Journal of Experimental Marine Biology and Ecology 413 (2012) 150–158

Contents lists available at SciVerse ScienceDirect

Journal of Experimental Marine Biology and Ecology

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

Foraging ecology of five toothed whale species in the Northwest Iberian Peninsula, inferred using carbon and nitrogen isotope ratios

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ARTICLE INFO

Article history:
Received 2 October 2011
Received in revised form 14 December 2011
Accepted 16 December 2011
Available online 13 January 2012

Keywords:
Stable isotopes
Toothed whales
Trophic position
Trophic relationships
Isotopic mixing model
North West Iberian Peninsula

ABSTRACT

The feeding ecology and habitat use of the most frequently sighted and/or regularly reported stranded or by-caught toothed whale species of the North Western Iberian Peninsula (NWIP) were examined, with a special focus on their trophic position (TP) and relationships with their prey. With this aim, the stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) of common dolphin (*Delphinus delphis*), bottlenose dolphin (*Tursiops truncatus*), harbour porpoise (*Phocoena phocoena*), striped dolphin (*Stenella coeruleolba*) and long-finned pilot whale (*Globicepahala melas*) were analyzed in muscle samples taken from stranded and by-caught animals between 2004 and 2008. Stable isotopes were also measured in 17 species of fish and cephalopods previously identified as prey species, based on stomach content analyses, and in plankton. The trophic enrichment factors (TEF) were calculated for all five species and in addition, isotopic mixing models were applied to estimate the proportional contribution of each prey source to the diet of the common dolphin, which was the toothed whale species best sampled in our study. Plankton, fish and cephalopods exhibited an increasing trend in their $\delta^{13}C$ values (from −19.6‰ to −15.3‰) along the offshore-inshore axis, with a less clear spatial pattern observed for $\delta^{15}N$ values. Striped dolphins exhibited the lowest mean $\delta^{13}C$, $\delta^{15}N$ and TP values (−17.6‰, 10.8‰ and 4.3, respectively), which confirms the oceanic character of this species and its lower trophic position when compared to the other toothed whales analyzed. The common dolphin exhibited mean $\delta^{13}C$, $\delta^{15}N$ and TP values that were at an intermediate level (−17.0‰, 11.7‰ and 4.7, respectively) and results of the mixing model indicated that blue whiting (*Micromesistius poutassou*) was the main component of the diet. The harbour porpoise, bottlenose dolphin and pilot whale exhibited higher and very similar isotopic compositions and TPs. The mean TEF obtained between predators and their main prey were 1.4‰ for $\delta^{15}N$ and 0.8‰ for $\delta^{13}C$. These results provide information on stable isotope incorporation data for toothed whales, which are essential if conclusions are to be drawn in issues concerning trophic structures and habitat use in the NWIP.

1. Introduction

Marine mammals are recognized as top predators in marine trophic webs but little is known about their role in the structuring of marine ecosystems (Bowen, 1997). The main limitation is that the ecological needs of such large animals often exceed the temporal and spatial scales used to define community boundaries. This role is especially important in habitats with enhanced productivity such as upwelling areas, where high species richness contributes to high trophic linkage density and exceptional resource abundance (Bode et al., 2003). This is the case of the Northwest Iberian Peninsula (NWIP) waters. This area is characterized by high marine biodiversity and productivity, supported by strong nutrient enrichment during seasonal upwelling periods (Fraga, 1981), and a relatively narrow (20–35 km wide) shelf. From April to September, the prevalent northerly winds favor the upwelling of the nutrient-rich Eastern North Atlantic Central Water (Fraga, 1981), sustaining a high level of productivity when compared to adjacent areas. The marine fauna of the NWIP includes at least 19 marine mammal species (16 cetaceans and 3 pinnipeds; López et al., 2002). Based on strandings and sightings data, the most common cetacean species are all toothed

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doi:10.1016/j.jembe.2011.12.007

whales: common dolphin (*Delphinus delphis*), bottlenose dolphin (*Tursiops truncatus*), harbour porpoise (*Phocoena phocoena*), long-finned pilot whale (*Globicephala melas*), striped dolphin (*Stenella coeruleoalba*) and Rissos's dolphin (*Grampus griseus*) (López et al., 2002, 2004; Pierce et al., 2010). Despite the high proportion of cetaceans inhabiting the NWIP little is known about their role into the food web and their trophic relationships. Knowledge of feeding habits, habitat use and trophic relationships within a community is needed to underpin sound management measures, in particular in areas such as the NIWP where fishery by-catch mortality (López et al., 2002, 2003), prey depletion due to overfishing, and oil spills (Ridoux et al., 2004) are the main threats to cetacean populations.

Previous studies based on stomach contents analyses, have investigated the diet of the five toothed whales in the NWIP. Striped dolphin and pilot whale are known to be mainly cephalopods eaters. However striped dolphin exhibits dietary plasticity since some crustacean species, oceanic fish such as silvery lightfish (*Maurolicus muelleri*) as well as pelagic fish species (e.g. scad *Trachurus trachurus*, sand smelt *Atherina presbyter*) were found in stomach contents of individuals stranded in the NWIP (Sollmann, 2011; Spitz et al., 2006). Common dolphin mainly feeds on fish species, and the blue whiting (*Micromesistius poutassou*), sardine (*Sardina pilchardus*) and sand smelt are the most important prey species in the studied area (Santos et al., 2004b). Bottlenose dolphins have a varied diet in the NIWP, although it was strongly dominated by blue whiting and hake (*Merluccius merluccius*) (Santos et al., 2007a, 2007b). Finally harbour porpoise from the NWIP manly feeds on pelagic and coastal fish species such as pouting (*Trisopterus luscus*) and scad (Pierce et al., 2010; Santos et al., 2004a).

These differences in diet are also supported by differences in habitat uses (Pierce et al., 2010) and could thus lead to segregation among the five toothed whale species in the area. However, it is widely recognized that stomach content analyses have a number of limitations, since information provided by stomach contents normally allows the identification of the prey consumed shortly before the stomachs were collected (Pierce and Boyle, 1991) and varying time of digestion of different prey species can result in a overestimation of some species (Santos et al., 2001). Thus, insights into the trophic relationships and feeding habits of marine mammals can be obtained by measuring the ratios of naturally occurring isotopes such as those of carbon and nitrogen, in specific tissues (Hobson and Welch, 1992; Muir et al., 1995; Ostrom et al., 1993). This chemical analysis constitutes a powerful complementary method to the stomach content analyses, and is based on the assumption that predator stable isotope compositions are a reflection of those of their prey (DeNiro and Epstein, 1978, 1981). Ratios of the natural abundance of stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) have been extensively used in studies of cetacean ecology to assess dietary variation in space and time (Abend and Smith, 1995; Knoff et al., 2008; Mendes et al., 2007). Turnover rates vary among tissues depending on their metabolic activity, e.g. faster turnover rates have been measured for skin than for teeth (Walker and Macko, 1999). The difference in turnover rates between tissues allows the exploration of the dietary history of individual animals over different time windows from few days to several years (Abend and Smith, 1995). In addition to information on diet, $\delta^{13}C$ and $\delta^{15}N$ signatures can act as chemical tracers that reflect characteristics of the ecosystem where an animal forages, to determine the trophic position of species in marine food webs (Bode et al., 2003, 2007; Fry and Sherr, 1984) but also to study migration patterns (see Hobson, 1999 for review) and population substructure (Borrell et al., 2006). Stable isotopes of carbon and nitrogen show enrichment (an increase in the abundance of the heavier isotope) through food webs with increasing trophic level. The enrichment of $\delta^{13}C$ is generally small or insignificant (DeNiro and Epstein, 1978; Vander Zanden and Rasmussen, 2001) and, therefore, $\delta^{13}C$ is primarily used to provide information on the origin of the base of the food chain (France, 1995) and can reveal information such as inshore *vs* offshore feeding preferences (Hobson and Welch, 1992). On the other hand, $\delta^{15}N$ enrichment per trophic level in marine food webs is normally considerably higher, with an estimated mean trophic enrichment factor (TEF) ranging from 2 to 5‰ (DeNiro and Epstein, 1978, 1981; Hobson and Welch, 1992; Vander Zanden and Rasmussen, 2001). Nitrogen isotope ratios are thus more useful as an indicator of trophic position although some variability of $\delta^{15}N$ has also been demonstrated, for example an inshore *vs* offshore enrichment of $\delta^{15}N$ signatures (Chouvelon et al., in press) due to the use of different nitrogen sources by phytoplankton. TEF also vary depending on the tissue analyzed (Hobson et al., 1996). For example, metabolically active tissues show less enrichment in $\delta^{13}C$ (or $\delta^{15}N$) relative to the diet than inactive or keratinous tissues (Hobson et al., 1996). This represents a potential confounding factor when using isotope ratios in different tissues to infer information on feeding ecology over different time periods.

In this context, the aim of the present study was to investigate the feeding ecology and habitat use of five toothed whales species inhabiting the NWIP waters through the use of stable isotopes analysis ($\delta^{13}C$ and $\delta^{15}N$) and based on previous stomach content studies. The carbon and nitrogen isotope ratios of known prey species (eight fish species and nine cephalopod species; see below for details) and plankton (selected as the base of the food web in the research area) were also analyzed, in order to position the predators and their potential prey in the food web and to study their trophic relationships. Following this aim, the TEF of toothed whales and prey species were calculated. For the common dolphin, which is the most abundant cetacean species in the Iberian Peninsula and also the best represented in the samples available, isotopic mixing models were also applied to estimate the proportional contribution of each prey source to its diet.

2. Materials and methods

2.1. Sample collection

The fieldwork was carried out in the North West of the Iberian Peninsula, in an area extending from the northern limit of the Galician coast (43° 31′ N, 7° 2′ W) to Nazaré on the Portuguese coast (39° 36′ N, 9° 3′ W; Fig. 1). Stranded cetaceans were attended by experienced personnel of the Galician (*Coordinadora para o Estudo dos Mamiferos Mariños*, CEMMA) or Portuguese (*Sociedade Portuguesa de Vida Salvagem*, SPVS) stranding networks. Animals were identified to species, measured, sexed and, if the state of preservation of the carcass allowed it, full necropsies were performed and samples collected following a standard protocol defined by the European Cetacean Society (after Kuiken, 1996). For this study, between 2004 and 2008, muscle tissues were sampled from stranded and by-caught individuals of five toothed whale species: common dolphin ($n=114$), bottlenose dolphin ($n=9$), harbour porpoise ($n=19$), striped dolphin ($n=21$) and long-finned pilot whale ($n=9$) (see Table 1). After collection, muscle samples were stored at −20 °C until processed in the laboratory.

Muscle tissues of 17 species of fish and cephalopods previously identified in the literature as prey of the sampled cetacean species in the study area (see Santos et al., 2004a, 2004b, 2007a, 2007b) were also analyzed (see Table 2). All the fish samples and those of common squid (*Loligo vulgaris*) were collected with a pelagic trawl, during the PELACUS0409 survey. This survey, carried out by *Instituto Español de Oceanografía* (IEO) in spring 2009 aimed to acoustically assess pelagic marine living resources of northwestern and northern Spanish shelf waters. Plankton was also collected during the survey, at night by vertical tows (0–100 m depth) of a conical net deployed at regularly distributed stations over the shelf up to the shelf-break throughout the surveyed area (Fig. 1). Plankton samples were