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*Applying welfare science to bottlenose dolphins (*Tursiops truncatus*)*

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Abstract

*Animal welfare science is a burgeoning field, but research on cetaceans (whales, dolphins and porpoises) is lacking. Bottlenose dolphins (*Tursiops truncatus*) are the most well-known and studied cetaceans, particularly in captivity, and thus are used in this review as a model for other cetacean species. Despite the public interest and need for such research, studies specifically investigating dolphin welfare are lacking. This review uses the three broad categories of behaviour, health, and cognition, to discuss how dolphin welfare has been assessed thus far, and could be assessed in future. We present welfare indicators validated in other species that could be applied to dolphins, including innovative measures, such as cognitive appraisal of emotions. We provide a summary of practical recommendations for validating the indicators of bottlenose dolphin welfare. This paper aims to stimulate further research into dolphin welfare which could improve the lives of the animals themselves and ultimately support regulatory decisions. We recommend uniting expertise in cetology and welfare science in order to develop a holistic approach to dolphin welfare assessment.*

Keywords: *affective states, animal-based measures, animal welfare, bottlenose dolphins, cetaceans, welfare assessment*

Introduction

Research into welfare assessments for zoo and aquarium (hereafter referred to as 'zoo') animals is increasing as farm animal welfare assessment is proven to be feasible and valid (Barber 2009; Whitham & Wielebnowski 2013). There is much support for the adaptation of farm animal measures to zoo animals (Swaisgood 2007; Hill & Broom 2009; Mason & Veasey 2010), and zoological institutions are well set-up for conducting measures due to the individualised care and multiple daily interactions (Barber 2009).

In this review, we conceptualise welfare using Spruijt *et al*'s (2001) description of a "…balance between positive (reward, satisfaction) and negative (stress) experiences or affective states. The balance may range from positive (good welfare) to negative (poor welfare)". This 'feelings-based' definition aligns with positions taken recently by many others (eg Yeates & Main 2008; Mason & Veasey 2010; Watters 2014; Dawkins 2015), and specifies measurement of both positive and negative welfare. Our review also prioritises animal-based over resource-based measures, since they are more likely to accurately reflect welfare (Webster 2005; Roe *et al* 2011; Whitham & Wielebnowski 2013). We also give equal consideration to indicators of positive and negative welfare (Désiré *et al* 2002; Paul *et al* 2005; Boissy *et al* 2007; Yeates & Main 2008).

There is very little existing research on the welfare of cetaceans (Ugaz *et al* 2013; Clegg *et al* 2015), in captivity or the wild. Given that public interest often stimulates research in the associated areas (eg with farm animal welfare; Rushen *et al* 2011), cetacean welfare studies are likely to increase markedly in the near future since the public's interest is at a high level and intensity (Grimm 2011; Ventre & Jett 2015). Although many questions posed are, in fact, ethical dilemmas (eg 'Should we keep dolphins in captivity?'), objective data on the animals' welfare state would aid in these personal decisions (Jiang *et al* 2007; Clegg *et al* 2015). Published farm welfare assessments have shown how this type of data can be gathered, for instance the Welfare Quality® project for farm animals (2009a,b,c) and its subsequent cross-species adaptations (eg Mononen *et al* 2012; Clegg *et al* 2015; Barnard *et al* 2016).

While cetology, the study of cetaceans, has burgeoned (Hill & Lackups 2010), there are very few studies on cetacean welfare and methods of assessment (Galhardo *et al* 1996; Clark 2013; Ugaz *et al* 2013; Clegg *et al* 2015). Bottlenose dolphins (*Tursiops truncatus*) are the most studied cetacean species (Hill & Lackups 2010), and the most common in captivity (Pryor & Norris 1998; Wells & Scott 1999), thus we choose them as the focus species for this review of how welfare science could be applied to cetaceans. We arrange the relevant cetology knowledge

into behaviour, health-related and cognition research, all well-established specialities (Wells 2009). These three categories are derived from Webster's (2005) 'Triangulation' principle for the measurement of welfare, where accumulating information from each specialty increases overall validity. Importantly, while our review includes wild research and welfare applications (wild animal welfare should be measured: Jordan 2005; Ohl & van der Staay 2012), our discussions orientate towards captive dolphins since their environment is closely controlled by humans. The necessity for dolphin welfare research is clear: there are 250 bottlenose dolphins in the European Association of Zoos and Aquaria facilities (EAZA 2015), 444 animals listed in US and Canadian dolphinaria (in 2011; Ceta-base), and many others worldwide not registered on an official record, all maintained in a huge range of facility types that differentially impact welfare (Joseph & Antrim 2010).

This review compiles what we believe to be literature on wild and captive bottlenose dolphins most relevant to welfare, suggesting some farm and zoo animal approaches which could be adapted to cetaceans, with final recommendations on initial studies and how the dolphin welfare discipline might evolve. A strong focus is maintained on those areas of cetology that merit further investigation to answer questions on bottlenose dolphins' quality of life.

Published work on dolphin welfare

There are very few studies of dolphin welfare, either in captivity or the wild (Ugaz *et al* 2013; Clegg *et al* 2015). Thus, there are no validated measures, ie ones that we know are linked to positive or negative affective states, as yet. Given the dearth of welfare research, in some cases findings from other cetacean species are extrapolated to bottlenose dolphins.

Studies of wild dolphin welfare

Only a handful of studies have focused on welfare concepts with regard to wild cetaceans, and even within these direct mentioning of the word 'welfare' is rare. A popular topic has been assessments of the impacts of tourist boats on various cetacean species (eg Stockin *et al* 2008; Christiansen & Lusseau 2015), although the focus remains at population-level indicators. Long-term data revealed that rate and repetitions of wild bottlenose dolphin whistles were potential indicators of short-term stress (Esch *et al* 2009). A more recent study suggested that an upward shift in whistle frequency was linked to increased emotional arousal (Heiler *et al* 2016). Butterworth *et al* (2013) empirically evaluated dolphin welfare in the Taiji drive hunts, an annual harvesting of dolphins in Japan, but this research only concentrated on welfare at the point of death. In the first and only teaming of wild marine mammal research with animal welfare science to our knowledge, Butterworth *et al* (2012) used the Five Freedoms to discuss how entanglement affects individual animal welfare in a number of species, including dolphins.

Studies measuring captive dolphin welfare

Similarly, there are only a handful of captive dolphin studies that have endeavoured to develop welfare measures. Ugaz *et al* (2013) correlated salivary cortisol to behavioural parameters in 23 *T. truncatus*, concluding that welfare was better in open (enclosed area of the sea) than closed (artificial water and pool) facilities due to lower cortisol levels and less floating and circular swimming. Castellote and Fossa (2006) suggested acoustic activity as a welfare measure for belugas (*Delphinapterus leucas*) and found it dropped to low levels during stressful events, but they did not correlate it with other parameters and only studied two animals. In a multi-disciplinary approach, Waples and Gales (2002) looked at inappetence, social behaviour, lethargy, weight loss and blood parameters in three *T. truncatus* with substantially deteriorating welfare likely due to social stress, revealing useful associations although again limited by sample size.

The C-Well© Assessment

In the first development of a welfare assessment protocol for dolphins, Clegg *et al* (2015) studied 20 *T. truncatus* in three facilities and adapted a well-established farm animal assessment (Welfare Quality® 2009a,b,c) to this species (the C-Well© Assessment). The research used 36 multi-dimensional measures, 58% of which were animal-based, to yield individual welfare scores comparable on many different levels (eg by measure, criteria, in total; among pools, sex, age class, facilities). Although the measures were unweighted, they were validated through expert opinion and application in specific contexts, and have associated standardised methods and thresholds. Some are reviewed in the relevant categories in *Research relevant to dolphin welfare*.

Given the lack of existing studies on dolphin welfare indicators, the next section is a review of cetology disciplines relevant to welfare. We expanded Webster's (2005) welfare measurement categories to behaviour, health (from Webster's 'physiology') and cognition (from 'neurobiology'). Health, while still including physiology, encompasses longer-term welfare indicators, and cognition includes experimental psychology methods potentially valuable for assessing welfare.

Research relevant to dolphin welfare

Health

Health-welfare interface

Health and welfare interact directly and indirectly as part of a complex relationship (Walker *et al* 2012). A reasonable level of health is considered a prerequisite for good animal welfare (Webster 2005; Hill & Broom 2009), while poor health is a likely contributing factor to poor welfare (Fraser *et al* 1997; Dawkins 2004; Boissy *et al* 2007; Mason & Veasey 2010). But do all components of poor health affect welfare? We refer back to our definition of welfare (Spruijt *et al* 2001) to address this: the balance of affective states and health and should only be impacted when poor health

either directly impacts affective state through, for example, nausea, lethargy or pain, or indirectly through loss of function. Poor health (eg an asymptomatic tumour) does not always affect emotional state and hence welfare, as we define it (Fraser *et al* 1997; Mason & Veasey 2010).

Health parameters in dolphins

An infection or disease can cause pain and/or 'sickness behaviour', which includes inappetence, lethargy, depression, and anti-social behaviours, all of which have direct or indirect effects on affective state (Broom 1991; Millman 2007; Sneddon *et al* 2014). Dolphins tend to mask symptoms of pain and disease as a survival adaptation (Waples & Gales 2002; Castellote & Fossa 2006), which therefore may only become obvious when the health problem is severe. Perhaps, as a consequence, little is published about indicators of pain in dolphins, with exceptions for extreme situations, such as their behavioural response to killing methods in the wild (Butterworth *et al* 2013). Weary *et al* (2006) and Sneddon *et al* (2014) provide cross-species advice for identifying behavioural and physiological pain markers, such as studying behavioural differences after analgesia administration. Inappetence and lethargy in dolphins have been correlated with many different diseases and together are generally reliable as poor health indicators (Joseph *et al* 1986; Johnson *et al* 2009). However, they can also be caused by social stress or even reproductive events such as oestrus (Waples & Gales 2002), where the associated affective states may vary from negative to positive. Studies on the behavioural and haematological characteristics of inappetence, where differentiations are made depending on whether it was caused by poor health or social stressors, are much needed.

In lieu of reliable pain indicators, physical bodily damage has been used as a health-related welfare measure in other captive species (Broom 1991; Welfare Quality® 2009a,b,c; Mononen *et al* 2012), and for wild animals as well (eg Jordan 2005; Cattet *et al* 2008). Clegg *et al* (2015) proposed the percentage of rake marks (superficial lesions and scars caused by conspecifics in play, sexual and aggressive behaviours; Scott *et al* 2005) on the body as a welfare measure for bottlenose dolphins, since such marks can be used as a proxy indicator of aggression levels and social stress (Scott *et al* 2005; Orbach *et al* 2015). However, this measure requires further investigation, for example to differentiate rake-mark levels due to high levels of play and aggression while controlling for age and sex differences.

Longer-term measures of dolphin health could also be useful for assessing welfare. Body Condition Scoring (BCS), an assessment of the extent of body fat present (Roche *et al* 2009), has been favoured as a general welfare measure (eg wild: Mann & Kemps 2003; Pettis *et al* 2004; Cattet *et al* 2008; captive: Roche *et al* 2009; Welfare Quality® 2009a,b,c; Mononen *et al* 2012) and it has already been used in wild health assessments of *T. truncatus* (Fair *et al* 2014; Schwacke *et al* 2014). Joblon *et al* (2014) produced a standardised protocol using stranded short-beaked common dolphins (*Delphinus delphis*), and Clegg *et al* (2015) developed a standardised BCS graphic for *T. truncatus* but did not test its reliability. The next step for these BCS tools is to correlate the results to other measures of affective state: Roche *et al* (2009) conducted this with cows, concluding that BCS may serve as a proxy indicator for hunger, satiety or feeling ill (leading to inappetence). Other health-related conditions such as diarrhoea, skin inflammation, eye condition, and coughing, have been used as farm animal welfare measures (Welfare Quality® 2009a,b,c; Mononen *et al* 2012), some of which were proposed for *T. truncatus* welfare (skin and eye condition, coughing; Clegg *et al* 2015), but have not been studied in relation to affective states. Haematological indices can be measures of disease states, especially when the pathology is advanced, but so far have had limited use in welfare assessments due to potential high inter- and intra-individual variation. Although wild dolphin health assessments have published their data and established baselines (Thomson & Geraci 1986; Dierauf & Gulland 2001; Wells 2009), and captive dolphin voluntary blood sampling is readily achievable using positive reinforcement training (Brando 2010), studies have not yet linked ranges of blood values to health-related welfare.

Population measures of longer-term health and welfare such as longevity and reproductive rate should also be considered (Dawkins 1998; Barber 2009). However, as with farm animals, parameters, such as high reproductive success, do not necessarily indicate that welfare is good (Dawkins 1980). For captive dolphin populations, baselines are being established by projects (notably in the US) allowing access to their valuable multi-species databases (Small & DeMaster 1995; Innes *et al* 2005; Venn-Watson *et al* 2011). Welfare conclusions from fitness measures should be supported by other data (Swaisgood 2007), such as in Christiansen and Lusseau's study (2015) linking disturbance behaviour from whale-watching boats, body condition and foetal growth rate in minke whales (*Balaenoptera acutorostrata*). Data on the incidence and severity of diseases can also be used as population-level health parameters: such wild studies are available (eg Reif *et al* 2008; Schwacke *et al* 2014), but data are not published for captive dolphins. However, extensive records are kept for most captive dolphins (C van Elk, personal communication 2016) and, thus, peer-reviewed publications on the nature of their diseases would be beneficial for establishing standardised health assessments.

Physiological parameters

Measures of physiological responses can contribute to assessments of emotions and affective states (Désiré *et al* 2002; Webster 2005; Boissy *et al* 2007). Endocrine responses to stressors are most commonly used (eg Moberg & Mench 2000), but as interest increases in positive welfare, other markers are being considered: for example, the balance of sympathetic and parasympathetic systems (for a review, see Boissy *et al* 2007), and indicators of eustress (positive stressors, eg mate acquisition, experienced by the animal; Selye 1975). Within dolphin physiology research, numerous studies of physiological measures

of stress for wild *T. truncatus* (eg Ortiz & Worthy 2000; Fair *et al* 2014; Schwacke *et al* 2014) have provided useful baselines, which will start to elucidate individual variation and repeatability questions (Atkinson *et al* 2015). Sample collection in the wild is challenging since taking blood is not possible without restraint and faecal samples are difficult to obtain (Atkinson *et al* 2015). This area, specifically, is where training for voluntary samples in captivity has exceptional advantages; for example, voluntary saliva collection is feasible and can provide accurate cortisol measurements in *T. truncatus* (Pedernera-Romano *et al* 2006; Ugaz *et al* 2013). Other sampling protocols are also possible with training, such as blood, faecal, blow (expiration of air) and biopsy collection. As for terrestrial animals, marine mammals experience diurnal and seasonal variation in cortisol levels (for a review, see Atkinson *et al* 2015), which would need to be taken into account in any welfare assessment and suggests that a conservative range would need to be used in any conclusions made, as opposed to a single threshold. Additionally, a recent review advised caution when applying terrestrial animal stress models to marine mammals. While corticosteroid pathways seem to be similar, evidence indicates other neuroendocrine hormones (eg catecholamines) may be regulated very differently (Atkinson *et al* 2015). Further, long-term studies on cetaceans in captivity could start to answer such questions on hormone regulatory systems. Innovative new collection techniques enabling accurate animal identification (example with cetaceans: whale blow), and insightful behavioural correlations, must also guide future progress (Möstl & Palme 2002): advice very applicable to dolphin studies.

Behaviour

Social behaviour

Behavioural measures are an important component in welfare frameworks (Dawkins 2004; Maple 2007), with some believing that they are more informative about welfare than health since behaviours are likely more indicative of emotional state (Gonyou 1994; Joseph & Antrim 2010). There have been a number of long-term studies of wild dolphin behaviour (Wells 1991; Mann *et al* 2000; Parsons *et al* 2006), including social relationships within their fission-fusion societies (Mann *et al* 2000; Wells 2009). Surprisingly, ethological studies of captive populations have not, until recently, been commonplace (Dudzinski 2010). Social behaviour measures will foreseeably be one of the most important tools in assessing dolphin welfare: as highly social mammals (Pryor & Norris 1998; Mann *et al* 2000), they are susceptible to social stress. Sudden changes in conspecific associations, aggression levels and social isolation have been correlated with declines in welfare (Waples & Gales 2002). Excessive or abnormal aggression levels are used as farm animal welfare measures (Webster 2005; Welfare Quality® 2009b; Mononen *et al* 2012), and using existing ethograms of aggressive behaviours to analyse frequencies over time could reveal dolphins' 'excessive' and 'normal' thresholds (Samuels & Gifford 1997; Scott *et al* 2005). Increased quantity and severity of rake marks could serve as a proxy indicator for levels of aggression and social stress (Waples & Gales 2002; Scott *et al* 2005). Clegg *et al*'s (2015) rake-mark assessment, currently using very conservative thresholds, might be validated to allow monitoring of aggression levels. Rake-mark quantification is an example of a method where collaboration between wild and captive researchers might be fruitful, since aggression is harder to observe in the wild and rake-mark levels could be used as proxy measures (Clegg *et al* 2015; Scott *et al* 2005).

While social stress is a negative consequence of being a social mammal, the highly social life of dolphins also has positive effects. Positive social (ie affiliative) behaviour has been proposed as an indicator of good welfare in other species (Boissy *et al* 2007; Buchanan-Smith *et al* 2013). Affiliative behaviour has been well-documented in wild *Tursiops* spp (Herman & Tavolga 1980 (early review); Connor *et al* 2000, 2006; Sakai *et al* 2006), and a little less so in captivity (Tamaki *et al* 2006; Dudzinski 2010). Gentle rubbing behaviours between dolphins are thought to be analogous to allogrooming in terrestrial mammals (Tamaki *et al* 2006; Kuczaj *et al* 2013) and may have potential as a measure of good welfare (Boissy *et al* 2007), along with synchronous swimming (thought to reflect social bonds; Connor *et al* 2006). Dudzinski (2010) and Kuczaj *et al* (2013) reviewed both wild and captive social affiliative behaviour, agreeing that in both settings tactile behaviours seem to be used to express emotions.

Play

Play behaviour is one of the strongest potential welfare indicators for animals, mainly because it is more likely to occur in the absence of threats and utilitarian needs (Bel'kovich *et al* 1991) and is linked to positive emotions (Held & Špinka [2011] reviewed link with welfare). Play is also likely to improve long-term fitness and health, as well as being socially contagious and therefore capable of spreading good welfare in groups (Held & Špinka 2011); these less-acknowledged benefits are especially relevant to the welfare of group-living dolphins. Despite this, play is not commonly used as a measure in welfare assessments (Welfare Quality® 2009a,b,c), most likely because of its inherent variability (Held & Špinka 2011) and difficulty of measurement There is also evidence for some species that play may not always be linked to a positive emotional state (Blois-Heulin *et al* 2015).

Evidence for wild and captive dolphin play is abundant (for reviews, see Paulos *et al* 2010; Kuczaj & Eskelinen 2014), including copious examples of object play (recent papers: Kuczaj & Makecha 2008; Paulos *et al* 2010; Greene *et al* 2011; Delfour & Beyer 2012), and evidence of inventing games (Pace 2000). McCowan *et al* (2000) showed that captive dolphins monitored their bubble quality as well as 'planned' for the behaviour; suggesting involvement of conscious thought and appraisal and strengthening the notion that play impacts affective state. Hill and Ramirez (2014) studied play in 14 belugas (*Delphinapterus leucas*) over three years, revealing differences between adult and

young preferences and showing that bouts were longer and more diverse when enrichment devices were involved. Where play is studied in captivity, the influence of any prior conditioning should be noted: Neto *et al* (2016) showed that when trainers positively reinforced dolphins' interactions with toys, their interest in the objects increased outside of the sessions. This technique could be used to increase the benefits of the toys to the dolphins but, until we have other measures of positive affective states available in this situation, the motivation to play may be influenced. In any case, as with all species, standardised measurements are needed. A study of African elephants (*Loxodonta africana*) addressed this using a play index (Vicino & Marcacci 2015), and a similar approach might be possible with dolphins. Such a behavioural measure could easily be applicable to wild dolphin welfare assessments, for example to investigate whether exposure to more environmental or social stressors results in reduced play frequencies.

Abnormal behaviour

Abnormal behaviours are most often studied in the context of stereotypic behaviour, which has been most recently defined as "…repetitive behaviour induced by frustration, repeated attempts to cope, and/or CNS dysfunction" (Mason & Rushen 2008). Abnormal behaviours are seldom observed in wild animals, although Miller *et al* (2011a) suggest they observed stereotypic swimming in lemon sharks (*Negaprion brevirostris*). In one of the only studies describing abnormal behaviour in wild dolphins, the causes and effects of solitary living for *T. truncatus* were investigated, and certain aspects were concluded as abnormal (eg behaviour oriented excessively towards humans; Müller & Bossley 2002). Stereotypic behaviour is commonly investigated as a welfare measure for captive animals (for a review, see Mason & Rushen 2008). There are scarcely any published studies with captive dolphins, and the small handful existing are outdated (Gygax 1993 and Clark 2013 describe this literature), making it hard to identify any common explanatory variables. Stereotypic swimming has been discussed in the literature as a concern for captive dolphins. There are disparities among definitions of this behaviour (Gygax 1993; Miller *et al* 2011b), but terrestrial animal studies also suffered similar problems with pacing behaviours and found that the variability and possible functions must be meticulously analysed for it to be defined as a stereotypy (Mason & Rushen 2008). Sobel *et al* (1994) observed preferences in the directionality of circular swimming, but did not measure whether the route around the pool was fixed and whether the animal was vigilant at the time. There is little evidence correlating stereotypic swimming with other potential factors of welfare. For example, although Ugaz *et al* (2013) found that in closed facilities there were higher rates of circular swimming as well as higher cortisol levels, they did not statistically test for a correlation between these two factors. Clegg *et al* (2015) included a stereotypy measure but based thresholds on terrestrial animal frequencies, since there was no data from dolphin species. Since there are ongoing questions about whether higher stereotypy frequency infers poorer welfare, even in terrestrial animals (Mason & Latham 2004; Dawkins 2006; Mason & Rushen 2008), future studies on this phenomenon in dolphins should aim to correlate suspected stereotypic behaviour with other indicators of welfare to validate it as an indicator. Basic work regarding the appearance of stereotypies is also needed, for example, the two main types of stereotypy defined in terrestrial mammals are 'oral' and 'movement' (Webster 2005; Mason & Rushen 2008), so a fundamental investigation would be to ascertain whether the same is true for dolphins.

Anticipatory behaviour

Recently, anticipatory behaviour (a measure of 'reward-sensitivity'; Spruijt *et al* 2001) has been used as a welfare measure in farm and zoo animals; low intensity anticipatory behaviour is thought to reflect positive affective states and high intensity anticipation indicates poorer welfare as the animal is heavily dependent on the reward (Spruijt *et al* 2001; Watters 2014). While one preliminary study focused on anticipatory behaviour in captive bottlenose dolphins (Jensen *et al* 2013), further work is necessary given the different training methods (ie conditioning to 'rewards') in dolphin facilities, which might ultimately be closely linked to welfare. Based on the reward-sensitivity paradigm it is likely that dolphins showing moderate anticipatory behaviour might experience positive affective states, while those that perform it for excessive amounts of time might be frustrated or have little other stimulation (Watters 2014). In order to evaluate its utility for welfare assessment, future studies with dolphins and other species should investigate the association between anticipatory behaviour frequencies and other welfare indicators, in order to understand what might qualify as 'excessive' levels.

Cognition

Emotions

Emotions are defined as intense, short-lived affective responses to an event, usually associated with specific physiological changes (Dantzer 1988). Animals with higher cognitive abilities may be capable of more complex emotions (eg guilt) (Paul *et al* 2005), and while this might result in increased chances of suffering, it could also lead to higher potential for positive affective states. Research beyond the 'basic emotions' (eg fear, rage, play; Mendl *et al* 2010) is essential to understand the valence and arousal levels of affective states which make up overall welfare (Leliveld *et al* 2013; Siegford 2013). Désiré *et al* (2002) and Boissy *et al* (2007) provide reviews on measuring animal emotion and the relevance to welfare.

Although dolphin emotion studies are scarce, there have been more studies on negative than positive ones. Most studies have looked at how sounds might reflect emotions, for example, burst pulse sounds have been associated with agonistic and aggressive behaviours (Overstrom 1983), and long-term etho-acoustical projects have made headway in pairing sounds to behaviour (eg Herzing 1996; Janik & Sayigh

2013). Animal emotion research is now widening to measure positive emotions as well (Boissy *et al* 2007), but there are no strongly supported indicators as yet in dolphins (Kuczaj *et al* 2013). Tactile behaviour was suggested by Dudzinski (2010) and Kuczaj *et al* (2013) to be linked to positive emotions in dolphins, but has not yet been analysed in conjunction with other indicators. Motivation and preference testing are applicable to captive dolphins and could reveal indicators of emotion (Gonyou 1994; Mendl *et al* 2010).

Environmental enrichment

This sub-section is applicable to dolphins under human care only. Environmental enrichment is any technique designed to improve biological functioning of captive animals through environmental modification (Newberry 1995). Bottlenose dolphins are good candidates for enhanced welfare through enrichment due to their cognitive abilities (Schusterman *et al* 2013) and propensity to, and creativity within, play (Kuczaj & Eskelinen 2014). Enrichment has been provided to captive dolphins for several decades, but there are few published studies describing the animals' responses (for a review, see Clark 2013). Furthermore, enrichment is often assumed to automatically enhance welfare even if it is unclear whether the animal's affective state will be improved (for reviews, see Swaisgood 2007; Würbel & Garner 2007). Enrichment strategies should be monitored to ensure that they are true enrichment by monitoring the animals' responses and looking for signs of habituation so that decisions can be made as to when, where and how the enrichment is presented again (Kuczaj *et al* 2002; Hoy *et al* 2010; Siegford 2013).

Recently, cognitive challenges have been presented as enrichment, with positive results as long as the animals possess the resources and skills to solve the problem (Meehan & Mench 2007; Siegford 2013). Clark (2013) supports cognitive enrichment with dolphin species, hypothesising that floating, simplistic objects are not sufficient to hold the dolphins' interest in the long-term. However, behaviour should be monitored to investigate whether this is indeed the case (Hill & Broom 2009), and such data, which shows responses to definable, repeatable contexts, could also aid in finding welfare indicators (Delfour & Beyer 2012). The Human-Animal Relationship (HAR) is only just beginning to be investigated in other species in relation to cognitive enrichment and welfare (Whitham & Wielebnowski 2013) and, due to the multiple, daily, and often close-contact interactions, is very likely to contribute to the welfare state of captive dolphins (Brando 2010; Clegg *et al* 2015). Future investigations assessing the HAR might aim to disentangle the effects of food reinforcement with the dolphins' attitude towards the humans themselves. An example of such an approach is shown by Perelberg and Schuster (2009), who demonstrated that outside of feeding sessions, a captive bottlenose dolphin group approached humans to receive rubs and petting in the absence of any other rewards. Given that many cetacean species show much tactile behaviour during intra-specific social affiliation (Dudzinski 2010; Kuczaj *et al* 2013), investigating the frequency and dimensions of voluntary human contact by the animals, during and outside of training sessions, might be a meaningful measure of their affective states.

Cognitive measures of dolphin welfare

Dolphins' cognitive abilities are frequently compared to those of great apes (Delfour 2010; Schusterman *et al* 2013), and may be linked to their fusion-fission society (Connor *et al* 2000; Maze-Foley & Würsig 2002). Dolphins display co-operative hunting (Connor *et al* 2000), use tools (eg Smolker *et al* 1997), and recognise their mirror image (Reiss & Marino 2001; Delfour 2006). Studies of cognitive bias, which investigate how emotional experiences affect cognitive processes, may aid in our interpretation of welfare, and constitute measures themselves (Paul *et al* 2005; Mendl *et al* 2009). Given the dolphins' learning capabilities (Brando 2010), many of the non-invasive cognitive bias methods reviewed in Mendl *et al* (2009) used with other species could be adapted. Paul *et al* (2005) also reviewed evidence for memory and attention bias processes in animals, concluding that if confirmed they could have implications for measuring welfare.

In humans as well as non-humans, the brain hemispheres process information differently, producing lateralised behaviours, ie a preference for either the left or right eye or body part (Rogers 2002). It seems that animals may predominantly use the right hemisphere when stressed (see Rogers 2010), with Leliveld *et al*'s (2013) review going further to conclude that negative emotions are managed by the right hemisphere and positive emotions by the left ('emotional lateralisation'). Examples of lateralised behaviours in wild and captive cetaceans are common, eg during foraging (Clapham *et al* 1995; Silber & Fertl 1995), flipper-rubbing (Sakai *et al* 2006), and visual discrimination tasks (Yaman *et al* 2003; Delfour & Marten 2006). Most notably, Karenina *et al* (2010, 2013) showed that belugas and killer whales (*Orcinus orca*) placed calves on their right side in non-threatening situations, with killer whales preferring the left when the situation became increasingly threatening (in this case proximity to boats). Sakai *et al* (2006) suggested a link with positive affective state since the left pectoral fin and eye were favoured during affiliative flipper-rubbing behaviour in Indian Ocean bottlenose dolphins (*Tursiops aduncus*). These last examples concerning lateralised behaviour and affective states should form a basis for future research into welfare implications of this phenomenon.

In the field of cognition, in particular, but also within health and behaviour, researchers rarely study both wild and captive dolphins, resulting in a skewed perspective of particular topics in certain environments, and leading us to an initial recommendation to increase collaborative efforts and reviews (in accordance with Hill & Lackups 2010; Pack 2010). Finally, although we must understand the dolphins' cognitive abilities, we should do so bearing in mind their *umwelt*, ie their 'subjective universe', and the focus of ethophenomenological studies (Delfour 2006, 2010). For example, an intermodal associative task was completed

very differently by bottlenose dolphin subjects due to the dominance hierarchy at the time dictating participation and mode of learning (Delfour & Marten 2006). Being cognisant of the dolphins' *umwelt* may help in determining what is important to the dolphins, and thus how to provide them with a good quality of life.

Considerations for developing dolphin welfare measures

In this section we review recommendations on the design of studies to investigate the measures discussed above. Welfare measures should be developed *in situ*, thus ensuring applicability to the dolphins and their environment (Dawkins 2006; Maple 2007). The measures must also be species-specific (Blokhuis 2008; Barber 2009; Hill & Broom 2009), and examine welfare at an individual level where possible (Siegford 2013). Zoological institutions have been advised to employ scientists specifically dedicated to assessing welfare (Maple 2007; Barber 2009), and facilities maintaining dolphins should take this step also.

The first proposed measures for *T. truncatus* should be validated through correlations with other parameters. Our review addresses the potential measures for validation which we identified with respect to cetacean health, behaviour and cognition (Table 1). When establishing welfare measures, studies of captive rather than wild dolphins, are more likely to be successful due to greater access to the subjects, their history, and their environment. International, inter-facility collaborations are vital to combat problems of low sample sizes and to control for inevitable environmental variation. For wild dolphin welfare indicators, long-term studies are the natural starting point since most have individual behavioural, physiological, as well as life history data (Wells 2009; Fair *et al* 2014). While it would be inaccurate to apply all measures for wild and captive animals without validation (Jordan 2005), it is likely that many welfare indicators, at least behaviourally, will be consistent between wild and captive *T. truncatus* since their repertoires show similarities (Mann *et al* 2000; Dudzinski 2010).

When validating measures, pre-existing conditions can be used where it is likely the animal has very good or poor welfare (Jordan 2005; Castellote & Fossa 2006; Whitham & Wielebnowski 2013). For example, transportation offers opportunities to assess welfare as it is assumed to induce a substantial, but short-term, welfare change for captive cetaceans (eg Castellote & Fossa 2006). Long-term states associated with social contexts may be more salient for welfare measurement: for example, the period after transport when the animals are introduced to a new group. Group changes are frequent enough in dolphinaria networks to provide adequate sample sizes for analysis. The selected behaviours and physiological parameters should then be measured during these events (and cognitive data if possible), with focal qualitative data (eg trainer ratings) taken concurrently to support the presumed change in welfare. Welfare measures should be conducted regularly, and also separately from full assessments. For example, behavioural measures of welfare could be applied on a weekly basis to dolphin groups since behavioural monitoring has been advised as essential for ensuring good welfare (Maple 2007), and especially with captive dolphins (Waples & Gales 2002; Clegg *et al* 2015). Eventually, comparing results from measures and assessments between individuals can highlight associations with good or poor welfare, thus indicating where changes in management protocols should occur and stimulating improvements in welfare of the animals themselves.

Table 1 Summary of the welfare-related topics in dolphin health, behaviour and cognition which merit further investigation in order to develop measures of welfare. Evidence supporting each topic has been taken from bottlenose dolphins (*Tursiops truncatus*) where possible, but where these were lacking studies from other cetacean species had to be used.

Category	Aspects meriting further investigation as dolphin welfare measures
Health	Epidemiological measures (eg mortality, reproductive success)
	Disease prevalence
	Body Condition Scoring
	Cortisol (and other 'stress' hormone) levels
	Rake mark percentage cover
Behaviour	Excessive aggression
	Affiliative behaviour
	Play
	Anticipatory behaviour
	Abnormal and stereotypic behaviours
Cognition	Emotions linked with sound production
	Indicators of basic emotions (eg fearful, playful, rage)
	Indicators of more complex emotions (eg contentedness, depression)
	Cognitive bias testing
	Visual and behavioural laterality

Conclusion

We have reviewed the literature on animal welfare science and cetology in order to identify the most successful intersections for developing bottlenose dolphin welfare measures. A general theme is that collaborations, whether wild-captive, across different cetology fields, or between multiple captive facilities, are necessary if we want to address this multi-dimensional concept.

We suggest that indicators, such as cortisol levels, inappetence and bodily injuries, as well as body condition and population fitness measures in the longer term, may help us assess health-related welfare. Behavioural measures are

likely to be the most informative for dolphin welfare, and we have shown evidence that tactile affiliation, play, anticipatory behaviour and stereotypic behaviours may be closely linked to affective states. Cognitive measures reflect how behavioural and physiological components are integrated to form the affective states experienced by the animals, and thus recent techniques, such as cognitive bias testing hold much promise for welfare assessment.

Lastly, we identified practical recommendations for validating the first measures, concluding that although captive studies should take the lead, long-term wild studies are also rich sources of potential indicators. Any proposed measures should be tested in situations likely to elicit changes in welfare with adequate sample sizes to allow the major environmental variations to be controlled for. Established measures would allow facility managers to monitor and improve the dolphins' welfare, aid in regulatory decisions, and could enrich wild dolphin research by revealing changing affective states. This review's findings are species-specific to bottlenose dolphins, but the general principles and selected measures could be adapted to other cetacean species. Our overall aim was to present current cetology knowledge in terms of measuring welfare, with the hope of stimulating researchers globally to take up the challenge.

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