



# The use of stable isotope analyses from skin biopsy samples to assess trophic relationships of sympatric delphinids off Moorea (French Polynesia)

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## ABSTRACT

Defining trophic relationships among organisms of a community is critical in ecology. However, the access to data is sometimes difficult, particularly in remote environments. Ecological niche segregation among the most common delphinid species was investigated: the spinner dolphin (*Stenella longirostris*), the rough-toothed dolphin (*Steno bredanensis*), the short-finned pilot whale (*Globicephala macrorhynchus*), and the melon-headed whale (*Peponocephala electra*). Resource partitioning was explored by analysing  $\delta^{13}\text{C}$  (reflecting foraging habitats) and  $\delta^{15}\text{N}$  stable isotopes (reflecting trophic level) from skin biopsies collected around Moorea from July to October 2002 to 2004. Results revealed that spinner dolphins had the lowest trophic level. The three other species had similar  $\delta^{15}\text{N}$  signatures. The most significant result is the differentiation of *S. longirostris* from *S. bredanensis* and *G. macrorhynchus* but not from the *P. electra*. For the latter three species, some degrees of overlap were apparent. For *S. longirostris*, *S. bredanensis* and *G. macrorhynchus*, variation of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  stable isotope was not significant between sexes. This study suggests that stable isotopes reveal some degree of segregation and overlap within this delphinid community. However, fine-scale segregation processes may be concealed by stable isotope analyses, meaning that traditional dietary analyses investigations are complementary in answering questions related to niche segregation.

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## 1. Introduction

Sympatric species with similar ecological requirements can compete for resources and thus their coexistence requires some degree of habitat and resource segregation (Pianka, 1974). Indeed, similar species that co-occur are thought to compete for resources unless they occupy different physical locations and/or feed on different prey. A shared resource in limited supply will bring about competition between members of the same species (intra-specific competition) or between individuals of different species (inter-specific competition) (Roughgarden, 1976).

Oceanic delphinids belong to 35 species worldwide (Jefferson et al., 2008). Many of them, have similar morphological characteristics, feeding habits and habitat preferences. This phenomenon has been documented around tropical oceanic islands, where delphinid diversity and biomass is generally high and where closely-related species co-occur (Gross et al., 2009). Around these islands, high cetacean diversity may be explained by the presence of a wide range of marine habitats in close proximity to one another (Kiszka et al.,

2007). In addition, oceanic islands appear to constitute areas of particular density of top predators due to an “island mass” effect. Similar to continental margins, insular slopes of islands potentially provide more abundant resources in the oligotrophic tropical marine environment (Guilmartin and Revelante, 1974). This situation of sympatry suggests that fine-scale mechanisms allow for the partitioning of habitats and/or resources. A study of the tropical delphinid community around the island of Mayotte, in the Comoros Archipelago (south-western Indian Ocean), has shown that the ecological niches of the delphinids occurring there do not overlap (Gross et al., 2009). Indeed, these species capture prey at different depths of the water column, where prey communities are segregated according to species and size. In other areas, such as the Bahamas, the cetacean community shares habitat and resources but only during the season when prey abundance is sufficient to support its needs, while competitive exclusion exists for the rest of the year (MacLeod et al., 2004). On the other hand, top predators may overlap in their feeding habits due to low productivity of tropical waters (Cherel et al., 2008). If these shared resources are limited quantitatively, inter-species competition can occur.

The dietary ecology of cetaceans and their trophic level can be determined using different methods. The most extensively used

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consist in analysing the stomach contents of dead animals. However, the specimens required for performing such analyses are often unavailable. The use of naturally occurring nitrogen and carbon stable isotopes has provided alternative information from which to better understand top predator feeding ecology, including marine mammals (Hobson and Welch, 1992; Abend and Smith, 1995; Das et al., 2003; Zhao et al., 2004; Gross et al., 2009). This approach is generally considered as complementary to stomach content studies as it integrates feeding habits on a longer-term basis. Various tissues, having varying temporal resolution (turnover rates), may be used in stable isotope analyses, including skin (Gross et al., 2009). Turnover rate for this tissue has been estimated for the beluga whale (*Delphinapterus leucas*; St Aubin et al., 1990) and the common bottlenose dolphin (*Tursiops truncatus*; Hicks et al., 1985). The estimated time required for cell migration, from the basal lamina to the outermost surface, is at least two months. The carbon and nitrogen isotope ratios ( $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$ , expressed hereafter as  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of a consumer reflect those of its diet, with a slight retention of the heavier isotope and excretion of the lighter one (Das et al., 2003). As a consequence, tissues will be enriched with heavy isotopes at every trophic level (1‰ for  $\delta^{13}\text{C}$  and 3‰ for  $\delta^{15}\text{N}$ ). The minor stepwise trophic enrichment of the carbon-isotope ratio limits its use in assessing trophic levels but enhances its use in tracking carbon sources through a food chain. The carbon isotope ratio of secondary and tertiary consumers should thus reflect the source of carbon at the base of their food chain (Kelly, 2000).

Moorea, a volcanic tropical island in French Polynesia (South Pacific), is characterized by the presence of many species of cetaceans, including several resident odontocetes, mostly delphinids (Poole, 1993, 1995; Oremus et al., 2007). At least thirteen species of dolphins may coexist around the island. Of these, the most common are the spinner dolphin (*Stenella longirostris*), the rough-toothed dolphin (*Steno bredanensis*), the short-finned pilot whale (*Globicephala macrorhynchus*) and the melon-headed whale (*Peponocephala electra*) (Gannier, 2000). The present study aimed to investigate ecological niche partitioning in the dolphin community of Moorea, especially for the spinner dolphin, the rough-toothed dolphin, the short-finned pilot whale and the melon-headed whale. We concentrated on these four species as they can be found within the same proximity around the island, in closely-related habitats within a small area and at all seasons (Poole, 1993). We hypothesised that these four species have different feeding niches that could be reflected in diverging stable isotope signatures. We also investigated some potential segregation processes that may occur intra-specifically, especially between sexes. Resource partitioning between sexes has been documented for a number of species, including mammals such as the giraffe (*Giraffa camelopardalis*) and several primate species (Beier, 1987; Young and Isbell, 1991). Sexual segregation in foraging habitats has also been documented for some marine mammals, such as the grey seal (*Halichoerus grypus*) (Breed et al., 2006). Females may use higher quality food, especially during gestation and lactation; therefore, it is often assumed that the energetic costs are greater for females than they are for males (Key and Ross, 1999). This could result in diverging stable isotope signatures if females develop sex-specific foraging strategies to fulfil their elevated energy requirements. On the other hand, in dimorphic species, such as long-finned pilot whales (*Globicephala melas*), males seem to have higher energetic needs (due to their larger size and weight) and potentially higher diving capabilities, and consequently use larger and deeper-living prey than females (Desportes and Mouritsen, 1993). As a consequence, males may have a higher trophic level than females.

In order to answer the question of niche segregation among the four most common dolphin species around Moorea Island, and intra-specifically between sexes, we analysed  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  stable isotopes from skin biopsies collected from 2002 to 2004.

## 2. Material and methods

### 2.1. Study area

Moorea (17°30'S, 149°50'W) is a high volcanic island of the Society Archipelago (134 km<sup>2</sup>), French Polynesia, located in the central South Pacific (Fig. 1). The island is almost entirely surrounded by a barrier reef which delimits a lagoon system connected to the open ocean by twelve passes varying in width and depth. Depth drops to more than 1000 m just 2 to 3 km outside the barrier reef. All species are usually observed outside the barrier reef, except the spinner dolphin (*Stenella longirostris*) which commonly enters the lagoon through passes during daytime (Poole, 1995) and feed in the open ocean only at night (Norris et al., 1994).

### 2.2. Sample collection

Samples were collected from 2002 to 2004, during small-boat-based surveys (2002, n = 107; 2003, n = 32, 2004, n = 63), in sea conditions not exceeding Beaufort 3. Most of the observation effort concentrated in austral winter (July–October). Efforts were made to survey the entire coastline. However, the targeted species during these surveys were the spinner dolphin and the humpback whale (*Megaptera novaeangliae*), and efforts were primarily concentrated in nearshore waters (i.e., within 500 m from the barrier reef or within the lagoon), where these species are preferentially distributed during daytime (Poole, 1995; 2002). Therefore, it must be noted that search efforts were not optimal for encounters of more oceanic species. During each encounter with dolphins, geographical position was recorded, group size was estimated by visual counts, and photographs were taken using a digital camera equipped with a 70–300 mm lens. Skin samples for genetic analyses were collected from adult dolphins using a small stainless-steel biopsy dart fired from a modified veterinary capture rifle equipped with a variable pressure valve (Krützen et al., 2002). Behavioural responses to biopsy attempts were recorded and reported in Oremus (2008). Level of short-term responses was low for all species and similar to that reported elsewhere (e.g. Krützen et al., 2002). All samples were preserved in 70% ethanol and stored at –20 °C for subsequent analysis.

### 2.3. Stable isotope analyses

Blubber and skin were separated for each biopsy. Stable isotope analyses were only performed on the skin. The ethanol was evaporated at 45 °C over 48 h and the samples were ground and freeze-dried (Hobson et al., 1997). The preservative used (ethanol) was the most suitable that could be used due to logistical constraints. Ethanol storage may have variable and organism-dependent effects on stable isotope signatures, generally higher on  $\delta^{13}\text{C}$  values than on  $\delta^{15}\text{N}$  values (Kaehler and Pakhomov, 2001). It does not affect stable isotope signatures in freshwater zooplankton and benthic macro-invertebrates (Svåvanta et al., 2008), bird eggs, blood and muscle (Hobson et al., 1997; Gloutney and Hobson, 1998). The increase in  $\delta^{13}\text{C}$  values is generally considered to be due to the extraction of some lipids but because lipids are depleted in  $\delta^{13}\text{C}$ , they have anyway to be extracted to avoid a bias in the isotopic signature of  $\delta^{13}\text{C}$  (De Niro and Epstein, 1978; Tieszen et al., 1983), that likely cancels any potential effect of storage in ethanol. Lipid extraction was done by shaking (1 h at room temperature) in cyclohexane (C6H12), and subsequent centrifugation prior to analysis. After drying, small subsamples (0.35 to 0.45 mg + 0.001 mg) were prepared for analysis. Stable isotope measurements were performed with a continuous-flow isotope-ratio mass spectrometer (Delta V Advantage, Thermo Scientific, Germany) coupled to an elemental analyser (Flash EA1112 Thermo Scientific, Italy). Results are expressed in notation relative to

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