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Comparative foraging ecology and ecological niche of a superabundant tropical seabird: the sooty tern *Sterna fuscata* in the southwest Indian Ocean

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Abstract:

Over 6-million pairs of sooty terns Sterna fuscata breed once a year in the southwest Indian Ocean, mostly on three islands of the Mozambique Channel (Europa, Juan de Nova and Glorieuses) and in the Seychelles region. Seasonal reproduction in either winter or summer is the dominant strategy in the area, but non-seasonal reproduction also occurred in some places like at Glorieuses Archipelago. The feeding ecology of the sooty tern was investigated during the breeding seasons to determine whether terns showed significant differences in their trophic ecology between locations. Regurgitations were analyzed to describe the diet of individuals when breeding, and stable isotopes and mercury concentrations were used to temporally integrate over the medium-term of the trophic ecology of both adults and chicks. Overall, the diet was composed of fish, flying squid and fish larvae in different proportions. At Europa and Aride in the Seychelles, where winter reproduction occurs, large epipelagic prey like flying fish or squid dominated the diet. At Juan de Nova, sooty terns reproduce in summer and rely mostly on fish larvae. At Glorieuses (non-seasonal breeding), the diet was intermediate with fish larvae and flying squid being important prey items. The stable-carbon and nitrogen isotope values in blood confirm the differences observed in dietary analysis, and demonstrate different feeding strategies between colonies. $\delta^{13}C$ values of feathers showed spatial segregation between birds from the Mozambique Channel and the Seychelles region. Terns from the Seychelles had also higher $\delta^{15}N$ values. Feather $\delta^{13}C$ values also suggest a significant shift from summer to wintering habitat for birds from Juan de Nova. This study emphasizes the high phenotypic plasticity of the species, which may explain its numerical dominance in all tropical waters of the World's Ocean.

Keywords: Seabirds, feeding ecology, flying squid, fish larvae, $\delta^{13}C$, $\delta^{15}N$, mercury

Introduction

Tropical oceanic waters are considered since a long time less productive and less seasonal than waters from higher latitudes (Ashmole 1971, Longhurst and Pauly 1987). Then resources are highly variable at most spatial and temporal scales, and are consequently more unpredictable than in colder waters (Ainley & Boekelheide 1983, Bertrand et al 2002, Weimerskirch et al 2005). Paradoxically tropical waters support a huge biomass of top predators like tunas and billfish, marine mammals, and seabirds (Harrison et al 1983, Longhurst & Pauly 1987, Le Corre & Jaquemet 2005). Thus high-level marine predators have to cope with constraining conditions to forage, and need to develop specific adaptations to live in the tropical marine environment.

The sooty tern *Sterna fuscata* is the most abundant marine bird species in all tropical waters. Its distribution is pan-tropical and the species nests in large synchronised dense colonies, sometimes numbering hundreds of thousands of pairs (Schreiber et al 2002). This surface-feeder (Ashmole 1971) is able to forage over oligotrophic oceanic waters, and generally get access to its food in association with schools of surface tunas (Au & Pitman 1986, Jaquemet et al 2005). With an annual estimated consumption of marine resources averaging 3 Mt, this superabundant species ranks fourth amongst the world’s seabirds, being the first-ranked tropical species (Brooke 2004).

Surprisingly, little is known of the food and feeding ecology of sooty terns worldwide. The diet and basic biology of the species have been described in the Atlantic and Pacific oceans (Ashmole 1963, Harrison et al 1983), in the Seychelles (Feare 1976), and more recently in Australia (Surman & Wooller 2003, Erwin & Congdon 2007). During the breeding season, sooty terns prey mainly on epipelagic fish, reef-fish larvae and on the flying squid *Sthenoteuthis oualaniensis* (Ashmole 1963, Feare 1976, Harrison et al 1983, Hensley and

Hensley 1995, Surman and Wooller 2003). During the non-breeding season, the species is known to disperse over large oceanic areas (Schreiber et al 2002), and juveniles can undertake transoceanic migrations (Robertson 1969).

In the tropical Indian Ocean the species is widely distributed (Schreiber et al 2002), although the main populations are located in its western part (Feare et al 2007). The species is especially abundant in the Mozambique Channel (Le Corre and Jaquemet 2005) and at the Seychelles Archipelago (Feare et al 2007), where it represents 99% (> 3,050,000 pairs) and 83% (> 3,420,000 pairs) of the total number of seabird breeding pairs, respectively (Rocamora & Skerrett 2001, Le Corre & Jaquemet 2005). Interestingly, breeding phenology varies considerably within the southwest Indian Ocean. In the Mozambique Channel, breeding is annual and seasonal at Europa Island (760,000 pairs) and at Juan de Nova Island (2,000,000 pairs), occurring in winter at Europa and in summer at Juan de Nova (Le Corre 2001). Breeding is non-seasonal at a third place, Lys Island (270,000 pairs), located in the north of the Channel, within the Glorieuses Archipelago (Le Corre and Jaquemet 2005). At Aride Island and other islands in the Seychelles Archipelago, sooty terns also breed seasonally in winter as in southern Mozambique Channel. These differences in breeding phenology seem to be driven by large oceanic patterns related to the climate in the western Indian Ocean, which influence the oceanic production and prey availability (Jaquemet et al 2007).

The main goal of this study was to better understand why sooty terns are so abundant in the tropical western Indian Ocean and more generally in tropical waters. During reproduction, individuals have to compete with congeners and other species for resources (Jaquemet et al 2005), and during the non-breeding period adults have to restore their body condition and moult. This last period is very important in shaping dynamics of seabird populations by affecting the survival of individuals or their breeding performance in the subsequent season

(Barbraud & Weimerskirch 2003). To achieve our aim we described the dietary habits and compare the ecological niches of sooty terns across the southwest Indian Ocean at four major colonies both during and outside the breeding season. We described the diet through stomach content analyses and investigated the feeding ecology over different time periods with stable isotopes and mercury concentrations. Stable isotopes of carbon and nitrogen, and heavy metals are naturally incorporated in the body of animals from their diet. The signatures of these chemical tracers in the tissues of organisms reflect differences in trophic level and / or in foraging habitats (Hobson 1993, Monteiro & Furness 1995, Cherel et al 2002). Analyses of these tracers in tissues with different turnover rate of elements provide different time-integrated dietary information (Hobson 1993), and they are useful to elucidate trophic ecology of organisms at different stages of their life (Hobson 1993, Monteiro & Furness 1995, Hobson et al 1997, Cherel et al 2002). Mercury concentrations are used to investigate exposure to contaminant uptake and the trophic position of animals in the food chain (Monteiro & Furness 1995). A recent study in the southwest Indian Ocean (Ménard et al 2007) revealed latitudinal effects on $\delta^{15}N$ and $\delta^{13}C$ values of two migratory highly opportunistic predators: yellowfin tuna (*Thunnus albacares*) and swordfish (*Xiphias gladius*). The authors concluded however that the baseline (POM) isotopic signatures and of intermediate trophic level organisms are needed to further investigate spatial variations in stable isotopes in the region (Ménard et al 2007). Similarly very few data are available on mercury concentration in marine organisms for the area, but a recent study on tuna and billfish suggested that the Mozambique Channel may be considered as a pristine area concerning heavy metal pollution (Kojadinovic et al 2007).

We first investigated whether individuals breeding at different locations, different seasons and with different modes (seasonal *vs* non-seasonal) in the same oceanographic province rely or not on the same food resources during the chick-rearing period. Secondly, we compared the diet at colonies located in different oceanic provinces (Mozambique Channel *vs* Seychelles). Finally, we used stable isotopes of carbon and nitrogen together with mercury concentration in sooty tern tissues to test whether spatial, temporal, and age-related differences in the feeding ecology and trophic niche of the species occur.

Materials and methods

Study sites and data collection

The study was conducted at the three main sooty tern colonies located within the Mozambique Channel and at a single colony within the central islands of the Seychelles Archipelago (Figure 1). From south to north of the Mozambique Channel, we focused on Europa Island (22°20’S, 40°22’E), Juan de Nova Island (17°03’S, 42°44’E), and Lys Island (Glorieuses Archipelago 11°31’S, 47°22’E). In the central Seychelles, we conducted our study at Aride Island (4°10’S, 55°40’E). We collected stomach contents of sooty terns, mainly from chicks (> 90%), during two consecutive breeding seasons in the Mozambique Channel (2002 and 2003 at Europa, and 2003 and 2004 at Juan de Nova and Glorieuses), and during a single breeding season in the Seychelles in 2005 (Table 1). Food samples were primarily collected at dusk when adults return to the colonies to feed their chicks. They were mostly taken from randomly selected chicks by spontaneous regurgitation when handled, after a returning parent had completed feeding them.

For the birds from the Mozambique Channel, the tip of the first primary feather and whole blood (red cells and plasma) were sampled from adults and chicks older than 20 days for stable isotope analyses. Five to 6 small covered body feathers were collected for mercury analysis. Between 10 and 32 individuals were sampled according to age and location. At Aride, body feathers were collected on 10 adults and 10 chicks for stable isotopes and mercury analysis. Every sample was frozen in the field, stored at –20°C, and subsequently analysed in laboratory. To limit disturbance every sampled bird was marked with a unique ring to ensure that no individual was sampled more than once during a breeding season.

Diet analysis

In the laboratory stomach contents were thawed and weighed. Then the different prey items were separated and weighed individually (wet weight to the nearest 0.1g). The total number of individuals of each prey was estimated in each sample.

For samples from the Mozambique Channel (Europa, Juan de Nova, Glorieuses) only, all prey items were identified to the lowest taxa possible using published keys on whole specimens and on specific items (cephalopod beaks, fish otoliths and bones) (Smith & Heemstra 1986, Clarke 1986, Smale et al 1995), and by comparison with material held in our own reference collection. In addition, biometric measurements were used to determine allometric equations allowing us to estimate the length and body mass of ingested individuals. For this purpose (i) fork and caudal length of fish, (ii) dorsal mantle length of cephalopods, and (iii) total and telson length of crustaceans were measured to the nearest 0.01mm for OL and LRL, and to the nearest 0.1mm for the other lengths. The body mass of every individual was measured to the nearest 0.1g. The importance of each prey item in the diet was assessed using three indexes, the frequency of occurrence, and percentages by number and by reconstituted mass. Reconstituted mass of prey was estimated using published allometric (Clarke 1986, Smale et al 1995, Le Corre et al 2003) and our own equations. For some species no equation was available. In such cases, we used the equation of a taxonomically related species or that of a species with a similar morphology (Cherel et al 2002). The overall importance of each taxon in the diet was ranked using the index of relative importance (IRI), which is a combination of the occurrence, numerical abundance, and reconstituted mass of the prey (Pinkas et al 1971).

Feeding overlaps using percentages by number and by reconstituted mass were calculated between locations (with pooled data from the two years) and between years for a given location, using the Morisita-Horn index based on taxonomic classification (Cmh; Magurran 1988). An index of 1 represents a complete dietary overlap whereas 0 indicates no similarity in diet composition. Significant overlap is assumed for index values ≥ 0.6 (Magurran 1988).

Stable isotope analysis

The carbon and nitrogen stable isotope signatures of sooty terns were measured on whole blood and feathers of both chicks and adults, and on muscle tissues of some important prey items. Blood and whole specimens of the main prey (fish and cephalopods) found in stomach contents were preserved in 70% ethanol before isotope analysis. Preservation in ethanol does not change stable-carbon and nitrogen isotope ratios of samples (Hobson et al. 1997).

In order to remove lipids feathers were cleaned by sonication (2min) in a 2:1 chloroform:methanol rinse. Samples were then rinsed with methanol, dried in an oven at +60°C and cut with stainless steel scissors into small homogeneous fragments. Avian blood does not necessitate lipid extraction (Cherel et al. 2005), but lipids were removed from muscle tissue of prey using cyclohexane. Prey samples were freeze-dried and finely ground using a Retsch MM2000 ball mill, and then 100mg were mixed with 4ml of cyclohexane in screw glass tubes, and agitated using a tube rotator during 1h. They were then centrifuged (10min at 1500g), the supernatant was discarded, and the remaining pellet mixed again with 2ml cyclohexane, sonicated during 1min and centrifuged a second time. The resulting pellet was dried in a dry bath at +60°C and ground again. Stable-carbon and nitrogen isotope measurements were performed on 1mg subsamples of homogenized materials by loading them into tin cups and combusting them at 1800°C in a Robo-Prep elemental analyzer. Resultant CO_2 and N_2 gases were then analyzed using a Europa 20:20 IRMS interfaced to a

Roboprep elemental analyzer (Europa Scientific, Crewe, UK). Stable isotope abundances were expressed in δ notation as the deviation from standards in parts per thousand (‰) according to the following equation: $\delta X = [(R_{sample} / R_{standard}) - 1] * 1000$, where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The R standard values were based on the Pee-Dee Belemnite (PDB) for ^{13}C and atmospheric N_2 (AIR) for ^{15}N. Replicate measurements of internal laboratory standards (albumen) indicate measurement errors of ± 0.1‰ and ± 0.3‰ for stable-carbon and nitrogen isotope measurements respectively.

Mercury analysis

Mercury concentration was measured in body feathers of adult birds. Feathers were washed vigorously in two series of triple baths of 0.25 N sodium hydroxide solution alternated with triple baths of deionized water in order to remove adherent external deposits and airborne contamination (Walsh 1990, Schreiber & Burger 2001), which could alter the results of the analysis of mercury sequestrated in feathers. They were then dried for 24 h at 50°C in an oven. Total mercury analyzes were carried out with an Advanced Mercury Analyzer (ALTEC AMA 254) on aliquots ranging from 5 to 20 mg of dried samples weighed to the nearest 0.01mg. The detection limit, accuracy, and reproducibility of the preparation were tested by preparing replicates of lobster hepatopancreas (TORT-2) reference standards (National Research Council, Canada) and blanks along with each set of samples. The detection limit, determined as three times the value of at least eight blanks, was equal to 2.5 $ng.g^{-1}$. Accuracy was estimated as the closeness of each measured value to the certified value of TORT-2 (0.27±0.06 $\mu g.g^{-1}$). Measured values were always within 6% of this reference value. Reproducibility was estimated as the closeness of repeated measurements from the same sample. The coefficient of variation given by relative standard deviations (SD) was always lower than 20%. Mercury levels are expressed in $\mu g.g^{-1}$ of dry weight.

Data analysis

One-way analyses of variances were performed with the software Statistica. All samples were first tested for normality using the Shapiro-Wilk test and for homogeneity of the variance using the Bartlett test. When these conditions of application of parametric analysis were not met, or when sample size was too small, non-parametric and *post-hoc* multiple comparison non-parametric Tukey-type tests (Nemenyi test) for the analysis of variance for independent samples were used (Zar 1999). Values are means ± SD, and the level of significance for statistical analysis was always set at $\alpha < 0.05$.

Results

We analysed 491 stomach contents of sooty terns from the four colonies, which overall contained 5560 prey items. Stomach contents were heavier at Europa and Juan de Nova for every year than at Glorieuses and Aride. They were always the lightest at Glorieuses (Table 1). The mean number of prey items per stomach content did not differ between years for a given location and was significantly smaller at Europa and Aride than at Juan de Nova and Glorieuses. The sooty terns consumed the widest variety of prey at Europa in 2003 (23 different families) and the diet was less diverse at Glorieuses and Aride (≤ 10 families). The number of prey families was constant over years at Juan de Nova and Glorieuses (Table 1).

Diet composition

Sooty terns from the Mozambique Channel fed mainly on fish, fish larvae, and squid (Table 2). Crustaceans and other organisms were scarce in the diet at all localities (Tables 2 & 3, Figure 2). Cephalopods and fish occurred in most samples from Europa, fish and fish larvae in most samples from Juan de Nova, and the three groups in those from Glorieuses. Fish dominated the diet by numbers at Europa, and fish larvae at Juan de Nova and Glorieuses. By reconstituted mass, however, cephalopods were the main prey group at Europa and Glorieuses, and fish at Juan de Nova. When compared to the other localities, a main characteristic of the diet of sooty terns at Europa was the minor importance of fish larvae in terms of their frequency of occurrence and percentages by numbers and reconstituted mass (Table 2). At Aride fish were the dominant prey items by fresh mass, frequency of occurrence, and number. Squids were present in more than half of the samples but their fresh mass and number represented less than 22% of the overall diet (Table 3).

Fish preyed by sooty terns were mostly small juveniles and larvae of epipelagic, mesopelagic and reef species. In the Mozambique Channel, important families of epipelagic fish were Carangidae, Exocoetidae, Hemiramphidae, Scombridae and Sphyraenidae (Figure 3). Mesopelagic fish (Nomeidae) were almost exclusively eaten at Europa where they were numerically important in the diet (Figure 3). In the Seychelles, Exocoetidae, Carangidae, Scombridae and Engraulidae were other important families. Proportion of fish larvae and their taxonomic composition were closely related at Juan de Nova and Glorieuses, and they differed widely from Europa. At this latter locality the dominant family was Mullidae although a large number of larvae was not identified (42%). At the two former localities Engraulidae were numerically dominant, with Mullidae and Holocentridae being also important. Difference in the mass of individuals, however, led to a dominance of the Mullidae in the diet at Juan de Nova (IRI ranks first), and the family was also of major importance at Glorieuses. Mullidae was the dominant fish family also at Aride.

Cephalopods were mainly composed of flying squid (Ommastrephidae), with a major dominance of *Sthenoteuthis oualaniensis*. The species was present in 53% of the samples at Europa and Glorieuses, where it ranked first using IRI values (Table 2). At Juan de Nova, the IRI value of *S. oualaniensis* ranked third and the species was present in 33% of the samples.

At Aride, *S. oualaniensis* also occurred frequently in the food samples, and was the dominant squid prey. The other cephalopod species were much less abundant for all locations and years. Crustaceans found in the diet of sooty terns from the Mozambique Channel were crabs, pelagic shrimps, and stomatopods. However, only the pelagic stomatopod *Natosquilla investigatoris* represented more than 1% of the number of prey at Europa. No crustaceans occurred in the dietary samples from Aride.

Dietary overlap indices for the colonies of the Mozambique Channel differed when using either the number of prey or their reconstituted biomass (Table 4). A significant overlap in number was only found between Juan de Nova and Glorieuses (0.93) while the overlap was small between Europa and both Juan de Nova and Glorieuses (< 0.23). In contrast the overlap by reconstituted mass was significant between almost all locations. It was more important between Europa and Glorieuses (0.89) than between Juan de Nova and Glorieuses (0.67), and between Europa and Juan de Nova (0.54). The feeding overlap between years for a given location was important for all sites, reaching its highest value at Juan de Nova and its lowest one at Europa (Table 4).

Prey size

Using OL or LRL measurements we compared the mean size and length-frequency distribution of some important prey from the Mozambique Channel collected in food samples of 20±8 days old chicks (Table 5, Figure 4). Whatever the species, prey were always smaller at Glorieuses than at the two other locations. However, no significant difference was noted for Exocoetidae between Europa and Glorieuses, and for *Oxyporamphus micropterus*, and Holocentridae between Glorieuses and Juan de Nova (all Mann-Whitney tests $p > 0.05$). On the other hand, flyingfish (Exocoetidae) from Juan de Nova were significantly larger than at

Europa and Glorieuses, whereas *Decapterus* sp. were significantly smaller at Juan de Nova than Europa (all Mann-Whitney tests $p < 0.01$).

The mean size (Mann-Whitney test $U = 23$ $p > 0.05$) and the length-frequency distribution (Kolmogorov-Smirnov test $D = 0.864$ $p > 0.05$) of the main fish larvae *Mulloïdes* sp. were not significantly different between Europa and Juan de Nova, but both differed significantly from Glorieuses (all Mann-Whitney test $p < 0.01$ and Kolmogorov-Smirnov test $p < 0.01$; Table 5, Figure 4). At Europa and Juan de Nova, there were at least two distinct size-classes whereas at Glorieuses only one size-class was present. At the three islands the first mode was similar, with OL between 0.9 and 1.0 mm. *Sthenoteuthis oualaniensis* were larger at Europa and smaller at Glorieuses (Table 5), and their length distribution differed significantly according to the locations (all Kolmogorov-Smirnov tests $p < 0.01$, Figure 4). As observed for the Mullidae, squid were almost all distributed in a single size-class at Glorieuses, whereas at Europa and Juan de Nova several size-classes occurred. At Juan de Nova, however, small individuals were more abundant than at Europa.

Stable isotope analysis

Carbon and nitrogen stable isotope signatures differed among locations and between adults and chicks (Figure 5). At Europa adults and chicks were significantly segregated by their blood isotopic signatures, with $\delta^{13}C$ being enriched and $\delta^{15}N$ being depleted in adults compared to the chicks (all Mann-Whitney tests $p < 0.01$). The carbon signature in feathers was not significantly different between adults and chicks (Mann-Whitney test $U = 105.5$, $p = 0.286$), while that of nitrogen was significantly lower in adult feathers (Mann-Whitney test $U = 1$, $p < 0.001$). At Juan de Nova both adult and chick carbon and nitrogen signatures did not differ significantly in blood (all Mann-Whitney tests $p > 0.05$). In contrast, both carbon and nitrogen signatures in adult feathers were significant lower in stable isotope ratios than chick feathers (all Mann-Whitney tests $p < 0.01$). At Aride adult and chick carbon feather signature did not differ significantly (Mann-Whitney test $U = 44$, $p > 0.05$), while nitrogen signatures were significantly higher in chick feathers (Mann-Whitney test $U = 20$, $p < 0.05$).

Comparison among locations indicated that for both adults and chicks, $\delta^{13}C$ values in blood of birds from Juan de Nova were significantly higher compared to that of birds from Europa, and $\delta^{15}N$ values were significantly lower (all Mann-Whitney tests $p < 0.01$). For feathers, $\delta^{13}C$ values segregated birds from the Seychelles from those from the Mozambique Channel (Nemeneyi test $p < 0.05$). Segregation was less obvious with $\delta^{15}N$ values, although three distinct groups can be identified. Individuals from the Seychelles and Glorieuses had significantly higher $\delta^{15}N$ values, while adults from Juan de Nova had significantly lower $\delta^{15}N$ values. Adults from Europa and chicks from Juan de Nova constituted a homogeneous group at an intermediate position (Nemeneyi test $p < 0.05$).

The main sooty tern prey clearly differed by their $\delta^{13}C$ values (Kruskal-Wallis $H = 43.2$ $p<0.001$, Nemeneyi test $p < 0.05$; Figure 6). The carbon signatures differentiated the cephalopods diet at Europa (*S. oualaniensis*) from the fish diet at Juan de Nova and Glorieuses. Prey also exhibited significant differences in their $\delta^{15}N$ values (Kruskal-Wallis $H = 38.4$ $p < 0.01$, Nemeneyi test $p < 0.05$). The nitrogen signatures significantly segregated three main groups of species. Engraulidae from the Glorieuses occurred at a lower trophic level followed by fishes and fish larvae from Juan de Nova and Glorieuses. *S. oualaniensis* from Europa had the highest $\delta^{15}N$ values, being enriched by at least 3‰ when compared to the other prey.

Mercury levels

Mercury concentrations found in feathers of adult sooty terns differed significantly between localities (Kruskal-Wallis test $H=24.2$, $p<0.01$). Feather concentrations were lower in the

Mozambique Channel than at the Seychelles (Europa 0.21 ± 0.08 $\mu g.g^{-1}$, Juan de Nova 0.39 ± 0.15 $\mu g.g^{-1}$, Glorieuses 0.23 ± 0.1 $\mu g.g^{-1}$, Aride 0.59 ± 0.60 $\mu g.g^{-1}$), but they showed relatively high inter-individual variability at every location. Mercury concentrations at Europa and Glorieuses were similar, but significantly different from those at Juan de Nova and Aride (Nemeneyi test $p<0.05$). There was no significant correlation between mercury concentrations in feathers and their $\delta^{13}C$ and the $\delta^{15}N$ values, or between mercury concentration and latitude.

Discussion

Until recently little was known about the feeding ecology of sooty terns in southwestern Indian Ocean, and generally worldwide (Table 6). Similarly, very few data exist on the stable isotope signatures and mercury concentrations in marine organisms and at the baseline of the ecosystems (Ménard et al 2007, Kojadinovic et al 2007). In the southwest Indian Ocean, during reproduction, the large diversity of prey underlies the opportunistic feeding habits of sooty terns, as found in Hawaii (Harrison et al 1983), the Dry Tortugas (Hensley and Hensley 1995), and western Australia (Surman and Wooller 2003). Individuals at each colony however depend upon a few key species, and flying squid, larvae and juveniles of fish form the bulk of sooty terns' food, as usually observed elsewhere (Ashmole 1963, Feare 1976, Harrison et al 1983, Surman and Wooller 2003). Stable isotope analyses confirm the trophic differences between localities that were observed from direct analysis of food samples during chick-rearing period. The feather isotopic signatures also showed that during the non-breeding season, adults feed on lower trophic level prey than those given to their chicks. This supports the hypothesis that seasonal reproduction occurs when trophic conditions are the most favourable (Jaquemet et al 2007), to fulfil high-energy requirements of reproduction.

Ecological niche of sooty terns in the Mozambique Channel

In the three colonies of the Mozambique Channel, the differences in mass of food loads and number of prey per food samples are related to the nature of the main prey items (i.e. larger food loads include a few larger prey, and conversely). At Europa chicks are fed with juveniles of fish and flying squids, at Juan de Nova with fish larvae, and at Glorieuses with large prey and fish larvae. In many seabird species, composition and mass of food loads have been related to the availability of prey (Croxall et al 1999). Thus, differences in food loads delivery to sooty tern chicks reflected more likely the availability of marine resources in the local foraging habitats, as already showed for other species (Croxall et al 1999, Forero et al 2002, Tremblay & Cherel 2003). In waters surrounding Europa and Juan de Nova, during reproduction, different seasonal aggregations of prey items supply breeding sooty terns, and demonstrate that the species is able to adapt to local resources to reproduce. In contrast, the non-seasonal reproduction at Glorieuses strongly suggests that aggregations of prey in the vicinity of the colony are not seasonal. If no seasonal change of the marine environment occurs, or if it has limited effect on breeding success, breeding at less than annual intervals might be advantageous for sooty terns (Ashmole 1963).

Feeding overlaps between successive years computed from prey mass was significant at each location but feeding overlaps from prey number were significant at Juan de Nova only. This indicates that a minimum mass of meal is required whatever the nature of prey, and that chick-rearing adults strive to collect the “target payload mass” as quickly as possible (Schaffner 1990, Le Corre et al 2003). For this, they secure any prey of appropriate size that is available in the surface waters around breeding colonies (Harrison et al 1983). At Juan de Nova, although in 2004 the diet samples were collected during two days at the end of the chick-rearing period, the high feeding overlap both by number and by mass between 2003 and 2004 suggests a similar availability of prey during two consecutive breeding seasons. A consistently high availability of prey from year to year would explain why Juan de Nova is the largest colony of sooty terns in the Indian Ocean (Le Corre and Jaquemet 2005).

Analyses of stable isotopes in blood and chick feathers revealed a pattern of geographic and seasonal differences in diet that complement the results from dietary analyses. Such differences are attributable to the nature of prey consumed but also to different strategies adopted by adults provisioning their chicks. Interestingly, at Europa, adults tend to feed their chicks with higher quality prey than they themselves subsist on (higher δ^{15}N values in chicks), as demonstrated for other seabirds (Hobson 1993, Hodum & Hobson 2000, Forero et al 2002). In contrast, at Juan de Nova, adults and chicks show the same blood isotopic signatures indicating that they rely on the same prey (mostly fish larvae). This difference of feeding strategy is probably related to the prey assemblage at sea around colonies and the adaptation of sooty terns to contrasted oceanic conditions. Stable isotope signatures of some important prey items exhibit the same trends as terns. Carbon isotope signatures segregate flying squid sampled in Europa fish prey sampled in Juan de Nova and Glorieuses. Nitrogen signatures of prey are consistent with a higher trophic level of terns at Europa during reproduction than at Juan de Nova and Glorieuses. These differences in trophic position of both individuals and their main prey show clear differences in the structure of food chains ending to sooty terns between the different localities of the Mozambique Channel. Sooty terns occupy different ecological niches during their breeding season in response to differences in the assemblages of prey in their foraging habitats.

Isotopic signatures of adult feathers also reveal different foraging habitats and ecological niche during the non-breeding season. Comparisons of feather carbon signatures between adults and chicks suggest firstly that overall adult sooty terns remain in tropical waters year round, thus contrasting with higher-latitudes seabird species that undertook extensive wintering migrations (Cherel et al 2000, Quillfeld et al 2005, Cherel et al 2006). Secondly, birds from the Seychelles had different $\delta^{13}C$ values from those from the Mozambique Channel, suggesting distinct foraging area during both breeding and non-breeding seasons. Thirdly, the difference in $\delta^{13}C$ values between chicks and adults is larger at Juan de Nova than at Europa, and suggesting that individuals from the former locality disperse over wider areas during the non-breeding season. This result reinforces the idea that surface waters in the central Mozambique Channel are few productive most of the year (Donguy & Meyer 1996, Jaquemet et al 2007). Individuals from Glorieuses probably disperse in the Mozambique Channel as well, toward southern waters as suggested by their carbon signatures.

Ecological niche of sooty terns in the Seychelles

Winter breeding of sooty terns in the Seychelles, as in Europa, is related to the overall enhancement of surface water primary production associated to the southwest monsoon (Jaquemet et al 2007, Monticelli et al 2007). This makes juveniles of epipelagic fish highly available for marine birds at that time. Mullidae, Scombridae, and Exocoetidae were the dominant prey, and Ommastrephidae were also frequently consumed, as previously found in Hawaii (Harrison et al 1983). Overall the diet at Aride was less diversified than in the Mozambique Channel and dominated by oceanic species, suggesting that adults forage far offshore outside the shelf (Seychelles plateau). The identical $\delta^{13}C$ values of adult and chick feathers moreover suggest that sooty terns from Aride forage over the same water masses during both the breeding and non-breeding seasons, with no extensive migration elsewhere.

Stable isotopes and mercury in sooty terns in relation to oceanic provinces

At large spatial scales $\delta^{13}C$ signatures in sooty tern tissues segregate the Mozambique Channel from the Seychelles region. This segregation is in accordance with the global trend of plankton $\delta^{13}C$ with latitude (Rau et al 1982). It also confirms recent findings of distinct isotopic regions between the Mozambique Channel and the Somali-Seychelles region, where $\delta^{13}C$ signatures in tuna and billfish ranged between -17.4 and -15.0 (Ménard et al 2007). Moreover, carbon values measured on muscles of tuna caught in the Mozambique Channel and around the Seychelles fit well with the sooty tern data. Changes in tuna carbon signatures were overall small along the 20° of latitude. In addition to a limited dispersion of adult sooty terns during the non-breeding period, it is highly probable that the carbon isotopic gradient is not strongly marked in tropical waters compared to higher latitudes, as recently suggested for the western Indian Ocean (Ménard et al 2007). Similarly to $\delta^{13}C$ values, a gradient of $\delta^{15}N$ values from the Mozambique Channel to the Seychelles exists with higher values in the Seychelles. In comparison with the similarities of diet composition between Europa and Aride in the Seychelles, this result supports the idea of a higher nitrogen baseline level in the Seychelles region compared to the Mozambique Channel (Ménard et al 2007).

No correlation occurs between mercury concentrations in feathers of sooty terns and both carbon and nitrogen isotopic ratios. However mercury concentrations segregate overall the Mozambique Channel and the Seychelles provinces, with higher concentrations observed in birds from the Seychelles. Piscivorous feeding habits in marine birds have been related to higher mercury concentrations (Sanpera et al 2007). Then a high proportion of fish in diet of adults during the non-breeding period may explain the higher levels of mercury display by individuals at Juan de Nova and Aride. Further investigations have to be conducted, however, to understand the mechanisms for the incorporation of mercury in sooty tern feathers during and outside the breeding period in the tropical environment.

Conclusion

To our knowledge this study is the first to compare the trophic ecology of sooty terns during both breeding and non-breeding periods at a regional scale. In addition demonstrating strong intercolonial dietary differences, our results support the view that during the non-breeding period adults disperse from their colonies but remain in tropical waters. This confirms the specialisation of the species to the tropical marine environment and its capacity to adapt to different oceanic conditions, which explain its numerical dominance in tropical waters (Schreiber et al 2002). In an oceanic province with contrasting environmental conditions like the Mozambique Channel, the species demonstrates a high phenotypic plasticity, expressed by differences in its food habits, breeding season, and breeding strategy. This plasticity is also demonstrated at a larger spatial scale, with birds from the Seychelles region showing a distinct feeding ecology. In the context of climate change it will be of interest to investigate the responses of different populations to the modifications of their oceanic environments. It would be especially interesting to determine whether adults will be able to compensate for food variation by an adjustment of the effort devoted to foraging, and to assess the influence of inter-annual changes in primary productivity and of local and regional scale ocean indices on the breeding performance of sooty terns as has been recently done for a tropical marine bird of the Seychelles, the roseate tern (Monticelli et al 2007).

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Legend to the figures

Figure 1-Map of southwestern Indian Ocean showing the location of the study colonies (★)

Figure 2- Relative contribution of the main prey categories to the diet of sooty terns according to the location. For wet mass, fish category includes both fish and fish larvae.

Figure 3- Composition of the diet by number for the main families of fish and fish larvae according to the locations.

Figure 4- Frequency distributions of otolith length (OL) of fish larvae (*Mulloïdes* sp.), and of lower rostral length (LRL) of beak of cephalopod (*Sthenoteuthis oualaniensis*) for localities from the Mozambique Channel. N: number of food samples, n: number of individuals.

Figure 5- Mean stable-carbon and stable-nitrogen isotopic signatures (± SD) in blood and feathers of breeding adults and chicks according to the locations.

Figure 6- Mean stable-carbon and stable-nitrogen isotopic signatures (± SD) of some important prey of sooty terns during the breeding season. E: Europa, J: Juan de Nova, G: Glorieuses

Table

Table 1- Main characteristics of the dietary samples of sooty terns in the southwest Indian Ocean, according to the years and the locations. sd: standard deviation. Values per line with different letters are significantly different at $p < 0.05$

	Mozambique Channel						Seychelles
	Europa		Juan de Nova		Glorieuses		Aride
	2002	2003	2003	2004	2003	2004	2005
Sampling period (days)	45	69	21	2	10	9	15
Number of samples	84	110	101	44	50	48	54
Mean wet mass of content ± sd (g)	18.8 ± 12.4^{a}	20.3 ± 14.5^{a}	15.8 ± 8^{b}	18.8 ± 8.9^{a}	6.7 ± 4.5^{c}	10.0 ± 4.8^{d}	$11.9 \pm 6,4^{e}$
Number of prey	424	659	2003	740	813	615	306
Number of families	13	23	17	16	11	10	9
Mean number of prey per content ± sd	5.0 ± 5.5^{a}	6.0 ± 6.7^{a}	19.8 ± 22.4^{b}	17.0 ± 16.5^{b}	17.6 ± 30.4^{b}	12.8 ± 14.2^{b}	5.7 ± 3.8^{c}

Table

Table 2 – Composition of the diet of sooty terns in the Mozambique Channel during the chick-rearing period

Prey Species	Europa							Juan de Nova							Glorieuses						
	Occurrence		Number		Reconstituted mass		IRI	Occurrence		Number		Reconstituted mass		IRI	Occurrence		Number		Reconstituted mass		IRI
	n	%	n	%	M (g)	%	rank	n	%	n	%	M (g)	%	rank	n	%	n	%	M (g)	%	rank
Cephalopods	145	74.7	339	31.3	3704.6	59.5		67	46.2	136	5.0	797.3	21.4		71	72.4	254	17.8	761.1	54.6	
Decapoda																					
Unid. Decapoda								1	0.7	3	0.1	12.6	0.3	21							
Enopleuthidae																					
Unid. Enoploteuthidae	1	0.5	1	0.1	0.8	< 0.1	27	2	1.4	3	0.1	1.2	<0.1	22	3	3.1	4	0.3	1.1	0.1	17
Ommastrephidae																					
Sthenoteuthis oualaniensis	104	53.6	215	19.9	2308.6	37.1	1	48	33.1	91	3.3	561.7	15.1	3	52	53.1	169	11.8	512.5	36.7	1
Ornithoteuthis volatilis	32	16.5	41	3.8	142.9	2.3	6														
Unid. Ommastrephidae	40	20.6	55	5.1	1012.9	16.3	3	23	15.9	29	1.1	190.8	5.1	10	43	43.9	76	5.3	234.2	16.8	3
Onychoteuthidae																					
Moroteuthis lonnbergii	2	1.0	2	0.2	2.0	<0.1	26														
Unid. Onychoteuthidae	1	0.5	1	0.1	4.4	0.1	27								1	1.0	1	0.1	0.8	0.1	20
Sepiidae																					
Unid. Sepiidae								1	0.7	1	< 0.1	0.5	< 0.1	24							
Spirulidae																					
Spirula spirula								1	0.7	1	<0.1	1.0	< 0.1	24							
Unid. Cephalopods	19	9.8	24	2.2	233.0	3.7	10	7	4.8	7	0.3	29.4	0.8	17	4	4.1	4	0.3	12.4	0.9	13
Crustaceans	13	6.7	80	7.4	30.7	0.5		2	1.4	2	0.1	7.3	0.2		0	0	0	0	0	0	
Aristeidae																					
Unid. Aristeidae	3	1.5	6	0.6	18.0	0.3	20														
Oplophoridae																					
Acanthephyra sanguineus								1	0.7	1	<0.1	6.5	0.2	23							
Peneidae																					
Unid. Peneidae	4	2.1	6	0.6	2.4	< 0.1	21														
Portunidae																					
Unid. Portunidae								1	0.7	1	<0.1	0.8	< 0.1	24							
Squillidae																					
Nastosquilla investigatoris	5	2.6	66	6.1	9.7	0.2	14														
Unid. Crustaceans	2	1.0	2	0.2	0.6	< 0.1	26														
Fish	158	81.4	540	49.9	2409.5	38.7		123	84.8	553	20.2	1722.7	46.3		66	67.3	180	12.6	349.9	25.1	
Balistidae																					
Balistoïdes viridescens								1	0.7	3	0.1	1.8	< 0.1	23							
Unid. Balistidae	1	0.5	1	0.1	1.3	< 0.1	27														

Carangidae																					
Caranx sp.								5	3.4	5	0.2	13.1	0.4	19							
Decapterus macarellus	2	1.0	2	0.2	32.6	0.5	23	15	10.3	43	1.6	186.4	5.0	12							
Decapterus macrosoma	3	1.5	5	0.5	43.5	0.7	19	24	16.6	70	2.6	242.7	6.5	7							
Decapterus russelli	1	0.5	1	0.1	7.4	0.1	27														
Decapterus sp.	47	24.2	103	9.5	799.1	12.8	2	15	10.3	45	1.6	157.1	4.2	14							
Unid. Carangidae	16	8.2	30	2.8	289.2	4.6	9	25	17.2	57	2.1	213.8	5.7	8	3	3.1	3	0.2	6.0	0.4	15
Carapidae																					
Echion sp.	1	0.5	1	0.1	0.6	< 0.1	27	1	0.7	1	< 0.1	0.5	< 0.1	24							
Diretmidae																					
Diretmichthys parini	1	0.5	1	0.1	4.0	0.1	27														
Exocoetidae																					
Cheilopogon sp.								1	0.7	1	< 0.1	10.6	0.3	22	1	1.0	1	0.1	2.2	0.2	18
Cypselurus oligolepis								1	0.7	1	< 0.1	1.9	0.1	24							
Cypselurus sp.	1	0.5	1	0.1	2.2	< 0.1	27	1	0.7	1	< 0.1	4.0	0.1	23							
Exocoetus sp.	2	1.0	2	0.2	4.3	0.1	25	1	0.7	1	< 0.1	5.3	0.1	23							
Exocoetus volitans	1	0.5	1	0.1	2.0	< 0.1	27	1	0.7	2	0.1	21.4	0.6	20							
Hirundichthys sp.	1	0.5	1	0.1	1.3	< 0.1	27														
Paraexocoetus brachypterus	1	0.5	1	0.1	15.1	0.2	26														
Paraexocoetus mento	1	0.5	1	0.1	2.5	< 0.1	27														
Prognichtys sealei	2	1.0	3	0.3	8.7	0.1	24														
Unid. Exocoetidae	27	13.9	47	4.3	99.5	1.6	17	25	17.2	37	1.3	89.6	2.4	13	31	31.6	59	4.1	87.9	6.3	5
Hemiramphidae																					
Oxyporamphus micropterus	5	2.6	6	0.6	40.4	0.6	18	51	35.2	82	3.0	301.7	8.1	5	21	21.4	31	2.2	73.9	5.3	7
Myctophidae																					
Diaphus sp.	1	0.5	1	0.1	3.3	0.1	27														
Unid. Myctophidae	1	0.5	1	0.1	3.2	0.1	27														
Nomeidae																					
Cubiceps capensis	10	5.2	43	4.0	121.7	2.0	12														
Cubiceps pauciradiatus	10	5.2	14	1.3	34.1	0.5	16	1	0.7	1	< 0.1	3.0	0.1	23							
Cubiceps sp.	33	17.0	128	11.8	319.9	5.1	4	1	0.7	1	< 0.1	3.0	0.1	23							
Psenes arafurensis								5	3.4	5	0.2	33.0	0.9	18							
Scombridae																					
Auxis sp.	1	0.5	2	0.2	40.0	0.6	24														
Unid. Scombridae	11	5.7	15	1.4	129.6	2.1	13	48	33.1	117	4.3	185.4	5.0	6	9	9.2	9	0.6	21.2	1.5	11
Sphyraenidae																					
Sphyraena acutipinnis	4	2.1	26	2.4	61.0	1.0	7														
Sphyraena sp.	23	11.9	46	4.2	104.4	1.7	8	22	15.2	31	1.1	92.8	2.5	15	30	30.6	47	3.3	93.4	6.7	6
Sternoptychidae																					
Unid. Sternoptychidae								1	0.7	1	<0.1	3.3	0.1	23							
Trichiuridae																					

Unid. Trichuridae	3	1.5	5	0.5	22.7	0.4	20														
Unid. Fish	36	18.6	52	4.8	216.1	3.5	5	23	15.9	48	1.7	151.5	4.1	11	22	22.4	30	2.1	65.2	4.7	8
Fish Larvae and Post-Larvae	22	11.3	122	11.2	85.0	1.4		122	84.1	2051	74.7	1192.9	32.1		59	60.2	986	69.0	282.5	20.2	
Acanthuridae																					
Acanthurus sp.								1	0.7	3	0.1	2.1	0.1	23							
Unid. Acanthuridae	1	0.5	1	0.1	1.0	< 0.1	27														
Apogonidae																					
Apogon cookii								1	0.7	2	0.1	0.4	< 0.1	23	1	1.0	3	0.2	0.6	< 0.1	19
Engraulidae																					
Unid. Engraulidae	1	0.5	5	0.5	0.8	< 0.1	26	42	29.0	1060	38.6	169.6	4.6	2	22	22.4	689	48.2	110.2	7.9	2
Hemiramphidae																					
Unid. Hemiramphidae								1	0.7	1	< 0.1	0.3	< 0.1	24							
Hemulidae																					
Pomadasys sp.	1	0.5	1	0.1	0.9	< 0.1	27														
Unid. Hemulidae															1	1.0	14	1.0	4.2	0.3	16
Holocentridae																					
Myripristis sp.								23	15.9	41	1.5	19.3	0.5	16	9	9.2	13	0.9	5.8	0.4	12
Sargocentron sp.								61	42.1	208	7.6	128.9	3.5	4	13	13.3	58	4.1	34.6	2.5	9
Unid. Holocentridae	2	1.0	3	0.3	2.1	< 0.1	25	1	0.7	1	< 0.1	0.7	< 0.1	24							
Istiophoridae																					
Unid. Istiophoridae								1	0.7	1	< 0.1	3.0	0.1	23							
Monachantidae																					
Unid. Monachantidae								1	0.7	1	< 0.1	1.7	0.1	23							
Mullidae																					
Mulloïdes sp.	13	6.7	56	5.2	70.0	1.1	11	78	53.8	559	20.4	840.8	22.6	1	33	33.7	147	10.3	117.7	8.4	4
Synodontidae																					
Synodus sp.	3	1.5	5	0.5	1.8	< 0.1	22														
Tetraodontidae																					
Lagocephalus lagocephalus								2	1.4	2	0.1	1.0	0.0	23							
Unid. Fish Larvae	5	2.6	51	4.7	8.4	0.1	15	23	15.9	172	6.3	25.8	0.7	9	13	13.3	62	4.3	9.3	0.7	10
Others	2	1.0	2	0.2	0.6	< 0.1		1	0.7	1	< 0.1	0.2	< 0.1		5	5.1	8	0.6	1.6	0.1	
Unid. algae	2	1.0	2	0.2	0.6	<0.1	26														
Insects																					
Orthoptera sp.								1	0.7	1	0.1	0.2	< 0.1	23	5	5.1	8	0.6	1.6	0.1	14
Total	194		1083	100.0	6230.5	100.0				2743	100.0	3720.4	100.0				1428	100.0	1395.0	100.0	

Table

Table 3 – Composition of the diet of sooty terns at Aride Island in the Seychelles during the chick-rearing period. N= number and M= mass

	Occurrence		Number		Wet Mass	
	n	%	n	%	M (g)	%
Cephalopods	**30**	**55.6**	**52**	**17.0**	**136**	**21.2**
Ommastrephidae	24	44.4	45	14.7	124.9	19.4
Unidentified Ommastrephidae	4	7.4	9	2.9	21.4	3.3
Sthenoteuthis oualaniensis	20	37.0	36	11.8	103.5	16.1
Other cephalopods	6	11.1	7	2.3	11.1	1.7
Fish	**52**	**96.3**	**254**	**83**	**506.7**	**78.8**
Caesionidae	5	9.3	10	3.3		
Carangidae	9	16.7	42	13.7		
Coryphaenidae	2	3.7	2	0.7		
Engraulidae	5	9.3	23	7.5		
Exocoetidae	11	20.4	33	10.8		
Hemiramphidae	2	3.7	2	0.7		
Mullidae	21	38.9	81	26.5		
Scombridae	10	18.5	23	7.5		
Unidentified fish	18	33.3	38	12.4		
Total	**54**		**306**	**100.0**	**642.7**	**100.0**

Table

Table 4-Morisita-Horn's overlap index of dietary composition based upon number and reconstituted mass per year for each location. Comparisons between the same locality are for different years and between localities for pooled years. Underlined values indicate a significant overlap (i.e: Morisita index > 0.6)

	Glorieuses	Juan de Nova	Europa
	Number of prey		
Europa	0.229	0.188	0.436 0.681
Juan de Nova	0.927	0.949 0.708	0.543
Glorieuses	0.573 0.709	0.667	0.889
	Reconstituted mass		

Table

Table 5–Size comparison of some important prey of the diet of the sooty terns according to the location in the Mozambique Channel, values given are mean ± standard deviation. OL: otolith length, LRL: lower rostral length of cephalopod beak, FL: fork length, DML: dorsal mantle length of cephalopods. Values with different letters by line are significantly different at $p < 0.05$

		Europa			Juan de Nova			Glorieuses		
		n	OL/LRL (mm)	Reconstituted FL/DML (mm)	n	OL/LRL (mm)	Reconstituted FL/DML (mm)	n	OL/LRL (mm)	Reconstituted FL/DML (mm)
Fish	Exocoetidae	18	1.49 ± 0.41^{a}	45 ± 22	18	2.08 ± 0.85^{b}	49 ± 15	26	1.42 ± 0.59^{a}	38 ± 11
	Oxyporamphus micropterus	3	3.20 ± 0.99	91 ± 20	41	2.67 ± 1.03^{a}	71 ± 23	25	2.14 ± 0.80^{a}	60 ± 17
	Decapterus sp.	22	2.27 ± 0.46^{a}	87 ± 20	98	1.65 ± 0.42^{b}	59 ± 18			
	Sargocentron sp.				109	1.41 ± 0.36^{a}	26 ± 7	27	1.35 ± 0.24^{a}	25 ± 4
	Myripristis sp.				30	1.89 ± 0.57^{a}	26 ± 9	7	1.69 ± 0.51^{a}	29 ± 16
	Mulloïdes sp.	13	1.23 ± 0.21^{a}	40 ± 5	256	1.31 ± 0.29^{a}	43 ± 7	13	1.08 ± 0.13^{b}	38 ± 4
Cephalopods	*Sthenoteuthis oualaniensis*	215	1.28 ± 0.38^{a}	66 ± 9	91	0.95 ± 0.41^{b}	58 ± 10	169	0.72 ± 0.24^{c}	53 ± 6

Table 6- Comparison of the diet of the sooty terns at different breeding localities by number of prey (%N), volume (%V), reconstituted mass (%M) or wet mass (%W) according to available data

	Hawaii[1]		**Ascension**[2]	**Dry Tortugas**[3]	**Seychelles**[4]	**Western Australia**[5]		**Europa**[6]		**Juan de Nova**[6]		**Glorieuses**[6]		**Aride**[6]	
	(n = 356)					(n = 449)		(n = 194)		(n = 145)		(n = 98)		(n = 54)	
	% N	% V	% N	% N	% N	% N	% V	% N	% M	% N	% M	% N	% M	% N	% W
Cephalopods	**33.5**					**23.6**	**68.1**	**31.3**	**59.5**	**5.0**	**21.4**	**17.8**	**54.6**	**17.0**	**21.2**
Ommastrephidae	26.1	40.7	Present	Present	Regularly present			28.8	55.7	4.4	20.2	17.1	53.5	14.7	19.4
Fish	**66**					**45.9**	**27.8**	**61.1**	**40.1**	**94.9**	**78.4**	**81.6**	**45.3**	**83.0**	**78.8**
Carangidae	3.8	6.7		Regularly present	Present	3.9	1.6	13.1	18.7	8.1	21.8	0.2	0.4	13.7	

Engraulidae				Present	Present	< 0.1	0.1	0.5	< 0.1	38.6	4.6	48.2	7.9	7.5
Exocoetidae	12.1	8.5	Present	Regularly present	Regularly present	0.2	0.3	5.8	2.1	1.6	3.6	4.2	6.5	10.8
Hemiramphidae	0.2	0.1	Present	Regularly present	Present			0.6	0.6	3	8.1	2.2	5.3	0.7
Holocentridae	4.9	1.5		Regularly present				0.3	< 0.1	9.1	4	5	2.9	
Mullidae	20.7	14.0		Regularly present	Regularly present	10.8	7.3	5.2	1.1	20.4	22.6	10.3	8.4	26.5
Nomeidae	3.3	2.8	Present	Regularly present				17.1	7.6	0.3	1.1			

1: Harisson et al 1983, 2: Ashmole 1963, 3: Hensley & Hensley 1995, 4: Feare 1976, 5: Surman & Wooller 2003, 6: Present study

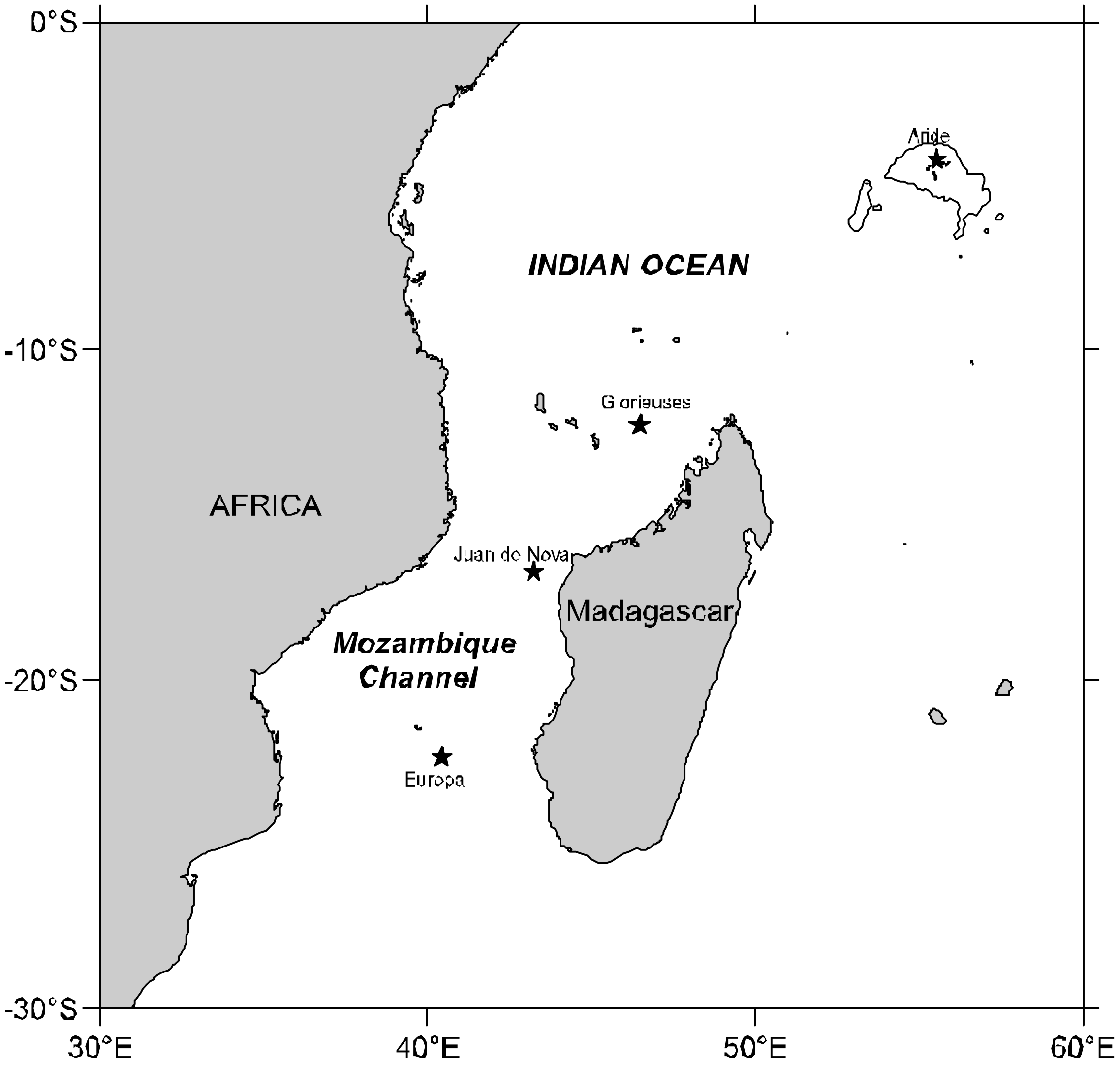
0°S
-10°S
-20°S
-30°S
30°E
40°E
50°E
60°E
Aride
INDIAN OCEAN
Glorieuses
AFRICA
Juan de Nova
Madagascar
Mozambique Channel
Europa

Figure 1

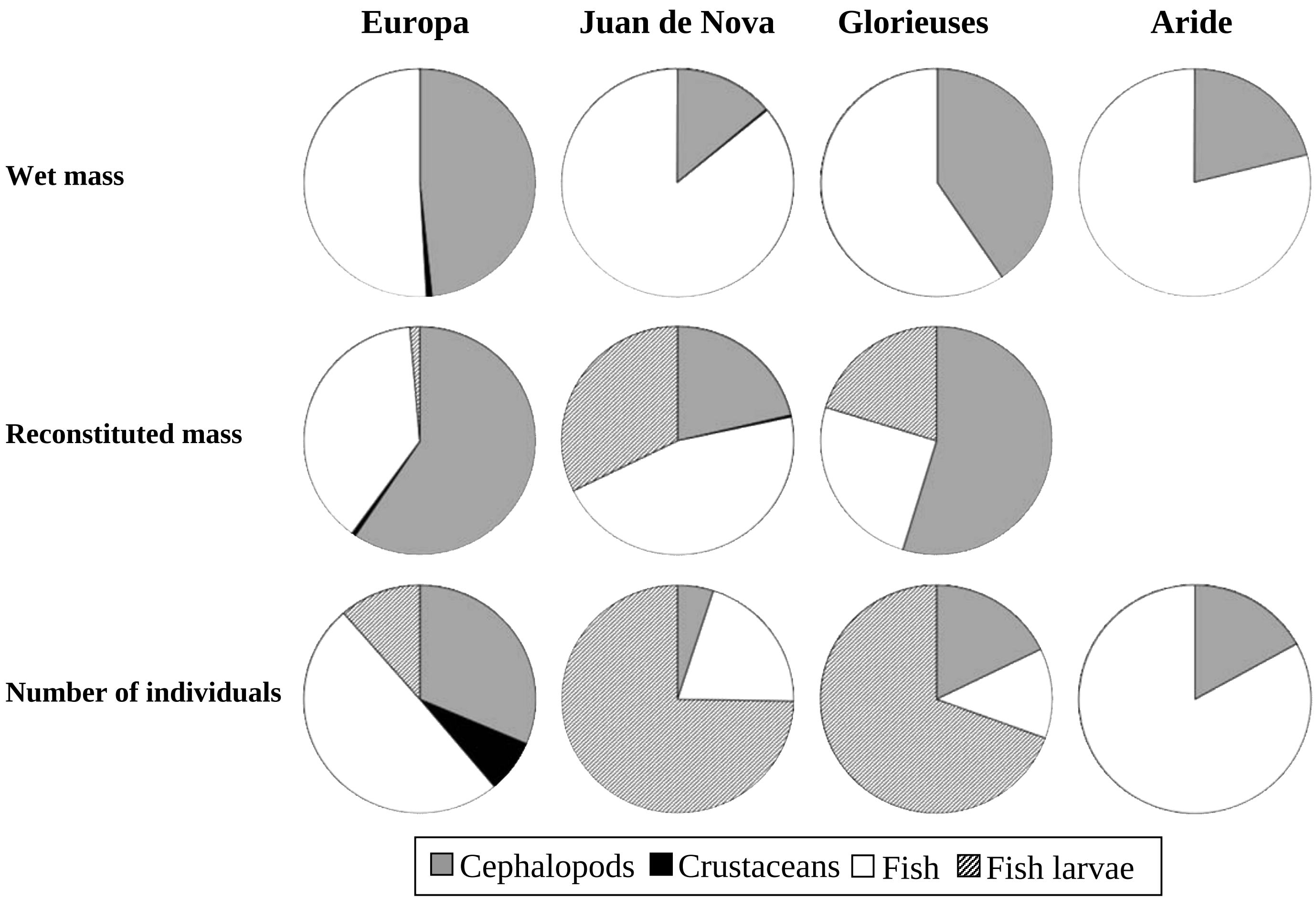
Europa
Juan de Nova
Glorieuses
Aride
Wet mass
Reconstituted mass
Number of individuals
Cephalopods
Crustaceans
Fish
Fish larvae

Figure 2

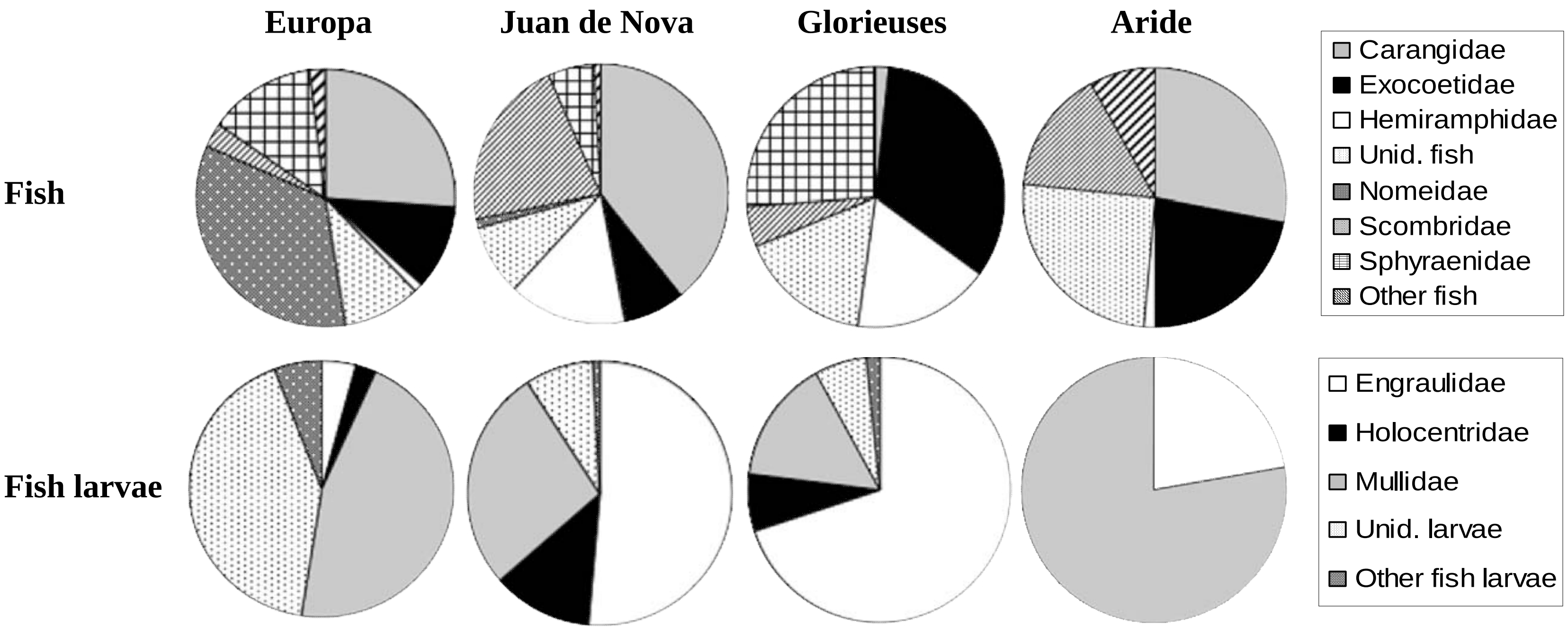
Europa
Juan de Nova
Glorieuses
Aride
Fish
Fish larvae
▨ Carangidae
■ Exocoetidae
☐ Hemiramphidae
☐ Unid. fish
▨ Nomeidae
▨ Scombridae
▤ Sphyraenidae
▧ Other fish
☐ Engraulidae
■ Holocentridae
▨ Mullidae
☐ Unid. larvae
▨ Other fish larvae

Figure 3

Figure

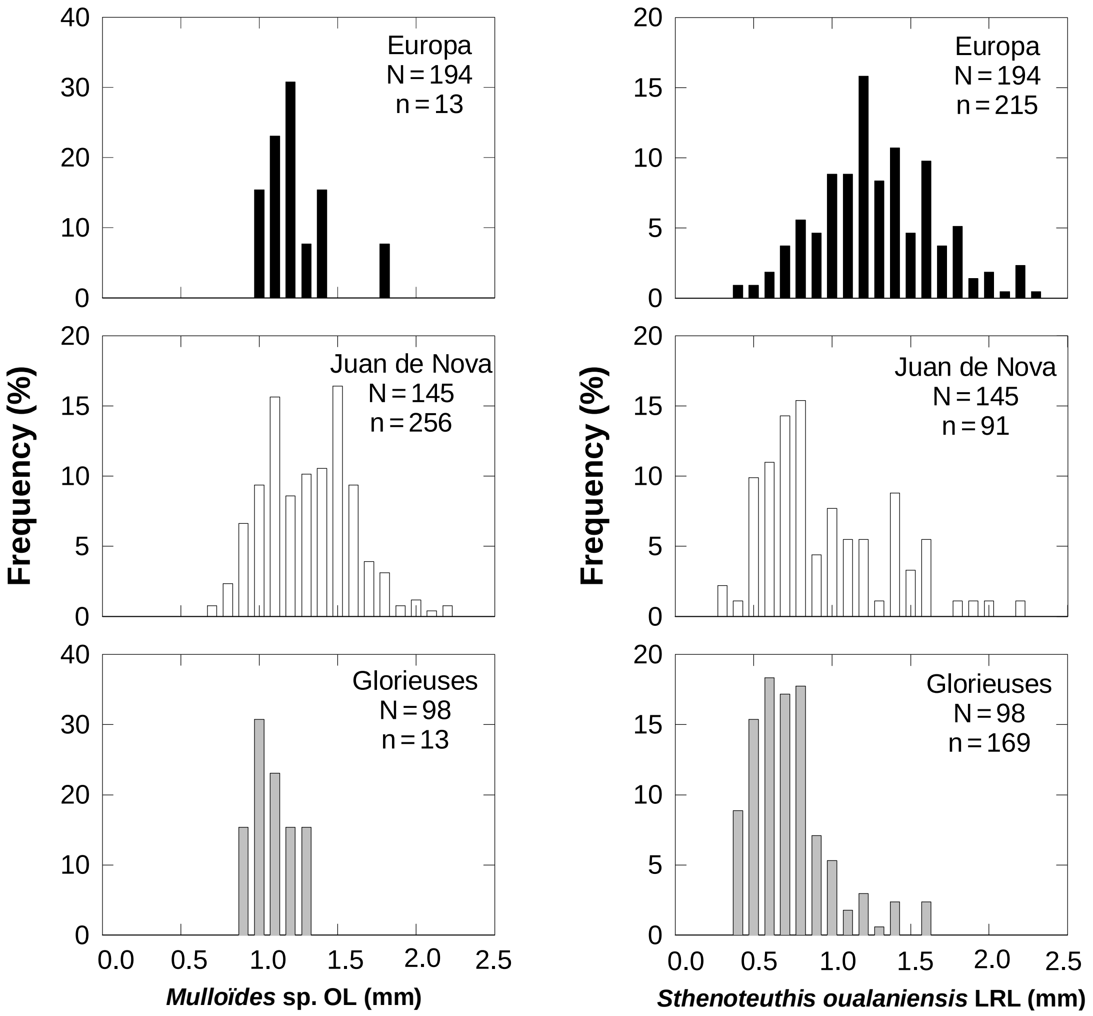

Figure 4

Figure

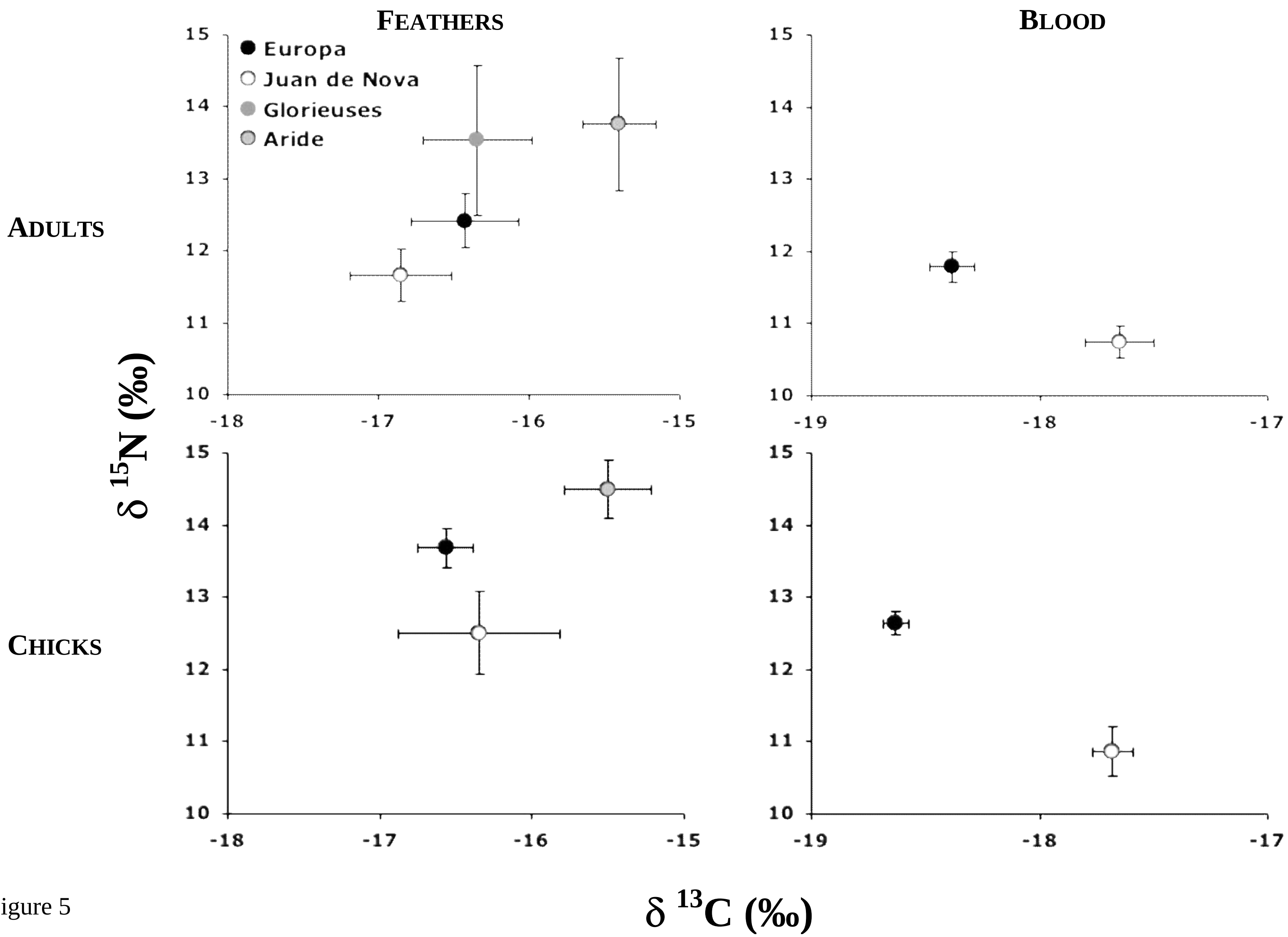

Figure 5

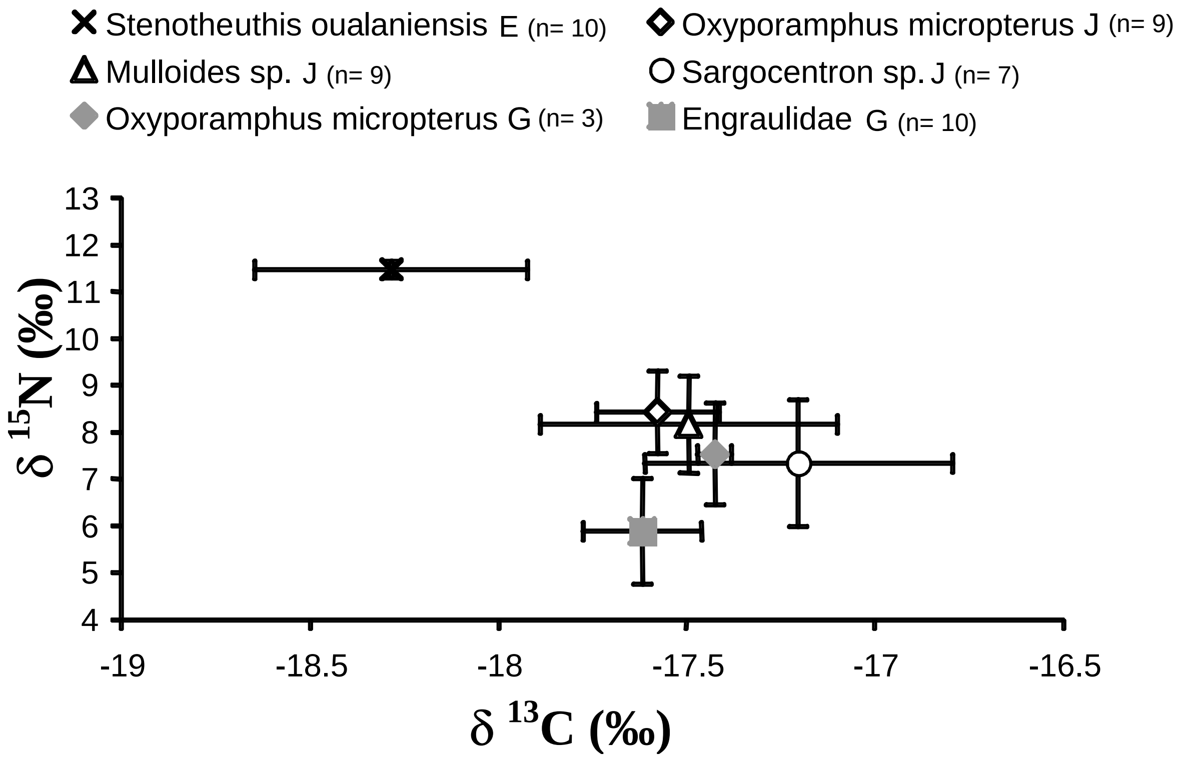
Stenotheuthis oualaniensis E (n= 10)
Oxyporamphus micropterus J (n= 9)
Mulloides sp. J (n= 9)
Sargocentron sp. J (n= 7)
Oxyporamphus micropterus G (n= 3)
Engraulidae G (n= 10)
13
12
11
10
9
8
7
6
5
4
δ 15N (‰)
-19
-18.5
-18
-17.5
-17
-16.5
δ 13C (‰)

Figure 6