Energetic Cost of Behaviors Performed in Response to Vessel Disturbance: One Link in the Population Consequences of Acoustic Disturbance Model

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1 Introduction

Several studies have shown that cetaceans respond to the physical presence and/or acoustic emissions from marine vessels. For example, cetaceans perform surface-active behaviors (SABs) in response to an increase in the number of and/or close approaches by vessels (Lusseau 2006; Noren et al. 2009; Williams et al. 2002, 2009). SABs are often performed in bouts of one or more behaviors performed sequentially, and the majority of SABs provide both visual and acoustic signals that are important to social marine mammals. Indeed, the use of sound is essential to the survival and reproduction of cetaceans (National Research Council 2003), and because of this, anthropogenic sound exposure in marine mammals is a concern. Individuals may compensate for increased vessel noise by changing the amplitude (Holt et al. 2009; Scheifele et al. 2005), duration (Foote et al. 2004), repetition rate, and/or frequency of the sounds they produce.

Although many studies have described changes in the performance of SABs and acoustic signals in cetaceans relative to changes in vessel presence and background noise, it is difficult to quantify whether these changes in behavior impact marine mammal populations. The population consequences of acoustic disturbance (PCAD) model provides a framework to assess the biological significance of behavioral responses to disturbance (National Research Council 2005). This model describes several stages required to relate acoustic disturbance to the effects on a marine mammal population. Data on the physiological effects of sound exposure, including the energetic costs of performing behaviors in response to increased exposure to vessel noise, are critical to the PCAD model.

The aim of this study is to fill a data gap in the PCAD model by determining the metabolic cost of behaviors performed in response to vessel presence and associated noise. Specifically, in terms relative to the PCAD model (National Research Council 2005, Fig. 3–1), this study provides data on transfer function 2 (metabolic cost) of behavioral changes (performing SABs and vocalizations)

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A.N. Popper and A. Hawkins (eds.), *The Effects of Noise on Aquatic Life*, Advances in Experimental Medicine and Biology 730, DOI 10.1007/978-1-4419-7311-5_97, © Springer Science+Business Media, LLC 2012 427

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that can immediately affect life functions (e.g., feeding rates). For example, if metabolic costs associated with these behavioral changes are significant, it is possible that cetaceans would need to increase their daily food consumption to meet their increased metabolic demands.

It is interesting to note that vessels can also disrupt foraging behavior in cetaceans. For example, *Orcinus orca* (killer whales) switch from foraging behavior to travel in the presence of vessels (Lusseau et al. 2009). Thus foraging opportunities and, consequently, energy acquisition can be reduced in the presence of vessels. If energetic demand is also increased due to the performance of SABs and vocalizations, then vessel impacts to cetaceans' daily energy budgets could be exacerbated.

2 Methods

Two trained adult male *Tursiops truncatus* (Atlantic bottlenose dolphins) were used in experiments to determine the metabolic cost of behavioral responses (SABs and vocalizations) to vessels by free-ranging animals. To determine the metabolic costs of performing SABs, oxygen consumption from the two dolphins was measured via flow-through respirometry immediately after they swam the length of the research pool, had bouts of tail slaps, and had bouts of bows (a proxy for breaches; Fig. 1). Oxygen consumption values were recorded continuously until levels reached resting values. To assess the energetic cost of sound production, oxygen consumption from the same dolphins was measured via flow-through respirometry before performing distinct stereotypical vocalizations, during the performance of the vocalizations, and during recovery after the performance of vocalizations. For both studies, respiration rates were also measured before, during, and after the performance of behaviors.



Fig. 1 Schematic of experimental trial to measure the energetic cost of performing surface-active behaviors

3 Results

Respiration and oxygen consumption rates after the performance of behaviors differed across trial types for both dolphins. Not surprisingly, respiration rates were highest after bouts of 10 bows and lowest after swimming. Metabolic rates measured after 10 bow bouts were higher than those after 5 bow bouts, whereas metabolic rates after tail slaps and slow swimming were the lowest. Energetic costs of slow swimming and bouts of tail slaps were similar to metabolic rates measured during rest. Recovery periods required for metabolic rates to return to resting values were greatest for the most energetically costly SAB bouts (10 bows and 5 bows). Furthermore, recovery periods after bouts of 10 bows were surprisingly long (\geq 14 min), particularly compared with the time required for the performance of these bouts (\leq 1 min). Data on the metabolic cost of sound production are still being analyzed so the results are not yet available. However, results from studies on sound production in other organisms suggest that these costs could be significant (e.g., Oberweger and Goller 2001).

4 Discussion

Experimental studies on trained marine mammals can be used to determine the energetic costs of behaviors performed in response to increased vessel presence and anthropogenic noise. These studies can provide useful data to populate information gaps in the PCAD model. Quantifying the energetic costs of behaviors performed in response to vessel disturbance will help us determine if short-term behavioral responses to disturbance have long-term individual- and/or population-level impacts.

The results of this study show that behaviors performed in response to increased vessel presence and anthropogenic noise can increase metabolic rates in cetaceans. As a consequence, the performance of energetically expensive SABs (e.g., breaches) in response to vessel presence and/or close approaches by vessels may impact daily energy requirements. For example, if the frequency of disturbance and the resulting behavioral responses are great enough to increase daily metabolic rates, daily food consumption will need to increase to meet these higher energetic demands. Furthermore, because cetaceans utilize sound to find food and/or coordinate feeding activities with conspecifics, increased noise due to vessel activity can also have the confounding effect of masking cetacean acoustic signals during foraging, consequently reducing the efficiency of foraging efforts. Moreover, some cetaceans actually cease foraging behavior in the presence of vessels (Lusseau et al. 2009). Thus vessel presence and the associated increase in ambient noise levels have the potential to increase energetic demand, reduce the efficiency of energy intake, and/or reduce opportunities for energy intake.

Acknowledgments This research was funded by Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, WA, and Office of Naval Research (ONR), Arlington, VA, grants to T. M. Williams, D. P. Noren, and M. M. Holt. These experiments were made possible through the efforts of dolphin trainers Traci Kendall, Jen Walsh, Brett Long, and Beau Richter from the Mammalian Physiology Laboratory, University of California, Santa Cruz, Santa Cruz, CA. All protocols were approved by the University of California, Santa Cruz, Institutional Animal Care and Use Committee.

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