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Building time-budgets from bioacoustic signals to measure population-level changes in behavior: a case study with sperm whales in the Gulf of Mexico

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ABSTRACT

Evaluating changes in the collective behavior of a population can be an indirect method for inferring organismal responses to changing environmental conditions. Apex predators, such as the sperm whale *(Physeter macrocephalus)*, can provide valuable insights into the ecosystem processes of the deep sea, where little direct observation can be made. Sperm whales are often difficult to observe at sea, as they inhabit deep, offshore waters and spend most of their lives beneath the surface. However, sperm whales are extremely amenable to passive acoustic monitoring, as their vocalizations are well-studied, highly distinguishable, produced regularly, and can be detected at relatively long ranges (>10 km). Sperm whales produce distinct clicks in two behavioral contexts (social interaction or foraging/prey capture); thus, we can use acoustic detection of these vocalizations to infer patterns of large-scale, collective behavior, which is similar to studying calling frogs or insects indicating their reproductive phenology. We recorded behaviorally-specific sperm whale vocalizations at three sites in the Northern Gulf of Mexico in July 2010 and 2011. We used these recordings to construct population-level time budgets, an empirical collective metric of behavior, based on the ratio of hours in a day with social clicks to the hours in a day with foraging clicks, and represented this as an "acoustic activity index." Our index showed significant differences in the proportions of social and foraging behavior across the range of sperm whales in the Northern Gulf of Mexico, and the proportion of social activity increased by more than a factor of two from 2010 to 2011. These differences support previous evidence of differential habitat use by sperm whales in the Gulf of Mexico, and suggest possible changes in environmental conditions between years. Thus, the acoustic activity index may provide a powerful way to evaluate changes in behavior and link them to changing ecological conditions. This novel application of bioacoustics to constructing time budgets and creating a behaviorally-based index at the population scale can serve as an indicator of ecological change, and greatly enhance our ability to understand the behavior and ecology of many acoustically active species.

1. Introduction

While direct assessment of an ecosystem can often be difficult, observations of animal behavior can act as indicators of ecosystem change, as animals modify their behavior due to changing environmental conditions. We can measure behavioral changes by analyzing an animal's time budget—an empirical measure that categorizes behavior types as the proportion of a time period that an animal spends engaged in that behavior (MacArthur and Pianka, 1966). Time budgets can provide detailed insights into how animals use resources and interact with their environment, and they have been used to study behavior in a variety of animals, such as birds (Cucco and Malacarne, 1997), primates (Dunbar, 1992; Kalan et al., 2015; Menon and Poirier, 1996), pinnipeds (Boyd et al., 1991), and cetaceans (Whitehead and Weilgart, 1991). An animal's time bud-

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get is often influenced by ecological and environmental conditions. For example, animals have been shown to alter their foraging effort in response to predation pressure and food availability, spending more time engaged in foraging activities when prey items are scarce (Anthony et al., 1981; Cucco and Malacarne, 1997; Friedlaender et al., 2011). Environmental factors, such as habitat degradation and weather, can change the timing of foraging and social activity (Boyd, 1999; Dunbar, 1992; Menon and Poirier, 1996). As such, time budgets constructed from behavioral observations of individuals can be used to examine how behavior patterns shift with changes to the environment.

Traditionally, time budgets have been focused on the behavior of individuals, and require many hours of careful observation of many different individuals to be able to infer anything about behavior patterns of the general population. Population-level time budgets, in contrast, look at general trends in behavior across the population to identify important large-scale shifts in behavior within short timescales (Bridges and Noss, 2011; O'Connell et al., 2010). Evaluating behavior at the population level allows us to quickly identify rapid changes with large implications, without having to monitor multiple individuals over a long period of time, and have been used to gather valuable information on social and foraging behaviors in cryptic and endangered species (Bridges et al., 2004; Cui et al., 2011; de Almeida Jácomo et al., 2004; Yoo and Jang, 2012).

Understanding the foraging behavior of top predators can be especially useful for studies of ecology and conservation, because changes in foraging behavior can reflect changes of abundance in lower trophic levels, as predators will modify their foraging behavior based on the availability of preferred prey species, spending more time engaged in foraging activities when prey items are scarce (Beckerman et al., 1997; Crocker et al., 2006; Estes and Duggins, 1995; Friedlaender et al., 2011; Garshelis et al., 1986; MacArthur and Pianka, 1966; Menon and Poirier, 1996; Norberg, 1997; Pichegru et al., 2010). As a deep-water apex predator, sperm whales (*Physeter macrocephalus*) play a major role in marine ecosystems around the globe, and have been suggested to be a valuable indicator species due to their high trophic level (Savery et al., 2013). Sperm whales feed almost exclusively on deep-water squid, routinely diving to depths greater than 400 m for up to an hour at a time (Watwood et al., 2006; Whitehead, 2003). Because sperm whales spend more than 70% of their lives below the surface of the ocean diving in deep water, they can be difficult to visually observe and study at sea (Watwood et al., 2006; Whitehead, 2003); thus, passive acoustic monitoring can be a useful tool for long-term study of sperm whale populations (Mellinger et al., 2007; Mellinger et al., 2002; Zimmer, 2011).

The use of passive acoustic monitoring has increased dramatically in recent years, especially in studies of marine mammals (Mellinger et al., 2007; Van Parijs et al., 2009). Passive acoustic technology is relatively inexpensive and easy to employ (compared to other survey methods), while offering a non-invasive and data-rich method for studying often difficult to observe species. In most cases, studies using passive acoustics in the marine environment have been mainly limited to discussing spatial and temporal presence and absence of a particular species. However, when there is contextual information in the acoustic signals, more detailed behavioral information can be extracted. Previous studies of sperm whales have shown that they produce stereotyped vocalizations that correspond to specific behavioral contexts (Watkins and Schevill, 1977). For example, studies using acoustic recording tags have linked clicks that sperm whales produce at regular intervals at depth to echolocation used for foraging, and more variable clicks produced at the surface to a communicative function (Madsen et al., 2002b; Watwood et al., 2006). In the Eastern Tropical Pacific, passive acoustics and visual observations have been used conjunctively to link particular vocalizations to observed social and foraging behaviors (Whitehead and Weilgart, 1991). Thus, the occurrence of these vocalization types can be used to infer sperm whale behavior, and we can assess the behavioral patterns of a population acoustically by measuring the relative temporal proportion of foraging and social behaviors.

Here, we present a novel method of monitoring behavior at the population level using passive acoustics which could be used to study trophic ecology and ecosystem processes. As a case study, we demonstrate using passive acoustic data to examine trends in group-level behavior of sperm whales over spatial and temporal scales. We classified vocalizations from three locations across the Northern Gulf of Mexico as pertaining to foraging or social behavior and created time budgets from these behaviors. We then compared time budgets across our study sites and between our study years to assess whether sperm whales changed their behavior with respect to time spent foraging or socializing.

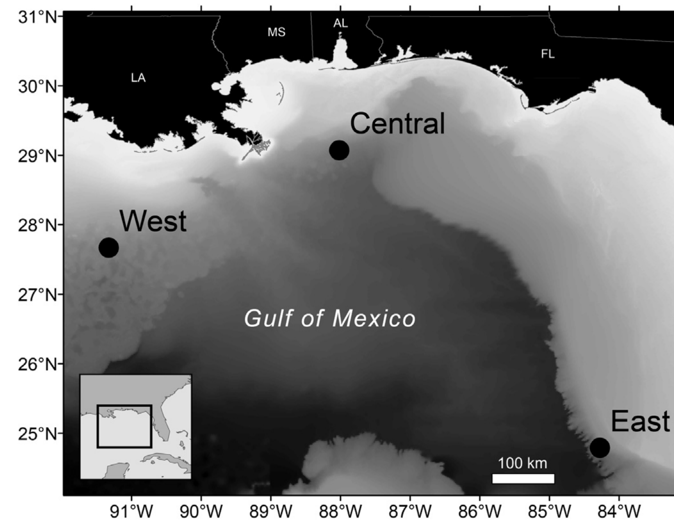

Fig. 1. Map showing the locations of the acoustic recording sites (West, Central, East) in the Northern Gulf of Mexico. Shading on the map shows the bathymetry and relative water depths.

Table 1
Location of the MARUs at three study sites.

	Depth (m)	Latitude (°)	Longitude (°)
West	771	27.67000	−91.32533
Central	1092	29.07500	−88.01033
East	1370	24.79562	−84.27557

Table 2
Mean Acoustic Activity Index values (Mean ± SE).

	2010	2011
West	0.0308 ± 0.0176	0.0592 ± 0.0217
Central	0.0658 ± 0.0194	0.1442 ± 0.0409
East	0.0217 ± 0.0099	0.0333 ± 0.0133

2. Materials and methods

Underwater acoustic data in the Northern Gulf of Mexico were recorded using Marine Autonomous Recording Units (MARUs) (Calupca et al., 2000). The MARUs were anchored on the sea floor at three study locations ("West," "Central," and "East") with depths ranging from 771 to 1370 m (Fig. 1, Tables 1 and 2). These locations were chosen to achieve a large spatial coverage for the home range of the Northern Gulf of Mexico sperm whale population (Jochens