Eds), *Whales and Dolphins: Cognition, Culture, Conservation and Human Perceptions,* (pp. 113-128). Earthscan: London, 125.

99 Reiss, D. (2011). The Dolphin in the Mirror: Exploring Dolphin Minds and Saving Dolphin Lives. Houghton Mifflin Harcourt, 167.

100 Statement of Lori Marino, Ph.D., Neuroscience and Behavioral Biology

Program, Emory University, Atlanta, Georgia to The House Committee on Natural Resources Subcommittee on Insular Affairs, Oceans and Wildlife regarding educational aspects of public display of marine mammals 27 April, 2010.

101 White, T. (2011). What is it like to be a dolphin? In Brakes, P., & Simmonds, M. (Eds), *Whales and Dolphins: Cognition, Culture, Conservation and Human Perceptions,* (pp. 188-206). Earthscan: London, 190.

102 White, T. (2007). *In Defense of Dolphins: The New Moral Frontier*.Malden, MA: Blackwell Publishing.

103 Herzing, D.L. & White, T. (1999). Dolphins and the Question of Personhood. *Etica Animali, 9(*98), 64-84.

104 Smith, J.D., Schull, J., Strote, J., McGee, K., Egnor, R., & Erb, L. (1995). The uncertain response in the bottlenose dolphin (*Tursiops truncatus*). *Journal of Experimental Psychology, 124*, 391-408.

105 S Smith, J.D. (2012). Inaugurating the Study of Animal Metacognition. *International Journal of Comparative Psychology, 23(*3), 401-413.

106 Carruthers, P. (2009). How we know our own minds: the relationship between mindreading and metacognition. *Behavioral and Brain Sciences*, *32*(2), 121-138.

107 Smith, J. D., Coutinho, M. V. C., Boomer, J., & Beran, M. J. (2012). Metacognition across species. In J. Vonk & T. Shackelford (Eds.), *Oxford Handbook of Comparative Evolutionary Psychology,* (pp. 271-296). Oxford: Oxford University Press, 285.

108 Pack, A. A., & Herman, L. M. (2004). Bottlenosed dolphins (*Tursiops truncatus*) comprehend the referent of both static and dynamic human gazing and pointing in an object-choice task. *Journal of Comparative Psychology, 118*(2), 160-171.

109 Tschudin, A., Call, J., Dunbar, R. I. M., Harris, G., & van der Elst, C. (2001). Comprehension of signs by dolphins (*Tursiops truncatus*). *Journal of Comparative Psychology, 115*, 100 –105.

110 Herman, L., Pack, A. A., & Morrel-Samuels, P. (1993). Representational and Conceptual Skills of Dolphins. In H. L. Roitblat, L. M. Herman & P. E. Nachtigall (Eds.), *Language and Communication: Comparative Perspectives,* (pp. 403-442). Hillsdale, NJ: Lawrence Erlbaum Associates.

111 Herman, L. M., Abichandani, S. L., Elhajj, A. N., Herman, E. Y. K., Sanchez, J. L., & Pack, A. A. (1999). Dolphins (*Tursiops truncatus*) comprehend the referential character of the human pointing gesture. *Journal of Comparative Psychology, 113*(4), 347-364.

112 Herman, L. M., & Uyeyama, R. U. (1999). The Dolphin's Grammatical Competency: Comments on Kako. *Animal Learning and Behavior 27*(1), 18-23.

113 Pack, A. A., & Herman, L. M. (2004). Bottlenosed dolphins (*Tursiops truncatus*) comprehend the referent of both static and dynamic human gazing and pointing in an object-choice task. *Journal of Comparative Psychology, 118*(2), 160-171.

114 Miklósi, Á., & Soproni, K. (2006). A comparative analysis of animals' understanding of the human pointing gesture. *Animal Cognition, 9*(2), 81-93.

115 Tschudin, A., Call, J., Dunbar, R. I., Harris, G., & van der Elst, C. (2001). Comprehension of signs by dolphins (*Tursiops truncatus*). *Journal of Comparative Psychology, 115*(1), 110-115.

116 Xitco, M. J., Gory, J. D., & Kuczaj, S. A. I. (2001). Spontaneous pointing by bottlenose dolphins (*Tursiops trucatus*). *Animal Cognition, 4*, 115-123.

117 Xitco, M. J., Jr., Gory, J. D., & Kuczaj, S. A., II. (2004). Dolphin pointing is linked to the attentional behavior of a receiver. *Animal Cognition, 8*, 231-238.

118 Herzing, D. (2011). Dolphins Diaries: My 20 Years with Spotted Dolphins in the Bahamas. New York: St. Martin's Press

119 Dudzinski, K. M., Sakai, M., Masaki, K., Kogi, K., Hishii, T., & Kurimoto, M. (2003). Behavioural observations of bottlenose dolphins towards two dead conspecifics. *Aquatic Mammals, 29*(1), 108-116.

120 For a review see: Tschudin, A. (2006). Belief attribution tasks with dolphins: What social minds reveal about animal rationality. In S. Hurley & M. Nudds (Eds.), *Rational Animals?* (pp. 411-436). Oxford: Oxford University Press.

121 Connor, R.C., Wells, R.S., Mann, J. & Read, A.J. (2000). The bottlenose dolphin: Social relationships in a fission-fusion society. In J. Mann, J., R.C. Connor, P.L. Tyack, & H. Whitehead (Eds.), *Cetacean Societies: Field Studies of Dolphins and Whales*, 91-126. Chicago: The University of Chicago Press, Page 91.

122 Connor, R. C., Smolker, R. A. & Richards, A.F. (1992). Two levels of alliance formation among bottlenose dolphins (*Tursiops* sp.) *Proceedings of the National Academy of Sciences, 89*, 987-990.

123 Connor, R. C., Heithaus, M. R. & Barre, L.M. (2001). Complex social structure, alliance stability and mating access in a bottlenose dolphin 'super-alliance'. *Proceedings of the Royal Society B: Biological Sciences, 268*, 263-267.

124 Connor, R.C., Watson-Capps, J., Sherwin, W.B. & Krutzen, M. (2010), A new level of complexity in the male alliance networks of Indian ocean bottlenose dolphins (*Tursiops* sp.), *Biology Letters*, *6*(20), 1 -4

125 Randic, S., Connor, R. C., Sherwin, W. B., & M. Krützen. (2012). A novel mammalian social structure in Indo-Pacific bottlenose dolphins (*Tursiops* sp.): complex male alliances in an open social network. *Proceedings of the Royal Society B: Biological Sciences.* doi:10.1098/rspb.2012.0264.

126 Connor, R.C. (2007). Dolphin social intelligence: Complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals*. Philosophical Transactions of the Royal Society B: Biological Sciences, 362* , 587-602

127 The benefits of mutualism: a conceptual framework. *Biological Reviews, 70*, 427-457.

128 Vaughn, R., L., Muzi, E., Richardson, J.L, and Würsig, B. (2011). Dolphin bait-balling behaviors in relation to prey ball escape behaviors. *Ethology, 117*, 859–871.

129 Benoit-Bird, K. J., & Au, W. W. L. (2009). Cooperative prey herding by the pelagic dolphin, *Stenella longirostris*. *Journal of the Acoustical Society of America, 125*, 125–137.

130 Duffy- Echevarria, E. E., Connor, R. C., & St. Aubin, D. J. (2008).

Observations of strand-feeding behavior by bottlenose dolphins (*Tursiops truncatus*) in Bull Creek, South Carolina. *Marine Mammal Science, 24*, 202-206.

131 Gazda, S.K, Connor, R.C., Edgar, R.K., Cox, F. (2005). A division of labour with role specialization in group-hunting bottlenose dolphins (*Tursiops truncatus*) off Cedar Key, Florida. *Proceedings of the Royal Society B Biological Sciences*, *272*(1559), 135-140.

132 Daura-Jorge, F.G., Cantor, M., Ingram, S.N., Lusseau, D., & Simões-Lopes, P.C. (2012). The structure of a bottlenose dolphin society is coupled to a unique foraging cooperation with artisanal fishermen. Biology Letters, doi: 10.1098/rsbl.2012.0174

133 Neil, D. T. (2002). Cooperative fishing interactions between Aboriginal Australians and dolphins in eastern Australia. *Anthrozoös, 15*, 3-18.

134 Biju Kumar, A., Smrithy R., & Sathasivam, (2012). Dolphin-assisted cast net fishery in the Ashtamudi Estuary, south-west coast of India. *Indian Journal of Fisheries, 59*(3), 143-148.

135 Busnel, R.G. (1973). Symbiotic relationship between man and dolphins. *Transactions of the New York Academy of Sciences, 35*, 112–131.

136 Baird, R.W. & L.M. Dill. (1997). Ecological and social determinants of group size in transient killer whales. *Behavioral Ecology 7*(4), 408-416

137 Smith, T. G., Siniff, D.B., Reichle, R. & Stone, S. 1981. Coordinated behavior of killer whales, *Orcinus orca*, hunting a crabeater seal, *Lobodon carcinophagus*. *Canadian Journal of Zoology, 59*, 1185–1189.

138 Visser, I. N., Smith, T.G., Bullock, I.D., Green, G.D., Carlsson, O. G. L., & Imberti, S. (2008). Antarctic peninsula killer whales (*Orcinus orca*) hunt seals and a penguin on floating ice. *Marine Mammal Science, 24*, 225–234.

139 Pitman, R. L., & Durban, J. W. (2012). Cooperative hunting behavior, prey selectivity and prey handling by pack ice killer whales (*Orcinus orca*), type B, in Antarctic Peninsula waters. *Marine Mammal Science, 28*(1), 16-36.

140 Connor, R. C. & Norris, K. S. (1982). Are dolphins reciprocal altruists*? The American Naturalist, 119*, 358-374.

141 Warren-Smith, A.B., & Dunn, W.L. (2006). Epimeletic behaviour toward a seriously injured juvenile bottlenose dolphin (*Tursiops* sp.) in Port Phillip, Victoria, Australia. *Aquatic Mammals, 32*(3),357-362.

142 Mann, J. & H. Barnett. (1999). Lethal tiger shark (*Galeocerdo cuvieri*) attack on bottlenose dolphin (*Tursiops* sp.) calf: Defense and reactions by the mother. *Marine Mammal Science, 15*(2), 568-575.

143 Wood, F.G., Caldwell, D.K. & Caldwell, M.C. (1970). Behavioral interactions between porpoises and sharks. *Investigations on Cetacea, 2*, 264–277.

144 Heithaus, M.R. (2001). Predator-prey and competitive interactions between sharks (order Selachii) and dolphins (suborder Odontoceti): a review. *Journal of Zoology, 253*, 53-68.

145 Saayman, G.S. and Tayler, C.K. (1979). *The socioecology of humpback dolphins* (*Sousa* spp.). In H.E. Winn, & B.L. Olla (Eds.), *Behaviour of Marine Animals Vol. 3: Cetaceans*, 165-226. New York: Plenum Press.

146 Bearzi G. (1997). A "remnant" common dolphin observed in association with

bottlenose dolphins in the Kvarneric (northern Adriatic Sea). *European Research on Cetaceans, 10*, 204.
147 Simard, P. & Gowans, S. (2004). Two calves in echelon: An alloparental association in Atlantic white-sided dolphins (*Lagenorhynchus acutus*). *Aquatic Mammals 30*(2), 330-334.
148 Mann, J., & Smuts, B. B. (1999). Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour, 136,* 529-566.
149 Karczmarski, L., Thornton, M., & Cockcroft, V. G. (1997). Description of selected behaviours of humpback dolphins *Sousa chinensis*. *Aquatic Mammals, 23*(3), 127-133.
150 Gaspar, C., Lenzi, R., Reddy, M. L., & Sweeney, J. (2000). Spontaneous lactation by an adult *Tursiops truncatus* in response to a stranded *Steno bredanensis* calf. *Marine Mammal Science, 16*, 653-658.
151 Ford, J.K. (2008). Killer Whale. In W.F. Perrin, B. Würsig, & H.C.M. Thewissen, (Eds.). *Encyclopedia of Marine Mammals, second edition,* 650-657. Academic Press, Inc.
152 McAuliffe, K., Whitehead, H. (2005) Eusociality, menopause and information in matrilineal whales. *Trends in Ecology & Evolution, 20*, 650.
153 Tyack, P. (2008). Behavior, overview. In W.F. Perrin, B. Würsig, & H.C.M. Thewissen, (Eds.). *Encyclopedia of Marine Mammals, second edition, 101--108.* Academic Press, Inc.
154 Grellier, K., Hammond, P.S., Wilson, B., Sanders-Reed, C.A., & Thompson, P.M. (2003). Use of photo-identification data to quantify mother–calf association patterns in bottlenose dolphins. *Canadian Journal of Zoology, 81*, 1421–1427.
155 Cockcroft, V.G., & Ross, G.J.B. (1990). Observations on the early development of a captive bottlenose dolphin calf. In by S. Leatherwood and R.R. Reeves (Eds.), *The Bottlenose Dolphin*, 461-478. New York: Academic Press.
156 Herman, L. M. (2009). Language learning and cognitive skills. In W.F. Perrin, B. Würsig, & H.C.M. Thewissen (Eds.). *Encyclopedia of Marine Mammals, Second Edition*, (pp. 657-663). Orlando: Academic Press.
157 Herman, L. M., Richards, D. G. & Wolz, J. P. (1984). Comprehension of sentences by bottlenosed dolphins. *Cognition, 16,* 129-219.
158 Herman, L. M. (1986). Cognition and language competencies of bottlenosed dolphins. In R.J. Schusterman, J. Thomas, and F. G. Wood (Eds.) *Dolphin Cognition and Behavior: A Comparative Approach*, (pp. 221-251). Hilladale, NJ: Lawrence Erlbaum Associates.
159 Herman, L. M., Richards, D. G. & Wolz, J. P. (1984). Comprehension of sentences by bottlenosed dolphins. *Cognition, 16*, 129-219.
160 Herman, L. M. & Forestell, P. H. (1985). Reporting presence or absence of named objects by a language-trained dolphin. *Neuroscience and Behavioral Reviews,* 9, 667-691.
161 Herman, L.M., Kuczaj, S. A. II, & Holder, M. D. (1993). Responses to anomalous gestural sequences by a language-trained dolphin: Evidence for processing of semantic relations and syntactic information. *Journal of Experimental Psychology, General, 122*, 184-194. Pg 185

162 Herman, L. M. (2006). Intelligence and rational behaviour in the bottlenosed dolphin. In S. Hurley & M. Nudds (Eds.), *Rational Animals?* (pp. 439-467). Oxford, England: Oxford University Press. Pg. 443.

163 Herman, L. M., Kuczaj, S. A., & Holder, M. D. (1993). Responses to anomalous gestural sequences by a language-trained dolphin: evidence for processing of semantic relations and syntactic information. *Journal of experimental psychology General*, *122*(2), 184-194.

164 Herman, L. M., Richards, D. G. & Wolz, J. P. (1984). Comprehension of sentences by bottlenosed dolphins. *Cognition, 16*, 129-219.

165 Herman, L. M. (1987). Receptive competences of language-trained animals. In J. S. Rosenblatt, C. Beer, M. C. Busnel, & P. J. B. Slater (Eds.), *Advances in the Study of Behavior. Vol. 17* (pp. 1-60). Petaluma, CA: Academic Press.

166 Pack, A. A. (2010). The synergy of laboratory and field studies of dolphin behavior and cognition. *International Journal of Comparative Psychology, 23*, 538-565.

167 Herman, L. (n.d.) Retrieved from http://www.dolphin-institute.org/resource_guide/animal_language.htm

168 Perner, J. (1991). Understanding the representational mind. Learning development and conceptual change. Cambridge, MA: MIT Press.

169 Herman, L. M., Richards, D.G., & Wolz, J. P. (1984). Comprehension of sentences by bottlenosed dolphins. *Cognition, 16,* 129-219.

170 Kako, E. (1999). Elements of syntax in the systems of three language-trained animals. *Animal Learning and Behavior, 27*, 1–14.

171 Mercado, E., Killebrew, D., Pack, A., Mácha, I., & Herman, L. (2000). Generalization of “same-different” classification abilities in bottlenosed dolphins. *Behavioural Processes*, *50*(2-3), 79-94.

172 Jaakkola, K., Fellner, W., Erb, L., Rodriguez, M., & Guarino, E. (2005). Understanding of the concept of numerically “less” by bottlenose dolphins (*Tursiops truncatus*). *Journal of Comparative Psychology*, *119*(3), 296-303.

173 Kilian, A., Yaman, S., Von Fersen, L., & Güntürkün, O. (2003). A bottlenose dolphin discriminates visual stimuli differing in numerosity. *Learning behavior a Psychonomic Society publication*, *31*(2), 133-142

174 Murayama, T., Usui, A., Takeda, E., Kato, K., & Maejima, K. (2012) Relative size discrimination and perception of the Ebbinghaus illusion in a bottlenose dolphin (*Tursiops truncatus*). *Aquatic Mammals, 38*(4), 333-342.

175 Ralston, J. V., & Herman, L. M. (1995). Perception and generalization of frequency contours by a bottlenose dolphin (*Tursiops truncatus*). *Journal of Comparative Psychology, 109*, 268-277.

176 Harley, H. (2008). Whistle discrimination and categorization by the Atlantic bottlenose dolphin (*Tursiops truncatus*): A review of the signature whistle framework and a perceptual test. *Behavioural Processes*, *77*(2), 243-268.

177 Janik, V. M., Sayigh, L. S., & Wells, R. S. (2006). Signature whistle shape conveys identity information to bottlenose dolphins. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(21), 8293-8297

178 Jaakkola, K., Guarino, E., Rodriguez, M., Erb, L., & Trone, M. (2010).

What do dolphins (*Tursiops truncatus*) understand about hidden objects? *Animal Cognition*, *13*(1), 103-120.

179 Jaakkola, K., Guarino, E., Rodriguez, M., Erb, L., & Trone, M. (2010). What do dolphins (*Tursiops truncatus*) understand about hidden objects? *Animal Cognition*, *13*(1), 103-120.

180 Herman, L. M., Morrel-Samuels, P., & Pack, A. A. (1990). Bottlenosed dolphin and human recognition of veridical and degraded video displays of an artificial gestural language. *Journal of Experimental Psychology General*, *119*(2), 215-230

181 Herman, L. M., Hovancik, J. R., Gory, J. D., & Bradshaw, G. L. (1989). Generalization of visual matching by a bottlenosed dolphin (*Tursiops truncatus*): Evidence for invariance of cognitive performance with visual and auditory materials. *Journal of Experimental Psychology Animal Behavior Processes*, *15*(2), 124-136.

182 Harley, H. E., Putman, E. A., & Roitblat, H. L. (2003). Bottlenose dolphins perceive object features through echolocation. *Nature, 424*, 667-669.

183 Pack, A. A., Herman, L. M., Hoffmann-Kuhnt, M., & Branstetter, B. K. (2002). The object behind the echo: dolphins (*Tursiops truncatus*) perceive object shape globally through echolocation. *Behavioural Processes*, *58*(1-2), 1-26.

184 Pack, A. A., & Herman, L. M. (1995). Sensory integration in the bottlenosed dolphin: immediate recognition of complex shapes across the senses of echolocation and vision. *Journal of the Acoustical Society of America*, *98*, 722-733.

185 Pack, A. A., & Herman, L. (1996). Dolphins can immediately recognize complex shapes across the senses of echolocation and vision. *Journal of the Acoustical Society of America*, *100*(4), 2610.

186 Harley, H. E., Roitblat, H. L., & Nachtigall, P. E. (1996). Object representation in the bottlenose dolphin (*Tursiops truncatus*): integration of visual and echoic information. *Journal of Experimental Psychology Animal Behavior Processes*, *22*(2), 164-174.

187 White, T. (2007). *In Defense of Dolphins: The New Moral Frontier*. Malden, MA: Blackwell Publishing, 39-40.

188 Herman, L. M. (2011). Body and self in dolphins. *Consciousness and Cognition*, *21*(1), 526-45.

189 Shimojo, S., & Shams, L. (2001). Sensory modalities are not separate modalities: plasticity and interactions. *Current Opinion in Neurobiology*, *11*(4), 505-509.

190 Thompson, R. K. R. and Herman, L. M. (1977). Memory for lists of sounds by the bottlenosed dolphin: Convergence of memory processes with humans? *Science, 195*, 501-503.

191 See for an overview: Jaakola, K. (2012). Cetacean Cognitive Specializations. In J. Vonk & T. Shackelford (Eds.), *Oxford Handbook of Comparative Evolutionary Psychology,* (pp. 144-165). Oxford: Oxford University Press. Pg. 148.

192 Thompson, R. K. R. and Herman, L. M. (1977). Memory for lists of sounds by the bottlenosed dolphin: Convergence of memory processes with humans? *Science, 195*, 501-503.

193 Bruck, J.N. (2013) Decades-long social memory in bottlenose dolphins,

20131726-20131726. In *Proceedings of the Royal Society B: Biological Sciences 280* (1768).
194 Raby, C. R. & Clayton, N. S. (2012). Episodic memory and future planning. In J. Vonk & T. Shackelford (Eds.), *Oxford Handbook of Comparative Evolutionary Psychology,* (pp217-235). Oxford: Oxford University Press, 217.
195 Zentall, T. R., (2008). Representing past and future events. In E. Dere, A. Easton, L. Nadel, & J. P. Huston (Eds.), *Handbook of Episodic Memory Research*, (pp.217-234). Oxford, UK: Elsevier. Page 230
196 Mercado, E., Murray, S. O., Uyeyama, R. K., Pack, A. A., & Herman, L. M. (1998). Memory for recent actions in the bottlenosed dolphin (*Tursiops truncatus*): Repetition of arbitrary behaviors using an abstract rule. *Animal Learning Behavior*, *26*(2), 210-218.
197 For an overview of dolphin planning see Kuczaj, S.A. II, Xitco, M.J. Jr. & Gory, J. D. (2010). Can dolphins plan their behavior? *International Journal of Comparative Psychology, 23,* 664-670. And also Kuczaj, S. A., II, Gory, J . D., & Xitco, M. J., Jr. (2009). How intelligent are dolphins? A partial answer based on their ability to plan their behavior when confronted with novel problems. *Japanese Journal of Animal Psychology, 59*, 99–115
198 Connor, R. C., & Krützen, M. (2003). Levels and patterns in dolphin alliance formation. In F. de Waal, & P. L. Tyack (Eds.), *Animal Social Complexity* (pp. 115-120). Cambridge, MA: Harvard University Press
199 Visser, I. N., Smith, T. G., Bullock, I. D., Green, G. D., Carlsson, O. G., & Imberti, S. (2008). Antarctic peninsula killer whales (*Orcinus orc*a) hunt seals and a penguin on floating ice. *Marine Mammal Science, 24*, 225-234.
200 Smolker, R., Richards, A., Connor, R., Mann, J., & Berggren, P. (1997). Sponge carrying by dolphins (*Delphinidae, Tursiops sp*.): A foraging specialization involving tool use? *Ethology, 103*, 454-465.
201 Fertl, D. & Wilson, B. (1997). Bubble use during prey capture by a lone bottlenose dolphin *(Tursiops truncatus). Aquatic Mammals, 23(2), 113--114.*
202 Duffy-Echevarria, E.E., Connor, R.C., St. Aubin, D.J. (2008). Observations of strand-feeding behavior by bottlenose dolphins (*Tursiops truncatus*) in Bull Creek, South Carolina. *Marine Mammal Science, 24,* 202–206.
203 Kuczaj, S. A., & Makecha, R. (2008). The role of play in the evolution and ontogeny of contextually flexible communication. In U. Griebel & K. Oller (Eds.), *Evolution of communicative flexibility: Complexity, creativity, and adaptability in human and animal communication* (pp. 253-277). Cambridge, MA: MIT Press.
204 Kuczaj, S.A. II, Xitco, M.J. Jr. & Gory, J. D. (2010). Can dolphins plan their behavior? *International Journal of Comparative Psychology, 23*, 664-670.
205 Finn, J., Tregenza, T., & Norman, M. (2009). Preparing the perfect cuttlefish meal: Complex prey handling by dolphins. *PLoS ONE 4*(1), e4217. doi:10.1371/journal.pone.0004217
206 Kuczaj, S. A., Gory, J. D. & Xitco, M. J. (2009). How intelligent are dolphins? A partial answer based on their ability to plan their behavior when confronted with novel problems. *Japanese Journal of Animal Psychology, 59*, 99-115.
207 Kuczaj, S.A. II & Walker, R.T. (2012). Dolphin problem solving. In T. Zentall

& E. Wasserman (Eds.), *Handbook of Comparative Cognition*. Oxford University Press.

208 Kuczaj, S.A. II, Xitco, M.J. Jr. & Gory, J. D. (2010). Can dolphins plan their behavior? *International Journal of Comparative Psychology, 23*, 664-670. Pg 668

209 Kuczaj, S.A. II & Walker, R.T. (2012). Dolphin problem solving. In T. Zentall & E. Wasserman (Eds.), *Handbook of Comparative Cognition*. Oxford University Press.

210 Herman, L. M. (2006). Intelligence and rational behaviour in the bottlenosed dolphin. In S. Hurley & M. Nudds (Eds.), *Rational Animals? (*pp. 439-467). Oxford, England: Oxford University Press, 441.

211 Paulos R.D., Trone, M., Kuczaj, S.A. II (2010). Play in wild and captive cetaceans. *International Journal of Comparative Psychology, 23*, 701—722. Pg. 702.

212 Herzing, D. (2011). Dolphin Diaries: My 20 Years with Spotted Dolphins in the Bahamas. St. Martin's Press, New York.

213 Trone, M., Kuczaj, S., & Solangi, M. (2005). Does participation in dolphin–human interaction programs affect bottlenose dolphin behaviour? *Applied Animal Behaviour Science, 93* , 363–374

214 Slooten, E., & Dawson, S. M. (1994). Hector's dolphins. In S. H. Ridgway & R. Harrison (Eds.), *Handbook of Marine Mammals* (pp. 311-334). London: Academic Press.

215 Brown, D. H., & Norris, K. S. (1956). Observations of captive and wild cetaceans. *Journal of Mammalogy, 37* (3), 311-326.

216 Kuczaj, S.A. II & Walker, R.T. (2012). Dolphin problem solving. In T. Zentall & E. Wasserman (Eds.), *Handbook of Comparative Cognition*. Oxford University Press.

217 Paulos R.D., Trone, M., Kuczaj, S.A. II (2010). Play in wild and captive cetaceans. *International Journal of Comparative Psychology, 23*, 701—722. Pg 707

218 Delfour, F., & Aulagnier, S. (1997). Bubbleblow in beluga whales (*Delphinapterus leucas*): A play activity? *Behavioural Processes, 40*, 183-186.

219 Marten, K., Shariff, K., Psarakos, S., & White, D. J. (1996, August). Ring bubbles of dolphins. *Scientific American, 275*, 83-87.

220 For an overview of all these behaviors, see Paulos R.D., Trone, M., Kuczaj, S.A. II (2010). Play in wild and captive cetaceans. *International Journal of Comparative Psychology, 23*, 701—722

221 Mccowan, B., Marino, L., Vance, E., Walke, L., & Reiss, D. (2000). Bubble ring play of bottlenose dolphins (*Tursiops truncatus*): Implications for cognition. *Journal of Comparative Psychology*, *114*(1), 98-106.

222 Gewalt, W. (1989). Orinoco freshwater dolphins (*Inia geoffrensis*) using self-produced air bubble rings as toys. *Aquatic Mammals, 15* (2), 73-79.

223 Mccowan, B., Marino, L., Vance, E., Walke, L., & Reiss, D. (2000). Bubble Ring Play of Bottlenose Dolphins (*Tursiops truncatus*): Implications for Cognition. *Journal of Comparative Psychology*, *114*(1), 98-106.

224 Panksepp, J. (1998). Affective Neuroscience: The Foundations of Human and Animal Emotions. New York: Oxford University Press, 26.

225 Panksepp, J. (2011). Cross-Species Affective Neuroscience Decoding of the Primal Affective Experiences of Humans and Related Animals. *PLoS ONE*, *6*(9), 15
226 Prinz, J. (2004). *Gut Reactions: A Perceptual theory of Emotions*. Oxford: Oxford University Press.
227 Herzing, D.L. & White, T. (1999). Dolphins and the Question of Personhood. *Etica Animali, 9(*98), 64-84.
228 Simmonds, M. (2006). Into the brains of whales. *Applied Animal Behaviour Science, 100*(1-2), 103-116.
229 Reiss, D. (2011). The Dolphin in the Mirror: Exploring Dolphin Minds and Saving Dolphin Lives. Houghton Mifflin Harcourt, 202.
230 Herzing, D.A. (2000). Trail of Grief. In M. Bekoff (Ed.), *The Smile of a Dolphin: Remarkable Accounts of Animal emotions* (pp. 138-139). London: Discovery Books.
231 Rose, N. (2000). A Death in the family. In M. Bekoff (Ed.), *The Smile of a Dolphin: Remarkable Accounts of Animal emotions* (pp. 144-145). London: Discovery Books.
232 Frohoff, T. (2000). The Dolphin's Smile. In M. Bekoff (Ed.), *The Smile of a Dolphin: Remarkable Accounts of Animal emotions* (pp. 78-79). London: Discovery Books.
233 Herzing, D. (2011). Dolphins Diaries: My 20 Years with Spotted Dolphins in the Bahamas. New York: St. Martin's Press, 106.
234 Kuczaj, S., Tranel, K., Trone, M., & Hill, H. (2001). Are animals capable of deception or empathy? Implications for animal consciousness and animal welfare. *Animal Welfare, 10*(1), S161-S173.
235 Santos, M.C.O., Rosso, S., Siciliano, S., Zerbini, A., Zampirolli, E., Vicente, A.F., Alvarenga, F., (2000). Behavioral observations of the marine tucuxi dolphin (*Sotalia fluviatilis*) in Sao Paulo estuarine waters, Southeastern Brazil. *Aquatic Mammals, 26*(3), 260-267.
236 Cockcroft, V. G., & Sauer, W. (1990). Observed and inferred epimeletic (nurturant) behaviour in bottlenose dolphins. *Aquatic Mammals, 16*(1), 31-32.
237 Fertl D., & Schiro A. 1994. Carrying of dead calves by free-ranging Texas bottlenose dolphins (*Tursiops truncatus*). *Aquatic Mammals, 20*(1), 53- 56.
238 Ritter, F. (2007). Behavioral responses of rough-toothed dolphins to a dead newborn calf. *Marine Mammal Science, 23*(2), 429-433.
239 Ritter, F. (2002). Behavioral observations of rough-toothed dolphins (*Steno bredanensis*) off La Gomera, Canary Islands (1995–2000), with special reference to their interactions with humans. *Aquatic Mammals, 28*(1), 46–59.
240 Harzen. S. & dos Santos. M.E. (1992), Three encounters with wild bottlenose dolphins (*Tursiops truncatus*) carrying dead calves. *Aquatic Mammals, 18*(2), 49-55.
241 Hauser, M. (2000). *Wild Minds: What Animals Really Think*. Henry Holt and Company: New York. See discussion of intelligence on pg. xviii
242 Dawkins, M.S. (2012). Why Animals Matter: Animal Consciousness, Animal Welfare, and Human Well-being. Oxford: Oxford University Press
243 Sherwin, C. M. (2001). Can Invertebrates Suffer? Or, How Robust is Argument-

By-Analogy? *Animal Welfare, 10(Supplement 1),* S103-S118.
244 Elwood, R. W. (2011). Pain and suffering in invertebrates? ILAR journal National Research Council Institute of Laboratory Animal Resources, 52(2), 175-184.
245 Chalmers, D. J. (1995). Facing Up to the problem of consciousness. *Journal of Consciousness Studies, 2*(3), 1-27.
246 Dawkins, M.S. (2001). Who needs consciousness? *Animal Welfare 10*, S19–29. Pg. S28.
247 Kuczaj, S., Tranel, K., Trone, M., & Hill, H. (2001). Are animals capable of deception or empathy? Implications for animal consciousness and animal welfare. *Animal Welfare, 10*(1), S161-S173.
248 Connor, R. C., & Norris, K. S. (1982). Are dolphins reciprocal altruists? *The* American Naturalist, 119(3), 358-374.
249 Dudzinski, K.M., Gregg, J.D., Ribic, C.A., & Kuczaj, S.A. (2009). A comparison of pectoral fin contact between two different wild dolphin populations. *Behavioural Processes, 80*,182-190
250 de Waal, F. B. M. (2008). Putting the altruism back into altruism: the evolution of empathy. *Annual Review of Psychology*, *59*(May 2007), 279-300.
251 Connor, R. C., & Norris, K. S. (1982). Are dolphins reciprocal altruists? *The American Naturalist*, *119*(3), 358-374.
252 Panksepp, J. (2011). Cross-Species Affective Neuroscience Decoding of the Primal Affective Experiences of Humans and Related Animals. *PLoS ONE 6*(9), e21236. doi:10.1371/journal.pone.0021236
253 Panksepp, J. (1992). A critical role for "affective neuroscience" in resolving what is basic about basic emotions. *Psychological review, 99*(3), 554–560.
254 Panksepp, J. (2005). Affective consciousness: Core emotional feelings in animals and humans. *Consciousness and Cognition, 14*, 30–80
255 Low, P. (2012, July 7). The Cambridge Declaration on Consciousness in Non-Human Animals. Signed at the Francis Crick Memorial Conference on Consciousness in Human and non-Human Animals, at Churchill College, University of Cambridge.
256 Mann, J., Stanton, M. A., Patterson, E. M., Bienenstock, E. J., & L. O. Singh. (2012). Social networks reveal cultural behaviour in tool-using using dolphins. *Nature Communications, 3*, 980. doi:10.1038/ncomms1983
257 Smolker, R., Richards, A., Connor, R., Mann, J., & Berggren, P. (1997). Sponge carrying by dolphins (Delphinidae, *Tursiops* sp.): a foraging specialization involving tool use? *Ethology, 103,* 454–465.
258 Mann, J., Sargeant, B. L., Watson-Capps, J. J., Gibson, Q. A., Heithaus, M. R., Connor, R. C., & Patterson, E. (2008). Why Do Dolphins Carry Sponges? (R. Brooks, Ed.) *PLoS ONE*, *3*(12), 7.
259 Patterson, E. M., & Mann, J. (2011). The Ecological Conditions That Favor Tool Use and Innovation in Wild Bottlenose Dolphins (*Tursiops* sp.). (S. F. Brosnan, Ed.) *PLoS ONE*, *6*(7), 7.
260 See for example: Pearson, H.C., & Shelton, D.E. (2010). A large-brained social animal. In Würsig, B., & Würsig, M., (Eds.), *The Dusky Dolphin: Master*

Acrobat off Different Shores (pp. 333-353). San Diego, CA: Elsevier.
261 Krützen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L., & Sherwin, W. B. (2005). Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(25), 8939-8943.
262 Bacher, K., Allen, S., Lindholm, A. K., Bejder, L., & Krützen, M. (2010). Genes or culture: are mitochondrial genes associated with tool use in bottlenose dolphins (*Tursiops* sp.)? *Behavior Genetics*, *40*(5), 706-714
263 Kopps, A.M., & Sherwin, W.B. (2012). Modelling the emergence and stability of a vertically transmitted cultural trait in bottlenose dolphins. *Animal Behaviour*, doi:10.1016/j.anbehav.2012.08.029.
264 This definition was taken from: Boyd, R. & Richerson, P. J. (1996). Why culture is common but cultural evolution is rare*. Proceedings of the British Academy, 88*, 77–93.
265 Rendell, L., & Whitehead, H. (2001). Culture in whales and dolphins. *Behavioral and Brain Sciences*, *24*(2), 309-24; discussion 324-82.
266 Mann, J. (2001). Cetacean culture: Definitions and evidence. *Behavioral and Brain Sciences, 24*(2), 343.
267 Janik, V. M. (2001). Is cetacean social learning unique? *Behavioral and Brain Sciences*, *24*(2), 337-338.
268 Donaldson, R., Finn, H., Bejder, L., Lusseau, D., & Calver, M. (2012). The social side of human–wildlife interaction: wildlife can learn harmful behaviours from each other. *Animal Conservation.* doi: 10.1111/j.1469-1795.2012.00548.x
269 Bender, C., Herzing, D., & Bjorklund, D. (2009). Evidence of teaching in Atlantic spotted dolphins (*Stenella frontalis*) by mother dolphins foraging in the presence of their calves. *Animal Cognition, 12*, 43-53.
270 Janik, V. M. (2001). Is cetacean social learning unique? *Behavioral and Brain Sciences*, *24*(2), 337-338.
271 *Kuczaj, S.* (2001). Cetacean culture*:* Slippery when wet. *Behavioral and Brain Sciences, 24*, 340-341.
272 Sargeant, Brooke L., and Janet Mann. From Social Learning to Culture: Intrapopulation Variation in Bottlenose Dolphins. The Question of Animal Culture. Ed. Kevin N. Laland and Bennett G. Galef. Cambridge, Mass: Harvard UP, 2009. 152-73.
273 Nowacek, D.P. (2002). Sequential foraging behaviour of bottlenose dolphins, *Tursiops truncates*, in Sarasota Bay, Florida. *Behaviour 139*(9): 1125–1145.
274 Connor, R. C., Heithaus, M., Berggren, P., & Miksis, J. L. (2000). “Kerplunking”: Surface fluke splashes during shallow-water bottom foraging by bottlenose dolphins. *Marine Mammal Science, 16*, 646-653.
275 Sargeant, B. L., Mann, J., Berggren, P., & Krützen, M. (2005). Specialization and development of beach hunting, a rare foraging behavior, by wild bottlenose dolphins (*Tursiops* sp.). *Canadian Journal of Zoology*, *83*(11), 1400-1410.
276 Mann, J. (2001). Cetacean culture: Definitions and evidence. *Behavioral and Brain Sciences, 24*(2), 343.

277 Galef, B.G., Jr. (2001). Where’s the beef? Evidence of culture, imitation and teaching in cetaceans? *Behavioral and Brain Sciences, 24*,(2) 335.

278 Premack, D., & Hauser, M. D. (2001). A whale of a tale: Calling it culture doesn't help**.** *Behavioral and Brain Sciences, 24(2)*, 350-351.

279 Mitchell, R.W. (2001). On not drawing the line about culture, Inconsistencies in interpretation of nonhuman cultures. *Behavioral and Brain Sciences, 24(2)*, 348.

280 Sargeant, B. L., & Mann, J. (2009). Developmental evidence for foraging traditions in wild bottlenose dolphins. *Animal Behaviour*, *78*(3), 715-721.

281 For overview see Sargeant, B. L., & Mann, J. (2009). Developmental evidence for foraging traditions in wild bottlenose dolphins. *Animal Behaviour*, *78*(3), 715-721.

282 For Example see: Mann, J., Stanton, M. A., Patterson, E. M., Bienenstock, E. J., & L. O. Singh. (2012). Social networks reveal cultural behaviour in tool-using using dolphins. *Nature Communications, 3*, 980. doi:10.1038/ncomms1983

283 Whitehead, H. (2011). The culture of whales and dolphins. In P. Brakes & M. Simmonds (Eds.), *Whales and Dolphins: Cognition, Culture, Conservation and Human Perceptions* (pp. 149-169). Earthscan: London.

284 Sargeant, B.L., & Mann, J. (2009). Social learning to culture: Intrapopulation variation in bottlenose dolphins. In K.N Laland & B.G Galef, *The Question of Animal Culture*, (pp. 152-173). Cambridge, Mass: Harvard University Press.

285 *Kuczaj, S.* (2001). Cetacean culture*:* Slippery when wet*.* *Behavioral and Brain Sciences, 24*, 340-341.

286 Bastian, J., Wall, C., & Anderson, C.L. (1968). Further investigation of the transmission of arbitrary environmental information between bottle-nose dolphins. Naval Undersea Warfare Center. Report no. TP 109, 38

287 Bastian, J. (1967). The transmission of arbitrary environmental information between bottlenosed dolphins. In R.G. Busnel (Ed.), *Animal Sonar Systems* (pp. 803-873). New York: Plenum Press.

288 Herman, L. M. and Tavolga, W. N. (1980). The communication systems of cetaceans. In L. M. Herman (Ed.), *Cetacean Behavior: Mechanisms and Functions* (pp. 149-209). New York: Wiley Interscience.

289 Evans, W. E., & Bastian, J. (1969). Marine mammal communication; social and ecological factors. In H. T. Anderson (Ed.), *The Biology of Marine Mammals* (pp. 425-476). New York: Academic Press.

290 Dudok van Heel, W.H. (1974). *Extraordinaires dauphins.* Paris: Rossel.

291 Markov, V. I., & Ostrovskaya, V.M. (1990) Organization of communication system in *Tursiops truncatus* Montague. In J.A. Thomas, & R.A. Kastelein (Eds), *Sensory Abilities of Cetaceans --Laboratory and Field Evidence* (pp. 599-602). NATO ASI Series, Series A: Life Sciences, vol 196. New York: Plenum Press.

292 Zanin, A.V., Markov, V.I., & Sidorova, I.E. (1990). The ability of bottlenose dolphins, *Tursiops truncatus*, to report arbitrary information. In J.A. Thomas, & R.A. Kastelein (Eds), *Sensory Abilities of Cetaceans --Laboratory and Field Evidence* (pp. 685-697). NATO ASI Series, Series A: Life Sciences, vol 196. New York: Plenum Press.

293 Herman, L. M. and Tavolga, W. N. (1980). The communication systems of cetaceans. In L. M. Herman (Ed.), *Cetacean Behavior: Mechanisms and Functions* (pp. 149-209). New York: Wiley Interscience.
294 Dreher, J. J. (1966). Cetacean communication: small-group experiment. In K. Norris (Ed.), *Whales, Dolphins and Porpoises*, (pp. 529-543). Berkley and Los Angeles: University of California Press.
295 Dreher, J. J. (1961). Linguistic considerations of porpoise sounds. *Journal of the Acoustical Society of America, 33*, 1799-1800.
296 Dreher, J. J. & Evans, W. E. (1964). Cetacean communication. In W. N. Tavolga, (Ed.), *Marine Bio-Acoustics* (pp. 473-393). Oxford, UK: Pergamon.
297 Ferrer-i-Cancho, R., & McCowan, B. (2009). A law of word meaning in dolphin whistle types. *Entropy*, *11*(4), 688-701.
298 McCowan, B., Doyle, L. R., Jenkins, J. and Hanser, S. F. (2005). The appropriate use of Zipf's law in animal communication studies. *Animal Behaviour*, 69. Pages F1 and F3 respectively.
299 McCowan, B., Hanser, S. F. & Doyle, L. R. (1999). Quantitative tools for comparing animal communication systems: information theory applied to bottlenose dolphin whistle repertoires. *Animal Behaviour, 57*, 409–419.
300 Suzuki, R., Buck, J. R., & Tyack, P. L. (2005). The use of Zipf's law in animal communication analysis. *Animal Behaviour*, 69(1)
301 Lang, T. G. & Smith, H. A. P. (1965). Communication between dolphins in separate tanks by way of an acoustic link. *Science, 150*, 1839-1843.
302 Lilly, J. C., & Miller, A. M. (1961). Vocal exchanges between dolphins. *Science, 134*, 1873-76.
303 Hawkins, E. & Gartside, D. (2010). Whistle emissions of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) differ with group composition and surface behaviours. *Journal of the Acoustical Society of America, 127* (4), 2652-2663.
304 Harley, H.E. (2008). Whistle discrimination and categorization by the Atlantic bottlenose dolphin (*Tursiops truncatus*): a review of the signature whistle framework and a perceptual test. *Behavioural Processes, 77*, 243-68.
305 Hernandez, E. N., Solangi, M., & Kuczaj, S. A. (2010). Time and frequency parameters of bottlenose dolphin whistles as predictors of surface behavior in the Mississippi Sound. *Journal of the Acoustical Society of America*, *127*(5), 3232-3238.
306 For example, Hawkins, E. & Gartside, D. (2009). Patterns of Whistles Emitted by Wild Indo-Pacific Bottlenose Dolphins (*Tursiops aduncus*) during a Provisioning Program. *Aquatic Mammals, 35* (2), 171-186.
307 Azevedo, A. F., Flach, L., Bisi, T. L., Andrade, L. G., Dorneles, P. R., & Lailson-Brito, J. (2010). Whistles emitted by Atlantic spotted dolphins (*Stenella frontalis*) in Southeastern Brazil. *Journal of the Acoustical Society of America, 127*(4), 2646-2651.
308 Janik, V. M. (2009). Acoustic Communication in Delphinids. In M. Naguib & V. M. Janik (Eds.), *Advances in the Study of Behavior Volume 40* (pp. 123-157). Elsevier.
309 Janik, V. M. (2013). Cognitive skills in bottlenose dolphin communication.

Trends in Cognitive Science, 17(4), 157-159

310 Janik, V. M., Sayigh, L. S., & Wells, R. S. (2006). Signature whistle shape conveys identity information to bottlenose dolphins. *Proceedings of the National Academy of Sciences of the United States of America, 103*(21), 8293-8297.

311 King, S.L., and Janik, V. (2013). Bottlenose dolphins can use learned vocal labels to address each other. *Proceedings of the National Academy of Sciences of the United States of America*, 110(32); 13216-13221.

312 Jaakola, K. (2012). Cetacean Cognitive Specializations In J. Vonk & T. Shackelford (Eds.), *Oxford Handbook of Comparative Evolutionary Psychology* (pp. 144-165). New York: Oxford University Press.

313 Smolker, R., & Pepper, J. W. (1999). Whistle convergence among allied male bottlenose dolphins (Delphinidae, *Tursiops* sp.). *Ethology*, *105*(7), 595-617.

314 Reiss, D., & McCowan, B. (1993). Spontaneous vocal mimicry and production by bottlenose dolphins (*Tursiops truncatus*): evidence for vocal learning. *Journal of Comparative Psychology*, *107*(3), 301-312.

315 Reiss, D., McCowan, B., & Marino, L. (1997). Communicative and other cognitive characteristics of bottlenose dolphins. *Trends in Cognitive Sciences*, *1*(4), 140-145

316 Richards, D. G., Wolz, J. P. & Herman, L. M. (1984). Vocal mimicry of computer generated sounds and vocal labeling of objects by a bottlenosed dolphin, *Tursiops truncatus*. *Journal of Comparative Psychology, 98*, 10-28.

317 Miksis, J. L., Tyack, P. L., & Buck, J. R. (2002). Captive dolphins, *Tursiops truncatus*, develop signature whistles that match acoustic features of human-made model sounds. *Journal of the Acoustical Society of America*, *112*(2), 728-739.

318 Tyack, P. L. (1997). Development and social functions of signature whistles in bottlenose dolphins *Tursiops truncatus*. *Bioacoustics, 8*(1-2), 21-46.

319 Sayigh, L. S., Tyack, P. L., Wells, R. S., & Scott, M. D. (1990). Signature whistles of free-ranging bottlenose dolphins, *Tursiops truncatus*: Stability and mother-offspring comparisons. *Behavioral Ecology and Sociobiology, 26*, 247–260.

320 Ford, J. K. B. (1991). Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Canadian Journal Of Zoology*, *69*(6), 1454-1483.

321 Ford, J. K. B. (1991). Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Canadian Journal Of Zoology*, *69*(6), 1454-1483.

322 Filatova, O. A., Burdin, A. M., & Hoyt, E. (2011). Horizontal transmission of vocal traditions in killer whale (*Orcinus orca*) dialects. *Biology Bulletin*, *37*(9), 965-971

323 Reiss, D., & McCowan, B. (1993). Spontaneous vocal mimicry and production by bottlenose dolphins (*Tursiops truncatus*): Evidence for vocal learning. *Journal of Comparative Psychology, 107*(3), 301-312.

324 Lilly, J. C. (1967). The mind of the dolphin: a nonhuman intelligence. Doubleday.

325 Reiss, D. (2011). The Dolphin in the Mirror: Exploring Dolphin Minds and Saving Dolphin Lives. Boston, MA: Houghton Mifflin Harcourt.

326 Sigurdson, J. (1993). Frequency-modulated whistles as a medium for communication with the bottlenose dolphin. In H. L. Roitblat, L. M. Herman, & P. E. Nachtigall (Eds.), *Language and Communication Comparative Perspectives* (pp. 153-173). Hillsdale, NJ: Lawrence Erlbaum Associates.
327 Richards, D. G., Woltz, J. P., & Herman, L. M. (1984). Vocal mimicry of computer-generated sounds and labeling of objects by a bottlenose dolphin (*Tursiops truncatus*). *Journal of Comparative Psychology* , *98*, 10-28.
328 Hooper J. (1983, January). John Lilly: Altered States. *Omni Magazine*.
329 Reiss, D. (2011). The Dolphin in the Mirror: Exploring Dolphin Minds and Saving Dolphin Lives. Boston, MA: Houghton Mifflin Harcourt.
330 Obituary for Kenneth Lee Marten, Ph.D. (2010). *Aquatic Mammals*, *36*(3), 323-325.
331 Xitco, M. J., Jr., Gory, J.D., & Kuczaj, S.A., II (1991). An introduction to The Living Seas' dolphin keyboard communication system. Presented at the 19th Annual Conference of the International Marine Animal Trainers Association, October, Concord, CA.
332 Herzing, D.L. (2010). SETI meets a social intelligence: Dolphins as a model for real-time interaction and communication with a sentient species. *Acta Astronautica,* 67, 1451-1454
333 Herzing, D. (2011). Dolphins Diaries: My 20 Years with Spotted Dolphins in the Bahamas. New York: St. Martin's Press.
334 Campbell, M. (2011) Talk with a dolphin via underwater translation machine. New Scientist, 2811.

Appendix B: List of persons or organizations replying to the request for information.

As part of the solicitation for relevant information, the Committee sought input via a notice on the MARMAM listserve in the following notice.

From: David Rosen <ontario.cetaceans@gmail.com>

Date: Tuesday, 17 December 2013 21:47

To: MARMAM <MARMAM@lists.uvic.ca>

Subject: [MARMAM] Input requested: Humane treatment of captive cetaceans

The Government of Ontario (Canada) has convened a Committee to provide research-based options and recommendations regarding how best to ensure the most humane treatment of captive cetaceans.

The Committee is seeking advice from the scientific community to highlight areas of scientific information on potential benefits or detrimental effects of keeping cetaceans in captivity in non-research institutions. This includes (but is not limited to) published, peer-reviewed studies of animal health, both physical and behavioural, as well as published studies on the potential educational benefits of display animals.

To that end, individuals or organizations may provide a 2-page [161] submission to the Committee. Please note that this is not an invitation to provide opinions, but to ensure the Committee has taken into consideration and has access to all of the relevant science-based evidence. Those individuals making submissions may be subsequently contacted for further information or input. Also, please be aware that all submissions may potentially be included in the Committee's final report to the Government of Ontario.

Submissions (and related inquiries) may be made by email to: ontario.cetaceans@gmail.com by no later than January 31, 2014.

Regards,

David Rosen, PhD.

The following individuals and organizations responded directly to this request by providing initial submissions.

- Kathleen Dezio, Executive Director, Alliance of Marine Mammal Parks
- & Aquariums
- Larry and Helen Fast
- Jared S. Goodman, Director of Animal Law, PETA
- Paul Nachtigall, DVM, University of Hawai'i

- Naomi A. Rose, Ph.D., Animal Welfare Institute
- Cathy Williamson, Captivity Programme Manager, Whale and Dolphin
- Conservation (formerly Whale and Dolphin Conservation Society)
- Julie Woodyer, Campaigns Director, Zoocheck Canada Inc.

The Committee would like to thank these individuals and organizations for their contributions.