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ABSTRACT

Marine mammals include cetaceans, pinnipeds, sirenians, sea otters and polar bears, many of which are charismatic and popular species commonly kept under human care in zoos and aquaria. However, in comparison with their fully terrestrial counterparts their welfare has been less intensively studied, and their partial or full reliance on the aquatic environment leads to unique welfare challenges. In this paper we attempt to collate and review the research undertaken thus far on marine mammal welfare, and identify the most important gaps in knowledge. We use 'best practice case studies' to highlight examples of research promoting optimal welfare, include suggestions for future directions of research efforts, and make recommendations to strive for optimal welfare, where it is currently lacking, above and beyond minimum legislation and guidelines. Our review of the current literature shows that recently there have been positive forward strides in marine mammal welfare assessment, but fundamental research is still required to validate positive and negative indicators of welfare in marine mammals. Across all marine mammals, more research is required on the dimensions and complexity of pools and land areas necessary for optimal welfare, and the impact of staff absence for most of the 24-h day, as standard working hours are usually between 0900 and 1700.

1. Introduction

Marine mammals are a diverse group of around 120 species including cetaceans (whales, dolphins, porpoises), pinnipeds (seals, sea lions, walruses), sirenians (manatees, dugongs), the sea otter (*Enhydra lutra*) and the polar bear (*Ursus maritimus*). Some species have a worldwide distribution, from the Arctic to the Antarctic, while others are more localized (Stewart et al., 2002). Marine mammals rely on aquatic and terrestrial environments to varying degrees over different life stages, making them an interesting and complex group to manage under human care.

Marine mammals have lived in zoos and aquaria (hereafter referred to as zoos), as well as other captive settings such as rehabilitation facilities, sanctuaries and research centres, for more than a century. Often, facilities have dual purpose such as a zoo and rehabilitation centre, but in most cases in this paper we refer to a traditional zoo setting. Captive environments vary greatly: marine mammals are housed in open and semi-open sea-pen structures, or more traditional concrete structure exhibits (Couquiaud, 2005a). Their water may be sea or treated fresh water, and the environment may be furnished with natural or simulated rocks and other landmasses. The first verifiable record of a marine mammal under human care appears to be a polar bear in 1060 (Reeves and Mead, 1999). Earlier accounts of Mediterranean sea creatures (likely dolphins and seals) in the year 879 BCE are mentioned in a paper by Foster (1999, p. 53). Beluga whales (*Delphinapterus leucas*) were the first cetaceans reported under human care, transported from the St. Lawrence River and housed at the Barnum's Museum in New York City in the early 1860's (Sorenson, 2008). Marine Studios in Florida, opened circa 1938, was the first 'Oceanarium' facility specialized in housing cetaceans and pinnipeds (Reeves and Mead, 1999).

There are around 2000 marine mammals housed in major zoos according to the Species 360 database (previously known as the International Species Information System; Species 360, 2016). Of the individuals on this public record, 71% are pinnipeds and 14% are cetaceans. The bottlenose dolphin (*Tursiops truncatus*) is the most numerous cetacean, representing 87% of cetaceans and 12% of all marine mammals. The most numerous marine mammal species, however, is the California sealion (*Zalophus californianus*) which represents 27% of all marine mammals. To put these figures into a broader context, Species 360 reports that there are approximately 36,000 primates housed in major zoos worldwide (Species 360, 2016). The vast majority of marine mammals under human care are permanent residents; however there is a relevant population of marine mammals who live temporarily in captivity while they are rehabilitated from boat injuries, beaching, natural disasters and so on. These individuals may be found in dedicated rehabilitation facilities, or zoos. The numbers of rehabilitants fluctuate, depending on events, but the Marine Mammal Center in California reports that since 1975, they have rescued and treated more than 20,000 marine mammals (Gulland, 2009). SeaWorld parks report that they have rescued and rehabilitated over 7500 marine mammals to date including cetaceans, pinnipeds and sirenians (SeaWorld Parks and Entertainment Inc., 2017).

Concern for the welfare of marine mammals has increased over the past several decades, in line with other animals in captive settings. Although the welfare implications of wild capture and transport are important, we shall not consider them in this paper, but rather the welfare of marine mammals already under human care, including marine mammals temporarily in captivity for rehabilitation purposes. This paper will not include ethical debate of whether certain species should be in captivity now, or in the future. We discuss the research undertaken thus far on marine mammals under human care, focussing on peer-reviewed sources but also acknowledging the importance of non-peer-reviewed sources where appropriate. We make recommendations to strive for optimal welfare, above and beyond minimum legislation and guidelines. We highlight where animal welfare-related evidence is present or currently lacking, and emphasise future directions for research. Where relevant, we provide 'best practice case studies' highlighting examples of research on optimal welfare. We focus on the most common species such as the bottlenose dolphin, California sea lion, common seal (*Phoca vitulina*), grey seal (*Halichoerus grypus*), and polar bear. Research and practical examples of other species such as walrus (*Odobenus rosmarus*), manatee (*Trichechus spp*.), beluga whale (*Delphinapterus leucas*), orca (*Orcinus orca*), and sea otter will also be described where available.

2. Animal welfare science

2.1. Animal welfare assessment

This paper will focus on the welfare of marine mammals, but in order to provide some context we first consider the wider sphere of animal welfare science. Modern animal welfare science focuses on a holistic approach to welfare, considering physical and psychological perspectives. Broom's (1986) animal welfare definition referred to health and feelings as a part of welfare: " the welfare of an individual is its state as regards its attempts to cope with its environment". Researchers consistently view welfare as a dynamic state of an animal, which varies over time on a spectrum from very good to very poor (Broom, 1988, 1991a, 1991b, 2014). In recent years, there has been an improvement in our ability to evaluate animal feelings and emotions or 'affective state', particularly positive states (e.g. Duncan, 1996; Mellor, 2015; Yeates and Main, 2008). Furthermore, there has been increased interest in assessing 'quality of life', which is essentially the same as welfare but does not refer to short periods (Wemelsfelder, 2007; Broom, 2007). For context, Appleby et al. (2011) and Hemsworth et al. (2015) provide comprehensive reviews of modern animal welfare science.

The 'Five Freedoms' concept is a method of animal welfare assessment where an animal's 'freedom' from issues such as hunger and pain are measured (Brambell Report, 1965). This was helpful after its inception as a general guide; however for species where there is now precise information about animal needs, it is better to consider needs rather than freedoms (Špinka, 2006; Broom, 2014). The first step in assessing welfare, for example in relation to living and management conditions, is to find out about the needs of animals of the particular species and compile a comprehensive list. A need is a requirement, which is part of the basic biology of an animal, to obtain a particular resource or to respond to a particular environmental or bodily stimulus (see Broom and Fraser, 2015). In animals that are little studied, an understanding of the general biology helps to determine needs, and evidence from scientific studies on related species can also be helpful. For more widely studied species, in addition to information about basic biology, research on the strength of their positive and negative preferences and studies on the consequences of presence or absence of a resource should be used to identify needs.

A holistic approach to animal welfare now exists, with an interdisciplinary approach including animal physiology, behaviour, affective states, husbandry, transport, housing, social life, enrichment efficacy, animal training, and human-animal relationships (Broom, 2014; Mellor, 2016; Mellor and Beausoleil, 2015; Panksepp, 2005). Animal welfare scientists now advocate animal-based measures and place less emphasis on animal resources; for example Fraser et al. (1997) emphasise the importance of accommodating an animal's 'natural adaptations and capabilities', and striving for good health, minimising negative affective states such as fear and pain, and promoting experience of pleasures.

2.2. Animal welfare science in the zoo

Before broaching the topic of marine mammal welfare under human care, it is necessary to understand the culture of animal welfare science in zoos. For any captive system, one must consider who are the stakeholders driving the study of animal welfare and what is their motivation. Aside from the ethical incentive to ensure good welfare for the animals themselves, from the perspective of zoo staff and visitors, zoos have several other incentives necessary for them to achieve their goals as tourist businesses, charities and centres for conservation and research. Animals with good welfare are better at educating and entertaining guests, are more valid research models for their wild counterparts, and are more likely to be successful if reintroduced into the wild (Mellor et al., 2015).

The Association of Zoos and Aquariums (AZA) Animal Welfare Committee defines animal welfare as "… an animal's collective physical, mental, and emotional states over a period of time, and is measured on a continuum from good to poor" (AZA, 2016). This adds to the words of Broom's definition (Broom 1986) by referring to the continuum but is too broad because "collective physical, mental, and emotional states" includes every part of the biology of the animal. Welfare has to be limited to the animal's "state as regards its attempts to cope with its environment" (Broom, 1986). This includes positive and negative aspects of coping systems including feelings and other high-level brain functions, as well as other mechanisms for dealing with homeostatic displacements. We suggest that the AZA definition is a useful starting point for the welfare of zoo-housed animals, but in order to effectively assess and enhance the welfare of any animal, including marine mammals, more precision is needed.

Zoo animal welfare assessment has benefitted from farm animal welfare frameworks and approaches (see Hill and Broom, 2009 for a review), and behavioural measures of welfare are widely used in zoos (Watters et al., 2009). Behavioural measures typically include stereotypic and other 'abnormal' behaviours, a 'normal' range of activity, for example as compared with wild conspecifics, and behavioural flexibility, e.g. how animals adapt to changes in their environment. Watters et al. (2009) suggest that behavioural monitoring should be a core component of a zoological institution's care programme and point out that this type of monitoring complements information gathered through physiological measures, to provide information on many important indicators of animal welfare, such as atypical behaviour and responses

Table 1
Summary of Marine Mammal Welfare Legislation and Guidance Documents for Europe, North America and the Caribbean.

Governmental Agency/Organisation	Relevant Documents
European Union	European Union Zoos Directive (1999)
United States Congress	Marine Mammal Protection Act (1972)
	Animal Welfare Act (AWA) (1966)
United Nations Environment Program	Action Plan for The Conservation Of Marine Mammals (MMAP) in The Wider Caribbean Region (2008)
World Association of Zoos and Aquariums (WAZA)	WAZA Welfare Strategy: Mellor et al. (2015)
European Association of Zoos and Aquaria (EAZA)	EAZA Standards for the Accommodation and Care of Animals in Zoos and Aquaria (2014)
	EAZA Guidelines on the Use of Animals in Public Demonstrations (2014)
American Society of Mammalogists	Guidelines for the Use of Wild Mammals in Research (Sikes and Gannon, 2011).

to environmental enrichment. Whitham and Wielebnowski (2009) and Kagan and Veasey (2010) have discussed the importance of an integrated approach to zoo animal welfare, including both resource-based (input) and animal-based (outcome) assessment tools.

Zoo biologists are increasingly using physiological welfare indicators originally validated for laboratory and farm animals (e.g. Baird et al., 2016; Clark et al., 2012; Miller et al., 2016). Adrenal hormone measures are valuable to indicate the extent of short-term behaviour problems, such as those associated with handling and transport (Broom and Johnson, 1993; Möstl and Palme, 2002) and are thus a useful measure of the welfare effects of environmental or social disturbances. Glucocorticoid metabolites, resulting from activation of the hypothalamic–pituitary–adrenal axis, are a measure of the physiological stress response that can be obtained non-invasively from faeces (Möstl and Palme, 2002; Schwarzenberger, 2007). Compared with behavioural monitoring there are protracted costs involved in collecting, processing and analysing physiological samples, as well as difficulties with interpretation of the biological relevance of amplitude changes in hormone levels (reviewed by Hill and Broom, 2009; Clark et al., 2012).

In contrast with behavioural and physiological indicators of welfare, other measures such as body condition scoring, nest condition and signs of illness (e.g. diarrhoea) are seldom used in zoos (Hill and Broom, 2009). Whitham and Wielebnowski (2009) describe the utility of more animal-based measures in zoos, including the animal's physical condition, and behavioural changes over time rather than the traditional 'snapshot in time'. Whitham and Wielebnowski (2009) make the point that these animal-based measures could be used in conjunction with the more typical resource-based or input measures and environmental variables; use of qualitative assessment by experienced caretakers is a rapid method of integrating and filtering information to provide an overall picture of an animal's welfare. Whitham and Wielebnowski (2009) also discuss various approaches for the validation of qualitative assessments, such as correlating trait-ratings with behavioural and physiological measures (Gosling, 2001), and correlating personality and temperament ratings with animal's responses to behavioural tests (Bousquet et al., 2015; Nawroth et al., 2017; Wielebnowski, 1999).

When assessing positive or negative effects on welfare, it is important to combine multiple measures (triangulation: see Clark et al., 2012) and also to evaluate the effects of multiple impacts on welfare. Some measures are of the same response whilst others are of different responses. For example, an increase in cortisol and an increase in heart-rate can sometimes occur at the same time and both can indicate a certain level of emergency response. However, periods with active responses indicating poor welfare, such as stereotypies and periods of reduced activity and unresponsiveness, usually without adrenal correlates, should be added together if the duration of indicators of poor welfare is to be measured. In all cases, a function of intensity of response and duration of response, i.e. the magnitude of good or poor welfare, should be calculated (Broom, 2014).

Animals under human care are often subject to multiple impacts on their welfare. Human proximity, high noise level, poor water quality, insufficient space for normal movement and inability to escape may all act at the same time. These multiple negative impacts may be multiplicative rather than additive in their consequences for the animals. There might also be positive impacts counter-balancing some of their effects. Hence the evaluation of welfare should take account of all measurable factors and how they might interact. A relevant example of a study in which there would have been multiple impacts is that of Kyngdon et al. (2003), where zoo-housed common dolphins (*Delphinus delphis*) were participating in a swim-with-dolphins programme. Dolphins increased the use of a refuge area (which could not be accessed by human swimmers) when swimmers were in the water. Unfortunately the study did not attempt to tease apart what aspects of the swim programme affected dolphin refuge use; dolphins might have been affected by a disruption of normal routine, sounds and behaviour of spectators, the sight, sound and odour of unfamiliar swimmers in the water, or swimmer behaviour. If one or more specific factors could be identified, these could be managed in order to improve welfare.

3. Marine mammal welfare: an overview

3.1. Legislation and guidance

The main legislation and guidance pertaining to the welfare of marine mammals under human care in Europe, North America and the Caribbean is listed in Table 1. Although beyond the scope of this paper, we are aware of the rapid expansion of marine mammal facilities in the Middle East and Asia. It is important to note that each country and each U.S. state usually has its own specific legislation governing the welfare of zoo animals, including marine mammals. Furthermore, marine mammal facilities will have their own institutional standards and policies in place, and may be guided by zoo association regulations such as the European Association of Zoos and Aquariums (EAZA), AZA and the World Association of Zoos and Aquariums (WAZA). Facilities may be accredited if they meet the standards the association has established, and these standards are typically higher than the minimum requirements established under government law.

Within the European Union, countries are allowed to differ in how the EU Zoos Directive is interpreted and transcribed into national law. The Italian Zoo Directive, for example, requires bottlenose dolphins to have one day free per week from show performances (Ministero dell'Ambiente, 2001), but this is not the case for all EU countries, nor is it clear on what basis this decision was made. Within the United States, The Animal Welfare Act (1979) establishes standards a facility must adhere to, in order to house marine mammals, as with other animals. The high density of facilities across the Caribbean is due to high demand from tourists to take part in human-animal interaction programmes (Section 6.6). Efforts from 16 countries to regulate these programmes can be found in the United Nations Action Plan for The Conservation of Marine Mammals in The Wider Caribbean Region (2008).

A detailed analysis of all these documents is beyond the scope of this paper. Some aspects are referred to in later sections of this paper, but readers interested in the finer details of animal welfare law are encouraged to refer to Kohn (1994), and Cao and White (2016).

3.2. Research trends

A review of peer-reviewed and non-peer-reviewed literature published between 1948 and 2015 on marine mammals housed under human care (Brando and Hosey, in prep.) found a moderate but growing body of research, with a taxonomic bias towards cetaceans and pinnipeds. Professionals involved with the care of marine mammals have sometimes preferred to publish in non-peer reviewed literature, for example, the International Marine Animal Trainer's Association (IMATA) quarterly newsletter 'Soundings'. In a review of publications on cetaceans between 1950 and 2009, Hill and Lackups (2010) found limited publications on cetaceans under human care, compared with those in the wild. In a review of publications between 1964 and 2014 on bottlenose dolphins and orcas, Hill et al. (2016a, 2016b) found that 68% of dolphin and 10% of orca publications were on animals living under human care.

According to the analyses of and Hill and Lackups (2010), published topics of marine mammal care include physical health, physiology, behaviour, breeding and neonatal care, nutrition, training, housing and husbandry practices, and environmental enrichment. The number of peer-reviewed papers on these topics has been rising steadily in each decade since the 1960s; however, environmental enrichment and animal welfare assessment were the least studied topics across all taxa (). This contrasts with the rapid increase in the number of scientific publications on the welfare of other animals under human care (see articles in this special issue). More detail on where research has been focussed and overlooked across these topics will be discussed in due course.

3.3. Overview of research variables

Table 2 gives an overview of the marine mammal husbandry and individual variables, concerning natural and individual life history, that have been studied in relation to their impact on welfare.

Table 2
Input Variables Previously Used in Studies of Marine Mammal Welfare.

Category	Variable	References
Animal Husbandry	Exhibit Size	Bassos-Hull and Wells (1997); Shyan et al. (2002); Shepherdson et al. (2013)
	Habitat access	Ross (2006)
	Public Viewing Area	Shepherdson et al. (2013)
	Exhibit View	Shepherdson et al. (2013)
	Life Support	Garibaldi (1998)
	Feeding Times	Shepherdson et al. (2013)
	Environmental Enrichment	Shepherdson et al. (2013); Hunter et al. (2002); Delfour and Beyer (2012)
	Animal Training	Shepherdson et al. (2013); Miller et al. (2011); Brando (2010)
	Social Grouping	Shepherdson et al. (2013); Waples and Gales (2002)
	Staff Experience	Brando (2010)
	Human-Animal Relationship	Ward and Melfi (2013)
Natural History	Home range	Clubb and Mason (2003, 2007)
	Habitat Type	Clubb and Mason (2003, 2007); Ugaz Ruiz et al. (2009); Ugaz et al. (2013); Luna Blassio et al. (2012)
	Activity Budgets	Wells (2009)
	Social System	Wells (2009)
	Mating System	Wells (2009)
	Diet	Geraci (1972); Slifka et al. (2013)
Individual History	Behavioural Type (Personality)	Shepherdson et al. (2013)
	Medical History	Venn-Watson et al. (2007)
	Rearing History	Shepherdson et al. (2013)

3.4. Behavioural indicators of welfare

Given that behaviour is the predominant welfare indicator used in zoos, as described above in Section 2.2, we shall now examine to what extent behavioural indicators have been formally identified and studied in marine mammals. Certain behaviours will be re-visited in the later section on enrichment (Section 5). Compared with primates, there is very little hypothesis-driven research on behavioural indicators of welfare in marine mammals under human care, including the effects of current and previous rearing conditions and exhibit complexity on these behaviours. Whilst the aetiology of harmful behaviours in marine mammals lacks causal analysis, if obviously harmful behaviours are at all frequent in the activity budget, welfare will be poor. According to the published literature, the most common behaviours considered to be aberrant, abnormal, undesirable or otherwise problematic in cetaceans under human care are repetitive (possibly stereotypical) swimming, and high levels of aggressive or sexual behaviour directed towards conspecifics and humans. However, these reports must be considered with caution as they are based on very limited sample sizes and numbers of species.

The most commonly reported behavioural 'problem' in cetaceans is swimming in a fixed circular pattern around the pool (Gygax 1993; Miller et al., 2011; Sobel et al., 1994). Stereotypic behaviour is "repetitive behaviour induced by frustration, repeated attempts to cope, sometimes with CNS dysfunction" (Mason, 2006, p.347). In some cases the problem for the animal is that the current environment does not meet their needs. In other animals, welfare is still poor but stereotypies represent 'behavioural scars'; these are behavioural abnormalities continuing after the cause has gone, due to stimulus deficiencies during early rearing rather than inadequacy of the current environment (Mason, 2006; Mason and Latham, 2004). While repetitive swimming could be widespread across zoos, few data are published and Miller et al. (2011) found that dolphins in a multi-zoo study (N = 6 zoos and 18 dolphins) performed the behaviour in less than 5% of scans. Gygax (1993) was unable to conclude whether repetitive circular swimming in two dolphins was stereotypical, and suggested the behaviour requires more study whilst Clegg et al. (2017) concluded that adequate studies have not been carried out. Some repetitive circular swimming might not be a stereotypy because it is punctuated by the performance of other behaviours. However, stereotypies may be interrupted and resumed so the other behaviours would have to be a majority of the activity to allow the conclusion that the behaviour is not a stereotypy. It is sometimes argued that repetitive movements around an animal's enclosure border has a "patrolling" function, but the behaviour often continues for too long for it to be considered functional (Clubb and Mason, 2007). As described by Mason (2006) it is important to distinguish between behaviours; abnormal repetitive behaviours (ARBs) linked to a deficit in the captive environment (stereotypies) and other abnormal repetitive behaviours for which we do not really know (other ARBs).

The welfare implications of sexual behaviours, including the frequency or duration of behaviours above which they transition from being 'normal' to 'abnormal', crucially lack study in marine mammals. The overlap between socio-sexual behaviours and aggression in cetaceans makes them challenging to differentiate and thus examine in isolation (Hill et al., 2015). The performance of aggressive (e.g. charging, biting) and sexual behaviours (e.g. using the genitals for physical contact; attempted mounting) towards conspecifics by cetaceans has been suggested to stem from a lack of environmental complexity (Sweeney, 1990) although no evidence was provided in this study. Furthermore, it is still not clear whether or not behaviours that relate to reproduction have stressful consequences (Burgess et al., 2013). Couquiaud (2005a, 2005b) reported aggression directed to trainers by orcas, pygmy killer whales (*Feresa attenuata*), Amazon River dolphins (*Inia geoffrensis*), and melon-headed whales (*Peponocephala electra*). By interviewing caregivers, Kuczaj et al. (2012), reported 13 cases of dolphins housed in two facilities directing their aggression to other dolphins but only one case of a dolphin directing aggression to humans. There are some anecdotal reports of cetaceans being aggressive towards their trainers and visitors during 'swim with dolphin' programmes (Frohoff, 1993; Kyngdon et al., 2003; Samuels and Spradlin, 1995), which contrasts with the welfare benefits reported for the animal-trainer relationship (Section 6). Thus, the effect of human presence in the water on cetacean behaviour varies according to the situation, human actions and previous experience of the animals, both in captivity and in interactions in the wild. In a multi-zoo study (N = 4 zoos), Samuels and Spradlin (1995) reported that aggressive and sexual behaviours towards swimming visitors increased when trainers did not choreograph interactions. Laule (1984) reported that a young male dolphin who bit trainers performed this behaviour less when trainers increased the diversity and intensity of positive reinforcement training.

Frohoff (1993) suggested that 'abrupt' body movements and sudden changes in direction are indicative of stress in dolphins; these behaviours are seen at higher rates during dolphin swim programmes (Frohoff, 1993; Frohoff, 1993, 2004; Kyngdon et al., 2003) but currently the link between these behaviours and poor welfare is not clearly established. Despite the aggressive actions of dolphins reported above, self-injurious behaviour is apparently uncommon according to published literature. In some cases where aspects of the captive environment have thought to have provoked aggressive behaviour, caregivers have prevented further aggression by transferring individuals to larger enclosures (Acasuso-Signoret, 1981). In an anecdotal report, Greenwood (1977) described three cases of dolphins repeatedly pressing their melons, the fatty 'forehead' area which produces echolocative pulses, against pool walls. Greenwood (1977) attributed this behaviour to 'small' pool sizes (40–60,000 L), as the behaviour rapidly extinguished when subjects were moved to larger pools. Surface-directed behaviour may also be an indicator of poor wefare (Galhardo et al., 1996, see Section 5).

As in cetaceans, stereotypies involving repetitive swimming patterns are the most commonly cited potential behavioural issue in pinnipeds but there is little quantitative evidence of this (Hunter et al., 2002; Smith and Litchfield, 2010). In pinnipeds, flipper chewing, excessive self-grooming and body scratching against hard surfaces have been reported (Kastelein and Wiepkema, 1989; Smith and Litchfield, 2010). These self-directed or injurious behaviours are widely accepted as signs of poor welfare in other mammals (Moberg and Mench, 2000).

Stereotypical behaviour is prevalent in zoo-housed polar bears (Mason et al., 2007; Shepherdson et al., 2013) and in fact, pacing is so synonymous with polar bears that the Dutch use the verb '*ijsberen*', literally translated to 'to polar bear' when describing pacing, restless people (Clubb and Vickery, 2006). Mason et al. (2007) found that 55% of 124 zoo polar bears performed abnormal repetitive behaviour, including pacing and other repetitive locomotory movements, rocking and head-rolling. The mean amount of time carrying out stereotypies in a range of studies of polar bears in zoos was around 40% of waking time (e.g. Wechsler 1991; Clubb and Mason, 2003; Mason and Rushen, 2008; Ross, 2006). A more recent survey indicated that over 80% of polar bears in North American zoos pace (55 bears from 20 zoos, Shepherdson et al., 2013). Bears who responded more positively to novelty tended to display less stereotypic behaviour, and higher faecal glucocorticoid levels were associated with higher proportions of stereotypic pacing. An extensive analysis by Clubb and Mason (2003) shows that mammalian species with wider home ranges tend to perform more stereotypies in captivity, with polar bears and lions (*Panthera leo*) at the top of this list. Shepherdson et al. (2013) stated that variables associated with reduced pacing were: enrichment, social group size, and whether the bears had a view out of their enclosure.

With regard to positive indicators of welfare, the most common for cetaceans is play. Spontaneous occurrences of play and attempts to stimulate play using enrichment (Section 5) have been reported for captive dolphin species (see reviews by Kuczaj and Eskelinen, 2014; Paulos et al., 2010) and beluga whales (Delfour and Aulagnier, 1997). Consistent with other vertebrate mammals (see Held and Špinka, 2011), the use of play as a welfare indicator in cetaceans appears to be based more on tradition than due to any validation against other welfare indicators (Clegg et al., 2017; Serres and Delfour, 2017). Play will be considered further in Section 4.4 (social management). Other positive behavioural indicators, such as engagement with the environment, recreational sex, and behaviours such as 'optimism' and 'confidence' lack study (see Yeates and Main, 2008 for an overview of positive behavioural indicators in terrestrial mammals).

3.5. Multivariate studies of welfare

To our knowledge, there are only two studies where multiple variables have been analysed to assess marine mammal welfare: on bottlenose dolphins (Clegg et al., 2015) and polar bears (Shepherdson et al., 2013). In the first study of its kind, Clegg et al. (2015) developed a welfare assessment index for captive bottlenose dolphins dubbed 'C-Well', adapted from 12 farm animal welfare assessment criteria, using published literature on wild and captive dolphins as well as professional insights (see case study, Section 3.6). Factors influencing stereotypies in zoo polar bears (also see Section 3.4) have been examined in a number of relatively small studies, mainly in North American zoos (e.g. Canino and Powell, 2010 N = 1 bear; Kelly et al., 2015 N = 3 bears; Ross, 2006 N = 2 bears). Ames (2000) found that animals living in recently renovated enclosures containing more natural substrates had lower levels of stereotypies than traditional, concrete bear 'pits', and Ross (2006) found that simultaneous access to indoor and outdoor areas, allowing bears to choose where to reside, had a significant impact. But to our knowledge, only one multi-zoo study has investigated the relationship between polar bear stereotypies and *multiple* factors across zoos. Shepherdson et al. (2013) discovered that in a sample of 55 bears housed in 20 North American zoos, the strongest factors linked to a decrease in the performance of stereotypies were diversity of enrichment, a view out of the enclosure (i.e. of the wider environment), and increased social group size.

3.6. Best practice case study

Clegg et al. (2015) was a collaborative effort of three marine mammal facilities, multiple universities, and the collective expertise of professionals working with marine mammals (for example veterinarians, curators and trainers). The 'C-Well Index' contains 36 welfare measures including animal-based measures (e.g. body condition scores, swim speed, stereotypies and response to trainer) and resource-based measures (e.g. diet, shade, water quality). Compared with any previous examination of cetacean welfare, this framework allows analysis of behavioural and physiological measures together, and is an important first step in the development of comprehensive and practical bottlenose dolphin welfare assessment. A deficiency is that the tool overlooks the importance of species-specific foraging behaviours for optimal welfare. Three natural seawater facilities were used to develop the tool but this type of housing which may result in better than average welfare and is not representative of most zoo cetacean habitats so some indicators of poor welfare might have been missed. This type of habitat may prove more popular in future.

3.7. Future directions

We propose five complementary areas for future research, forming the backbone of an optimal welfare approach for marine mammals. (1) A detailed analysis of the current literature on marine mammal welfare legislation and guidance is needed at local and global levels; to assess where gaps in legislation exist, or where guidance could be transformed into legislation, thus ensuring the highest possible minimum standards. (2) It would be useful to survey institutions housing marine mammals, to quantify where and how minimum standards are already surpassed to optimise welfare. (3) These reports of best practice, or indeed case studies where a management practice has failed or could be improved, should be more widely disseminated; not only in specialist publications but also in peer-reviewed publications thus increasing their impact and input from the wider scientific community. (4) More multi-variate studies of welfare, similar to Clegg et al. (2015) and Shepherdson et al. (2013) are required in order to assess welfare trends in large samples of marine mammals, thus understanding what are the main welfare problems facing each species and the main variables which should be focussed on in future. Finally, (5) there is a clear need for more validated positive and negative indicators of welfare in marine mammals.

4. Health and husbandry

A holistic housing and husbandry programme includes habitat design and construction, nutrition, healthcare (preventive and responsive), social management, welfare monitoring, environmental enrichment and animal training (Miller et al., 2015). Training and enrichment play prominent roles in the care of marine mammals (see Sections 5 and 6).

4.1. Habitat design and construction

For a minority of marine mammal species housed in zoos, husbandry guidelines have been developed. Professional husbandry manuals cover a wide variety of topics pertaining to the species such as biology, ecology, anatomy, diet, social life, cognition, and behaviour as well as environmental requirements, environmental enrichment, and animal training. The content should be a combination of science, to inform evidence-based decision-making, and practical information based on experience and best practice, for example illustrated with a case study, technical drawings, or links to videos and other instructive materials. At the time of writing this paper only one reference-based marine mammal husbandry guideline could be located, the AZA Polar Bear Care Manual (2009). The European Association for Aquatic Mammals (EAAM) has published bottlenose dolphin standards and guidelines but is mainly a list of provisions without references on which these are based. Caregivers sometimes do not read the husbandry manual if their proficiency in English is poor (Brando, 2016a).

Legislation for the design and construction of marine mammal habitats is provided by the US Animal Welfare Act (1979), which gives the minimum pool dimensions, depth and water volumes for all known marine mammals under human care, based on their adult body lengths and group size. It is not known what these figures have been based upon, and what scientific evidence there is to support them, but these are minimum standards and should always therefore be exceeded. Beyond minimum space and water requirements, however, legislation and guidance becomes limited. At the time of writing, pinniped, sirenian and sea otter habitat guidelines were not available. However, the EAAM provides guidelines for the housing requirements of bottlenose dolphins. It is stated that a pool area of at least 275 m^2 should have a minimum depth of 3.5 m (EAAM, 2009, p. 13). As a point of reference, the average length of an adult bottlenose dolphin is 2.5–3.8 m (EAAM, 2009; US Animal Welfare Act, 1979). In a review of 44 cetacean facilities from in 22 countries, Couquiaud (2005a, 2005b) reported that the average area of traditional pools was 90.5 m^2 (range 14–195 m^2). Open facilities (i.e. sea pens and lagoons) were much larger, on average 400 m^2 (range 92–1633 m^2). For animals living in tropical areas, especially in open sea-pens, tropical storm and hurricane exposure has been proposed as a concern (Kuczaj et al., 2012). The importance of pool dimensions is an intuitive area of welfare research on zoo cetaceans, yet surprisingly we found only one study where preference for different pool sizes was quantified. In a study at one facility, Shyan et al. (2002) found that when given the choice, a pod of seven bottlenose dolphins chose to reside in fairly shallow areas of their habitat. In the wild, bottlenose dolphins reside in shallow waters approximately 2 m deep when resources are abundant (e.g. Irvine and Wells, 1972; Wells et al., 1980). Shyan et al. (2002) concluded that larger pools in captive facilities may not be the preferred environments for dolphins; but since this is an isolated study a larger sample size is required to replicate findings, and may have been confounded by animals choosing to reside in shallower areas if they were near to kitchen or trainer areas.

A recent study assessed ten bottlenose dolphins after their relocation from a sea pen enclosure with a capacity of 26,250 m^3 to five different closed facilities with 332, 549, 597, 1241 and 4610 m^3 (Ugaz Ruiz et al., 2009). Dolphins were more active and showed less circular swimming patterns in the sea pen facility. Similar research has shown that in sea pens dolphins spend more time swimming and less time floating/resting (Luna Blassio et al., 2012; Ugaz et al., 2013). Some studies have found that, despite the higher activity levels, dolphins in sea pens have lower cortisol levels than those in closed environments (reviewed in Ugaz et al., 2013). Myers and Overstrom (1978) observed that dolphins preferred to remain in comparatively large show pools following a show, and Bassos-Hull and Wells (1997) reported that dolphins were more active, i.e. they swam more as opposed to motionless floating, in a larger pool. In polar bears, Shepherdson et al. (2013) found that a view from the indoor to the outdoor habitat was associated with a significant reduction in stereotypical pacing, but other physical habitat features did not reduce or prevent stereotypies.

Marine mammals spend most, if not all, of their lives in the water and therefore good water quality is essential to their long-term health (McBain, 1999). The chemical composition of water determines its thermodynamics and microorganism content (Arkush, 2001; Van der Toorn, 1987). When composition measures are out of the normal suggested ranges, consequences are wide-ranging but include irritation of the eyes, skin and gut, loss of beneficial microflora, and changes in osmotic balance (Joseph and Antrim, 2010; Van der Toorn, 1987; Wallis, 1973).

An average adult dolphin (mass ≈ 190 kg), under an average feeding regime discards around 1.45 kg of faeces and 4 L of urine per day (Ridgway, 1972). Constant filtration and regular total replacement of water is thus vital to prevent the accumulation of harmful waste products (Van der Toorn, 1987). In order to maintain good water quality, a turnover of at least 9.6 times per day is suggested (Wallis, 1973) but these are minimum standards from an early source and are likely to be far from the optimum. Natural habitats, such as open-sea pens, have 'built-in' processes for self-purification; naturally occurring microorganisms digest and re-incorporate faeces and food scraps into the food chain (Van der Toorn, 1987; Wallis, 1973). In contrast, maintaining water quality, temperature and flow is a complex procedure in artificial pools, and requires specialist staff and considerable operating costs.

4.2. Nutrition

Nutrition plays an important role in sustaining healthy and active animals under human care (Kleiman et al., 2010). However, the link between animal welfare and food and water intake is perhaps not as direct as between welfare and other husbandry variables. An animal may have a poor diet (i.e. low nutrient, high fat) but has good welfare because she enjoys this type of diet. Similarly, an animal may have a nutritious diet but poor welfare due to other factors such as boredom. The important links between nutrition and welfare are as follows: the diet should meet dynamic energetic requirements and not cause disease which subsequently leads to pain and suffering; food presentation should be safe and hygienic so as to avoid disease, pain and injury; and food should be presented in a manner that encourages the expression of natural and pleasurable behaviours.

Nutritional requirements are dynamic and vary for numerous reasons, for example reproductive status (bottlenose dolphin: Kastelein et al., 2002); growth status (bottlenose dolphin: Kastelein et al., 2003;

Commerson's dolphin: Kastelein et al., 1993), seasonal fluctuations in water temperature (orcas: Kastelein et al., 2000c; dusky dolphin: Kastelein et al., 2000b; Pacific white-sided dolphins: Piercey et al., 2013); and resting metabolic rate (Rechsteiner et al., 2013). An example of dynamic nutritional requirements is that of adult sea otters, who normally consume 20–30% of their body weight in fish or shellfish daily, but this can be doubled when animals in rehabilitation suffer from thermal distress and require more sustenance to help control their body temperature (Geraci and Lounsbury, 2005). Pinnipeds experience vast changes in fat content during different life cycle stages such as breeding and moulting (Kirsch et al., 2000). In captive California sea lions for example, lower food intake is common in the summer months, associated with an increase in aggressive behaviour related to mating (Kastelein et al., 2000a). In an overview of marine mammal energy requirements, Lockyer (2007) found that female marine mammals have higher requirements during pregnancy (accounting for foetal growth, heat and placental maintenance), and lactating mothers can consume up to 63% more food than before pregnancy.

Marine mammals under human care, excluding sirenians which are maintained on lettuce, cabbage and aquatic plants, predominantly eat freshly thawed previously frozen fish. Important practical considerations related to feeding fish thus include how fish are caught, handled, frozen, transported, stored, unfrozen, selected for best quality, and presented to the animals in order to avoid risk of disease and illness (White and Francis-Floyd, 1988). To this end, many facilities operate according to the US Department of Agriculture guideline manual for fish-eating animals (Crissey and Spencer, 1998). It is common practice to feed stringently assessed restaurant-quality fish, and the process of preparation takes a substantial amount of time and care (Joseph and Antrim, 2010). As an example of the attention to detail given to fish preparation the lenses of frozen fish are checked and should be cloudy, which indicates the fish have been properly stored at or below −30 °C before purchase (higher temperatures often result in clear lenses) (Merck Veterinary Manual, 2015).

Feeding a variety of fish to captive marine mammals is important to ensure animals do not become conditioned to one particular type of fish that may in the future become less available; there are however practical problems including the high costs of sourcing a variety of fish, and constantly changing nutritional values of fish stocks. Until relatively recently, commercially manufactured alternatives to whole frozen fish had not been evaluated. In a study of captive beluga whales, Mazzaro et al. (2011) evaluated the effect of Fish Analog (Mazuri® Foods, Gray Summit, MO), an alternative to frozen fish. Over an eight-month period, the authors found no apparent gastric discomfort, as evidenced by little change to faecal consistency and no significant change in behaviour. Processed foods may become more commonplace in future if fish stock declines are significant in certain parts of the world. For example, the Merck Veterinary Manual (2015) recommends that only sustainable fish approved by the Marine Stewardship Council are fed. It remains to be seen how this will affect the welfare of marine mammals and other piscivorous zoo animals.

The freezing and thawing process causes significant nutrient loss in fish; for example when fish decay thiamine (vitamin B1) is lost as thiaminase enzyme is activated (Rigdon and Drager, 1955), and vitamin E is lost due to oxidation (Dierenfeld et al., 1991). Oily fish such as mackerel are particularly susceptible to vitamin E destruction and oxidation. Other micronutrients may be leached from fish and seafood such as squid (Huss, 1995). Nutritional vitamin A deficiency has been reported for sea otters (St. Leger et al., 2011). In order to prevent nutrient deficiencies which could lead to dietary disease, supplements are commonly supplied. For instance, commercially available supplements for marine mammals include vitamins A, C and E, thiamine and lutein. Although supplemental vitamin C is frequently given to captive cetaceans, there is no conclusive evidence it is beneficial. In fact, many facilities have experienced cases of iron storage disease in both pinniped and cetacean species and vitamin C supplementation may exacerbate this problem by increasing absorption of iron (Mazzaro et al., 2011). Although subject to some debate, the Merck Veterinary Manual (2015) also recommends salt (NaCl) supplementation for pinnipeds maintained in freshwater in order to prevent hyponatraemia (low blood sodium levels). Although over-supplementation of water-soluble vitamins may be tolerated by marine mammals, over-supplementation of some fat-soluble vitamins is potentially harmful owing to their large blubber content (Mazzaro et al., 2011). More details on methods of providing diets to stimulate desired behaviours, including the provision of live prey, are provided in Section 5 (enrichment).

Dehydration is a commonly cited welfare problem for rehabilitant marine mammals (Dierauf and Gulland, 2001). Marine mammals use water from food and from food metabolism for hydration, but also from metabolism of their own body fat stores. If such stores are not available and or no food has been obtained, as happens often with rehabilitation animals, then dehydration is likely to occur. Dehydration leads to poor gastrointestinal function and requires rehydration treatment, easily trained through voluntary collaboration. Most commonly, caregivers use a soft flexible rubber tube to deliver water directly into the stomach, known as 'tubing' (Dierauf and Gulland, 2001). As a preventive measure, marine mammals are often fed cubes of gelatine mixed with water to provide extra hydration; this is a frequently used dietary supplement in our experience, but no study could be found directly referencing the practice, but only as a secondary mention for other purposes (Reiss, 2011). Rescued orphan manatees, for instance, can enter human care with severe constipation, which increases their risk for enterocolitis and other illnesses related to or exacerbated by low water intake. It is only after several months of rehydration that their food intake can be recovered by incorporating a variety of luscious green plants into the diet (Geraci and Lounsbury, 2005).

4.3. Health care

Marine mammal health care is an important cornerstone in providing for optimal animal welfare and, whilst it cannot be extensively reviewed (nor are the authors trained as marine mammal veterinarians), the omission of the topic would not be appropriate. Knowledge of marine mammal disease has come as much from research on live animals as it has from research on deceased animals, the book Marine Mammal Medicine by Dierauf and Gulland (2001, 2nd edition) providing an invaluable overview. In this section we have attempted to illustrate a few short examples of marine mammal diseases and their relation to marine mammal welfare. Ocular diseases and tuberculosis in sea lions have been highlighted as pressing topics requiring immediate attention. Examples were not chosen solely with priority or prevalence in mind, but also to show the breadth of marine mammal veterinary science and the importance of attention to details in all aspects of marine mammal health care and management.

Preventive health care for marine mammals (further discussed in Section 6.2) is important for avoiding poor welfare and includes a variety of assessments, some of which will be familiar to animal care professionals working with terrestrial mammals and some of which are unique to their aquatic adaptations. To illustrate, Miller et al. (2015) described preventive assessments for bottlenose dolphins at one zoological facility. These included daily assessments by animal care staff and quarterly assessments by veterinary staff. Veterinary assessments included comprehensive blood tests examining complete blood count and chemistry panel, ultrasound examinations, cytological examinations for faecal, chuff and gastric samples. Morphometric measurements of body length, girth and weight in addition to blubber thickness are monitored weekly to ensure animals fall within reference ranges from wild bottlenose dolphins (e.g. Hart et al., 2013).

Respiratory disease is the major cause of illness and death in wild and captive marine mammals (Miller and Fowler, 2014). Much of the information about captive marine mammal disease comes from studies of small numbers of animals examined when they die but there are a few quantitative studies. Venn-Watson et al. (2012) conducted a retrospective study on 42 dolphins from the US Navy Marine Mammal Programme population; animals were selected from a database ranging from 1980 to 2010. A total of 21 (50%) of the dolphins evaluated had pneumonia confirmed by histopathology. Bacterial and fungal pneumonia was present in 43 and 29% of cases (9 and 6 cases), respectively, with *Staphylococcus aureus* as the most common confirmed pathogen (4 cases, 19%). Other pathogens identified as the cause of pneumonia were *Cryptococcus neoformans, Erysipelothrix rhusiopathiae, Histoplasma capsulatum*, parainfluenza virus, *Proteus* species, *Pseudomonas aeruginosa*, and *Streptococcus zooepidemicus*. Other bacterial and parasitic diseases have been implicated in the cause of death in marine mammals (e.g Acasuso-Signoret, 1981; Cordes and O'Hara 1979), as well as pathologies such as cancers (e.g. Newman and Smith, 2006). Publications that summarise the diseases of particular groups of animals, such as dolphins (Cordes, 1982), or a wider variety of wild and captive animals (Dierauf and Gulland, 2001; Aguirre et al., 2002) are recommended to interested readers.

Dermatomycosis, a common zoonotic skin disease caused by a fungus, typically results in an itchy and scaly rash and can include hair loss and blisters (Miller and Fowler, 2014). Dermatomycosis has been reported in California sea lions (Sós et al., 2013) steller sea lions, *Eumetopias jubatus* (Tanaka et al., 1994) and Patagonian sea lions (Quintard et al., 2015), causing ulcerative skin lesions. Sós et al. (2013) reported that the skin lesions were multifocal to coalescing, involved all flippers, and were most pronounced on the ventral surfaces of flippers, the lesions were depigmented and covered with crusts. Tanaka and Kohno (2015) reported extensive depilation and hyperkeratosis, as well as redness and depigmentation of the skin. Quintard et al. (2015) mention that epidemiological analysis revealed a dermatophytosis case in one of the carnivore section keepers a few weeks before the lesions were diagnosed in the sea lion, suggesting a possible transmission from man to sea lion, highlighting the importance of personal hygiene and the use of gloves (human-animal transmission are well-described: e.g. man-dog transmission: Van Rooij et al., 2012).

Fatal encephalitis has been described in zoo-housed polar bears (Donovan et al., 2009; Prüss et al., 2015). Dovovan et al. (2009) demonstrated the presence of equine herpes virus 9 in affected areas of the brain, concluding that this case resembles other fatal herpes virus encephalitis derived from interspecies transmission. Equids may be a source of infection, and Schrenzel et al. (2008) traced the source to Grevy's zebras (*Equus grevyi*) housed close to the polar bear exhibit. To diagnose encephalitis Szentiks et al. (2014) proposed a next generation sequencing-based diagnostic tool to identify pathogens. The One Health approach (Center for Disease Control, 2016) promotes the prevention of risks as well as the mitigation of diseases originating at the interface between humans, non-humans and their various environments.

A pressing topic in marine mammal health care is tuberculosis, found in sea lions and seals (Cousins et al., 1990, 2006). When fur seals and sea lions die under human care, tuberculosis has sometimes been found to be an important cause, with the initial infection likely present when the animals were captured from the wild (Forshaw and Phelps, 1991). However, Dierauf and Gulland (2001) state that the source of the pathogen in tuberculosis reported in both wild and captive cases remains a subject of conjecture, stressing that none of the many hypotheses postulated has been accepted. An outbreak in the Netherlands, described as a form *Mycobacterium pinnipedii* of the *M. tuberculosis* complex, was transmitted to animal keepers (Kiers et al., 2008), probably resulting from nebulisation when cleaning the sea lions' enclosure. Tuberculosis can be transmitted to other zoo animals as reported by Moser et al. (2008), describing the transmission from South American sea lion to Bactrian camel (*Camelus bactrianus*) and Malayan tapirs (*Tapirus indicus*).

Another pressing health topic is ocular health; eye conditions are prevalent in sea lions and seals, are known to cause function loss and pain, and are considered a welfare issue that needs urgent attention (Colitz et al., 2010; Gage, 2011). Research on eye problems reports that a large percentage of captive pinnipeds suffer from ocular conditions, such as corneal disease, premature cataracts, and lens luxations (Colitz et al., 2010; Gage, 2011). Causative factors such as exhibit design, water quality and water additives, and suggestions on how to correct them can be found in these papers and related references. Access to UV-protective shade should be readily available and the preferred colour of the pool should be earth tones, tan or brown colours to avoid glare and reflections (Colitz et al., 2010; Gage 2011). Suggestions on feeding and training during sunny conditions are also offered, such as not throwing the fish while animals stare up into the sun (Gage 2011).

Paterson et al. (2012) highlight how captive life may have energetic consequences for pinnipeds. The authors found that pregnant harbour seals hauled out more frequently during lactation and moult. The seals maintained higher body temperatures compared to pre-moult period, presumably trying to minimise the energetic cost of the moult, and maintain optimal high skin surface temperatures for hair growth. Kastelein and Wiepkema (1990), Kastelein et al. (1991) found differences in growth rate of grey seal pups and behavioural differences of the mother when comparing the suckling period of consecutive years, attributed to different climatic conditions. Robeck et al. (2012) describe the importance of monitoring expected foetal growth rates and hormone concentrations during pregnancy, and the characterization of hormones required during parturition to better understand how to treat bottlenose dolphins suffering from progesterone insufficiency.

4.4. Social management

Social life and groupings are important for marine mammal welfare (Caldwell and Caldwell, 1977; Waples and Gales, 2002; Wood, 1977). To this end, social structure, hierarchy, density, and group dynamics should all be considered. Social environments can provide for companionship, play opportunities and social learning, as well as pose challenges such as aggression, monopolisation of resources and displacement. However, studies of the social dynamics of zoo-housed marine mammals are scarce.

In the wild, the social lives of bottlenose dolphins are complex and flexible, with social groups varying from 2 to 140 individuals (Bearzi et al., 1997; Connor et al., 2000; Wells et al., 1987). The social system is often termed fission-fusion, as groups frequently fuse and split apart again (Connor et al., 2000). Bottlenose dolphins thus interact with and exchange with individuals from larger groups or communities, resulting in short-term and long-term relationships. The fission-fusion system is not achievable in captive settings; even though individuals move between zoos as part of zoo breeding plans (see next paragraph) the scale and frequency of these moves is low. Thus far in bottlenose dolphins, it appears that housing in larger social groupings leads to higher reproductive success (Wells, 2009), but more research is required to examine whether other factors may be at play. In an older reference, it was suggested that higher group density is preferable to low group density, in order to prevent 'loneliness' (Caldwell and Caldwell, 1972a). In addition to overall group size, the adult-sex ratio (i.e. male: female) may have an impact on welfare but again is not something which is easily changeable in zoos because it will involve inter-zoo transfer of individuals. In the wild, cetacean females group together sometimes including few males in their groups (e.g. Bearzi et al., 1997; Wells et al., 1987); aggression is more common amongst males, less common between males and females, and almost absent amongst females (Heyning, 1984; Scott et al., 2005).

The European studbook for bottlenose dolphins is maintained at Dolfinarium Harderwijk in the Netherlands (other dolphin studbooks are maintained in other regions in the world: Andrews, 2000; Robeck et al., 1994). Studbook management is primarily for captive breeding purposes (maximising genetic diversity), but should also take into account maintaining strongly affiliated conspecifics together, maintaining levels of aggression, and trying to arrange naturalistic social groupings.

To reduce the number of transfers, stress and the changing of social compositions and relying on intra-institutional transports, technologies such as artificial insemination (killer whales: Robeck et al., 2004; Pacific white-sided dolphin: Robeck et al., 2009) as well as the development of sperm sexing and associated assisted reproductive technology for sex preselection (bottlenose dolphin: O'Brien and Robeck, 2006) have been used.

The most common motives of aggression in wild cetaceans are intrasexual male competition and sexual coercion, which are enhanced during breeding seasons (Scott et al., 2005). 'Rake marks' are caused by the teeth raking along the body of a conspecific, and have been analysed as an indirect measure of aggression in cetaceans (Scott et al., 2005). Under human care, we believe that rake marks are an important measure of aggression since not all aggression can be observed by animal care staff, i.e. it also takes place overnight (personal communication, Brando, Clark, Acasuso-Rivero). More recently rake marks have been proposed as an animal-based welfare measure to monitor bottlenose dolphin welfare (Clegg et al., 2015). However, there has been no conclusion on the frequency or severity of rake marks above which welfare is poor, especially since rake marks are very frequently observed on wild cetaceans and are the expression of normal social behaviour (Lockyer and Morris, 1985, 1990). In contrast, affiliative body contact among zoo-housed bottlenose dolphins may repair deteriorated relationships or reduce tension within the group following aggressive interactions (Tamaki et al., 2006). In this study, the authors suggested that flipper-rubbing may contribute to restoring friendly relationships between former opponents, or reduce conflicts in juvenile-adult female associations.

An important social bond is the one between mothers and infants, aiding growth, development, sociality and protection. The importance of the bond and its fast development was demonstrated in wild Australian fur seals (*Arctocephalus pusillus doriferus*), who recognise the calls of their calves only after 48 h of birth (Pitcher et al., 2010). Some marine mammals such as bottlenose dolphins have a prolonged nursing period and a strong mother-calf bond, which are critical for calf survival (Gubbins et al., 1999). The specific swimming positions that bottlenose dolphin and other cetacean calves adopt, with respect to their mothers, evolve change with age; these positions are known to be preserved in captivity (Gubbins et al., 1999). In pinnipeds, mother-pup bonding and familial relationships extend over a number of years and may last a lifetime (Hanggi and Schusterman, 1990). Hanggi and Schusterman (1990) observed a colony of zoo-housed California sea lions and found siblings and half-siblings interact more with each other than with unrelated animals, and mothers interact predominantly with their offspring. Few aggressive interactions were found between relatives, and animals without relatives stayed mostly alone.

Most marine mammals wean in the wild between 1 and 3 years; for instance, 55% of polar bear cubs in their second year are independent of their mothers (Ramsay and Stirling, 1988). Weaning is an important social and physical process and thus likely to affect welfare (also see case study 4.5). Methods for weaning zoo-housed marine mammals differ; some facilities separate the mother from the infant to kick-start the eating of solid foods, other use play and training, or a combination of both. Implications of weaning on both mother and calf should be considered as calf independence is gradually acquired while mother and infant still spend much time together, up to 3–6 years (Hill et al., 2013; Reid et al., 1995). If necessary and in order to minimise the stress involved in the weaning process, we encourage caregivers to separate mother and calf into neighbouring enclosures permitting visual and acoustic communication, and invest time in pre-weaning training to make it gradual and voluntary.

Appropriate social structures improve welfare by offering play opportunities, developing problem-solving skills, stimulating innovation, and facilitating learning. For an overview of play and its relation to welfare, see Burghardt (2005) and Held and Špinka (2011). Pace (2000) observed fluke-made bubble rings and associated play behaviours in two zoo-housed bottlenose dolphin calves, who were usually seen together and mimicked each other during ring formation. Kuczaj et al. (2006) observed spontaneous play behaviours of bottlenose dolphins and found that play behaviour complexity increased with age. The study found that novel play behaviours were more likely to be produced by calves than adults, and calves would imitate novel play behaviours from other dolphins. The authors propose that through innovation and transmission of behaviours, interaction and play among peers contributes to the development of problem-solving skills. It has also been shown that dolphins use sponges as a tool for moving rocks and foraging for fish (Smolker et al., 1997). Such behaviour is transmitted not only from mother to calf, but also between other group members; this suggests a vertical cultural transmission involving important social learning and cognition (Mann et al., 2008; Smolker et al., 1997).

Social interaction and grouping obviously differ between marine mammal species, when comparing the social life of bottlenose dolphin to a polar bear for example. The line between solitary and social is blurring through a more detailed understanding of what social means for a certain species. Polar bears are typically described as solitary, but this species is often housed socially in zoos (Renner and Kelly, 2006). In zoos, negative interactions, including aggression, can occur in polar bears; but play, swimming and sleeping close together have also been observed (Ross, 2006; personal observations Brando). The use of landscape complexity and multiple pathways in exhibits allows bears to make behavioural decisions to spend time together or apart, and can thus aid in the management of possible aggression (Renner and Kelly, 2006), with open access to multiple areas providing choice and control (Ross, 2006).

Interaction with other species is part of the social life of marine mammals. In some facilities different species are sometimes housed together, such as bottlenose dolphins and California sea lions. Tayler and Saayman (1973) described the interaction between a zoo-housed Indian Ocean bottlenose dolphin (*Tursiops aduncus*) and a cape fur seal (*Arctocephalus pusillus*), including attempts of copulation culminating in aggression. This same paper describes the dolphin imitating sounds and activities, including the use of tools, of human divers (Tayler and Saayman, 1973), and some interactions between dolphins and seals in the wild. Co-housing different species potentially adds additional social management challenges, of which some will not be well known or understood and are therefore unpredictable. Co-housing several species in one enclosure can increase complexity in the environments (see Section 4.1) and can potentially enrich them (Section 5).

The breeding and moulting behaviour of pinnipeds can affect group behaviour and interaction, well as pup survival (Campagna et al., 1992; Trillmich and Wolf, 2008). Otariids are sexually dimorphic, polygynous and highly gregarious marine mammals (Campagna et al., 1992). The main causes of pup death are infanticide by conspecific young males, with pups in colonies being more protected from harassment by subordinate males, and females benefitting from group breeding through increased survival of their pups (Campagna et al., 1992). Behavioural changes such as competition and fighting between animals and guarding of females are more likely to occur during breeding season. Habitat features such as shallow areas and flat rocks might be defended from other animals and care staff.

4.5. Best practice case study

The rehabilitation of marine mammals is a major challenge for caregivers. Care is based on the limited evidence provided by previous cases, and animals are often extremely unwell by the time they reach a rehabilitation facility. Hundreds of stranded harbour seals pups are brought to wildlife rescue centres and zoos every year, stimulating MacRae et al. (2011) to investigate the most effective diet for these pups. 243 pups admitted to Vancouver Aquarium Marine Mammal Rescue Centre over two consecutive summers (2007–2008) were fed either an artificial milk replacement (Zoologic® 30/55 Milk Matrix, PetAg, Hampshire, IL), or macerated fish by tubing until weaning. Meticulous records of every feeding (volume per feed, food type, animals' most recent body weights) were assembled. It was found that pups on the milk replacement gained more weight, and pup survival was significantly higher for these pups, particularly in 2008 when the quantity of food (as a percentage of body weight) was increased. Neither of the diets in this study could completely match the fat and protein content of seal milk, but the milk replacement with 30% fat and 8% protein, was a closer match than the fish which only had 21% fat and 6% protein. Providing hand-reared seal pups with a diet that maximises weight gains is vital since they must achieve sufficient body fat and weight in order to survive once released. The higher fat content of the milk replacement appears to be the most important factor in allowing pups to gain weight and thus survive.

4.6. Future directions

This section on the health and husbandry of marine mammals has highlighted a number of areas of major importance to welfare that have been overlooked. In the order of discussion rather than order of importance: (1) Professional husbandry guidelines should be developed for all species of zoo-housed marine mammals. Manuals should be available as a reference and practical guide for all caregivers and managers, and be translated into different languages. (2) There is a pressing need to investigate the importance of pool area, depth and construction on welfare for cetaceans, and the legislation and guidelines available should be made accountable for the figures they provide; in other words they should be more evidence based. (3) Marine mammal nutrition is still a relatively unexplored area, and a review and justification of our supplementation practices for marine mammals is long overdue. This should take into account that many facilities have the ability to weigh their animals and collect biological samples. Rather than the use reference values that have been calculated for wild species, it is arguably more valid to construct reference values that are more appropriate for captive settings. In terms of marine mammal health, we believe (4) a central database of marine mammal diseases and treatments, contributed to by all zoos, would enhance this field of management. It is true that there are many peer-reviewed case studies available on marine mammal diseases, but not all cases can be reported in this way. The recent development of the medical module in Species 360 (Species 360, 2016), together with software that helps maximise genetic variation within groups by analysing and managing pedigrees (e.g. PMx: Lacy et al., 2012), can facilitate this practice. Finally, there are many research topics pertaining to the understanding of marine mammal social life and management due to an overall dearth of research in this area. In particular, we propose research to examine (5) how husbandry and/or management variables affect social life, such as the impact of separating individuals for daily activities such as presentations, or transfer to another facility. Finally, (6) the question of whether positive human-animal relationships can compensate for small or un-naturalistic group sizes in captivity is something worth considering.

5. Environmental enrichment

5.1. Summary

This section is necessarily larger than some previous sections, since any change to a captive environment in attempts to enhance welfare could be described as enrichment (Shepherdson, 1998). To follow convention in the field of zoo biology, we use the term enrichment to refer to any enrichment *attempt* in marine mammals, rather than limit discussions to environmental additions that have evidentially improved welfare. In a *meta*-analysis of 28 mammals, including polar bears, harbour seals and grey seals, Swaisgood and Shepherdson (2005) report that enriched environments were associated with a reduction of stereotypies about 53% of the time. Environmental enrichment for marine mammals has received little scientific attention; Alligood and Leighty (2015) excluded marine mammals from their *meta*-analysis of zoo enrichment due to a lack of data compared with primates and terrestrial carnivores. As stated in the introduction, substantially more primates than marine mammals are housed in zoos, which may account for some of the publication bias. However, we believe that the amount of published research on marine mammal enrichment does not reflect the frequency or diversity of enrichment actually undertaken for marine mammals, making it difficult to accurately assess current best practice. For example, artificial kelp and mirrors are enrichment attempts we commonly observe in dolphin and pinniped enclosures, but to our knowledge these methods have received hardly any empirical evaluation in these settings (see Amundin, 1974 for brief use of kelp in laboratory porpoises).

We ran Boolean literature searches for marine mammal enrichment in Google Scholar and Web of Science (Spring 2016). These returned less than 15 peer-reviewed articles and book chapters and less than 20 non-peer-reviewed publications or theses on marine mammal enrichment in zoos or research facilities. also discovered some interesting historical trends; according to their search criteria there were no enrichment studies on cetaceans prior to 2009 and to their knowledge there have been no peer-reviewed studies on sirenians.

The aims of marine mammal enrichment (according to published studies) are the same as those for most animals under human care (Young, 2003). Thus far, the main aim of marine mammal enrichment has been to reduce stereotypies (e.g. Amundin, 1974; Grindrod and Cleaver, 2001; Holden, 2003 cited in Shyne, 2006). Shyne (2006) quantified studies of enrichment which attempted to reduce stereotypies in zoo mammals, and found that approximately equal numbers of studies have been performed on marine mammals and primates (10 versus 13), but four times as many studies have been performed on terrestrial carnivores (37). Other aims have been to increase foraging behaviour (Forthman et al., 1992; Hocking et al., 2015; Kastelein and Wiepkema, 1989) and time spent underwater (Clark et al., 2013; Kastelein and Wiepkema, 1989). We found one study where the aim was to reduce destructive behaviour (self-injurious or destruction of the environment: Sweeney, 1990).

5.2. Floating objects

According to the published literature, there is a clear bias towards buoyant, floating plastic or rubber objects as enrichment, as opposed to objects placed under the water surface. These include balls or barrels (e.g. dolphins: Delfour and Beyer, 2012; orcas: Kuczaj et al., 1998, 2002; sea lions: Smith and Litchfield, 2010), rafts (e.g. dolphins: Delfour and Beyer, 2012; seals: Grindrod and Cleaver, 2001), and buoys (e.g. dolphins: Neto et al., 2016; seals: Grindrod and Cleaver, 2001; polar bears: Canino and Powell, 2010). It is understandable why these objects are desirable from a practical perspective: being made from one continuous piece of plastic they are easy to clean, and will not break into small parts which could be a choking hazard or clog filtration systems (Kastelein and Wiepkema, 1989; Goldblatt, 1993; Joseph and Antrim, 2010).

Many studies have referred to floating objects as 'toys' (e.g. Grindrod and Cleaver, 2001; Kuczaj et al., 2002; Sevenich, 1986). When these objects stimulate inspection behaviour this could be classified as a beneficial response and play is increasingly viewed as a positive indicator of welfare (Held and Špinka, 2011; Mellor, 2015 but see Blois-Heulin et al., 2015 for counterargument). According to a study by Delfour and Beyer (2012), where 21 objects were offered to bottlenose dolphins in random sets of four objects over a two-week period, only 50% of objects were manipulated by dolphins and the others did not elicit a behavioural response, positive or negative. Consistent with other zoo animals (see Young, 2003 for a review), simple contiguous objects with no moving parts rouse immediate interest and interaction but are quickly habituated to by marine mammals. For example, Kuczaj et al. (2002) evaluated eight enrichment items for six species of marine mammal (cetaceans, pinnipeds and polar bears), and found subjects interacted with items less than an average of ten times over a total of two hours (session length varied). Furthermore, objects elicited more interaction when they were provided randomly and for variable times, rather than being scheduled. In a large multi-zoo study of North American polar bears, Shepherdson et al. (2013) found that enrichment diversity, i.e. the number of different types, had a significant effect on reduced stereotypical pacing behaviour. These studies demonstrate the importance of evaluating and readjusting an enrichment programme to ensure we are meeting the needs of the animals to show certain behaviours (Alligood and Leighty, 2015).

5.3. Submerged objects

Compared with floating objects, submerged objects have been rarely used for cetaceans. Examples include: a submerged A-frame (Hunter et al., 2002), a weather vane (Amundin 1974) and artificial kelp created from rope or a fire hose (Amundin 1974; Berglind 2005). However, there could be significant benefits in providing more underwater stimulation. Amundin (1974) found that stereotypical swimming patterns were reduced in a pair of harbour porpoises (*Phocoena phocoena*) in the presence of submerged items. Berglind (2005) ran water through submerged fire hose so that it moved erratically, subsequently triggering group movements and increased sonar activity in bottlenose dolphins. Clark et al. (2013) designed an innovative submerged puzzle constructed from pieces from plumbing pipe, which decreased circular swimming and increased time spent underwater in bottlenose dolphins (see case study, 5.8). However, wild bottlenose dolphins inhabit relatively shallow waters and underwater enrichment may not be as important for this species as for other cetaceans (e.g. Pryor, 2004). For deep-diving species of pinniped such as the grey seal, submerged enrichment objects may help stimulate more deep-diving behaviours to help mimic their behaviour in the wild.

Compared with great apes, there have been few published studies examining complex cognitive challenges as enrichment for marine mammals (Clark, 2011; but see Harley et al., 2010 and case study 5.8). In a review of marine mammal cognition and care, Clark (2013) highlighted the similar cognitive skills of great apes, including humans, and cetaceans, and how complex cognitive challenges may be beneficial to animals. 'Puzzle feeders' which require effort to extract food are often used for pinnipeds (e.g. common seals: Grindrod and Cleaver, 2001; pacific walruses: Kastelein and Wiepkema, 1989; harbour seals: Holden, 2003 cited in Shyne, 2006; Hunter et al., 2002), but the degree of cognitive challenge actually bestowed by these objects is probably low. Research examining the degree of cognitive challenges and benefits of such challenges has not been empirically tested widely across marine mammals.

Clark (2013, p.1) proposes the need for 'cognitive enrichment' suggesting, "Tasks originally developed to test the limits of dolphin and sea lion cognitive skill could be modified and implemented as 'cognitive enrichment' in zoos and aquariums. To be enriching, cognitive challenges should be relevant, motivating, controllable, and possible to master." In cognitive behavioural studies that may have real implications for welfare, Kuczaj et al. (2010, 2015) demonstrated that bottlenose dolphins under human care, alone or cooperatively with conspecifics or humans, are capable of applying behavioural skills to solve novel problems, where the solution resulted in the acquisition of food rewards. There is also evidence that dolphins are motivated to participate in challenging tasks without an external reward. In another cognitive study with no focus on welfare at that time, Mackay (1981) noticed that dolphins trained to whistle to activate a food dispenser continued to do so without a food reward.

Dolphins have also shown interest in operating touchscreens with no food rewards and thus seem to be intrinsically motivated by the challenge itself (Delfour and Marten, 2006). For animals for whom food rewards are highly motivating, Goldblatt (1992) proposed a design for an automated cut fish dispenser, primarily for use by marine mammals in the laboratory setting but it could also be used in zoos, perhaps combined with a cognitive challenge.

Although it has received little previous consideration, the ability to use environmental features could be important for species of marine mammal that have regular contact with sand, rocks and other land masses. Casson (personal communication in Goldblatt, 1993) reported the destructive nature of sea otters in an enrichment study. The otters preferred using substrates that could either be broken or used to break other items, resembling their natural feeding strategy of breaking into mollusc shells using rock tools. In the only other published sea otter enrichment study we are aware of, Hanna et al. (2016) found that the female in a pair of otters interacted with a foraging tool use task, but was not successful in solving the task. Sea otters are certainly not the only tool-using marine mammals; dolphins have been observed using sponge tools in the wild to protect their rostrums while foraging in sharp rocks (Smolker et al., 2007) and there are numerous reports of cetaceans using tools in zoos (see Jaakkola, 2012). Polar bears often 'kill' enrichment items by performing naturalistic stalk-rush-kill hunting behaviours (personal communication, Clark), and the immense size and strength of polar bears makes indestructibility of enrichment almost impossible. For some species the destruction of items needs to be considered by animal care staff to ensure the health and safety of animals due to loose particles that could be ingested or cause problems for water filtration systems (Baer, 1998).

5.4. Food-based enrichment

There have been more studies published on object enrichment than food-based enrichment for marine mammals. Goldblatt (1993) reasoned that food-based enrichment is limited because food particles affect water quality and are also a choking hazard. However, there are many facilities that use food-based enrichment but have not published their efforts (Acasuso-Rivero personal communication). Food can present a choking hazard and this has been a legitimate concern of many animal care staff where captive-born animals are naïve to certain food types, or consume associated substrates such as ropes or sacking (Hare et al., 2007). In support of this, Kastelein and Wiepkema (1989) encountered problems when implementing a submerged feeding trough full small stones and molluscs for Pacific walruses (*Odobenus rosmarus divergens*); these put a strain on water quality and stones were ingested by the animals. Problems were eventually circumvented by stringing large rocks together on a chain so that they could not leave the trough. A positive side effect of this foraging enrichment was that walruses wore down their vibrissae (whiskers), which tend to become overgrown in zoos, on the abrasive substrates (Kastelein and Wiepkema, 1989).

Similar to the walrus example given above (Kastelein and Wiepkema, 1989), the most common form of food-based enrichment for marine mammals is hiding a portion of the normal daily diet within an object such as a ball, box or block of ice (e.g. seals: Grindrod and Cleaver, 2001; pacific walruses: Kastelein et al., 2007; polar bears: Canino and Powell, 2010). Hocking et al. (2015) found that food concealed within objects (a ball and a box) was more engaging than simply scattering food into the water for Australian fur seals (*Arctocephalus pusillus doriferus*). Hiding food also decreased stereotypical swimming and increased random swimming. The major limitation is that hidden food uses up some of the animal's allotted diet, and because some individuals may be more successful than others at finding hidden food this will affect their dietary intake via enrichment. Despite its popularity, there is no clear relationship between the success of enrichment and presence of food. Smith and Litchfield (2010) found Australian sea lions (*Neophoca cinerea*) spent more time interacting with non-food than food containing objects (balls), whereas Hunter et al. (2002) used a variety of enrichments for seals (harbour and grey) and found that they were more successful when they used food, although quickly consumed.

With the exception of the previously cited walrus examples (Kastelein and Wiepkema, 1989), live fish, molluscs and crustaceans are rarely provided to marine mammals as part of routine management, or perceived enrichment. The practical limitations are discussed in Section 4.2. An alternative to live prey is a simulated fish chase where fish are physically dragged through the water on wires; this strategy has decreased stereotypical swimming in common seals (*Phoca vitulina*: Grindrod and Cleaver, 2001). In one of the earliest documented reports of zoo enrichment, Morris (1960); as described in Rees, (2011) used an automatic device to feed seals (*Halichoerus* spp.) at London Zoo. The device moved dead fish around the pool before being caught by seals. Hocking et al. (2015) reasons that naturalistic foraging enrichment is lacking for marine mammals because we lack knowledge about their natural foraging behaviour at sea. Most studies on pinnipeds, for example, focus on easily observed behaviour occurring when animals are hauled-out on rocks and beaches (i.e. for breeding and moulting) rather than food-related behaviours.

As far as we are aware, with the exception of Berglind (2005) who stimulated group hunting movements in bottlenose dolphins with an underwater hose with water running through it, there has been no empirical research on stimulating the natural hunting strategies of cetaceans. It is understandable why it is not practical or safe to encourage cetaceans to hunt large prey items in a captive setting, but for large apex predators such as polar bears and orcas, the thwarting of hunting behaviour may be a cause of poor welfare, linked to the development of abnormal behaviour as is seen in large felids (Burgener et al., 2008). There are reports of cetaceans opportunistically capturing and eating wild birds (as cited in Kuczaj and Eskelinen, 2014), and of dolphins in sea pens capturing fishes, crabs and lobsters, sometimes eating them, some animals refusing their given diets, or simply playing with them by letting go repetitively (personal communication, Acasuso-Rivero). This suggests the urge to hunt can still present in captivity, even when free food is provided.

5.5. Structural enrichment

Enrichment which increases the structural complexity of enclosures is rare for marine mammals when compared with primates and terrestrial carnivores (Young, 2003). This is surprising since it could be used to compensate for bare concrete pools. Most marine mammals are housed in enclosures with little substratum (dirt, coral, seaweed etc.) to haul out on, rub on, hide or forage in. There is also little variation in land or water temperature, or water currents; however, some facilities are starting to experiment with altering water temperature for dolphins (personal communication, Brando, Clark). Amundin (1974) suggested that 'structure plates' could be added to the pool walls of marine mammals in order to create additional complexity; this potential type of enrichment may also be classified as object-based or even cognitive enrichment if the plates provide an appropriate level of cognitive stimulation. The cognitive maze puzzle provided to dolphins by Clark et al. (2013) was modular in design, and could theoretically be used across a much larger scale on pool walls or tethered to the floor similar to Amundin's vision. Amundin (1974) stated that simple plastic objects perpetuate the 'sterile' nature of marine mammal pools, and the logical alternative should be rocks, coral or seaweed or kelp. As stated at the beginning of this section, we have observed several attempts at providing artificial kelp in cetacean and pinniped enclosures, but scientific assessment of natural materials is apparently lacking.

5.6. Human interaction and training

For captive marine mammals, training has been suggested as "essential for any environmental enrichment programme" (Kuczaj et al., 1998). Training and other forms of human interaction are discussed in more detail in Section 6, but human contact, particularly training, is considered to be enriching for marine mammals. Eskelinen et al. (2015) reported that bottlenose dolphins preferred human contact, both in and out of the water, to object interactions. Training has also been used in an attempt to facilitate the enrichment process. Neto et al. (2016) trained four bottlenose dolphins to show increased interest in objects, and even to encourage object play. The criticism here is that rather than being intrinsically motivated to explore the objects, the dolphins' behaviour was 'engineered' (behavioural engineering *sensu* Markowitz, 1978). This brings us back once again to the functional-versus-naturalistic debate, and more specifically whether the performance of natural-looking behaviour is enough to enhance welfare, without there being strong internal motivation to perform that behaviour (i.e. an inherent interest in exploring objects as opposed to the interest in receiving fish rewards). But there is a paradox on these statements since rewards, particularly primary ones like food, enhance motivation *per se* independently of their intention (Skinner, 1938). It is out of the scope of this review to differentiate the "nature" of motivation; for instance, between a trainer reinforcing a cognitive trial versus a marine mammal learning to catch prey with a particular technique copied from conspecifics.

5.7. Sensory enrichment

Thus far we have described the physical enrichment objects that encourage simple manipulation or problem-solving, and food-based enrichment. Another subset of enrichment that is highly relevant to marine mammals is water itself, which could be classified as many forms of enrichment including structural or sensory. Self-produced bubbles are well documented in cetaceans; they are produced with the fins or blowhole and are usually subsequently played with, thus acting as a do-it-yourself enrichment. Studies of cetacean bubble production have focussed on cognitive processes rather than welfare (e.g. bottlenose dolphins: McCowan et al., 2000; Pace, 2000; beluga whales: Delfour and Aulagnier, 1997). In a study that had both cognitive and welfare aspects, Clark et al. (2013) found that bottlenose dolphins sometimes produced large bubbles from their blowholes in response to a cognitive maze. The authors hypothesised these bubbles were social signals to other dolphins about the task. Gewalt (1989) found that a pair of Inia freshwater dolphins (*Inia geoffrensis*) were more interested in creating and playing with bubbles than object 'toys'. Bubbles produced by machines also stimulated curiosity in cetaceans and pinnipeds; for example Hunter et al. (2002) found that for harbour and grey seals, a submerged machine producing bubble 'curtains' was used more and had a larger effect on reducing stereotyped swimming than floating objects or a submerged A-frame. Another type of self-stimulation is tactile; for cetaceans it is most probably due to the presence of longitudinal dermal ridges which provide the skin with particularly sensitive tactile functions (Palmer and Weddell, 1964). Cetaceans and in some cases pinnipeds rub their bodies, flippers and genitals against almost any object in the enclosures, including walls, fences, stairs, other dolphins, other species, etc. (e.g. Caldwell and Caldwell, 1972a, 1972b). Reasons for this behaviour could be many, ranging from pleasure and masturbation through touch, or reacting to itches or skin irritations (e.g. when water conditions are not optimal).

Other types of sensory enrichment for marine mammals have been rare according to the publication record. For polar bears, we have seen scent trails, for example blood or perfume, used to encourage generalised foraging in the enclosure (personal communication, Brando, Clark). Grindrod and Cleaver (2001) studied enrichment for common seals and claimed that 'playing a variety of music each day' was enriching but this was tested alongside 17 other enrichment attempts such as floating objects and hidden food in various combinations. Unfortunately there are no data on the specific effect of music in this. Kuczaj et al. (1998) exposed zoo-housed orcas to underwater tones, training them to associate one tone with a trained behaviour. This was evaluated by the authors to be enriching because it stimulated memory skills in an unpredictable manner for different combinations of behaviours. Revisiting the idea of using cognitive research apparatus as enrichment, Amundin et al. (2008) developed a sonar-activated touchscreen for dolphins that could be used for enrichment purposes.

5.8. Best practice case study

Clark et al. (2013) designed, implemented and evaluated a novel form of underwater enrichment for bottlenose dolphins housed at Six Flags Discovery Kingdom, California. The premise behind the research was to use knowledge of dolphin's well-documented cognitive skills, particularly physical cognition, to improve their welfare, using apparatus previously used for cognitive research. PVC plumbing pipe has been used previously to build frames for cognitive testing apparatus (see Herman, 2002) and its modular structure makes it practical for building novel items. The device was essentially a maze containing a ball, and dolphins had to navigate the ball through an array of pipes in order to retrieve it as a reward. Presence of the device had positive behavioural effects (increased time spent underwater, decreased circular swimming, increased exploration and problem-solving) on a group of male dolphins, but a separately housed group of female dolphins did not approach nor use the device. Male dolphins used the device without prior training, using a variety of problem-solving strategies. The device had no significant effect on circular, repetitive, swimming patterns, but males spent significantly more time underwater when the maze was present.

5.9. Future directions

We suggest two parallel approaches to marine mammal enrichment, and one general comment on its future evaluation. (1) We recommend more research to evaluate discrete tasks or devices, which ideally aim to stimulate cognitive skills. These do not necessarily need a food reward, and are therefore feasible alongside routine husbandry training with food rewards. To this end, we encourage researchers to investigate how the field of marine mammal cognition, both the knowledge already gained, and future developments, can serve the field of marine mammal welfare. In addition to physical manipulation, echolocating cetaceans have the ability to use their sonar for enrichment; echolocation is inherently challenging to observe and to study and is currently not well-understood from a welfare perspective. (2) More research is needed to enrich more of the aquatic environment, below the water's surface. This will entail making changes to water structure, for example with wave or bubble machines, introducing other aquatic plants and animals, or creating more structurally complex pool walls. One important consideration is giving animals the opportunity to retreat from or avoid stimuli if they are aversive. In terms of evaluating enrichment, this will necessarily evolve as we find novel and valid indicators of positive and negative welfare (Section 2). (3) We advise that every enriching effort should be followed by scientific and objective evaluation of its real enrichment value. It is often taken for granted that adding a stimulus will have positive effects in individuals or groups. However, this is not necessarily the case, and should be carefully inspected at individual and group levels. Every enriching attempt should be accompanied by behavioural observations and if possible physiological measurements that validate the use of the device or task or method. The best practice is to follow-up immediate and long-term effects through detailed records that can be easily examined over time.

6. Training and human-animal interactions

6.1. Overview

As with most animals under human care, marine mammals experience a range of interactions with humans on a daily basis. Animals are often in frequent and often prolonged contact with caregivers, trainers, veterinarians, researchers, TV teams, educational groups and members of the public. Here we will focus on how different human-animal interactions affect marine mammal welfare including: training, participation in shows, visitor interaction sessions and participation in research.

The training of marine mammals developed in the mid 1960s. Pryor (2004) described some of the first attempts to train marine mammals using traditional Skinnerian methods (Skinner, 1938) in order to enhance their survival and quality of life under human care. Over the past five decades, marine mammal carers have continuously explored and refined methods of husbandry training for animals who could not be managed otherwise due to the unique difficulties involved with contacting or moving them in water. Today, marine mammal training is still based on the foundations of Skinner but takes an interdisciplinary approach, focussing predominantly on positive reinforcement and is informed by advances in animal behaviour, emotion, cognition and communication. The training of marine mammals is viewed as a sophisticated branch of animal care, often performed by staff with specialist training in psychology, increasingly, in the growing field of behaviour analysis (Herman et al., 1994; Highfill and Kuczaj, 2007; Kastak and Schusterman, 1992; Schusterman and Kastak, 1995; Kuczaj et al., 2006, 2008, 2009; Marino, 2002; McCowan et al., 2000; Ross, 2006; Xitco et al., 2004).

6.2. Training to facilitate husbandry practices

The use of positive reinforcement training, where positive reinforcement is used to increase the frequency of desired behaviours (Skinner, 1938), is one of the many tools at the disposal of animal care staff and is now ubiquitous with modern zoo animal management. Positive reinforcement training contributes to optimal welfare as it reduces the negative stress often associated with husbandry procedures and unknown situations, and increases choice and control for the animal (Brando, 2010, 2016b). The effects of negative reinforcement, positive and negative punishment, and the possible negative effects interactions on animal welfare have been well described (general: Brando, 2012; dogs: Hiby et al., 2004; Schilder and van der Borg, 2004; marmosets: Bassett et al., 2003; horse: Warran et al., 2007). Reviews of marine mammal husbandry training are provided by Brando (2010) and Ramirez (2012). For example, marine mammals have been trained to participate in husbandry behaviours to facilitate routine preventive monitoring of clinical signs and inspection of body condition; reduce or eliminate the use of physical restraint or sedative and anaesthetic drugs: and facilitate invasive procedures (e.g. blood sampling) and surgery (Higgins and Hendrickson, 2013; Miller and Fowler, 2014; West et al., 2014). Furthermore, training can facilitate procedures such as weighing, and the collection of biological samples such as milk, semen and urine for longitudinal studies to improve health and husbandry (Kamolnick et al., 1994; Lima et al., 2005; Mellish et al., 2006; Odell and Robeck, 2002). The immobilisation of cetaceans and pinnipeds is associated with high rates of medical complications and mortality (Gales, 1989; Haulena, 2014).

The benefit of using training to provide optimal animal welfare is illustrated by a study conducted by Desportes et al. (2007). Long-term monitoring of cortisol levels in four harbour porpoises held in human care showed that voluntary collaboration between animal and humans while collecting routine husbandry samples significantly reduced cortisol levels. Cortisol levels of porpoises lifted by hand from the water were significantly higher than those of porpoises that collaborated voluntarily at the poolside. Even if animals can experience habituation to handling over time, regular and frequent handling might not suppress significant stress responses. Voluntary husbandry behaviours can aid in limiting stress in husbandry practices, therefore, increasing positive welfare (Brando, 2010, 2012).

Although training can facilitate voluntary preventive healthcare and has had many positive outcomes as cited above, the use of a singular routine and training method may be insufficient for dealing with complex welfare problems, highlighting the importance of understanding different animal training techniques and methods. Examples in bottlenose dolphins and sea lions illustrate the positive effects on training on welfare. For example, inadequate parental care by a female bottlenose dolphin who drowned three calves soon after birth was addressed by training the female to interact positively with an anatomically correct model of a calf. The female was trained using positive reinforcement to touch the model and present her mammary glands while continuing to swim (Kastelein and Mosterd, 1995). Regular training sessions over a six-week period reduced routine-like swimming of steller sea lions. On weeks when food was provided as rewards during training, play-like behaviour increased and routine swimming decreased in these subjects (Kastelein and Wiepkema, 1988).

In addition to husbandry training, the majority of marine mammals under human care participate in other forms of training, either in formal training sessions or less formal contexts such as *ad hoc* playful interactions with trainers. Different methods can be used to train animals, such as 'shaping': a common animal training method to acquire a wide variety of desired behavioural goals (Pryor and Ramirez, 2014), but many other methods such as 'chaining' and 'scanning' can be used too. Many training interactions require mental effort on the part of the animal because behaviours are continually shaped by trainers in order to maintain or perfect their expression. Studies investigating the amount of training, through shaping or other methods, required to perfect behaviours in marine mammals are currently lacking. Learning new behaviours or behavioural sequences, and engaging in novel interactions through the process of training, is widely accepted as being mentally stimulating for animals (Perlman et al., 2010). But like other forms of cognitive enrichment (Section 5.3) it is difficult to quantify the level of challenge to the animal.

6.3. Training to facilitate choice and control

Choice and control are becoming popular research topics in the field of animal welfare. Studies on perceived control in both humans and animals dating back to the late 1970′s already allude to their positive impact on welfare (Perlmuter and Monty, 1977). Perceived control refers to whether animals are aware of the choices and opportunities they have in their environment. Animals who are able to control supplementary light (Buchanan-Smith and Badihi, 2012), access indoor and outdoor areas (Owen et al., 2005), or activate a shower (Legrand et al., 2011) have shown signs of improved welfare. Marine mammal training facilitates choice and control if animals can actively decide whether or not they want to participate in a session or other activity by going to a certain point in the pool; choose what session or consequence they would like to do through the use of abstract concepts such as choosing from a range of symbols which each represent a certain object or activity; or choose with which trainer or other animals they want to spend time (Brando, 2009a, 2009b; for more on the concept of choice and control see Brando et al., 2016). Choices and control can be given through habitat design (as discussed in Section 4.1) as well as the use of technological aspects. For example, dolphins have been trained to use their echolocation to request different fish species (Starkhammar et al., 2007, case study 6.8).

The level, quantity and quality of choice and control is determined by many factors; a loss of motivation and possible boredom can come from a lack of perceived choice and control. "Finally the environment in question does not have to be of a purely physical nature. The chronically bored individual can be confined within a number of social structures and thus have their ability to creatively and actively break out of their boredom obstructed, not by the walls of rooms or cages, but by the walls of social systems or authoritative relations" Wemelsfelder (2005, p.79–80). The relevance of this quote to animal training programmes could be explored in that a lack of perceived choice and control, and a lack of motivation or possible boredom, can result not only from the physical environment and housing conditions, but also through what does or does not happen within and outside of training sessions and the types of human-animal relationships.

It has been proposed that some trained behaviours can become routine and eventually become second nature to animals that then appear to perform them without much effort or thought (Melfi, 2013). It is important to note that initiating and interacting with the trainer can be reinforcing in itself without a need for a food reward, and proves an opportunity to exercise control over the environment. Already established behaviours and well-known and practised routines could become monotonous over time and could be prone to causing boredom and loss of motivation (Melfi, 2013). Although data are lacking on marine mammals, the motivational challenges encountered by marine mammal trainers such as animals not coming to station, needing repeated requests to perform a behaviour, or low levels of criteria (Personal communication, Brando) indicate that the possibility of boredom and loss of motivation warrants further consideration and investigation. We should ask about specific training techniques and practices, consider the competencies of the practitioners and study individual differences in animals as well as trainers and how they interact.

6.4. Visitor effects on marine mammals

Human-animal interaction studies include topics such as the visitor effect, human attitudes to animals, or human-animal interactions during interactive programmes. Most papers have focussed on the effects of visitors on a variety of animals but have predominantly focussed on primates. For example, higher noise levels and viewing group sizes have been linked to negative behavioural indicators of welfare (Cooke and Schillaci, 2007; Wells, 2005). By contrast, no similar studies on visitor noise and density have been undertaken on marine mammals to our knowledge. However, animal responses to familiar and unfamiliar humans have been studied in belugas, dolphins and white-sided dolphins (Hill et al., 2016a, 2016b). The results indicated that cetaceans discriminate between familiar and unfamiliar humans, sometimes preferring active humans. Cetaceans and other marine mammals have also been observed to spontaneously interact with visitors (Trone et al., 2005; personal observation Brando). The effects of public demonstrations (6.4.1) and visitor interaction programmes (6.4.2) are discussed below.

6.4.1. Public demonstrations

Due to their inherently charismatic natures, cetaceans and pinnipeds perform in demonstrations for large groups of visitors. Major zoo organisations such as EAZA, EAAM and WAZA have issued animal welfare strategies and or guidelines on the use of animals performing in demonstrations. The EAAM (EAAM, 2009) only has a short description while EAZA and WAZA have clear guidelines and aims in their strategies to ensure both high welfare and the ethical treatment and representation of animals (EAZA, 2014a, 2014b). The EAAM husbandry guidelines state that bottlenose dolphins should not be unnaturally provoked for the benefit of the viewing public (EAAM, 2009). Both EAZA and WAZA documents contain recommendations and specifics highlighting a commitment to high animal standards for animals used in any interactive experience.

While there are guidelines to promote good standards of welfare for performing animals, as reviewed above, empirical data are lacking on animal's experiences of performing in demonstrations. However, recently Jensen et al. (2013) attempted to measure the anticipatory behaviour of bottlenose dolphins before shows and found that dolphins decreased their activity levels and chose to approach the demonstration area before the demonstration began. Vigilance behaviour also increased prior to the show with animals being alert towards trainers and other activities around the pool. The authors mention seeing the 'waiting' behaviour during the study but do not consider this behaviour to be abnormal or stereotypic, instead concluding that shows were not perceived to be stressful or adverse by the animals.

Research on terrestrial mammals suggest that stimuli eliciting anticipatory behaviour can be perceived as either positive or aversive (Bassett and Buchanan-Smith, 2007). Waitt and Buchanan-Smith (2001) found that anticipation of feeding routines in primates had a considerable negative impact on behaviour, with higher rates of self-directed behaviour, inactivity, vocalisation and abnormal behaviours. Furthermore, when feeding was delayed past the mean routine time, these behavioural patterns were prolonged.

6.4.2. Visitor interaction programmes

Interactive programmes between visitors and marine mammals take place in many facilities around the world, most commonly with dolphins, seals and sea lions. These programmes are exclusive and usually more expensive than the regular facility ticket price, allowing small groups of visitors to get closer to and learn more about animals. Programmes often feature an educational segment, such as natural history, behaviour and anatomy, as well as a health and safety briefing. Most interactive sessions involve visitors either sitting, wading or swimming in the water, with physical (e.g. hugging, stroking) and non-physical (e.g. waving, trained hand signals) interaction (Samuels and Spradlin, 1995).

Dolphin swim programmes have not only been developed for the general public but have for many years been employed in animal-assisted therapies (Nathanson, 1998). People with learning difficulties, or physical or psychological impairments may interact with animals, most frequently dolphins, normally alongside professionals such as psychologists, speech therapists or kinesiologists (Nathanson et al., 1997). There is some evidence that swimming or wading with dolphins can have positive effects on human learning and development. For example, Nathanson and de Faria (1993) reported a significant improvement in cognitive responses when children were reinforced with dolphin interactions in comparison to reinforcement with a toy. Parents of children participating in dolphin-assisted therapy reported positive behavioural changes such as being less socially withdrawn, inhibition and anxiety disorder changes (Dilts et al., 2011)

Unfortunately there has been very little parallel research to investigate the impacts of human therapy interactions on dolphin welfare. In fact, the effects of all dolphin swim programmes are poorly understood as research is lacking. However, a study by Trone et al. (2005) found no detrimental effects on the behaviour of the dolphins they studied. Kyngdon et al. (2003) reported that dolphins increased the use of a refuge area during swim programmes, returning to pre-programme levels of refuse use within 15 min. The authors concluded that the dolphin swim sessions did not appear to have a detrimental effect on the dolphins. Miller et al. (2011) describe positive welfare and enriching experiences of education programmes in bottlenose dolphins as the animals exhibited higher rates of behavioural diversity, diversity of swimming style, and play behaviour following shows and interaction programmes. The authors found that affiliative, aggressive and repetitive behaviour and time spent socialising appeared to be unrelated to participating in interaction programmes. More research is needed to understand the short-term and long-term effects of cetacean swim programmes and how human behaviour can be directed to ensure good welfare in the animals.

6.5. Participation in research

Since the 1950′s, captive marine mammals have been trained to participate in research within the fields of physiology, cognition and animal communication (e.g. dolphins: Herman et al., 1984; orcas: Abramson et al., 2013; Szymanski et al., 1999; harbour porpoises: Desportes et al., 2007; sea lions: Schusterman and Kastak, 1993; seals: Dehnhardt et al., 2001; manatees: Bauer et al., 2003). Some of these studies had the aim of using the animals for delivering weapons or defending against them. Marine mammals have also been trained to better understand and mitigate problems such as bycatch, the unintended catch of marine mammals during fishing activities (e.g. porpoises: Teilmann et al., 2006) and responses to anthropogenic noises in the ocean (various cetaceans: Romano et al., 2004).

Facilities such as the Marine Science Center (Germany), the Fjord and Baelt Centret (Denmark), and the Kewalo Basin Marine Mammal Laboratory, Pinniped Cognition and Sensory Systems Laboratory, Navy Marine Mammal Program, Dolphins Plus, Moss Landing Marine Laboratories, and the Dolphin Research Center (U.S.A) are some of the many examples of facilities where animals have previously or currently participate in research. In addition, animals housed in zoos participate in research (dolphin: Brill et al., 1988; Hill et al., 2016a, 2016b; white-sided dolphins: Yeater et al., 2014; beluga whales: Yeater et al., 2014; Robeck et al., 2005; walrus: Schusterman and Reichmuth, 2008; sea otter: Hanna et al., 2016).

Research into the welfare of marine mammals when participating in research is currently lacking but from our practical experiences, working in and visiting many different facilities and projects (personal communication, Brando, Clark) it seems that animals experience pleasure (Panksepp, 2005), can enjoy participating, and can spend much voluntary time and many trials with the trainer and equipment. Motivation to continue during a long session or a high number of trials, or being frustrated in the phase when they do not understand the task or problem can sometimes be a challenge. Well-planned shaping sessions, good behavioural analysis, not moving too fast from step to step in the programme, and understanding the prerequisite behaviour necessary for success can help in errorless learning (Skinner, 1938; Ramirez, 2012).

Besides food, many other stimuli can be reinforcing to marine mammals and can therefore be used to maintain and extend interest and motivation during participation in research. These include ‘toys’ and tactile stimulation (Kuczaj and Xitco, 2002). The relationship between cognitive task level and welfare has been studied fairly well in great apes (see Clark, 2011) but thus far is overlooked in marine mammals. The housing conditions for some of the research animals is a topic requiring further investigation, as some of the holding pools and haul out areas, or social opportunities are more limited than in many zoos.

6.6. Best practice case study

In an innovative study of choice and control for bottlenose dolphins, the EchoLocation Visualisation and Interface System (ELVIS) was developed at Kolmården Dolphinarium, Sweden (Starkhammar et al., 2007). This is a software-based system providing infinite possibilities and variations, and is only limited by imagination. Sonar pulses from dolphins are detected by hydrophones and translated into a coloured light on an underwater screen. This system provides dolphins with immediate visual feedback of their sonar input. First, dolphins were trained to use their sonar beam to ‘hit’ symbols on the screen that represented different types of fish (herring, mackerel, capelin, and squid). In this manner, dolphins could choose what fish they preferred. Personal communication with J. Starkhammar (September 24th, 2016) indicated some interesting points: (1) dolphins quickly learned the task and were highly motivated to explore it, although individual differences were observed in the distances individuals chose to interact with the system, and the duration. (2) three dolphins were trained to ‘hit’ the symbols with their sonar beam; one individual was so eager that she engaged with the task without prompting from trainers; (3) when the whole pod swam around spontaneously without trainers present, interest in the ELVIS-system decayed gradually. Additional interactive functionality and more unpredictable access can likely increase and maintain their interest over time.

6.7. Future directions

There are many aspects of animal training requiring further investigation in marine mammals. We propose five complementary areas for future research. (1) To begin, more research is necessary to evaluate under what circumstances training is enriching for the animal. This necessarily involves investigating how training may be a form of social enrichment (i.e. providing more opportunities for complex social interaction), cognitive enrichment (i.e. providing mental challenges), physical enrichment (i.e. stimulating increased physical activity) or gateway to other forms of enrichment (i.e. allowing animals to understand basic rules regarding the timing and placement of enrichment, and their movement between different exhibit areas). (2) How can facility design provide options for more choice and control? (3) What are the welfare effects of human interactions on marine mammals housed under human care? (4) Considering that animal care staff can seldom spend 24 h at the facility caring for marine mammals, what are the effects of no human presence in the 'night time' on animal welfare? Finally, (5) we also recommend a thorough review of performance animal guidelines, to ensure that animal performances provide a strong educational and/or conservation message, and highlight directions for research to understand how animal perceive presentations and related activities.

7. Overall conclusions

- Marine mammals are charismatic species that command considerable public attention, both in the wild and under human care.
- The welfare of any animal is complex, and it is important to appreciate that animals have a range of needs and a range of coping systems. Whilst it is considered best practice to utilise a range of indicators of welfare, validation of many positive and negative indicators is still required for all species of marine mammals under human care.
- Welfare should be considered throughout the day and night and across the lifespan, including aspects like habitat complexity, social needs, nutrition, choice and control.
- More research in all areas of marine mammal welfare, care and management is needed, from a theoretical as well as practical approach. All marine mammal holding facilities should be involved in research to further the knowledge and experience on marine mammal welfare.
- Environmental enrichment should be a core and daily aspect of marine mammal care, be goal-directed, and consider aspects such as cognition, food, and structural enrichment
- Marine mammal husbandry guidelines for all species should be developed, maintained and updated as new research and practical experiences become available, going above and beyond minimum legislation and guidelines.
- In order to make evidence-based decisions, we need a better fundamental understanding of what is optimal welfare for wild and captive animals, including marine mammals. Evidence-based decisions on how to best provide for optimal animal welfare can have ethical implications if data confirm a failure to do so adequately, i.e. if it is not possible to provide for optimal welfare. At this point an ethical decision on whether or not to keep each species of marine mammal is necessary. Minimising the gap in comprehension of marine mammals perceptions and choices, individualising their needs, diminishing anthropomorphic interpretations, and assuming our capabilities as caregivers, are key for future plans.

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