



An Inventory of Peer-reviewed Articles on Killer Whales (*Orcinus orca*) with a Comparison to Bottlenose Dolphins (*Tursiops truncatus*)

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Abstract - The welfare of killer whales (*Orcinus orca*) has received worldwide attention recently. The purpose of this study was to sample the peer-reviewed scientific research on killer whales with a complementary comparison to Atlantic bottlenose dolphins (*Tursiops truncatus*) to ascertain the primary topics of research conducted with these two cetaceans. A second objective of the study was to assess the relationship between the research topic and the setting in which the research was conducted. From a database-driven search of peer-reviewed academic journal articles, 759 unique articles involving killer whales, 2,022 unique articles involving Atlantic bottlenose dolphins, and 38 additional articles that included both species were retained for analysis. Coders categorized each article by topic (Anthropogenic Response, Cognition, Distribution, Echolocation, Foraging/Predation, Health/Physiology, Interactions with Humans, Sociality, and Vocalization) and research setting (Natural Habitat, Captivity, or Both). Most studies of killer whales involved animals in their natural habitat (90%) and the majority of killer whale studies, regardless of setting, concentrated on health and physiology, such as contaminants and genetic variability (31%), foraging and predation behaviors (26%), and geographic distribution (20%). The majority of the studies (68%) involving bottlenose dolphins were also conducted in their natural habitat, but there was significantly more research comparatively with captive animals and with greater diversity. The results suggested that research with killer whales has been dominated by a limited range of topics with relatively little research conducted on topics that directly address issues of welfare. Similar to killer whales, research with Atlantic bottlenose dolphins has been dominated by health and physiology (48.5%) and distribution (17.6%). In contrast to killer whales, topics such as sociality (9.5%) and cognition (5%) were more prominent in research incorporating Atlantic bottlenose dolphins. Both species are still in need of additional research on questions related to behavioral patterns.

Keywords – Atlantic bottlenose dolphin, Killer whale, *Orcinus orca*, Publication trends, *Tursiops truncatus*

The recent upsurge of the debate over housing killer whales (*Orcinus orca*) in captivity has led to calls for increased government regulations on facilities that manage captive populations (H. R. 4019, 2015; USDA Docket Marine Mammal, 2016). As focus on the controversy developed in response to popular cinematic depictions, public opinion on the welfare or well-being of captive killer whales and sentiment toward the humaneness of keeping killer whales in captivity have formed without much input

from the scientific community. Fundamental to disagreements over the utility of housing the animals in zoological facilities are conflicting assessments about the value and necessity of research conducted with captive killer whales and the overall well-being of these populations. Efforts have been made to evaluate debaters' claims point-by-point, but this tactic is at risk for cherry-picking favorable evidence or citing a handful of findings in areas where research is too sparse to produce reliable results. The distribution of peer-reviewed scientific literature on killer whales across topics has not been determined, leaving the capacity to which science can inform the debate over killer whales in captivity unknown. Determining the relative research coverage by topic would assist in establishing which claims can be empirically evaluated and what areas necessitate further investigations.

The Science of Animal Well-being

Initial conceptions of welfare specified expectations of the environment to satisfy basic animal care standards but have advanced to focus on increasing individual positive affect and the expression of natural behaviors (Barnett & Hemsworth, 2009; Yeates & Main, 2009). The most recent movement within animal welfare, and the viewpoint adopted here, focuses on the definition of welfare as the promotion of well-being across three broad aspects: physical health, psychological health, and naturalistic behaviors (Fraser, 2009; Maple, 2007; Swaisgood, 2007). Ultimately, determinations of welfare depend on supporting well-being and require a knowledge of health and physiology, cognition, and social interactions, of animals both in their natural habitat and in managed care (Baumans & Van Loo, 2013; Carlstead, Mench, Meehan, & Brown, 2013; Chua, Weary, Van Delen, & Coenen, 2002; Greenwald & Dabek, 2003; Hoy, Murray, & Tribe, 2010; Kuczaj, Makecha, Trone, Paulos, & Ramos, 2006; Paulos, Trone, & Kuczaj, 2010; Pomerantz & Terkel, 2009; Walker, Diez-Leon, & Mason, 2014; Whitham & Wielebnowski, 2013).

These changes have led to improvements in the welfare of laboratory animals (e.g., mice, rats, guinea pigs, gerbils, rabbits, dogs, cats, non-human primates) and a variety of animals housed at zoos through cognitively and behaviorally enriching activities and changes in their physical environments and social groupings (Baumans & Van Loo, 2013; Hoy et al., 2010; Whitham & Wielebnowski, 2013). For example, by observing the behavioral responses to different enrichments (e.g., devices, social partners, lights, noises, or food), researchers better understand the importance of environmental preferences, species differences, and individual differences when determining the welfare needs of animals in managed care (Baumans & Van Loo, 2013; Chua et al., 2002; Greenwald & Dabek, 2003; Hoy et al., 2010; Pomerantz & Terkel, 2009). Without sufficient research in these domains appropriate welfare regulations are difficult to construct. Research with animals in their natural habitats informs researchers of species-appropriate activities, physical environments, and social groupings whereas research with animals in managed care informs researchers of physiological and environmental constraints, particularly when large, inter-institutional studies are conducted (Whitham & Wielebnowski, 2013).

The Science of Cetaceans

Beyond the indirect benefits of welfare assessments and regulations, information gained from objective scientific studies on animal physical health, species-typical behavior, social interactions, offspring development and care have been shown to have a direct and positive influence on the population studied (Carlstead & Shepherdson, 2000; Sapolsky, 2004; Swaisgood, 2007; Whitham & Wielebnowski, 2013). Although individual studies are important to informing policy, periodic reviews of the scientific literature are particularly helpful in aggregating information. Literature reviews systematically quantify the areas that have progressed and identify areas that still need to be explored (Elwen, Findlay, Kiszka, & Weir, 2011; Mulrow, 1994). The debate surrounding killer whales demonstrates the need for such an empirical review. Currently, there is not a systematic review of the types of research conducted with killer whales and the settings in which this research occurred.

To address the paucity of a comprehensive view of research with killer whales and to evaluate the state of our scientific understanding, particularly with regard to welfare, the current study attempted to capture the distribution of research on killer whales. We conducted an inventory of a representative sample of peer-reviewed articles with killer whales and a complementary inventory with articles with Atlantic bottlenose dolphins (*Tursiops truncatus*). Much like killer whales, Atlantic bottlenose dolphins represent a species that is geographically distributed around the world in both natural habitats and captive facilities. Rather than review the findings of specific studies on various topics, the inventory summarized the types of studies and the contexts in which research has been conducted to address three major research questions.

The Major Questions

1. What broad topics have been investigated by peer-reviewed research involving killer whales as compared to Atlantic bottlenose dolphins?
2. What settings are these topics investigated within most often?
3. Have topics critical to assessing well-being been investigated, and if so, to what extent?

Method

Sample

To collect the initial sample of 3,062 unique, peer-reviewed academic journal articles pertaining to killer whales and bottlenose dolphins, we conducted three independent searches. The initial search was conducted between May and August of 2014 using the St. Mary's University subscription to 11 databases, which included Academic Search Complete, PsycINFO, Science & Technology Collection, GreenFILE, Psychology and Behavioral Sciences Collection, Health Source: Nursing/Academic Edition, PubMed, MedLine, PsycARTICLES, BIOSIS, and AGRICOLA. A second search of peer-reviewed articles using the index of *Cetacean Societies* (Mann, Connor, Tyack, & Whitehead, 2000) was conducted to capture publications produced prior to key word indexing. These two searches produced 1,383 unique articles (killer whales: $n = 424$, dolphins: $n = 959$). Given our desire to be as representative as possible, we conducted a third search with the Web of Science reference database. Producing an additional 1,679 articles, this final search doubled the original number of articles discovered in the first two searches. Out of the 3,062 articles, 243 articles were excluded due to the inability to identify a coded variable (e.g., research setting, research topic). The sample included 2,819 unique articles, which were published across 566 different journals. The goal of the search was to produce an objective, representative sample of the peer-review published literature and not an exhaustive review of all research produced on the two species examined. These journals represent research from around the world and are independent of any particular geographic location or facility.

Procedure

To control for the large number of irrelevant sources and rigor, the search was limited to peer-reviewed academic journals, beginning with the year 1964, which corresponded to the first scientific publication on killer whales captured in our search, and ending with September 2015. The initial database search separately utilized the keywords without quotation marks: killer whale, *Orcinus*, bottlenose dolphin, and *Tursiops*. The Web of Science search utilized the common name (in quotation marks) and scientific names for the species as keywords, combined using the Boolean "or" operator: "killer whale" or *Orcinus*; "bottlenose dolphin" or *Tursiops*. Dissertations, book chapters, presentations, reviews, and duplicated articles were excluded from the sample.

The title and the abstract of each article were examined to verify that the search term (killer whale, *Orcinus*, bottlenose dolphin, or *Tursiops*) appeared in the text. Additionally, articles retrieved by the keywords, *Tursiops* or dolphins, were added to the sample only if the species, *Tursiops truncatus* or Atlantic bottlenose dolphin, was specified.

Table 1

Categories of Articles

Category	Definition	Key Examples
Anthropogenic Response	Animal response to human activities (e.g., noise, vessels), which could alter the animals' behaviors.	Captivity: Hall & Johnson, 1972; Finneran et al., 2007 Wild: Miller et al., 2014; La Manna et al., 2013
Cognition*	Learning mechanisms and cognitive processes (e.g., problem solving, task performance, object recognition).	Captivity: Abramson et al., 2013; Kilian et al., 2003 Wild: N/A; Delfour & Herzing, 2013
Geographic Distribution	Geographic areas in which the animals were found.	Captivity: N/A; Zhang et al., 2012 Wild: Bolanos-Jiminez et al., 2014; Fruet et al., 2015
Echolocation	Ability of the animal to locate or discriminate distant or invisible objects or prey using sound waves.	Captivity: N/A; Harley et al., 2003 Wild: Eskesen et al., 2011; Wisniewska et al., 2014
Foraging/Predation	Techniques adopted by the animal to obtain sources of food; animal's preferred prey.	Captivity: N/A Wild: Vongraven & Bisther, 2014; Eierman & Connor, 2014
Health/Physiology*	Contaminant-caused illnesses, genetic variability, reproduction, hormone level, growth.	Captivity: Katsumata et al., 2006; Noren, 2013 Wild: Porter et al., 2014; Venn-Watson et al., 2015
Interactions with Humans (Humans)	Animal-human direct interaction.	Captivity: N/A; Breising et al., 2005 Wild: Westdal et al., 2013; Mustika et al., 2015
Sociality*	Maternal care, social interaction, social structure, play behaviors, courtship.	Captivity: Horback et al., 2012; Perlberg & Schuster, 2009 Wild: Riesch et al., 2012; Connor & Krützen, 2015
Vocalization	Different sounds/vocals the animal uses to communicate.	Captivity: Noonan & Suchak, 2005; van der Woude, 2009 Wild: Samarra et al., 2015; King & Janik, 2015

Note. An asterisk denotes topics that are related to assessing well-being. Key examples provide references for killer whales then dolphins for each setting per category. N/A indicates that no articles were captured for these categories.

The 2,819 unique articles were coded for their research setting, broad research topic, and the species. Each article received a code for all three categories and the three coding schemes were independent from each other. Internally, each coding scheme was mutually exclusive and comprehensive. Species was coded as either: killer whale (exclusively killer whales), dolphin (exclusively Atlantic bottlenose dolphins), or both (populations from both species were studied). The research setting of the article was classified as wild (conducted on free-ranging animals), captive (conducted within zoological

and aquatic parks), or both settings (research was conducted with animals representing both settings). Broad research topic was classified into one of nine categories (Anthropogenic Response, Cognition, Distribution, Echolocation, Foraging/Predation, Health/Physiology, Interactions with Humans, Sociality, and Vocalization) according to their topic defined in Table 1. To address reliability, an additional search with Google Scholar was conducted by a marine mammal expert (H. Hill) for every article to confirm coded data via an inspection of the methodology of available full-length articles.

As a descriptive summary, chi-square goodness-of-fit tests were conducted for each species to determine the distribution of articles by topic. Chi square tests of independence were conducted to examine relationships between various distributions: (1) setting x topic for each species, (2) species x topic, and (3) species x topic for each setting. Chi square tests of independence account for disparate sample sizes when the adjusted standardized residuals are examined. This process transforms residuals to z-scores following a weighted calculation such that values exceeding +/- 2 contribute significantly to the resulting chi square value and can be interpreted as a topic that was either significantly over-represented (positive values) or significantly under-represented (negative values) as compared to expected values. A logistic regression was performed as an omnibus test to predict the probability that an article was based on a bottlenose dolphin or a killer whale determined by two predictors: setting and topic. Each variable was dummy-coded per each level: setting had three levels and topic had nine levels. The reference categories for the two predictors included wild for setting and health and physiology for topic.

Results

General Findings

Overall, 2,819 peer-reviewed academic journal articles published across 566 different journals were retained for analysis. Articles in which only killer whales were studied represented 27% ($n = 759$) of the peer-reviewed research inventoried while articles in which only Atlantic bottlenose dolphins were studied represented 72% ($n = 2,022$) of the peer-reviewed research inventoried (Figure 1). Both species were studied in 1% ($n = 38$) of peer-reviewed articles. Research articles conducted with free-ranging populations represented 74% of the sample ($n = 2,078$), while 25% of articles were conducted with captive populations ($n = 713$) and 1% with both settings ($n = 28$). Based on the study sample, *Marine Mammal Science*, the *Journal of the Acoustical Society of America*, and *Aquatic Mammals* were the three journals that published research involving killer whales and Atlantic bottlenose dolphins most frequently (Tables 2A and Table 2B).

Topics

Killer whales. To investigate the current knowledge of research with killer whales, we examined the frequency of research topics (Figure 1). Per a chi square goodness of fit test, the most frequent topics published were health and physiology (31%, $n = 238$), foraging and predation (25%, $n = 194$), geographic distribution (20%, $n = 151$), and vocalization (13%, $n = 99$), $\chi^2(8, N = 759) = 770.89$, $p < 0.001$. Only 42 articles, less than 10% of the identified killer whale articles (sociality; cognition), investigated topics relevant to aspects related to the psychological and social well-being of killer whales.

Atlantic bottlenose dolphins. To provide a comparison to killer whales, a second chi square goodness of fit test was conducted to examine the distribution of topics across Atlantic bottlenose dolphins. The results indicated that the topics were distributed unequally, $\chi^2(8, N = 2,022) = 3,192.42$, $p < 0.001$. The most frequent topics published included health and physiology (48.5%, $n = 982$), geographic distribution (17.5%, $n = 354$), sociality (9%, $n = 192$), and vocalization (6%, $n = 114$). Figure 1 represents the breakdown of each category.

Table 2A

Top Ten Journals Publishing Killer Whale Articles Most Frequently from the Study Sample

Journal	Frequency	Percentage
Marine Mammal Science ^{ab}	71	9.4
Journal of the Acoustical Society of America ^{ab}	42	5.0
Aquatic Mammals ^{ab}	41	4.0
Canadian Journal of Zoology	22	2.9
Journal of the Marine Biological Association of the United Kingdom ^a	20	2.6
PLoS ONE ^a	19	2.5
Journal of Cetacean Research and Management ^a	17	2.2
Marine Ecology Progress Series	16	2.1
Marine Pollution Bulletin	16	2.1
Polar Biology	16	1.0

Note. All numbers are derived from the sample of unique articles examined in this study.

^aJournals publishing both killer whale and bottlenose dolphin research most frequently.

^bTop three journals publishing both killer whale and bottlenose dolphin research most frequently.

Table 2B

Top Ten Journals Publishing Dolphin Articles Most Frequently from the Study Sample

Journal	Frequency	Percentage
Marine Mammal Science ^{ab}	158	7.8
Aquatic Mammals ^{ab}	151	7.5
Journal of the Acoustical Society of America ^{ab}	128	6.3
Journal of the Marine Biological Association of the United Kingdom ^a	46	2.3
Journal of Wildlife Diseases	43	2.1
PLoS ONE ^a	42	2.1
Journal of Experimental Biology	38	1.9
Journal of Cetacean Research and Management ^a	33	1.6
Journal of Zoo and Wildlife Medicine	30	1.5
Science of the Total Environment	27	1.3

Note. All numbers are derived from the sample of unique articles examined in this study.

^aJournals publishing both killer whale and bottlenose dolphin research most frequently.

^bTop three journals publishing both killer whale and bottlenose dolphin research most frequently.

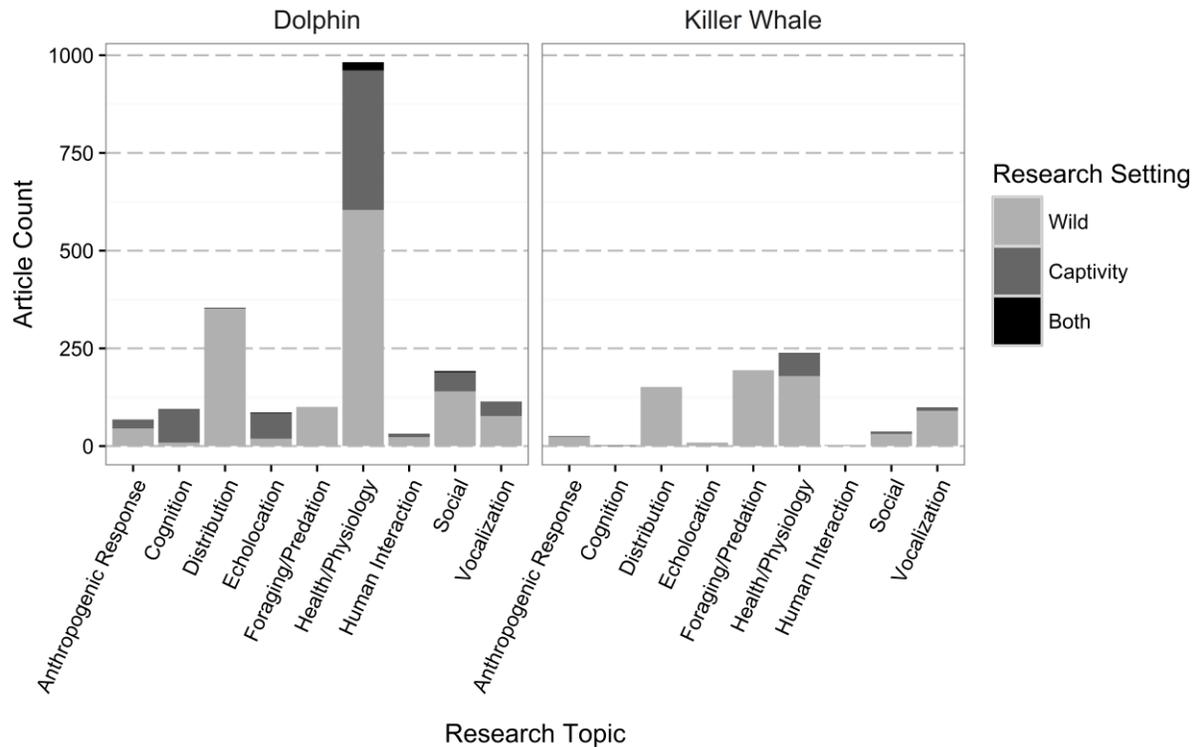


Figure 1. Number of articles per topic for each species divided across research setting. The three articles involving captive dolphins in the distribution category included articles that summarized the origin and current housing locations of captive animals (e.g., Zhang, Sun, Yao, & Zhang, 2012).

Setting

For killer whales, 90% ($n = 681$) of the published articles were conducted with wild animals, 10.8% ($n = 77$) with captive animals, and < 1% ($n = 1$) with both wild and captive animals. For Atlantic bottlenose dolphins, 67.7% ($n = 1,368$) of the published articles were conducted with wild animals, 31.0% ($n = 627$) with captive animals, and 1.3% ($n = 27$) with both wild and captive animals (Figures 2A and 2B).

Topics by setting – killer whales. A chi square test of independence was conducted to examine the distribution of articles published across topics (nine categories) per setting (three categories) for killer whales only. The results indicated that a significant relationship existed, $\chi^2(8, N = 797) = 128.04$, $p < 0.001$, $V = 0.28$. For killer whales, topics such as foraging and predation (28.5%, adjusted standardized residual = 5.7) and geographic distribution (22.2%, adjusted standardized residual = 5.0) were more likely to be represented in wild settings whereas topics such as health and physiology (75.3%, adjusted standardized residual = 8.9) and cognition (2.6%, adjusted standardized residual = 5.0) were more likely to be represented in captive settings. Topics like anthropogenic noise, echolocation, interactions with humans, sociality, and vocalizations were represented as expected per setting.

Topics by setting – Atlantic bottlenose dolphins. The follow-up chi square test of independence conducted to assess the distribution of articles published across topics per setting for Atlantic bottlenose dolphins indicated that a significant relationship existed, $\chi^2(8, N = 2,060) = 480.95$, $p < 0.001$, $V = 0.34$. For Atlantic bottlenose dolphins, topics such as geographic distribution (25.7%, adjusted standardized residual = 14.1) and foraging and predation (7.3%, adjusted standardized residual = 7.2) were more likely to be represented in wild settings whereas topics such as cognition (13.7%, adjusted standardized residual = 13.0), echolocation (10.4%, adjusted standardized residual = 9.0), and health and physiology (56.9%,

adjusted standardized residual = 5.2) were more likely to be represented in captive settings. Topics like anthropogenic noise, interactions with humans, sociality, and vocalizations were represented as expected per setting.

Killer Whales vs Dolphins

A logistic regression was conducted to determine if topic and/or setting significantly predicted the species with which research was conducted. The results of the full model indicated that species was significantly predicted by topic and setting, $R^2 = 0.14$ (Cox & Snell), $R^2 = 0.20$ (Nagelkerke), Model: $\chi^2(10) = 406.45$, $p < 0.001$ (Table 3). When compared to health and physiology, topics like foraging and predation ($p < 0.001$), vocalizations ($p < 0.001$), and geographic distribution ($p < 0.05$) were more likely to involve killer whales. In contrast, only research on cognition ($p < 0.01$) was more likely than health and physiology to involve dolphins. When controlling for the effect of topic compared to a wild setting, research was more likely to be conducted with dolphins in captive settings ($p < 0.001$) and in both wild and captive settings ($p < 0.05$).

Table 3

Logistic Regression Predicting Species by Topics and Setting

Predictor	B (SE)	Wald	p	95% CI for Odds Ratio		
				Lower	Odds Ratio	Upper
Anthropogenic response	-0.38 (0.25)	2.45	ns	0.42	0.68	1.10
Cognition	1.94 (0.72)	7.20	0.007	1.69	6.98	28.83
Geographic distribution	-0.29 (0.13)	5.46	0.020	0.58	0.75	0.95
Echolocation	0.54 (0.36)	2.21	ns	0.84	1.72	3.50
Foraging and predation	-1.80 (0.15)	150.95	< 0.001	0.12	0.17	0.22
Health and physiology ^a		223.06	< 0.001			
Interactions with humans	1.02 (0.61)	2.80	0.094	0.84	2.79	9.24
Sociality	0.32 (0.20)	2.68	ns	0.94	1.38	2.02
Vocalizations	-1.19 (0.16)	56.41	< 0.001	0.22	0.36	0.42
Wild ^a		43.73	< 0.001			
Captivity	0.90 (0.14)	40.42	< 0.001	1.87	2.46	3.25
Both	2.07 (1.02)	4.09	0.043	1.07	7.90	58.55

Note. Species was coded as a binomial outcome variable for the regression with dolphin as the reference group (1 = dolphin, 0 = not dolphin/killer whale). Positive coefficients represent increased odds of research being conducted with a dolphin sample. Negative coefficients represent the increased odds of research not being conducted with dolphins, but with killer whales. The three levels of setting included Wild, Captivity, and Both.

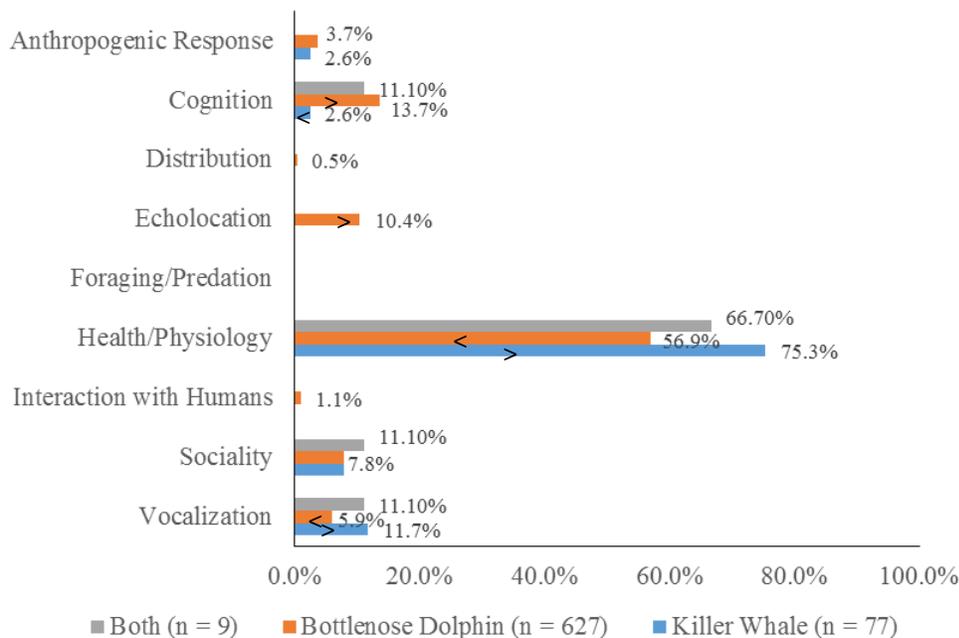
^aHealth and physiology and wild were selected as the reference groups for topic and setting, respectively.

Topic by Species per Setting. A chi square test of independence was conducted for each setting to examine the distribution of articles per topic comparing killer whales to Atlantic bottlenose dolphins. For articles in which both settings were investigated ($N = 28$), there was no significant trend for topics. Killer whales contributed a single article while Atlantic bottlenose dolphins contributed 27 articles, primarily including health and physiology (78%), social (11%), echolocation (7%), and interactions with humans (4%).

Articles involving captive settings produced a significant relationship between species (killer whales, Atlantic bottlenose dolphins, both) and topic (all nine categories), $\chi^2(14, N = 713) = 25.54$, $p = 0.03$, $V = 0.13$. When compared to killer whales, research on echolocation (10.4%, adjusted standardized residual = 3.1) and cognition (13.7%, adjusted standardized residual = 2.7) were over-represented in Atlantic bottlenose dolphins (denoted by > sign on Figure 2A). When compared to Atlantic bottlenose dolphins, research on health and physiology (75.3%, adjusted standardized residual = 3.1) and vocalizations (11.7%, adjusted standardized residual = 2.0) were over-represented in killer whales (denoted by > sign on Figure 2A). In contrast, topics such as echolocation (0%, adjusted standardized

residual = -2.9) and cognition (2.6%, adjusted standardized residual = -2.8) were significantly under-represented for killer whales while health and physiology (56.9%, adjusted standardized residual = -3.1) and vocalizations (5.9%, adjusted standardized residual = -2.0) were under-represented for Atlantic bottlenose dolphins (denoted by < sign on Figure 2A).

A) Captivity



B) Wild

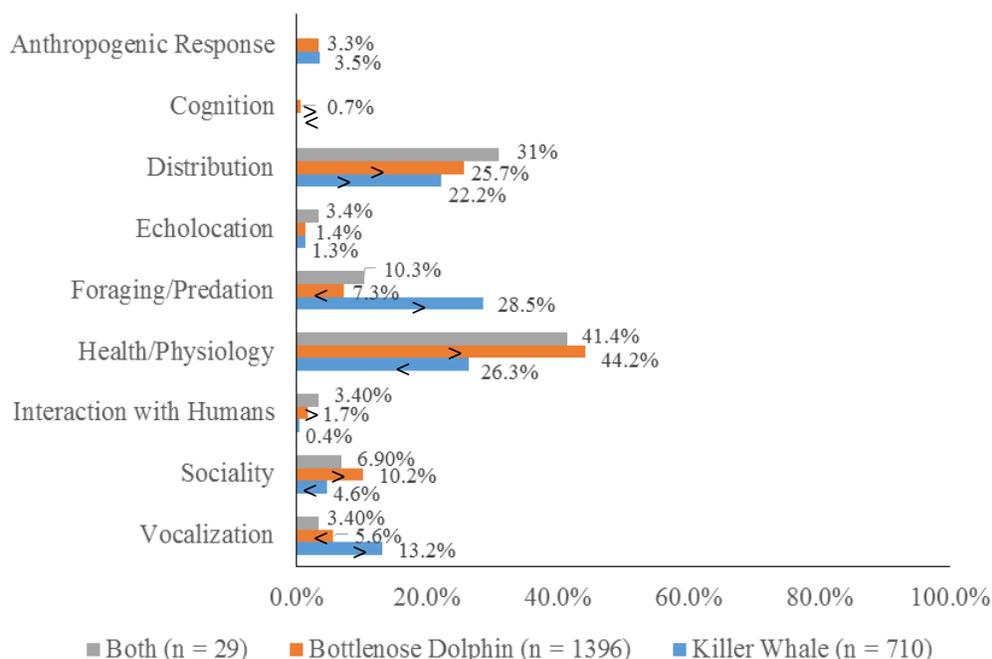


Figure 2. Distribution of articles for topic per species based on captivity (A) and wild (B) settings. A > sign indicates that a topic was represented significantly more often in the species comparison. A < sign indicates that a topic was represented significantly less often in the species comparison.

Articles involving wild settings also reflected a significant relationship between species and topic, $\chi^2(16, N = 2,078) = 247.66, p < 0.001, V = 0.24$. When compared to Atlantic bottlenose dolphins, research on foraging (28.5%, adjusted standardized residual = 12.9) and vocalizations (13.2%, adjusted standardized residual = 6.0) was over-represented in killer whales (denoted by > sign on Figure 2b). When compared to killer whales, research on health and physiology (44.2%, adjusted standardized residual = 7.7), social behaviors (10.2%, adjusted standardized residual = 4.4), interactions with humans (1.7%, adjusted standardized residual = 2.1), and cognition (0.7%, adjusted standardized residual = 2.2) were over-represented in Atlantic bottlenose dolphins (denoted by > sign on Figure 2b). In contrast, topics such as health and physiology (26.3%, adjusted standardized residual = -7.8), sociality (4.6%, adjusted standardized residual = -4.3), interactions with humans (0.4%, adjusted standardized residual = -2.4), and cognition (0%, adjusted standardized residual = -2.1) were significantly under-represented for killer whales while foraging and predation (7.3%, adjusted standardized residual = -12.6) and vocalizations (5.6%, adjusted standardized residual = -5.7) were under-represented for Atlantic bottlenose dolphins.

Evaluation of Topics Related to Well-being

Of the nine broad research topics, three were considered directly related to well-being: health and physiology, sociality, and cognition. Based on the relative distributions of articles as presented in the analyses above, the primary areas of published research on captive killer whale populations included health and physiology, vocalizations, and sociality, with three or fewer studies on all other psychological or behavioral well-being topics (Figure 1). In comparison to killer whales, the distribution of articles with Atlantic bottlenose dolphins reflected significantly more research with greater diversity in the well-being topics, including health and physiology, sociality, and cognition as supported by the direct comparison between the two species across the three tested settings, $\chi^2(16, N = 2,819) = 371.06, p < 0.001, V = 0.26$. Topics like foraging and predation (adjusted standardized residual = 15.8) and vocalizations (adjusted standardized residual = 6.6) have taken precedence when studying killer whales. When compared directly to Atlantic bottlenose dolphins, the topics relevant to well-being for killer whales that were under-represented included health and physiology (adjusted standardized residual = -8.2), cognition (adjusted standardized residual = -5.7), and sociality (adjusted standardized residual = -3.9). In contrast, research with Atlantic bottlenose dolphins was more diverse and represented more consistently across topics related to well-being: health and physiology (adjusted standardized residual = 7.9), cognition (adjusted standardized residual = 5.6), and sociality (adjusted standardized residual = 3.9).

Discussion

What is Missing?

Based on a database search of peer-reviewed scientific literature, we conclude that there is little empirical knowledge of killer whales as compared to a species of bottlenose dolphins, limiting the evidence available to inform public policy decisions on the welfare and management of killer whales. Although killer whale investigations are less numerous and more limited in scope compared to bottlenose dolphins, the most important results are the relative distributions of topics. From the total sample, three major topics emerged consistently across both species: 1) health problems caused by contaminants and physiological studies involving reproduction, genetics, and hormone levels, 2) geographic distribution of animals, and 3) vocalizations. Of these three topics, investigations into the health and physiology of killer whales and dolphins is the only one that may contribute to our understanding of physical well-being regardless of setting. Although vocalizations could provide some evidence of social or emotional well-being (e.g., presence of vocalizations indicating aggression/displacement vs affiliative interactions), research has yet to correlate many vocalizations with behavioral contexts or emotional state. The two

topics directly relevant to addressing the social and psychological aspects of well-being, sociality and cognition, remain under-explored in killer whales in particular, but in dolphins as well.

Setting Plays a Role

It is critical to recognize that research is needed from both wild and captive settings to inform the debate about the welfare of captive animals as has been recommended already for non-marine mammals (Walker et al., 2014). Whereas each setting is conducive for studying certain questions or topics (e.g., geographic distribution of populations and foraging and predation are more appropriate for wild investigations compared to studies involving experimental designs are more easily conducted in captivity), many of the topics examined by marine mammal researchers could benefit from research conducted in both settings. Research on anthropogenic noise should be conducted in both natural and controlled settings as the natural habitat allows for broader generalizability while the captive environment allows for manipulation of conditions under controlled circumstances. Research conducted on health problems caused by contaminants, reproductive physiology, genetics, and hormone levels has contributed significantly to the care of captive animals and to an increased awareness of the plight of animals in their natural habitat and many of these studies have been conducted with wild and captive populations (killer whales: health: LaMere et al., 2009; Robeck et al., 2015; St. Leger et al., 2009; physiology: Worthy, Worthy, Yochem, & Dold, 2013; reproduction, Asper, Young, & Walsh, 1988; Robeck et al., 2009). Even research on aspects of cognition and sociality of bottlenose dolphins has been conducted in both wild and captive settings and resulted in information that facilitated more species-appropriate forms of enrichment and social groupings for captive animals (Fabienne & Helen, 2012; Waples & Gales, 2002). Research with killer whales may benefit from similar studies.

Clearly, research on topics critical to evaluating and maintaining the well-being of captive marine mammals, such as killer whales and dolphins can be performed with animals researched in both settings. Of the studies in which wild and captive populations of bottlenose dolphins have been compared directly, few differences, if any, existed (Dudzinski et al., 2011; Dudzinski, Gregg, Paulos, & Kuczaj, 2010; Greene, Melillo-Sweeting, & Dudzinski, 2011). Studies that facilitate direct comparisons are critical to understanding if captive environments support the well-being of a species. The work with bottlenose dolphins suggests that dolphins have adapted to captive environments successfully. This research could serve as a model for the evaluation of behaviors displayed by killer whales in captivity.

Is the Current Research Adequate?

Periodic inventories of the published peer-reviewed literature serve as a template to facilitate increased use of scientific evidence in policy decisions by defining the state of relevant research evidence (Gagnon, 2011). Such summaries elucidate current knowledge and areas that need further investigation (Elwen et al., 2011). Addressing the evolving controversy over the role of animals in captivity for exhibition and research, this review provides a quantitative foundation to inform public policy decisions on this controversial and often emotion-laden issue. This study was not intended as a forum to address the philosophical disagreements on the humaneness of housing killer whales in captivity as it is beyond the scope of this review. Neither was this study intended as an exhaustive review of research on either killer whales or Atlantic bottlenose dolphins. To truly evaluate the results of the extant literature, meta-analyses would be important. However, until there is a sufficient number of articles in specific areas, such an undertaking is not feasible. Rather, this inventory provides an objective overview of a representative sample of research that has been published in peer-reviewed literature. Most importantly, this study identifies areas that are in need of empirical and objective knowledge. The complex variables that go into determining what species, topics, and settings, research is conducted with, such as availability, funding, and feasibility, were not examined. One variable that might have influenced the number of available articles for captive animals was the timeframe in which stable populations were established for both

species and when welfare research expanded. For example, when research began to focus on positive aspects of animal well-being, killer whale populations were not as established as bottlenose dolphins in zoological facilities across the world.

While even the major topics for killer whale research (health and physiology, foraging and predation behavior, vocalizations, and geographic distribution) are lacking when compared with research on Atlantic bottlenose dolphins, an emphasis on the under-represented categories relevant to the killer whale welfare debate would facilitate a timely production of empirical evidence necessary for objective evaluations. Studies of the social interactions, sociality, and species preferences from animals in their natural habitat are necessary to best determine appropriate social groupings and species-typical behavior exhibited by animals in captivity. Similarly, if social groupings and the physical habitat approximate those of the appropriate natural habitat, captive animals can inform science of the capabilities and constraints of their wild conspecifics. Embedded within research on sociality are the various communication systems. Killer whales and bottlenose dolphins seem to have complex acoustic systems that may serve a number of functions, including communicating location, identity, and current emotional state (Janik, 2009). Research on vocalizations was represented well for both species, but there is still much to be discovered. Similarly, our knowledge of health and physiology seems fairly robust for both species, yet many aspects remain unexplored, such as the relationship between physiological or hormonal states and behavioral states or social interactions exhibited by the animals. Finally, our understanding of the cognitive abilities of both species is limited at best. Research with both species is necessary before it can be assumed that cognitive abilities are similar in phylogenetically-related species, such as killer whales and bottlenose dolphins. To truly appreciate the cognitive requirements needed to support the physical, social, and cognitive well-being of these cetaceans in captivity, we must first understand how they perceive and interact with the world. Exploring topics such as learning mechanisms and characteristics, memory formation and recall, discriminations, representations of various mental states in self and others, social cues, among other abilities in adult and immature animals would begin to address the dearth of knowledge. Based on the current state of the literature, we issue a call for researchers, journal editors, and granting agencies to promote behavioral, cognitive, and well-being-oriented studies in both captive and wild killer whales.

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