The University of San Francisco
USF Scholarship: a digital repository @ Gleeson Library | Geschke Center

Biology Faculty Publications | Biology

2016

Comparative and Cumulative Energetic Costs of Odontocete Responses to Anthropogenic Disturbance

Dawn P. Noren

Marla M. Holt

Robin C. Dunkin

Nicole Thometz
University of San Francisco, nthometz@usfca.edu

Terrie M. Williams

Recommended Citation

Dawn P. Noren, Marla M. Holt, Robin C. Dunkin, Nicole M. Thometz, and Terrie M. Williams. Comparative and cumulative energetic costs of odontocete responses to anthropogenic disturbance. Proc. Mtgs. Acoust. 27, 040011 (2016); doi: http://dx.doi.org/10.1121/2.0000357

Proceedings of Meetings on Acoustics

Volume 27 http://acousticalsociety.org/

Fourth International Conference on the Effects of Noise on Aquatic Life

Dublin, Ireland

10-16 July 2016

Comparative and cumulative energetic costs of odontocete responses to anthropogenic disturbance

Dawn P. Noren and **Marla M. Holt**

Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, WA; dawn.noren@noaa.gov, marla.holt@noaa.gov

Robin C. Dunkin, Nicole M. Thometz and **Terrie M. Williams**

Ecology & Evolutionary Biology Department, University of California, Santa Cruz, CA; rdunkin@ucsc.edu, nthometz@ucsc.edu, tmwillia@ucsc.edu

Odontocetes respond to vessels and anthropogenic noise by modifying vocal behavior, surface active behaviors, dive patterns, swim speed, direction of travel, and activity budgets. Exposure scenarios and behavioral responses vary across odontocetes. A literature review was conducted to determine relevant sources of disturbance and associated behavioral responses for several odontocete species (bottlenose dolphin, killer whale, harbor porpoise, and beaked whales). The energetic costs of species-specific responses to anthropogenic disturbance were then estimated. The energetic impact varies across species and scenarios as well as by behavioral responses. Overall, the cumulative energetic cost of ephemeral behavioral responses (e.g., performing surface active behaviors, modifying acoustic signals) and modifying swim speeds and activity budgets likely increases daily energy expenditure by ≤4%. In contrast, the reduction in foraging activity in the presence of vessels and/or exposure to sonar has the potential to significantly reduce individuals' daily energy acquisition. Indeed, across all odontocete species, decreased energy acquisition as a result of reduced foraging undoubtedly has a larger impact on individuals than the increased energy expenditure associated with behavioral modification. This work provides a powerful tool to investigate the biological significance of multiple behavioral responses that are likely to occur in response to anthropogenic disturbance.

Published by the Acoustical Society of America

1. INTRODUCTION

Cetaceans (whales and dolphins) are exposed to noise produced by a variety of sources, including boats, sonar, and acoustic pingers, among others. Odontocete (toothed cetaceans) responses to anthropogenic noise and vessel presence include changes in vocal behavior, surface active behavior, dive patterns, swim speed, direction of travel, and behavioral activity states (Kruse, 1991; Williams et al., 2002a, 2002b, 2006, 2009; Holt et al., 2009; Lusseau et al., 2009; Noren et al., 2009; Tyack et al., 2011; DeRuiter et al., 2013; Kastelein et al., 2015). Yet, the consequences of such behavioral responses are not well understood. Measuring the energetic costs of behavioral responses is one method to assess the biological significance of anthropogenic disturbance to marine mammals. Previous studies have measured or estimated the metabolic costs of performing surface active behaviors (Noren et al., 2012), producing and modifying communicative sounds (Noren et al., 2013; Holt et al., 2015) and echolocation clicks (Noren et al., in prep), swimming over a range of speeds (Williams et al., 1992, 1993; Yazdi et al., 1999; Williams and Noren, 2009), and modifying daily activity budgets (Williams et al., 2006) in delphinids. However, little work has been done to estimate the cumulative energetic cost of multiple responses to disturbance. This study investigates the cumulative energetic cost of species-specific responses to disturbance in four odontocete groups. This is critical for linking short-term energetic impacts to long-term, population-level consequences (Lusseau and Bejder, 2007).

2. METHODS

A. SUBJECTS AND DATA SOURCES

This study focuses on four odontocete taxa [bottlenose dolphins (*Tursiops truncatus* and *Tursiops aduncus*), harbor porpoises (*Phocoena phocoena*), killer whales (*Orcinus orca*), and beaked whales (multiple species)] that are particularly sensitive to disturbance from vessels, sonar, and acoustic pingers. Studies in peer-reviewed journals and other literature sources were consulted to determine the scenarios of disturbance and associated behavioral responses that are relevant to each species. The focus of this effort was on acoustic and vessel disturbance only, and behavioral responses were limited to activities that have the potential to impact energy expenditure and/or energy acquisition. The energetic costs of relevant species-specific behavioral responses were then estimated.

B. ESTIMATED ENERGETIC COSTS OF RESPONSES

The energetic costs of species-specific responses to disturbance that have the potential to increase energy expenditure were estimated using results from earlier studies. Specifically, the mass-specific metabolic costs of performing surface active behaviors (tail slaps and breaches; Noren et al., 2012 and Noren et al., unpublished data), producing social sounds (whistles and squawks; Noren et al., 2013 and Holt et al., 2015) and echolocation clicks (Noren et al., in prep), and modifying social sounds (Holt et al., 2015) and echolocation clicks (Noren et al., in prep) in bottlenose dolphins were used to estimate the energetic costs of these responses in the four focal species. This was deemed appropriate because the mass-specific costs of these short-term responses are likely to be similar across most odontocetes. The energetic costs of altering swim speeds in response to disturbance were calculated from the energetic costs of swimming at specific speeds during disturbed and non-disturbed scenarios using species-specific cost of transport equations (see Table 1). The energetic costs for killer whales modifying swim speeds concomitant with modifying activity budgets in response to disturbance (northern resident killer whales: Williams et al., 2006; southern resident killer whales: Lusseau et al., 2009) were also estimated from swim speeds associated with activity states (Ford, 1989; Noren, 2011) and cost of transport equations (Williams and Noren, 2009) specific to killer whales (Table 2). The energetic costs of altering swim speeds with disturbance as well as modifying swim speeds as a result of modifying daily activity budgets with disturbance were calculated for 12-hour periods to estimate the change in energy expenditure when odontocetes are exposed to disturbance for 12 hours, compared to when they are free from disturbance (undisturbed) for 12 hours.

Table 1. Variables used to calculate the energetic costs of swimming during disturbed and undisturbed scenarios for four odontocetes.

Species	**Disturbance source (reference)**	**Undisturbed speed (ms^{-1}) (reference)**	**Disturbed speed (ms^{-1}) (reference)**	**Cost of transport equations (reference)**
Killer whales	Vessel presence (Williams et al., 2002a)	Males: 1.76 ms^{-1} Females: 1.31 ms^{-1} (Williams et al., 2002a)	Males: 2.19 ms^{-1} Females: 1.64 ms^{-1} (Williams et al., 2002a)	males and females without calves (Williams and Noren, 2009)
Killer whales	Vessel presence (Kruse, 1991)	1.44 ms^{-1} (Kruse, 1991)	2.02 ms^{-1} (Kruse, 1991)	males and females without calves (Williams and Noren, 2009)
Harbor porpoises	Acoustic pinger alarm (Culik et al., 2001)	0.52 ms^{-1} (Culik et al., 2001)	0.48 ms^{-1} (Culik et al., 2001)	females only (Otani et al., 2001)
Bottlenose dolphins	Vessel presence (multiple references, see Table 3)	Not available	Not available	females only (Yazdi et al., 1999)
Beaked whales	Sonar and vessels (multiple references, see Table 3)	Not available	2.6 ms^{-1}, 3.1 ms^{-1} (DeRuiter et al., 2013)	Not available

Table 2. Variables used to calculate the energetic costs of modifying swim speeds as a result of modifying activity budgets with disturbance for northern and southern resident killer whales.

Activity state	**Northern resident Swim speed (ms^{-1}) (Ford, 1989)**	**Southern resident Swim speed (ms^{-1}) (Noren, 2011)**	**Cost of transport equations (reference)**
Rest	0.8	0.8	males and females without calves (Williams and Noren, 2009)
Beach rub	0.8 (assumed slow speed)	Not applicable	males and females without calves (Williams and Noren, 2009)
Travel	2.9	2.2	males and females without calves (Williams and Noren, 2009)
Forage	1.7	1.1	males and females without calves (Williams and Noren, 2009)

Social	1.1	0.3	males and females without calves (Williams and Noren, 2009)

3. RESULTS AND DISCUSSION

A. ODONTOCETE SOURCES OF DISTURBANCE AND RESPONSES

The comprehensive review of previously published studies demonstrates that odontocetes are subjected to a wide range of anthropogenic disturbances, and behavioral responses are highly variable (Table 3).

Table 3. Summary of changes in behavior that may impact energy expenditure and/or acquisition in response to anthropogenic sources (e.g., vessels, sonar, noise) for bottlenose dolphins, killer whales, harbor porpoise, and beaked whales.

Species/group	**Disturbance Source**	**Behavioral Response**	**Reference(s)**
Bottlenose dolphins	Vessel presence	Change in surface active behaviors	Lusseau, 2006; Papale et al., 2012; Yazdi, 2005, 2007
Bottlenose dolphins	Vessel presence	Change in dive behavior	Goodwin and Cotton, 2004; Lusseau, 2003a, 2006; Miller et al., 2008; Nowacek et al., 2001; Papale et al., 2012; Yazdi , 2005
Bottlenose dolphins	Vessel presence	Change in swimming behavior	Goodwin and Cotton, 2004; Lemon et al., 2006; Lusseau, 2006; Mattson et al., 2005; Nowacek et al., 2001; Papale et al., 2012; Stensland and Berggren, 2007; Yazdi, 2005, 2007
Bottlenose dolphins	Vessel presence	Change in activity state	Arcangeli and Crosti, 2009; Christiansen et al., 2010; Constantine et al., 2004; Lusseau, 2003b, 2004; Lemon et al., 2006, 2008; Mattson et al., 2005; Miller et al., 2008; Papale et al., 2012; Steckenreuter et al., 2012; Stensland and Berggren, 2007; Yazdi, 2005, 2007
Bottlenose dolphins	Vessel presence/noise	Change in vocal behavior	Buckstaff, 2004; Gospić and Picciulin, 2016; Heiler et al., 2016; Luís et al., 2014; Pirotta et al., 2015; Scarpaci et al., 2000
Killer whales	Vessel presence,	Change in surface active	Noren et al., 2009; Williams et

	sonar	behaviors	al., 2009; Miller et al., 2012
Killer whales	Vessel presence, sonar	Change in dive behavior	Williams et al., 2009; Miller et al., 2012, 2014
Killer whales	Vessel presence, sonar	Change in swimming behavior	Kruse, 1991; Williams et al., 2002a, 2002b, 2009; Williams and Ashe, 2007; Miller et al., 2012, 2014
Killer whales	Vessel presence, sonar	Change in activity state	Williams et al., 2006; Lusseau et al., 2009; Miller et al., 2012, 2014
Killer whales	Vessel presence/noise, sonar	Change in vocal behavior	Foote et al., 2004; Holt et al., 2008, 2009, 2011, 2012; Miller et al., 2012, 2014
Killer whales	Sonar	Change in echolocation behavior	Miller et al., 2012
Beaked whales	Mid frequency sonar, vessel presence/noise	Change in dive behavior	Aguilar Soto et al., 2006; DeRuiter et al., 2013; Tyack et al., 2011
Beaked whales	Mid frequency sonar	Change in swimming behavior	DeRuiter et al., 2013
Beaked whales	Mid frequency sonar, vessel presence/noise	Change in echolocation behavior	Aguilar Soto et al., 2006, DeRuiter et al., 2013; Tyack et al., 2011
Harbor porpoises	Vessel presence, sonar	Change in surface active behaviors	Dyndo et al., 2015; Kastelein et al., 2015
Harbor porpoises	Acoustic alarms	Change in dive behavior	Teilman et al., 2006
Harbor porpoises	Acoustic alarms, sonar	Change in respiration rate	Kastelein et al., 2000, 2001, 2005, 2006, 2015
Harbor porpoises	Acoustic alarms, sonar, underwater ammunitions explosions, windpower generator	Change in swimming behavior	Culik et al., 2001; Cox et al., 2001; Johnston, 2002; Kastelein et al., 1997, 2000, 2001, 2005, 2006, 2015; Koschinski et al., 2006; Olesiuk et al., 2002; Teilman et al., 2006; Sundermeyer et al., 2012; Koschinski et al., 2003
Harbor porpoises	Acoustic alarms, air gun array, impact pile driving, windpower	Change in echolocation behavior	Culik et al., 2001; Koschinski et al., 2006; Teilman et al., 2006; Pirotta et al., 2014; Brandt et al., 2012; Lucke et al., 2012;

	generator	Tougaard et al., 2012; Koschinski et al., 2003

The prevalent disturbance sources as well as the most commonly observed behavioral responses vary across species. For example, both killer whales and bottlenose dolphins are routinely subjected to whale-watching vessels (see references within Table 3) and demonstrate similar behavioral responses to this type of disturbance (Table 3, Fig. 1). Killer whales also demonstrate a wide range of reactions to sonar (Table 3, Fig. 1). In contrast to responses observed during vessel disturbance, killer whales cease acoustic signal production (both calls and echolocation clicks) and tail slaps in response to sonar (Miller et al., 2012; Table 3; Fig. 1). These behavioral changes are associated with cessation of foraging (Miller et al., 2012). Similar to acoustic responses to vessel disturbance, killer whales have also demonstrated strong vocal responses to sonar, including increasing call coordination, increasing call "loudness", and/or increasing whistle frequency (Miller et al., 2014; Table 3; Fig. 1). The sources of disturbance for beaked whales and harbor porpoises are predominantly anthropogenic noise inputs, including sonar, acoustic alarms, and underwater explosions, as well as vessel presence. Although one study reported that harbor porpoises increased echolocation rates in response to an alarm (e.g., Koschinski et al., 2006), the most common responses for both harbor porpoises and beaked whales are to cease the production of echolocation clicks and leave the area (Table 3, Fig. 1). Harbor porpoises have also increased surface active behaviors in response to vessel noise (Dyndo et al., 2015) and sonar (Kastelein et al., 2015), but overall, that reaction is also rare in this species. Interestingly, increasing travel and decreasing foraging behavior is a ubiquitous response to disturbance across all four odontocetes (Fig. 1). These responses have the potential to not only increase energy expenditure but to also decrease energy acquisition at the same time.

	↑ SABs	↑ Speed	↑ Acoustic Signal rate/amplitude	↓ Acoustic Signal rate/amplitude	↑ Travel	↓ Forage
Killer Whale	X	X	X	X	X	X
Bottlenose Dolphin	X	X	X		X	X
Beaked Whales		X		X	X	X
Harbor Porpoise	X	X	X	X	X	X

Figure 1. Behavioral responses to acoustic disturbance that may impact energy balance in four odontocetes. Red X's denote responses that have been reported for each of the four odontocetes (see Table 3). Red columns depict responses that may increase energy expenditure while white columns depict responses that may reduce energy acquisition.

B. ESTIMATED ENERGETIC COSTS OF RESPONSES

The energetic impact of disturbance varies across species and scenarios, and the cumulative cost depends on the specific behavioral responses performed. For the two delphinids and harbor porpoises, the energetic cost of performing surface active behaviors, producing and modifying acoustic signals, and changing swimming speeds are relevant to determining the cumulative energetic cost of disturbance (Table 3, Fig. 1). The only response that has the potential to increase energy expenditure in beaked whales is increasing swimming speed and travel with disturbance, but there are currently insufficient data to estimate that cost.

The energetic costs of producing and modifying social sounds and echolocation clicks are considered to be small for delphinids and porpoises. Previous studies showed that the metabolic rate of dolphins producing social sounds continuously for 2 minutes ranges from 1.2-1.5 times resting metabolic rate (RMR; Noren et al., 2013; Holt et al., 2015). Increases in vocal effort, as a consequence of increasing vocal amplitude, repetition rate and/or duration, which has been observed in dolphins and killer whales in the presence of vessels (e.g. Buckstaff, 2004; Foote et al., 2004; Holt et al., 2009), result in higher metabolic rates. Yet, the estimated metabolic cost of modifying vocal behavior in response to noise is considered to be quite modest (Holt et al, 2015). Similarly, for harbor porpoises, the metabolic cost of increasing click rates (e.g., Koschinski et al., 2006) is likely to be small because the metabolic cost of producing and modifying echolocation click bouts is negligible (Noren et al., in prep).

The energetic cost of performing surface active behaviors in response to disturbance varies by species, the type of behavior(s) performed, and the level of disturbance. For example, although killer whales regularly perform several different surface active behaviors, northern and southern resident killer whales perform tail slaps more often than other surface active behaviors in response to disturbance (Williams et al., 2002 a, b; Noren et al., 2009). Because the performance of tail slaps does not significantly increase metabolic rates (Noren et al., 2012) and because surface active behavior bouts are regularly performed by resident killer whale populations, not always in response to close approaches by vessels (Noren et al., 2009), the cumulative energetic impact of performing surface active behaviors in response to vessel disturbance is likely to be low for killer whales. Similarly, the energetic impact of altering the frequency of performing surface active behaviors is likely to be low for bottlenose dolphins. Although tail slaps and the more energetically costly leaps (Noren et al., 2012) can be performed in response to vessels (Yazdi, 2007; Papale et al., 2012), some dolphins also reduce the number of breaches and/or the diversity of surface active behaviors performed (Papale et al., 2012) in the presence of vessels. The overall cumulative energetic impact of changes in the performance of surface active behaviors may be negligible. Thus far only two studies have reported that harbor porpoises increase surface active behaviors in response to disturbance. Porpoising (Dyndo et al., 2015) and leaping (Kastelein et al., 2015) out of the water can be energetically costly (Noren et al., 2012). However, it is important to note that these responses were observed for porpoises that were confined to net pens and pools and were therefore unable to leave the area, which is the most common response for harbor porpoises (see references in Table 3). Harbor porpoises that regularly respond to disturbance by porpoising and/or leaping could increase their energy expenditure, but it is important to first determine how often these responses occur in free-ranging porpoises before assessing the energetic impact.

The energetic cost of modifying swim speeds in the presence of vessels varied by species and population as well as by the method that was used to estimate energy expenditure. Northern resident killer whales increased their swim speed in response to vessel disturbance, which equates to a 0.7-1.4% increase in energy expenditure over a 12-hour period when vessels are present, compared to when there are no vessels (speeds from Kruse, 1991 and Williams et al., 2002, see Table 1). The increase in energy expenditure calculated from changes in activity budgets and associated swimming speeds was considerably lower for northern and southern resident killer whales and ranged from 0.02-0.5%, depending on the sex, disturbance scenario, and population. This result is likely because swim speeds associated with the activity states are relatively slow (Ford, 1989; Noren, 2011), and killer whales swim efficiently over a broad range of speeds (Williams and Noren, 2009). Interestingly, males from the southern resident killer whale population, the population that is typically associated with a higher number of boats, had the greatest increase in energy expenditure using this method. Nonetheless, increases in energy expenditure calculated by both methods are considered to be negligible for resident killer whales. The increase in energy expenditure for harbor porpoises responding to an acoustic pinger alarm was 0.33%. This was not expected because swimming speed actually decreased during disturbance. The result is due to the unusual shape of the cost of transport curve (Otani et al., 2001). Regardless, energy expenditure related to swim speed modification is also considered negligible for harbor porpoises.

It appears that responses involving changes in swimming speeds, either alone or in association with changes in activity budgets, do not equate to large changes in energy expenditure. However, it is important to note that beyond differences in swimming speed, activity states are associated with other behaviors that contribute to the energetic cost of being engaged in those states. The method used here does not account for those additional energetic costs. A study on northern resident killer whales utilized a different method to account for those costs and found that energy expenditure increased by 3-4% when whales were with vessels for 12 hours compared to when there were no vessels present for 12 hours (Williams et al., 2006). This method could be used with data from southern resident killer whales (Lusseau et al., 2009) and should be explored for use with data from bottlenose dolphins since swim speed data are not available (Table 1), yet several studies have investigated changes in daily activity budgets with disturbance in bottlenose dolphins (Table 3). Finally, an increase in energy expenditure of 3-4% could still be considered small, compared to the substantial decrease in energy acquisition from lost foraging opportunities as a result of vessel disturbance (Williams et al., 2006). The reduction of foraging behavior with a concomitant increase in travel appears to be a ubiquitous response across cetaceans (references in Table 3, Senigaglia et al., 2016). Thus, it is important to quantify this reduction in prey acquisition to better assess consequences of disturbance.

4. CONCLUSION

By combining data on the metabolic costs of behaviors with data on behavioral changes observed in the field, we can estimate the cumulative energetic cost of various disturbance scenarios. Overall, odontocetes may increase their energy expenditure in response to acoustic disturbance, but short-lived responses with relatively small metabolic costs (e.g., tail slaps, vocal compensation, moderate changes in swim speed), may not significantly impact individuals during ephemeral exposures. Certainly, the ability to estimate the metabolic consequences of disturbance for all odontocetes is hampered by lack of empirical data. Reduced energy acquisition resulting from lost foraging opportunities is likely to have a larger impact on individuals than modifying behaviors in a way that increases energy expenditure. Extended reduction in energy acquisition has the greatest potential to affect energy balance, consequently altering body condition, and ultimately affecting fitness of individuals. A better understanding of the consequences of reduced energy acquisition is warranted to better understand the cumulative effects of multiple responses to anthropogenic disturbance.

ACKNOWLEDGMENTS

We thank Emily Mazur, NOAA Hollings Intern, for assistance with literature searches, data calculations, and tables. This research was supported by the Office of Naval Research [N0001415IP00039, N0001414IP20045, and N0001416IP00023 to D.P.N. and M.M.H., and N000141410460 to R.C.D. and T.M.W.].

REFERENCES

Aguilar Soto, N., Johnson, M., Madsen, P.T., Tyack, P.L., Bocconcelli, A., and Borsani, J.F. (**2006**). “Does intense ship noise disrupt foraging in deep-diving cuvier’s beaked whales (Ziphius cavirostris)?” Mar. Mammal Sci. **22**, 690-699.

Arcangeli, A., and Crosti, R. (**2009**). “The short-term impact of dolphin-watching on the behaviour of bottlenose dolphins (Tursiops truncatus) in western Australia,” J. Mar. Anim. Ecol. **2**, 3-9.

Brandt, M. J., Diederichs, A., and Nehls, G. (**2012**). “Effects of offshore pile driving on harbor porpoises (Phocoena phocoena)” in The Effects of Noise on Aquatic Life, edited by A. N. Popper and A. Hawkins (Springer, New York), Ad. Exp. Med. Biol. **730**, 281-284.

Buckstaff, K. C. (**2004**). “Effects of watercraft noise on the acoustic behavior of bottlenose dolphins, Tursiops truncatus, in Sarasota Bay, Florida,” Mar. Mammal. Sci. **20**, 709-725.

Christiansen, F., Lusseau, D., Stensland, E., and Berggren, P. (**2010**). “Effects of tourist boats on the behavior of Indo-Pacific bottlenose dolphins off the south coast of Zanzibar,” Endang. Species Res. **11**, 91-99.

Constantine, R., Brunton, D.H., and Dennis, T. (**2004**). “Dolphin-watching tour boats change bottlenose dolphin (Tursiops truncatus) behavior,” Biol. Cons. **117**, 299-307.

Cox, T. M., Read, A. J., Solow, A., and Tregenza, N. (**2001**). “Will harbor porpoises (Phocoena phocoena) habituate to pingers?” J. Cetacean Res. Manage. **3**, 81-86.

Culik, B. M., Koschinski, S., Tregenza, N., and Ellis, G. M. (**2001**). “Reactions of harbor porpoises Phocoena phocoena and herring Clupea harengus to acoustic alarms,” Mar. Ecol. Prog. Ser. **211**, 255-260.

DeRuiter, S. L., Southall, B. L., Calambokidis, J., Zimmer, M. X., Sadykova, D., Falcone, E. A., Friedlaender, A. S., Joseph, J. E., Moretti, D., Schorr, G. S., Thomas, L., and Tyack, P. L. (**2013**). “First direct measurements of behavioural responses by Cuvier’s beaked whales to mid-frequency active sonar,” Biol. Lett. **9**, 20130223.

Dyndo, M., Wiśniewska, D. M., Rojano-Doñate, L., and Madsen, P. T. (**2015**). “Harbour porpoises react to low levels of high frequency vessel noise,” Sci. Rep. **5**, 11083.

Foote, A.D., Osborne, R.W., and Hoelzel, A.R. (**2004**). “Whale-call response to masking boat noise,” Nature **428**, 910.

Ford, J. K. B. (**1989**). “Acoustic behaviour of resident killer whales (Orcinus orca) off Vancouver Island, British Columbia,” Can. J. Zoolog. **67**, 727–745.

Goodwin, L., and Cotton, P. A. (**2004**). “Effects of boat traffic on the behaviour of bottlenose dolphins (Tursiops truncatus),” Aquat. Mamm. **30**, 279-283.

Gospić, N. R., and Picciulin, M. (**2016**). “Changes in whistle structure of resident bottlenose dolphins in relation to underwater noise and boat traffic,” Mar. Pollut. Bull. **105**, 193-198.

Heiler, J., Elwen, S. H., Kriesell, H. J., and Gridley, T. (**2016**). “Changes in bottlenose dolphin whistle parameters related to vessel presence, surface behaviour and group composition,” Anim. Behav. **117**, 167-177.

Holt, M. M., Veirs, V., and Veirs, S. (**2008**). “Noise effects on the call amplitude of southern resident killer whales (Orcinus orca),” Bioacoustics. **17**, 164-166.

Holt, M. M., Noren, D. P., Veirs, V., Emmons, C. K., and Veirs, S. (**2009**). “Speaking up: Killer whales (Orcinus orca) increase their call amplitude in response to vessel noise,” J. Acoust. Soc. Am. **125**, EL27-EL32.

Holt, M. M., Noren, D., and Emmons, C. (**2011**). “The effects of noise levels and call types on the source levels of killer whale calls,” J. Acoust. Soc. Am. **130**, 3100-3106.

Holt, M. M., Noren, D. P., and Emmons, C. K. (**2012**). “An investigation of sound use and behavior in a killer whale (Orcinus orca) population to inform passive acoustic monitoring studies,” Mar. Mammal Sci. **29**, E193-E202.

Holt, M.M., Noren, D.P., Dunkin, R.C., and Williams, T.M. (**2015**). “Vocal performance affects metabolic rate in dolphins: implications for animals communicating in noisy environments,” The Journal of Experimental Biology **218**, 1647-1654.

Johnston, D. W. (**2002**). “The effect of acoustic harassment devices on harbour porpoises (Phocoena phocoena) in the Bay of Fundy, Canada,” Biol. Conserv. **108**, 113-118.

Kastelein, R. A., de Haan, D., Goodson, A. D., Staal, C., and Vaughan, N. (**1997**). “The effects of various sounds on a harbour porpoise (Phocoena phocoena),” in *The Biology of the Harbour Porpoise*, edited by A. J. Read, P. R. Wiepkema, and P. E. Nachtigall (De Spil Publishers, Woerden, The Netherlands), pp. 367-383.

Kastelein, R. A., Rippe, H. T., Vaughan, N., Schooneman, N. M., Verboom, W. C., and de Haan, D. (**2000**). “The effects of acoustic alarms on the behavior of harbor porpoises (Phocoena phocoena) in a floating pen,” Mar. Mammal Sci. **16**, 46-64.

Kastelein, R. A., de Haan, D., Vaughan, N., Staal, C., and Schooneman, N. M. (**2001**). The influence of three acoustic alarms on the behavior of harbor porpoises (Phocoena phocoena) in a floating pen,” Mar. Environ. Res. **52**, 351-371.

Kastelein, R. A., Verboom, W. C., Muijsers, M., Jennings, N. V., and van der Heul, S. (**2005**). The influence of acoustic emissions for underwater data transmission on the behaviour of harbor porpoises (Phocoena phocoena) in a floating pen,” Mar. Environ. Res. **59**, 287-307.

Kastelein, R. A., Jennings, N. V., Verboom, W. C., de Haan, D., and Schooneman, N. M. (**2006**). “Differences in the response of a striped dolphin (Stenella coeruleoalba) and a harbor porpoise (Phocoena phocoena) to an acoustic alarm,” Mar. Environ. Res. **61**, 363-378.

Kastelein, R. A., van den Belt, I., Gransier, R., and Johansson, T. (**2015**). “Behavioural responses of a harbor porpoise (Phocoena phocoena) to 25.5- to 24.5-kHz sonar down-sweeps with and without side bands,” Aquat. Mamm. **41**, 400-411.

Koschinski, S., Culik, B. M., Damsgaard Henriksen, O., Tregenza, N., Ellis, G., Jansen, C., and Kathe, G. (**2003**). “Behavioural reactions of free-ranging porpoises and seals to the noise of a simulated 2 MW windpower generator,” Mar. Ecol. Prog. Ser. **265**, 263-273.

Koschinski, S., Culik, B. M., Trippel, E.A, and Ginzkey, L. (**2006**). “Behavioral reactions of free-ranging porpoises Phocoena phocoena encountering standard nylon and $BaSO_4$ mesh gillnets and warning sound,” Mar. Ecol. Prog. Ser. **313**, 285-294.

Kruse, S. (**1991**). “The interactions between killer whales and boats in Johnstone Strait, B.C.” in Dolphin Societies: Discoveries and Puzzles, edited by K. S. Norris and K. Pryor (University of California Press, Berkeley, CA), pp. 149-159.

Lemon, M., Lynch, T. P., Cato, D. H., and Harcourt, R. G. (**2006**). “Response of travelling bottlenose dolphins (Tursiops truncatus) to experimental approaches by a powerboat in Jervis Bay, New South Wales, Australia,” Biol. Conserv. **127**, 363-372.

Lemon, M., Cato, D., Lynch, T., and Harcourt, R. (**2008**). “Short-term behavioural response of bottlenose dolphins Tursiops aduncus to recreational powerboats,” Bioacoustics. **17**, 171-173.

Lucke, K., Dähne, M., Adler, S., Brandecker, A., Krügel, K., Sundermeyer, J. K., and Siebert, U. (**2012**). “Evaluating the effects of offshore pile driving on Phocoena phocoena (harbor porpoise) by using passive acoustic monitoring” in The Effects of Noise on Aquatic Life, edited by A. N. Popper and A. Hawkins (Springer, New York), Ad. Exp. Med. Biol. **730**, 285-287.

Luís, A. R., Couchinho, M. N., and dos Santos, M. E. (**2014**). “Changes in acoustic behavior of resident bottlenose dolphins near operating vessels,” Mar. Mammal Sci. **30**, 1417-1426.

Lusseau, D. (**2003a**). “Male and female bottlenose dolphins Tursiops spp. have different strategies to avoid interactions with tour boats in Doubtful Sound, New Zealand,” Mar. Ecol. Prog. Ser. **257**, 267-274.

Lusseau, D. (**2003b**). “Effects of tour boats on the behavior of bottlenose dolphins: using Markov chains to model anthropogenic impacts,” Conserv. Biol. **17**, 1785-1793.

Lusseau, D. (**2004**). “The hidden cost of tourism: detecting long-term effects of tourism using behavioral information,” Ecol. Soc. **9**, 2.

Lusseau, D. (**2006**). “The short-term behavioral reactions of bottlenose dolphins to interactions with boats in Doubtful Sound, New Zealand,” Mar. Mammal Sci. **22**, 802-818.

Lusseau, D., and Bejder, L. (**2007**). “The long-term consequences of short-term responses to disturbance experiences from whalewatching impact assessment,” Int. J. Comp. Psychol. **20**, 228-236.

Lusseau, D., Bain, D. E., Williams, R., and Smith, J. C. (**2009**). “Vessel traffic disrupts the foraging behavior of southern resident killer whales Orcinus orca,” Endang. Species Res. **6**, 211-221.

Mattson, M. C., Thomas, J. A., and St. Aubin, D. (**2005**). “Effects of boat activity on the behavior of bottlenose dolphins (Tursiops truncatus) in waters surrounding Hilton Head Island, South Carolina,” Aquat. Mamm. **31**, 133-140.

Miller, L. J., Solangi, M., and Kuczaj, S. A. II. (**2008**). “Immediate response of Atlantic bottlenose dolphins to high-speed personal watercraft in the Mississippi Sound,” J. Mar. Biol. Assoc. UK. **88**, 1139-1143.

Miller, P. J. O., Kvadsheim, P. H., Lam, F.-P. A., Wensveen, P. J., Antunes, R., Alves, A. C., Visser, F., Kleivane, L., Tyack, P. L., and Sivle, L. D. (2012). “The severity of behavioral changes observed during

experimental exposures of killer (*Orcinus orca*), long-finned pilot (*Globicephala melas*), and sperm (*Physeter macrocephalus*) whales to naval sonar" Aquat. Mamm. **38**, 362-401.
Miller, P. J. O., Antunes, R. N., Wensveen, P. J., Samarra, F. I. P., Alves, A. C., Tyack, P. L., Kvadsheim, P. H., Kleivane, L., Lam, F.-P. A., Ainslie, M. A., and Thomas, L. (**2014**). "Dose-response relationships for the onset of avoidance of sonar by free-ranging killer whales," J. Acoust. Soc. Am. **135**, 975-993.
Noren, D. P. (**2011**). "Estimated field metabolic rates and prey requirements of resident killer whales," Mar. Mammal Sci. **27**, 60–77.
Noren, D. P., Johnson, A. H., Rehder, D., and Larson, A. (**2009**). "Close approaches by vessels elicit surface active behaviors by southern resident killer whales," Endangered Species Research. **8**, 179-192.
Noren, D., Dunkin, R., Williams, T., and Holt, M. (**2012**). "Energetic cost of behaviors performed in response to vessel disturbance: one link in the population consequences of acoustic disturbance model" in The Effects of Noise on Aquatic Life, edited by A. N. Popper and A. Hawkins (Springer, New York), Adv. Exp. Med. Biol. **730**, 427-430.
Noren, D. P., Holt, M. M., Dunkin, R. C., and Williams, T. M. (**2013**). "The metabolic cost of communicative sound production in bottlenose dolphins (Tursiops truncatus)," J. Exp. Biol. **216**, 1624-1629.
Nowacek, S. M., Wells, R. S., and Solow, A. R. (**2001**). "Short-term effects of boat traffic on bottlenose dolphins, Tursiops truncatus, in Sarasota Bay, Florida," Mar. Mammal Sci. **17**, 673-688.
Olesiuk, P. F., Nichol, L. M., Sowden, M. J., and Ford, J. K. B. (**2002**). "Effect of the sound generated by an acoustic harassment device on the relative abundance and distribution of harbor porpoise (Phocoena phocoena) in Retreat Passage, British Columbia," Mar. Mammal Sci. **18**, 843-862.
Otani, S., Naito, Y., Kato, A., and Kawamura, A. (**2001**). "Oxygen consumption and swim speed of the harbor porpoise Phocoena phocoena," Fisheries Sci. **67**, 894-898.
Papale, E., Azzolin, M., and Giacoma, C. (**2012**). "Vessel traffic affects bottlenose dolphin (Tursiops truncates) behaviour in waters surrounding Lampedusa Island, south Italy," J. Mar. Biol. Assoc. UK. **92**, 1877-1885.
Pirotta, E., Brookes, K. L., Graham, I. M., and Thompson, P. M. (**2014**) "Variation in harbour porpoise activity in response to seismic survey noise," Biol. Lett. **10**, 20131090.
Pirotta, E., Merchant, N. D., Thomspon, P. M., Barton, T. R., and Lusseau, D. (**2015**) "Quantifying the effect of boat disturbance on bottlenose dolphin foraging activity," Biol. Conserv. **181**, 82-89.
Senigaglia, V., Christiansen, F., Bejder, L., Gendron, D., Lundquist, D., Noren, D.P., Schaffar, A., Smith, J.C., Williams, R., Martinez, E., Stockin, K., and Lusseau, D. (**2016**). "Meta-analyses of whale-watching impact studies: comparisons of cetacean responses to disturbance." Mar. Ecol. Prog. Ser. **542**, 251-263.
Scarpaci, C., Bigger, S. W., Corkeron, P. J., and Nugegoda, D. (**2000**). "Bottlenose dolphins (Tursiops truncatus) increase whistling in the presence of 'swim-with-dolphin' tour operations," J. Cetacean Res. Manage. **2**, 183-185.
Steckenreuter, A., Möller, L., and Harcourt, R. (**2012**). "How does Australia's largest dolphin-watching industry affect the behaviour of a small and resident population of Indo-Pacific bottlenose dolphins?" J. Environ. Manage. **97**, 14-21.
Stensland, E., and Berggren, P. (**2007**). "Behavioural changes in female Indo-Pacific bottlenose dolphins in response to boat-based tourism," Mar. Ecol. Prog. Ser. **332**, 225-234.
Sundermeyer, J. K., Lucke, K., Dähne, M., Gallus, A., Krügel, K., and Siebert, U. (**2012**). "Effects of underwater explosions on presence and habitat use of harbor porpoises in the German Baltic Sea" in The Effects of Noise on Aquatic Life, edited by A. N. Popper and A. Hawkins (Springer, New York), Adv. Exp. Med. Biol. **730**, 289-291.
Teilman, J., Tougaard, J., Miller, L. A., Kirketerp, T., Hansen, K., and Brando, S. (**2006**). "Reaction of captive harbor porpoises (Phocoena phocoena) to pinger-like sounds," Mar. Mammal Sci. **22**, 240-260.
Tougaard, J., Kyhn, L. A., Amundin, M., Wennerberg, D., and Bordin, C. (**2012**). "Behavioral reactions of harbor porpoise to pile-driving noise" in The Effects of Noise on Aquatic Life, edited by A. N. Popper and A. Hawkins (Springer, New York), Adv. Exp. Med. Biol. **730**, 277-280.
Tyack, P. L., Zimmer, W. M. X., Moretti, D., Southall, B. L., Claridge, D. E., Durban, J. W., Clark, C. W., D'Amico, A., DiMarzio, N., and Jarvis, S. et al. (**2011**). "Beaked Whales Respond to Simulated and Actual Navy Sonar," PLoS ONE **6**, e17009.
Williams, R., and Ashe, E. (**2007**). "Killer whale evasive tactics vary with boat number," J. Zool. **272**, 390-397.
Williams, R., and Noren, D. P. (**2009**) "Swimming speed, respiration rate and estimated cost of transport in adult killer whales," Mar. Mammal Sci. **25**, 327–350.
Williams, R. M., Trites, A. W., and Bain, D. E. (**2002a**). "Behavioural responses of killer whales (Orcinus orca) to whale-watching boats: opportunistic observations and experimental approaches," J. Zool., Lond. **256**, 255–270.

Williams, R. M., Bain, D. E., Ford, J. K. B., and Trites, A. W. (**2002b**) "Behavioural responses of male killer whales to a leap frogging vessel," Journal of Cetacean Research and Management. **4**, 305-310.
Williams, R., Lusseau, D., and Hammond, P. S. (**2006**). "Estimating relative energetic costs of human disturbance to killer whales (Orcinus orca)," Biol. Conserv. **133**, 301-311.
Williams, R., Bain, D. E, Smith. J. C., and Lusseau, D. (**2009**). "Effects of vessels on behaviour patterns of individual southern resident killer whales Orcinus orca," Endangered Species Research. **6**, 199-209.
Williams, T. M., Friedl, W. A., Fong, M. L., Yamada, R. M., Sedivy, P., and Haun, J. E. (**1992**). "Travel at low energetic cost by swimming and wave-riding bottlenose dolphins," Nature **355,** 821-823.
Williams, T. M., Friedl, W. A., and Haun, J. E. (**1993**). "The physiology of bottlenose dolphins (Tursiops truncatus): heart rate, metabolic rate and plasma lactate concentration during exercise," J. Exp. Biol. **179,** 31-46.
Yazdi, P., Kilian, A., and Culik, B. M. (**1999**). "Energy expenditure of swimming bottlenose dolphins (Tursiops truncatus)," Mar. Biol. **134,** 601-607.
Yazdi, P. (**2005**). Einfluss der Tourismusboote auf das Verhalten und die Energetik der Großen Tümmler (Tursiops truncatus) vor der Insel Choros, Chile (Impact of tour boats on the behaviour and energetic of bottlenose dolphins (Tursiops truncatus) off Choros Island, Chile). Dissertation, Christian-Albrechts-Universität, Kiel.
Yazdi, P. (**2007**). "Impact of tour boats on the behaviour and energetics of bottlenose dolphins (Tursiops truncatus) off Choros Island, Chile." International Whaling Commission SC/59/WW20.