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Decadal stability in top predator habitat preferences in the Bay of Biscay

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ABSTRACT

Most oceanographic systems, especially shelf ecosystems, are characterised by interannual variability in the timing, extent and intensity of their seasonal patterns. Such interannual variations have important consequences on top predator habitat preferences. Capitalising on oceanographic surveys performed every spring since 2004 in the Bay of Biscay (BoB), this study explored interannual variations in habitat preferences exhibited by five mobile top predator species: bottlenose and common dolphins, auks, fulmars and northern gannets. We expected to find species with similar habitat preferences every year or species exhibiting important variability in their habitat preferences. First, we identified with a Principal Component Analysis (PCA) three different habitats of varying extent depending on year: river plumes, central shelf waters and shelf edge. Second, the Principal Components were used to explore the habitat preferences of predators through Generalized Additive Models. We fitted two kinds of models, using and not using the year as an interaction term, to test whether habitat preferences changed across years. Our results showed a range of habitat strategies based on the specificity and stability of species preferences. Species exhibiting narrower habitat preferences also exhibited stronger stability in their preferences among years while the species with wider habitat preferences exhibited higher variability among years. The target habitats differed across studied species, with bottlenose dolphins targeting the shelf edge exclusively, auks preferring river plumes, fulmars exhibiting a gradual preference from the shelf edge to river plumes and gannets being present in any of the three habitats. In contrast, the habitat preferences of common dolphins, the most sighted cetacean species in the BoB, could not be reliably inferred.

1. Introduction

The marine environment, and especially pelagic ecosystems, is highly dynamic due to complex interactions between physical and biological processes. The resulting heterogeneous and dynamic structures vary in timing, extent and intensity at many scales (Barry and Dayton, 1991; Longhurst, 2007). Over continental shelves, for example, annual variations in river discharge determine nutrient inputs (Simpson, 1997), while the localisation and intensity of eddies associated with either currents or slope can fluctuate from year to year (Longhurst, 2007).

Heterogeneity is a challenge for species, as they must make accommodation for spatio-temporal variability in resources to ensure survival. Many species have evolved to target discrete and predictable oceanographic features (Ballance et al., 2006; Weimerskirch, 2007). This is the case of homeotherm top predators (cetaceans, seabirds and pinnipeds) which are associated with specific coarse and meso-scale habitats such as eddies and filaments (Tew-Kai et al., 2009; Cotté et al., 2011), tidal or river plume fronts (Jahncke et al., 2005; Skov and Thomsen, 2008) or shelf edges (Cañadas et al., 2002; Azzelino et al., 2008; Guilford et al., 2012). In addition to their sensory skills, most of these predators can rely on memories or social learning to locate these favourable habitats (Davoren et al., 2003) and they are highly dependent on spatial and temporal repetitiveness to find them.

Homeotherm top predator species exhibit a wide range of biological traits (Gaston, 2004; Perrin and Wursig, 2009): from plankton- to marine mammal-eating species, from tropical to polar regions, from species foraging at the sea surface to those hunting over a thousand metres deep and from resident to migrating species. The main difference between cetaceans and either seabirds or pinnipeds relates to reproductive strategies; the latter two require land to breed or moult (Gaston, 2004; Perrin and Wursig, 2009), while cetaceans have evolved a completely marine lifestyle (Chivers, 2009). Terrestrial reproduction and moulting have major consequences for seabirds and pinnipeds as they induce central-place foraging constraints, by which these species must rely on food available within a short distance from colonies and

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resting sites, whereas they can range freely the rest of the year (Gaston, 2004; Perrin and Wursig, 2009).

Although studies on the habitat of homeotherm marine predators are now common, especially over shelf areas, they often focus on short temporal scales due to methodological constraints (but see Ballance et al., 2006; Forney et al., 2015; Becker et al., 2016), which results in only a few investigations addressing the consistency of habitat preferences over time. However, some species may be expected to use several habitats depending on their availability and quality, while other species might be specialised towards a specific habitat type year after year.

Since 2004, the PELGAS ("PELagique GAScogne") oceanographic survey has been conducted in May in the Bay of Biscay (BoB; eastern North Atlantic) to study the ecosystem from physical oceanography to top predator ecology (Doray et al., 2018, this issue). This survey represents a unique opportunity to explore the temporal variability of species relationships to their habitats in a diversified top predator community, composed of species with contrasted lifestyles. The BoB is located at the intersection of cold and warm temperate biogeographic regions and is characterised by the occurrence of species with warm water as well as cold water affinities.

In this study, we focused on five cetacean and seabird taxa frequently encountered in the BoB (the sighting surveys were not appropriate for spotting pinnipeds). Bottlenose (*Tursiops truncatus*) and common dolphins (*Delphinus delphis*) are two species that are widely distributed, from estuaries to offshore waters. In the BoB, we know from previous studies in spring that bottlenose dolphins are aggregated over the slope, while common dolphins can also be encountered over the shelf (Certain et al., 2011). At the western Europe scale, bottlenose dolphins mostly occur over the slope in both winter and summer while common dolphins are abundant over the shelf in winter but are more widespread from shelf to oceanic waters in summer (Lambert et al., 2017, which focused on one-year seasonal ecological preferences of cetaceans and seabirds in the eastern North-Atlantic). Northern fulmars (*Fulmarus glacialis*) and auks (common guillemot *Uria aalge* and razorbill *Alca torda*) are two taxa with cold water affinities. The BoB represents the southern part of their range during both breeding and wintering periods (Lambert et al., 2017), and despite we know auks are more aggregated along the coast while fulmars are widespread over the shelf but avoid coastal waters (Certain et al., 2011; Lambert et al., 2017), information on their at-sea ecology remains poor. The northern gannet (*Morus bassanus*) is a more widely distributed species, breeding in northern Europe but wintering from the North Sea to western Africa (Nelson, 2002; Fort et al., 2012; Lambert et al., 2017). Although the species must face strong intra-specific competition during the breeding season, leading to sharp habitat preferences, during the wintering period gannets exhibit some flexibility with wintering grounds having different characteristics (for example, the Canary Current or the English Channel; Fort et al., 2012; Lambert et al., 2017).

In the BoB and during the PELGAS surveys, which occur during their breeding period, most of sighted auks and gannets are supposed to be non-breeders, the number of breeding auks being very low in the area (Cadiou et al., 2014) and the closest colony of gannets being in the English Channel (Nelson, 2002). Thus, the present study will provide valuable information on a poorly-known fraction of seabird populations, the non-breeding individuals (either juveniles or non-breeding adults).

Previous studies explored the averaged spatial distribution of predators over the 2003–2008 time period in the BoB (Certain et al., 2011) or unveiled the ecological preferences at the western Europe scale by contrasting winter and summer seasons (Lambert et al., 2017), but none focus on the long-term temporal variability of ecological preferences of predators. Thus, this study complements the knowledge brought by Certain et al. (2011); Lambert et al. (2017) on the habitat preferences of predators in the BoB by explicitly investigating the temporal variability of their springtime habitat preferences, thanks to the long time period of the PELGAS surveys. As suggested above, we expected two main patterns: (i) specialist species using the same pelagic habitat year after year, spatial variations of distribution reflecting spatial variations in habitat availability and (ii) species exhibiting a great variability in habitat preferences over time, either because generalist species are made up of specialist individuals with different habitat preferences, or because all individuals are generalists and remain within the same area irrespective of whether the corresponding habitat had changed.

We used in-situ environmental variables and top predator observational data collected during the decadal oceanographic surveys conducted in May every year from 2004 to 2013 within the BoB. We first characterised the habitats available in the study area in May. Given their dynamic nature, pelagic habitats are often difficult to define and distinguish (Barry and Dayton, 1991; Longhurst, 2007), but we chose to identify the different habitats available as well as their interannual variations, using a Principal Component Analysis (PCA). Springtime habitat preferences were explored with habitat modelling (generalized additive models (GAMs); Guisan and Zimmermann, 2000), highlighting potential associations to specific environmental conditions and their variation over time.

2. Material & methods

2.1. Study area

The BoB is a large bay in the eastern North Atlantic, spanning from France to Spain (Fig. 1). This bay is characterised by a broad continental shelf, which extends from 180 km in the northern part of the BoB, to 20 km in the southern part (Capbreton Canyon) and approximatively 30–40 km wide along the Iberian coasts (Koutsikopoulos and Le Cann, 1996). The oceanic part of the BoB is 2000–5000 m deep. In the southern BoB, the interaction between the slope current flowing from Iberian Peninsula to the northern BoB and the shelf break topography frequently results in meso-scale eddies that are relatively persistent in time (Pingree and Le Cann, 1992; Caballero et al., 2014). Over the shelf, currents are mainly driven by winds, tides or freshwater inputs, depending on the area (Koutsikopoulos and Le Cann, 1996). Seasonality is well marked, with a thermal stratification establishing during spring from south to north (Koutsikopoulos and Le Cann, 1996)

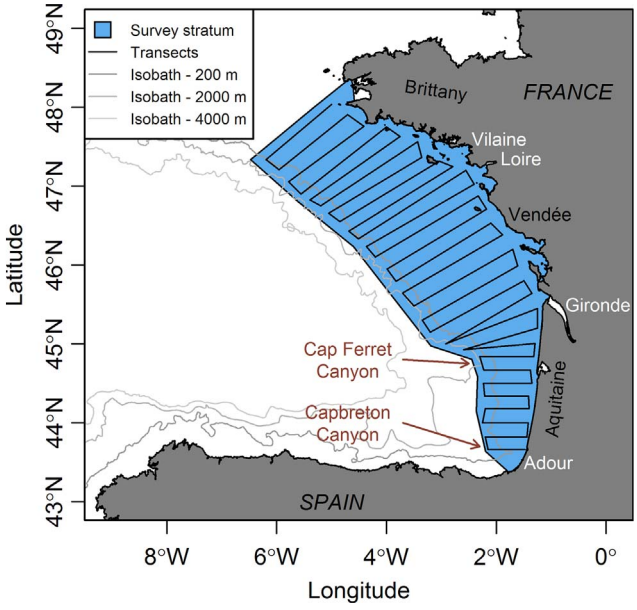

Fig. 1. Survey area and theoretical sampling design of the PELGAS survey. The isobaths are indicated in grey, the four main estuaries in white, the geographical localities in black and the main canyons in brown. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)