Deep–Sea Research Part II 141 (2017) 155–167

Contents lists available at ScienceDirect

Deep–Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Regular article

Habitat preferences of baleen whales in a mid-latitude habitat

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ARTICLE INFO

Keywords:
Environmental niche modeling (ENM)
Azores
Mid-Atlantic
Migration
MaxEnt
Niche overlap
Blue whale
Fin whale
Sei whale

ABSTRACT

Understanding the dynamics of baleen whale distribution is essential to predict how environmental changes can affect their ecology and, in turn, ecosystem functioning. Recent work showed that mid-latitude habitats along migratory routes may play an important role on the feeding ecology of baleen whales. This study aimed to investigate the function of a mid-latitude habitat for blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*) and sei (*Balaenoptera borealis*) whales occurring in sympatry during spring and summer months and to what extent their environmental niches overlap. We addressed those questions by developing environmental niche models (ENM) for each species and then making pairwise comparisons of niche overlap and relative habitat patch importance among the three species. ENMs were created using sightings from the Azorean Fisheries Observer Program from May to November, between 2004 and 2009, and a set of 18 predictor environmental variables. We then assessed monthly (April–July) overlap among ENMs using a modified Hellinger's distance metric (I). Results show that the habitat niches of blue and fin whales are strongly influenced by primary productivity and sea surface temperature and are highly dynamic both spatially and temporally due to the oceanography of the region. Niche overlap analyses show that blue and fin whale environmental niches are similar and that the suitable habitats for the two species have high degree of spatial coincidence. These results in combination suggest that this habitat may function as a mid-latitude feeding ground to both species while conditions are adequate. The sei whale model, on the other hand, did not include variables considered to be proxies for prey distribution and little environmental niche overlap was found between this species and the other two. We argue that these results suggest that the region holds little importance as a foraging habitat for the sei whale.

1. Introduction

Marine ecosystems are facing increasing changes and deteriorating rapidly, due to the combined effect of global climate change and of a significant increase in the human utilization of marine space and resources (McCauley et al., 2015; Worm et al., 2006, 2003). These changes may unbalance marine ecosystems, to the point of causing regime shifts, with detrimental effects not only on the natural communities but also to the ecosystem services they provide to human societies (Möllmann et al., 2015; Worm et al., 2006). To counteract the deterioration of marine ecosystems we need effective management and conservation policies that incorporate the most recent advances in population biology and community ecology (Soulé et al., 2005). In that respect, understanding the processes, functioning and interrelationships among ecosystem components is essential for proper ecosystem-based management (Borja, 2014).

Pelagic marine ecosystems are highly dynamic and vast, and many pelagic predators regularly move thousands of kilometers among different regions of the ocean (Block et al., 2011). Obtaining information to understand the ecology of pelagic species and ecosystems in order to be able to predict how changes may affect pelagic communities is a complex task that is further hampered by logistical and financial constraints (Borja, 2014; Game et al., 2009; McClellan et al., 2014). One of the great challenges for accurately predicting patterns and features of pelagic communities is to identify the mechanisms leading to the presence of a given species in a specific geographical area at a specific moment in time (Verity et al., 2002).

In face of the data scarcity for pelagic ecosystems, one of the approaches commonly used is to describe the habitat requirements of a species by fitting niche models and then use those models to identify its potential distribution by projecting the models on environmental space (Robinson et al., 2011; Tyberghein et al., 2012). Niche models can be

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http://dx.doi.org/10.1016/j.dsr2.2016.07.015

Available online 02 August 2016

(1) mechanistic, informed by species' physiological tolerances and behavior; (2) correlative, which try to identify statistical relationships between species occurrences and environmental conditions; (3) a combination of the above (Anderson, 2012, 2013). Mechanistic methods depend on a profound knowledge of the organism′s physiology and behavior that is not available for the vast majority of species, especially in the case of pelagic taxa (Anderson, 2013; Robinson et al., 2011). By far, most niche models utilize a correlative approach, taking advantage of the availability of a wealth of digital data sources on species occurrences and environmental conditions (Franklin, 2010; Guisan and Thuiller, 2005; Peterson et al., 2011; Tyberghein et al., 2012). The correlative approach is rooted in the Grinnellian notion of environmental niche, assuming that the natural distribution of a species is chiefly controlled by abiotic preferences, food requirements and microhabitat characteristics (Grinnell, 1904; Hutchinson, 1991).

In the present work we explore the potential of using environmental niche models to investigate the processes involved in the utilization of a mid-latitude pelagic habitat by different species of baleen whales.

It is a well-known fact that most baleen whales undertake large annual migrations to highly productive areas during the summer, where they store large amounts of energy in the form of fat deposits that are believed to finance most of the activities over the next season (Stern, 2009). Their breeding and calving success during the following season, and even their survival, is probably dependent on the outcome of this feeding period (Webster et al., 2002). Based on stomach contents obtained from whaling catches, it was long believed that baleen whales feed only opportunistically when on breeding grounds and during migration, although some energetic models suggest that they may actually need to consume some food between feeding seasons (Lockyer, 1981).

However recent work has shown that habitats along migratory routes may play an important role on the feeding ecology of baleen whales. There is mounting evidence that at least some individuals interrupt their migration to high-latitude feeding grounds to forage in mid-latitude waters. Feeding behavior in mid-latitude sites during spring and summer was reported for southbound humpback whales (*Megaptera novaeangliae*) off Australia and New Caledonia, as well as in the South Atlantic (Barendse et al., 2010; Garrigue et al., 2010; Stockin and Burgess, 2005); similarly, in the Northeast Pacific, sighting data and satellite telemetry suggest that blue whales (*Balaenoptera musculus*) forage at different latitudes in discrete sites during their entire migratory cycle (Bailey et al., 2009; Mate et al., 1999; Reilly and Thayer, 1990).

In the central North Atlantic, recent studies investigating the movements and behavior of blue, fin (*B. physalus*) and sei whales (*B. borealis*), occurring in sympatry in the Azores region (37–40°N) during their northbound migration to summering grounds, yielded distinct results.

Blue and fin whales instrumented with satellite transmitters in the Azores remained foraging at middle latitudes for periods varying from a few days to months (Silva et al., 2013). Foraging behavior in fin whales was only detected in the vicinity of the Azores islands and north of 56°N, suggesting the species alternate periods of active migration with periods of extended use of specific habitats along the migratory route (Silva et al., 2013). In contrast, sei whales tagged in the Azores did not interrupt their migratory journey and their movement patterns gave no indication of foraging activity until whales reached the Labrador Sea, a known feeding ground for this species (Prieto et al., 2014).

Visser et al. (2011) investigated the association between baleen whale relative abundance in the Azores with the timing of three stages of phytoplankton bloom development (the onset, maximum, and end of bloom). Peak relative abundance of baleen whales was better explained by the onset of the spring bloom and occurred with a lag of 11 to 14 weeks and standard deviation (SD) of 1.5 weeks, 14–16 weeks (SD=1.2 weeks), and 14 to 17 weeks (SD=2.1 weeks) respectively for the blue, fin and sei whales. Although the results by Visser et al. (2011) show some inter-annual variation, which is more pronounced in the case of the sei whale, they suggest that whales may synchronize their migration to the North Atlantic phytoplankton spring bloom.

Clearly, more investigation is necessary to understand the processes leading to the choice and utilization of mid-latitude pelagic habitats by migrating baleen whales, and to understand if these habitats have distinct ecological roles for these animals.

Our study focused on three baleen whale species (blue, fin and sei whales) occurring in sympatry in a mid-latitude habitat (the Azores islands) during their migratory season towards high-latitude feeding grounds. We developed dynamic monthly environmental niche models using a presence only modeling approach based on the maximum entropy principle (Phillips et al., 2006), in order to characterize the environmental niche of each of the three species in the study area, and to understand how the habitat conditions change over time. We then quantified the environmental niche overlap among the three species (Warren et al., 2008) to assess to which degree their environmental niches are similar while they are in the region.

2. Methods

2.1. Study region

Data were collected in waters off the Azores islands, between 36°30'N 24°30'W and 40°00'N 31°45'W (Fig. 1). The Azores are an isolated archipelago of nine volcanic islands disposed in three groups (Eastern, Central and Western) aligned along a NW–SE orientation, extending over 600 km. The archipelago is crossed by the Mid-Atlantic Ridge (MAR) between the Central and Western groups. The islands are positioned over the Azores plateau rising from the abyssal plain (~4000 m), and defined roughly by the 2000 m depth isobath. As other volcanic oceanic islands, the Azores are characterized by steep slopes and narrow or absent island-shelves (Tempera et al., 2012). Additionally to the islands, more than 460 seamounts and seamount-like features are found within the archipelago EEZ (Morato et al., 2008). These characteristics combine to create a wide range of habitat types and are responsible for complex circulation patterns that increase the ability of the archipelago to capture and retain particles and small organisms (Sala et al., 2015). The region is largely dominated by two eastward flows generating from the Gulf Stream: the cold southern branch of the North Atlantic Current that crosses the MAR to the north of the Azores (45–48°N), and the warm Azores Front/Current system,

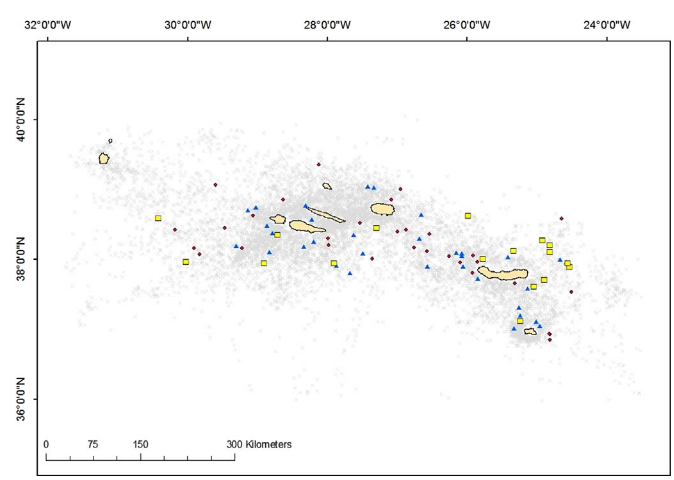

Fig. 1. Distribution of occurrences (2004–2009) of blue (*Balaenoptera musculus*) (squares), fin (*B. physalus*) (circles) and sei (*B. borealis*) (triangles) whales, and background points (crosses), used to fit the MaxEnt models. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)