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 roughed-toothed dolphin (*Steno bredanensis*), the short-finned pilot whale (*Globicephala macrorhynchus*), and the melon-headed whale (*Peponocephala electra*). Resource partitioning was explored by analysing δ^{13}C (reflecting foraging habitats) and δ^{15}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 δ^{15}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 δ^{13}C and δ^{15}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 ($^{13}C/^{12}C$ 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 (1‰ for $\delta^{13}C$ and 3‰ for $\delta^{15}N$). 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 intraspecifically between sexes, we analysed $\delta^{13}C$ and $\delta^{15}N$ 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 km²), 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 $\delta^{13}C$ values than on $\delta^{15}N$ values (Kaehler and Pakhomov, 2001). It does not affect stable isotope signatures in freshwater zooplankton and benthic macroinvertebrates (Syväranta et al., 2008), bird eggs, blood and muscle (Hobson et al., 1997; Gloutney and Hobson, 1998). The increase in $\delta^{13}C$ values is generally considered to be due to the extraction of some lipids but because lipids are depleted in $\delta^{13}C$, they have anyway to be extracted to avoid a bias in the isotopic signature of $\delta^{13}C$ (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 (C_6H_{12}), 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
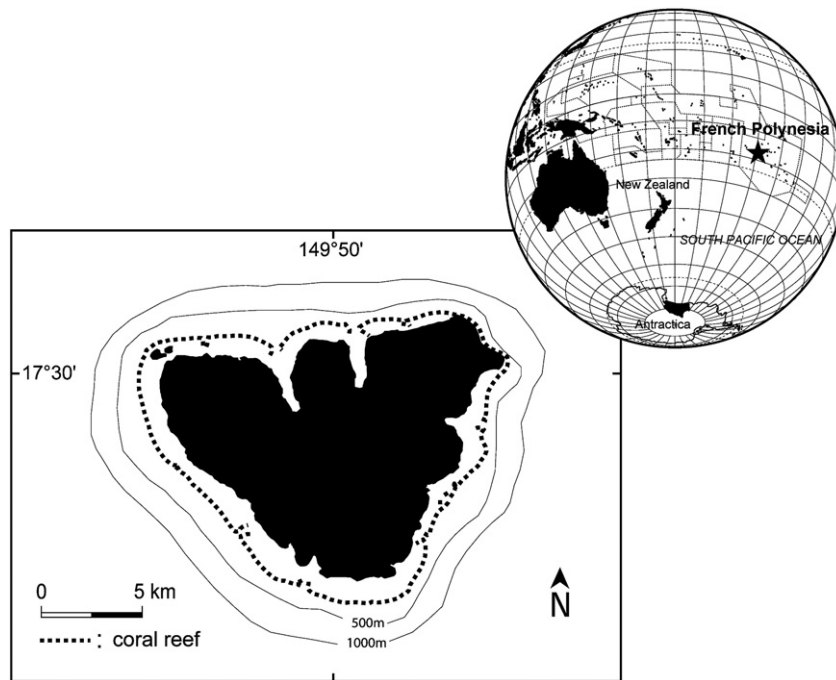
Fig. 1. Location of the study area.

PeeDee Belemnite and atmospheric N_2 for $\delta^{13}C$ and $\delta^{15}N$, respectively, according to the equation

$$\delta X = \left[\frac{R_{sample}}{R_{standard}} - 1 \right] \times 1000$$

where X is ^{13}C or ^{15}N and R is the isotope ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicated that measurement errors were <0.1‰ for $\delta^{13}C$ and $\delta^{15}N$. Percent C and N elemental composition of tissues were obtained using the elemental analyzer and used to calculate the sample C:N ratio, indicating good lipid removal efficiency when <4.

2.4. Species identification and molecular sexing

Species sampled for this study were identified visually and confirmed using photographic and genetic evidences. Mitochondrial DNA control region were sequenced for all samples, as reported in Oremus et al. (2007), and sequences were submitted to the program DNA-surveillance v. 3.01 (Ross et al., 2003) to determine species identity. Sex was identified by co-amplification of the male-specific *sry* gene and ZFX positive control gene (Gilson et al., 1998).

2.5. Data analysis

Differences of stable isotopes signatures of $\delta^{15}N$ and $\delta^{13}C$ among species were tested using non-parametric Kruskal–Wallis tests. Pairwise tests to compare $\delta^{13}C$ and $\delta^{15}N$ values between species were performed using Mann–Whitney-*U* tests. Variability of $\delta^{13}C$ and $\delta^{15}N$ signatures among sexes was also tested using *U* tests. For all statistical analyses, a significance level of $\alpha = 0.05$ was used.

3. Results

3.1. Sampling

We collected skin samples from 91 delphinids: spinner dolphin ($N = 40$; 29 males and 11 females), rough-toothed dolphin ($N = 35$; 23 males and 12 females), short-finned pilot whale ($N = 12$; 6 males and 5 females) and melon-headed whale ($N = 4$; not sexed). All samples were collected during the same season, i.e. austral winter (July to October). All sampled individuals were considered to be adults based on their size.

3.2. Resource partitioning

The distribution of $\delta^{15}N$ and $\delta^{13}C$ values is given in Fig. 2. Overall, overlap among species is present, and intra-specific variability appears high. However, significant statistical differences were found among the four species for $\delta^{15}N$ (H = 24; df = 3; P<0.001) and $\delta^{13}C$ values (H = 37; df = 3; P<0.001). Even with the melon-headed whale removed from the analysis, differences remained significant (for $\delta^{15}N$: H = 12.3; df = 2; P = 0.001 and $\delta^{13}C$: H = 13; df = 2; P = 0.002). Short-finned pilot whales had the highest $\delta^{15}N$ and $\delta^{13}C$ signatures, spinner dolphins had the lowest $\delta^{15}N$ values (Fig. 2), and melon-headed whales had the lowest
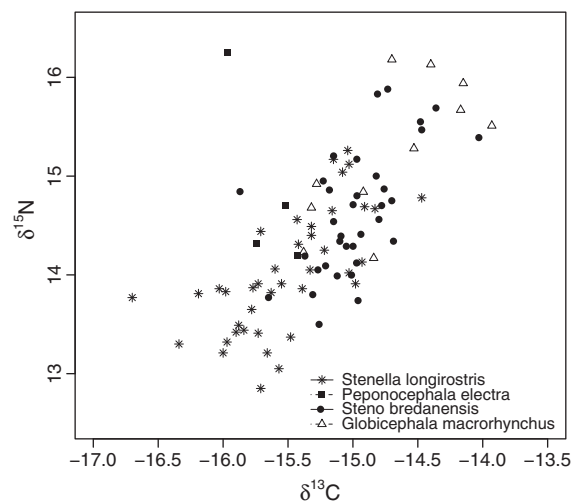

Fig. 2. Stable isotope distribution ($\delta^{13}C$ and $\delta^{15}N$ in ‰) in delphinid skin tissues from Moorea. *Stenella longirostris* (n = 40), *Steno bredanensis* (n = 35), *Globicephala macrorhynchus* (n = 12) and *Peponocephala electra* (n = 4).

δ^{13}C signatures. Rough-toothed dolphins had an intermediate position between spinner dolphins and short-finned pilot whales. At a finer scale, when looking at differences in δ^{13}C and δ^{15}N signatures between species, some degrees of overlap and differentiation can be observed (Table 1). In δ^{13}C, differences were not significant between the spinner dolphin and the melon-headed whale nor between the rough-toothed dolphin and the short-finned pilot whale. For other pairwise comparisons of δ^{13}C values, statistically significant differences were found. For δ^{15}N, overlap was statistically significant between the melon-headed whale, the rough-toothed dolphin and the short-finned pilot whale. The spinner dolphin could not be differentiated from the melon-headed whale but differed significantly from the rough-toothed dolphin and short-finned pilot whale (Fig. 3).

3.3. Differences between sexes

We tested differences in stable isotope signatures between males and females, both for δ^{15}N and a δ^{13}C, in all species except the melon-headed whale; in the latter case, sample size was too small and sex data unavailable. Box plots (Fig. 4) show stable isotope median values, 50, 75 percentiles and outliers of the three species. Male spinner dolphins and rough-toothed dolphins seem to have a lower trophic position than females. In addition, both species seem to feed on less ^{13}C-enriched preys (Fig. 4). An opposite situation was found for short-finned pilot whales, with males having higher mean δ^{15}N and δ^{13}C signatures. For the short-finned pilot whale, males seem to have a wider range of δ^{13}C signatures (Fig. 4). Conversely, females had a wider range of δ^{15}N values. However, none of the differences were statistically significant (spinner dolphins: δ^{15}N: $U=59$; $P=0.236$; δ^{13}C: $U=33$; $P=0.203$, rough-toothed dolphin: δ^{15}N: $U=51$; $P=0.266$; δ^{13}C: $U=57$; $P=0.409$ and short-finned pilot whales: δ^{15}N: $U=50$; $P=0.193$; δ^{13}C: $U=13$; $P=0.074$).

4. Discussion

4.1. General comments

Stable isotope approaches are powerful analytical tools to link the foraging ecology of top predators with habitat, diving behaviour and diet (Das et al., 2003; Zhao et al., 2004). This has been shown for a number of taxa, including seabirds (Cherel et al., 2008), sharks (Domi et al., 2005), pinnipeds (Zhao et al., 2004) and cetaceans such as tropical delphinids (Gross et al., 2009). These results were the first describing the isotopic niches of sympatric delphinids in French Polynesia; they can be used in the future to examine seasonal, year-to-year or long term variation in delphinid trophic ecology in the region. Lack of significance in some comparisons may partly result from insufficient sample size. Analytical resolution was <0.1‰ as shown by replicate measurements

Table 1

Pairwise Mann–Whitney U test p values for each pairs of delphinid species in carbon and nitrogen. Values in bold are significant, meaning that the two species do not overlap in their isotopic signatures. *Stenella longirostris*: spinner dolphin; *Peponocephala electra*: melon-headed whale; *Steno bredanensis*: rough-toothed dolphin; *Globicephala macrorhynchus*: short-finned pilot whale.

	Peponocephala electra	*Globicephala macrorhynchus*	*Steno bredanensis*
δ^{13}C			
Stenella longirostris	0.394	**0.0001**	**0.0001**
Steno bredanensis	**0.005**	0.131	
Globicephala macrorhynchus	**0.006**		
δ^{15}N			
Stenella longirostris	0.09	**0.00001**	**0.00004**
Steno bredanensis	0.235	0.06	
Globicephala macrorhynchus	0.07		

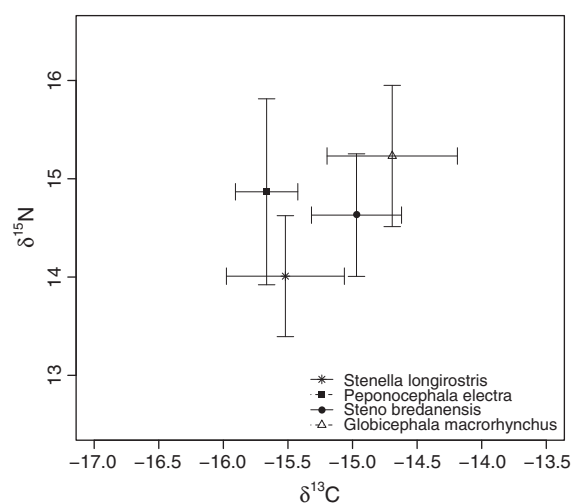**Fig. 3.** Stable isotopes (δ^{13}C and δ^{15}N in ‰) in delphinid skin tissues from Moorea. Graphs show average values and standard deviations. *Stenella longirostris* (n = 40), *Steno bredanensis* (n = 35) and *Globicephala macrorhynchus* (n = 12) and *Peponocephala electra* (n = 4).

of internal laboratory standards, and delipidation was successfully carried out on all samples since C:N ratios were always <4. Carbon sources and reference levels of nitrogen were not investigated in this work; hence isotopic data can only be interpreted in terms of relative values among the four species studied.

4.2. Isotopic niche segregation

Very few other studies have attempted to address issues regarding ecological segregation in delphinid assemblages by analysing isotopic signature in skin biopsies (Gross et al., 2009), but more work has been done on communities of other marine top predators including sharks, large teleost fishes, seabirds and marine mammals (Hobson and Welch, 1992; Abend and Smith, 1995; Das et al., 2003; Zhao et al., 2004; Domi et al., 2005; Ménard et al., 2007; Cherel et al., 2008; Jaeger, 2009). In top predator communities, significant habitat partitioning has been found in polar communities, such as in pinnipeds from the Antarctic (Zhao et al., 2004). Conversely, in tropical sympatric seabirds, significant overlap of feeding niches has been found at the community level (Cherel et al., 2008). This may be laid to the low productivity of tropical oligotrophic waters, leading top predators to share the same feeding resources. However, significant differences in isotopic niches were found in delphinids from the tropical island of Mayotte, in the south-western Indian Ocean (Gross et al., 2009). In the Southern Hemisphere, clearly structured latitudinal carbon isoscapes have been found from the Antarctic to the subtropical zones (Jaeger, 2009). This structured shape of latitudinal isoscapes may not exist in tropical waters, mainly due to the oligotrophic nature of these waters. However, around oceanic islands such as Mayotte, clear differences of δ^{13}C and δ^{15}N values were observed between the three delphinid genera investigated, which could be interpreted by the structured nature of marine habitats (high carbon gradients from coastal to oceanic surface waters; Kiszka et al., unpublished data) around the island, from lagonal to oceanic waters. In addition, diving predators such as small cetaceans use resources at varying depth, where carbon gradients are significant (from the surface to bottom, where organic matter accumulates and provides carbon sources). In conclusion, investigating trophic relationships of predators living in a structured system (such as around an oceanic island) and feeding at varying depth may result in diverging isotopic niches, while in surface feeders like seabirds, feeding in the homogenous oceanic system may result in low to no difference in isotopic niches.
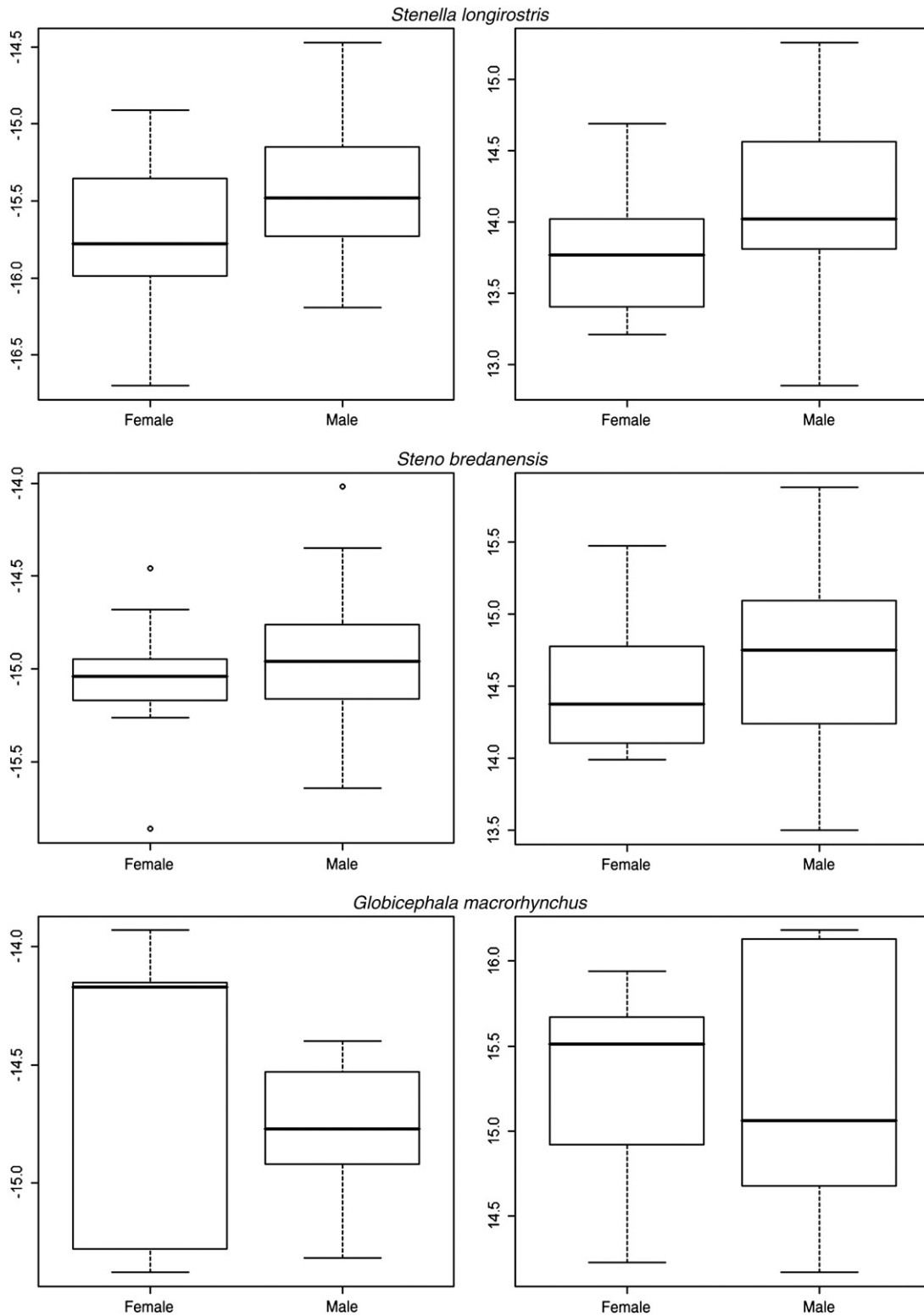
Fig. 4. Stable isotope (δ^{13}C and δ^{15}N in ‰) median values, 50, 75 percentiles and outliers of *Stenella longirostris* (n = 40), *Steno bredanensis* (n = 35) and *Globicephala macrorhynchus* (n = 12) males versus females.

In our study, overall analyses show some degrees of niche partitioning among the four species investigated, the most significant result being the differentiation in trophic level revealed by δ^{15}N values among spinner dolphin, rough-toothed dolphin and short-finned pilot whale, but not between spinner and melon-headed whale. In terms of foraging habitats, δ^{13}C values were significantly different between all species except two pairs of species that could not be discriminated: spinner dolphin/melon-headed whale and rough-toothed dolphin/short-finned pilot whale. No significant intra-specific difference was found between sexes. Finally, it must be kept in mind that differences in isotopic signatures are informative, whereas similarities do not necessarily imply that species share a similar trophic niche; indeed different foraging strategies may result in similar isotopic signatures. If stable isotope signatures and preys of two predators are effectively similar, other segregation processes may

occur, such as differential spatial and temporal use of habitat and resources. Published studies from other areas in the Pacific suggest that the community of delphinids around Moorea is likely to feed on pelagic and oceanic prey. The spinner dolphin had the lowest trophic level and, with the melon-headed whale, the lowest $\delta^{13}C$ values. The spinner dolphin feeds primarily on mesopelagic fishes and squids at night (Norris et al., 1994; Dolar et al., 2003). Vertical distribution of the prey items summarized from published literature indicate that spinner dolphins forage in the upper 200 m and probably occasionally as deep as 400 m (Dolar et al., 2003). Melon-headed whales are oceanic predators, mostly feeding on mesopelagic fishes and cephalopods throughout their range (Brownell et al., 2009). When considering the vertical distribution of these prey groups, melon-headed whales probably forage in the upper 700 m (Young, 1978). Like spinner dolphins, melon-headed whales seem to feed at night during vertical migrations of their preys, while they rest and socialize during daytime near oceanic islands (Brownell et al., 2009). Therefore, the two species may share some similar features of habitat and resource use, although at Moorea, melon-headed whales do not use inshore and nearshore waters like spinner dolphins do. This possible overlap was confirmed in this study, as stable isotope signatures were not significantly distinguishable. Note that this absence of significant difference could be due to small sample size for melon-headed whales. However, around the island of Mayotte (with similar habitats to those around Moorea) in the south-western Indian Ocean, stable isotope analyses on skin samples revealed significant differences in $\delta^{13}C$ and $\delta^{15}N$ values with similar sample size than in our study (Gross et al., 2009). Melon-headed whales were characterised by significantly higher $\delta^{13}C$ and $\delta^{15}N$ values (Gross et al., 2009). In our study, $\delta^{13}C$ signatures were very similar between spinner dolphins and melon-headed whales, suggesting they prey on species with similar $\delta^{13}C$ signatures or even similar prey. This could suggest that their prey are not limited quantitatively, allowing the two species to feed on similar resources without deleterious competition for one or the other. However, despite no statistical evidences, some differences in the $\delta^{15}N$ values suggest that melon-headed whale has a higher trophic level, and may probably feed on prey of higher trophic position (probably larger prey). The feeding ecology of the rough-toothed dolphin is poorly known, but it is known to feed on cephalopods (Aguiar dos Santos and Haimovici, 2001), deep water fishes (Miyazaki and Perrin, 1994) and occasionally on coastal prey (Shallenberger, 1981). Foraging on flying fishes and other surface fish has been regularly observed off Moorea (Oremus and Poole, personal observations). In the eastern tropical Pacific, rough-toothed dolphins regularly feed on dolphin fish (*Coryphaena hippurus*; Pitman and Stinchcomb, 2002). Short-finned pilot whales are deep-water cephalopod predators (Hernández-García and Martín, 1994). Recent evidence suggests that short-finned pilot whales can dive to depths reaching 1000 m on occasion (Aguilar Soto et al., 2008). Based on the available literature, making comparisons of the diet of the rough-toothed dolphin and the short-finned pilot whale appears highly hazardous, given the limited existing information. However, the latter seem to feed deeper in the water column. In our results, the rough-toothed dolphin and the short-finned pilot whale were not statistically different in their stable isotope signatures. However, *S. brenadensis* had lower $\delta^{13}C$ and $\delta^{15}N$ signatures than those in short-finned pilot whales. The later may feed on more carbon-enriched prey. As there is a bottom-surface gradient of $\delta^{13}C$, with higher carbon values from the sea bottom than at the surface (Hobson, 1999), higher $\delta^{13}C$ values observed in short-finned pilot whales could be due to their preference for prey occurring deeper in the water column, in closer proximity to bottom organic matter sources. This is consistent with published literature describing general ecology, prey preferences and diving behaviour of short-finned pilot whales (Aguilar Soto et al., 2008; Hernández-García and Martín, 1994). The lower $\delta^{15}N$ values observed in the rough-toothed dolphin may be attributed to its preference for preys of a lower trophic position than those consumed by pilot whales.

Overall, when looking at biometrical data of predators from our study (Jefferson et al., 2008), we observe that there is a correlation between trophic position and body size. Larger predators have a higher trophic level in this delphinid community, which is consistent with many other species communities.

Difference in feeding ecology between genders has been documented in delphinids (Desportes and Mouritsen, 1993). From our dataset, we did not observed statistically significant gender-specific variations of stable isotope signatures. However, mean values of carbon and nitrogen isotope values were higher for female spinner and rough-toothed dolphins. On the contrary, carbon and nitrogen isotope values were higher in male short-finned pilot whales. In other words, the feeding niches of delphinids from Moorea may not differ according to sex. However, some segregation processes may be not detected through the use of stable isotopes, and traditional dietary analyses may answer this question. Detailed studies of diving behaviour may also contribute to assessing gender-specific variation in feeding strategies. However, at least for short-finned pilot whales, our sample size was small, which could conceal potential differences related to sex. Indeed, it is known that males in sexually dimorphic species such as long-finned pilot whales feed on larger prey, and potentially have a higher trophic level (Desportes and Mouritsen, 1993). Nevertheless, no detailed studies of the diet of short-finned pilot whales have been published, and such gender-specific variation may not occur in this species.

5. Conclusions

When conventional dietary studies cannot be undertaken, such as around Moorea where dead animals from strandings and bycatch are unavailable, the use of stable isotopes can be recommended to assess trophic relationships in a community of cetacean predators, especially delphinids. The delphinids around Moorea seem to have different feeding niches, although statistical analyses do not always show significant differences among species. To complement the interpretation of these first results, documenting accurate data on local carbon sources and reference levels of nitrogen by analysing the isotopic content of particulate organic material that constitute the basis of the local food webs and/or of a range of putative prey taxa from coastal to oceanic habitats, would help in characterizing the three-dimensional isoscape (Jaeger, 2009) in which this assemblage of sympatric dolphins dwells. Additionally, any information on the diet, diving behaviour, activity budget and micro-scale spatial distribution of the four dolphin species constituting this community would considerably improve the potential for interpreting stable isotope data.

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