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A preliminary study of habitat and resource partitioning among co-occurring tropical dolphins around Mayotte, southwest Indian Ocean

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ABSTRACT

Mayotte in the southwest Indian Ocean is characterized by high dolphin diversity. They may coexist within a fairly small area around the island because they exploit neither the same preferential habitats nor the same resources. This preliminary study aimed to investigate ecological niche segregation among these delphinid communities: the Indo-Pacific bottlenose dolphin, *Tursiops aduncus*, the pantropical spotted dolphin, *Stenella attenuata*, the spinner dolphin, *Stenella longirostris*, and the melon-headed whale, *Peponocephala electra*. Two approaches were used. Habitat preferences were investigated by analysing dolphin sighting data and associated physiographical characteristics. Resource partitioning was explored by analysing C and N stable isotopes in skin and blubber biopsies. Only *T. aduncus*, which showed clear association with coastal habitats in the lagoon, differed from the others in terms of habitat preferences, characterised by shallow depth and slope, and proximity to the coast. All other species shared similar oceanic habitats immediately outside the lagoon, these being of higher depth and slope, greater distance from the coast and were not discernable by discriminant analysis. The two *Stenella* species and the melon-headed whale displayed very high overlap in habitat physiographic variables. The analysis of stable isotopes confirmed the ecological isolation of *T. aduncus* and revealed a clear segregation of *P. electra* compared to the two *Stenella* that was not apparent in the habitat analysis. This may reflect ecological differences that were not observable from diurnal surface observations.

1. Introduction

In biological communities, each species has its own unique niche, which provides the conditions and resources needed for its survival. 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). Competition can take two different forms: interference, which is a direct, often aggressive, interaction between individuals, or exploitation-competition, in which individuals interact with each other indirectly, by responding to a resource level which has been depressed by the activity of competitors (Begon et al., 1986). A niche occupied by a species in the absence of competitors is termed its fundamental niche, whereas in the presence of competitors, species may be confined to a realized niche, which is shaped by the presence of competing sympatric species (Begon et al., 1986). Hence, the coexistence of potentially competing species is often made possible by the differentiation of their realized ecological niches. The first mechanism that allows for niche differentiation is resource partitioning. In this case, different species living in the same habitat exploit the resources differently. For example, predators of different size may feed on prey of different size, hence minimising the overlap between the various predators' prey size ranges. Prey specialisation presumably allows for niche partitioning in areas of sympatry (Ballance, 2002). The second mechanism involves spatial (micro-habitat differentiation) or temporal separation in the availability of the different resources (these become available at different times of the day or different seasons of the year; Huisman and Weissing, 2001).

Small delphinids belong to numerous species which have similar morphological characteristics. This situation suggests that fine-scale mechanisms allow for the partitioning of habitats and

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resources when and where the different species live in sympatry. A study of the cetacean community of Great Abaco, Bahamas, has shown that the ecological niches of the four species that permanently live there do not overlap (Macleod et al., 2004). These species capture prey at different depths of the water column. Other cetacean species are observed in the study area only during the season when prey abundance is sufficiently high to support their presence, while they are competitively excluded for the rest of the year (Macleod et al., 2004). Indeed, the spatial distribution of marine predators is mainly determined by the distribution and availability of their prey, these in turn varying according to physical, chemical and biological characteristics of the water masses (Forcada, 2002).

The dietary ecology of marine mammals and their trophic level can be determined using different methods: traditional methods analyse faeces and regurgitated food of living animals, as well as the stomach contents of dead animals (from strandings or by-catch; e.g. Pusineri et al., 2007). A more recent method for studies of dietary ecology is stable isotope analysis of blubber, skin or muscle samples (Bearhop et al., 2004). The carbon and nitrogen isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$, expressed hereafter as $\delta^{13}C$ and $\delta^{15}N$) 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. 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). The higher enrichment of the nitrogen isotope ratio of consumers compared to their prey makes it very useful for the determination of their trophic level (Kelly, 2000). Thus, both ratios help elucidate trophic relations and habitat use.

Mayotte, a volcanic island in the northern Mozambique Channel (southwest Indian Ocean), is characterised by the permanent presence of more than 20 species of cetaceans (Kiszka et al., 2007). Of these, the most important in coastal waters are the Indo-Pacific bottlenose dolphin, *Tursiops aduncus* (Ehremberg, 1833), the pantropical spotted dolphin, *Stenella attenuata* (Gray, 1846), the spinner dolphin, *Stenella longirostris* (Gray, 1828), and the melon-headed whale, *Peponocephala electra* (Gray, 1846). The island has a great variety of marine ecosystems offering a large diversity of habitats: coasts, mangroves, an extended lagoon (1100 km^2), different kinds of reefs (fringing, pinnacles, and barrier), a steep insular slope with many submarine canyons and seamounts, and the open ocean (Quod et al., 2000). At least twelve species of delphinids may coexist in a fairly small area around the island because they exploit neither the same habitats nor the same resources (Kiszka et al., 2007). The present study aimed to investigate ecological niche segregation among the resident dolphin community of Mayotte, especially the Indo-Pacific bottlenose dolphin, the pantropical spotted dolphin, the spinner dolphin and the melon-headed whale. We concentrated on these four species as they are of fairly similar size and can be found within the same proximity around Mayotte, in closely-related habitats within a small area and at all seasons (Kiszka et al., 2007). This is particularly so for the two *Stenella* species and the melon-headed whale which are all encountered immediately outside the barrier reef and in the channels, whereas existing literature suggests that they would be more differentiated habitat-wise, with the spinner dolphin feeding offshore but resting inshore, the melon-headed whale being an oceanic squid-eater and the Indo-Pacific bottlenose dolphin dwelling in nearshore coastal habitats (Norris et al., 1994; Perryman, 2002; Wells and Scott, 2002; Silva et al., 2005). Two approaches were used for the study: a comparison of habitat by the analysis of dolphin sighting data and associated behavioural and physiographic characteristics (group size, depth, slope, distance to the coast and proximity to the different kinds of reefs), and the study of habitat and resource partitioning by the analysis of C and N stable isotopes from skin and blubber biopsies.

2. Material and methods

2.1. Study area

The volcanic island of Mayotte (45°10′E, 12°50′S), which is part of the Comoros archipelago, is located in the northern Mozambique Channel (Indian Ocean) between Madagascar and Southeast Africa. Its surface area is 376 km^2 and it is composed of two main islands and about 30 islets scattered within and around a lagoon. Mayotte is surrounded by a large lagoon-reef complex, whose width varies from 3 to 15 km. Fringing reefs surround the archipelago, an inner double-reef is present off the southwest end of Mayotte, and the barrier reef, which is interrupted by numerous channels, separates the lagoon itself (maximum depth 80 m) from the external slope and more oceanic habitats.

The four species of interest, the Indo-Pacific bottlenose dolphin, the pantropical spotted dolphin, the spinner dolphin, and the melon-headed whale, range in size from about 200 cm and 90 kg for the spinner dolphin to 250 cm and 250 kg for the melon-headed whale (Perrin, 2002a,b, Perryman, 2002, Wells and Scott, 2002).

2.2. Data and sample collection

Data were collected from 1997 to 2005, during small boat-based surveys dedicated to studying marine mammals (Fig. 1). Several types of boats were used: a 7 m catamaran equipped with two, four-stroke, 60-hp outboard engines; a 7 m boat equipped with two, two-stroke, 40-hp outboard engines; a 6.4 m cabin boat equipped with an inboard four-stroke and 150-hp outboard engine. Surveys were conducted during daylight hours, i.e. between 0700 h and 1800 h, in sea conditions not exceeding Beaufort 3. The survey vessels did not follow pre-defined transects but sampling covered all habitats within the lagoon and over the external insular slope (Fig. 1). Effort varied according to month (Fig. 2), with more effort being applied in the austral summer (November–January). When dolphins were encountered, preliminary information records included group size (maximum, minimum, best estimate), geographic position, activity (travelling, resting, foraging/feeding, socialising, milling, play), group classification on the basis of the relative size of individuals (adults, sub-adults, calves), research boat disturbance (bowride, approach, avoidance, no response) as well as group formation (tight, loose, dispersed, variable, convergent; Shane, 1990; Würsig et al., 1998). This study is still on-going and, therefore, only the sighting locations and associated physiographic variables are analysed here.

When conditions were optimal (good weather and sea state, dolphins closely approaching the boat), biopsies were collected using a cross-bow (*BARNETT Veloci-Speed® Class*) with Finn Larsen bolts and tips (20-mm). The dolphins were hit below the dorsal fin, when close (3–10 m) to the research boat. Sampling periods spanned all seasons but sample sizes did not allow seasonal comparisons (January, August and December for *Tursiops aduncus*, $N = 4$; January, February, March and October for *S. attenuata*, $N = 4$; February, March, May and October for *Stenella longirostris*, $N = 5$; March, July and December for *Peponocephala electra*, $N = 4$). It was not possible to determine sex, size or age of the individuals biopsied. Blubber and skin biopsy samples were preserved separately in 90° ethanol before shipping and subsequent analysis. Biopsy sampling was conducted under scientific permit #78/DAF/2004.