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Diet and trophic position of the devil rays *Mobula thurstoni* and *Mobula japanica* as inferred from stable isotope analysis

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*This study confirms the diet and determines the trophic position of the bentfin devil ray (*Mobula thurstoni*) and spinetail devil ray (*Mobula japanica*) in the south-west Gulf of California. There has been an active fishery in the area for these filter-feeding elasmobranchs, which are highly susceptible to exploitation due to low fecundity and long lifespan. However, information on their basic biology is scarce. δ^{13}C and δ^{15}N values of devil rays and zooplankton (sorted according to trophic level: herbivores, carnivores and omnivores) were determined over a period of 11 months, to allow for isotopic temporal variations in isotopic signals at the base of the food web. On the basis of fractionation factors we determined that bentfin and spinetail devil rays fed mainly on *Nyctiphanes simplex*, the most abundant euphausiid in neritic waters of the Gulf of California. The trophic positions obtained for the devil rays correspond to second level consumers.*

Keywords: devil rays, diet, *Nyctiphanes simplex*, stable isotopes, temporal variability

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INTRODUCTION

Stable isotope analysis (SIA) has been used extensively to infer diet (Frazer, 1996; Kibirige *et al.*, 2002), nutrient flow in ecosystems (Rau *et al.*, 1983; Pinnegar & Polunin, 2000; Sherwood & Rose, 2005) and trophic position (Estrada *et al.*, 2003; Vander Zanden & Rasmussen, 2001), and to differentiate between organisms feeding in nearshore and offshore areas (Burton & Koch, 1999; Perry *et al.*, 1999). Stable isotopes have allowed the determination of diet assimilated over a period of time ranging from days to months, whereas stomach contents analysis gives information on recently ingested items (Michener & Schell, 1994; Fry, 2006).

The use of SIA in ecological research relies on an approximately constant increase in the 'heavier' isotopes (^{13}C and ^{15}N) with progression up the food chain. δ^{13}C values increase by 0–1.5‰ from one trophic level to the next, and δ^{15}N values by approximately 3.4‰ (Rau *et al.*, 1983; Vander Zanden & Rasmussen, 2001; Post, 2002; McCutchan *et al.*, 2003). This enables the use of δ^{15}N to determine the trophic level of organisms in the wild, whereas δ^{13}C values are often used to differentiate between nearshore and offshore nutrient sources (France, 1995; Perry *et al.*, 1999).

Seasonal variability in isotopic signals at the base of the food web (producers and primary consumers) has been observed in marine coastal ecosystems (Simenstad & Wissmar, 1985; Vizzini & Mazzola, 2002). This seasonality is less pronounced higher up the food web (Simenstad & Wissmar, 1985), which has made it difficult to assign trophic positions to vertebrates high on the food chain on the basis of point sampling (O'Reilly *et al.*, 2002).

Devil rays (*Mobula* spp.) are a relatively unstudied group of myliobatiform ray. Of the nine recognized species within the genus *Mobula*, five are present in the Gulf of California (McEachran & Notarbartolo-di-Sciara, 1995), and have been the target of a directed artisanal fishery for decades. Like the majority of elasmobranchs, devil rays display life history traits such as production of few embryos at long intervals (Homma *et al.*, 1999), that make them vulnerable to overexploitation (Stevens *et al.*, 2000).

The most comprehensive study on the devil rays of the south-west Gulf of California was carried out in the early 1980s (Notarbartolo-di-Sciara, 1988). It was determined through stomach contents analysis that the bentfin devil ray (*Mobula thurstoni* Lloyd) and spinetail devil ray (*Mobula japanica* Müller & Henle) fed almost exclusively on *Nyctiphanes simplex* Hansen, the most abundant euphausiid species in the area (Brinton & Townsend, 1980; Notarbartolo-di-Sciara, 1988; De Silva-Dávila & Palomares-García, 2002). Notarbartolo-di-Sciara (1988) reported a high percentage of empty stomachs in his study, possibly due to the high digestibility of zooplanktonic prey (Chipps & Garvey, 2007).

We used SIA of carbon (δ^{13}C) and nitrogen (δ^{15}N) to confirm the diet of *M. thurstoni* and *M. japanica* in the south-west Gulf of California, Mexico, by comparing their isotopic signal to that of their most probable prey, *N. simplex*, as well as to other zooplanktonic groups representative of different trophic levels in the food web. We analysed zooplankton samples over several months in order to observe isotopic

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variability in the prey and relate this variability to the isotopic signal of the devil rays.

Our objectives were: (1) to confirm the diet of *M. thurstoni* and *M. japanica* through the use of stable isotopes of C and N; and (2) to determine the trophic position of these two rays in the Gulf of California food chain, within the context of a seasonally changing isotopic baseline.

MATERIALS AND METHODS

Sample collection

Samples of dorsal muscle of bentfin devil ray (*Mobula thurstoni*) and spinetail devil ray (*Mobula japanica*) were obtained from fishing camps on the island of El Pardito, the Bay of La Ventana and the sandbar of El Mogote (Figure 1), areas where devil rays are consistently caught (Notarbartolo-di-Sciara, 1988). In addition, a polespear with a modified tip was used to obtain biopsies from live devil rays swimming at the surface in the bay of La Paz.

The Gulf of California has a monsoonal wind pattern, with strong winds blowing from the north-west in winter (December to April) leading to strong upwelling of nutrient-rich waters primarily along the eastern shores of the gulf. During summer (May to November) weak winds blow from the south-east, resulting in weak upwelling along the western margin of the gulf and allowing warm Pacific waters to enter the gulf (Lavín & Marinone, 2003). The bays of La Paz and La Ventana are on the south-west margin of the gulf, and the entrance of Pacific water in the summer could potentially influence local isotopic signals. There are few published studies on SIA of phytoplankton or suspended matter for the study area. For the Carmen basin, north-west of the bay of La Paz, Altabet *et al.* (1999) determined that $\delta^{15}N$ values in the sediment ranged from 5.6‰ to 10.0‰ during the period 1990–1992.

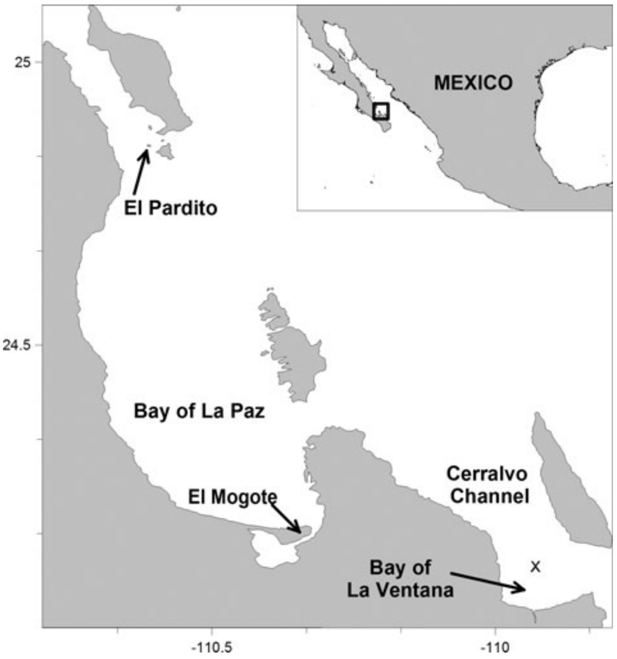

Fig. 1. Study area, showing zooplankton sampling station (X), El Pardito Island, El Mogote sandbar and bay of La Ventana fishing camps.

Zooplankton samples were collected monthly from March to November 2006 at a station in the bay of La Ventana, in the middle of the Cerralvo Channel (Figure 1). Diurnal and nocturnal samples were obtained in a 505 μm conical net towed at the surface for 10 minutes. The following were separated from the sample for isotopic analysis: *N. simplex* individuals, as well as carnivorous chaetognaths and copepods (genera *Candacia*, *Labidocera* and *Euchaeta*), omnivorous decapods and herbivorous zooplankton (copepods from the genus *Acrocalanus* and *N. simplex* calyptopes) (Suh, 1989; Ritz *et al.*, 1990; Suh *et al.*, 1991; Sánchez-Ortíz & Gómez-Gutiérrez, 1992; Palomares *et al.*, 1998). For each group, the number of individuals sorted was appropriate for the isotopic analysis (approximately 40 copepods, 10 euphausiids, 20 chaetognaths and 10 decapods). We were able to compare the isotopic signal of devil rays to that of their most probable prey as well as to those of other zooplanktonic groups present in the area that the rays could potentially consume.

All devil ray samples were kept in 96% ethanol for a maximum of 7 days then frozen. From March to May all zooplankton samples were kept frozen until processed; from June to November samples were kept in 96% ethanol for a maximum of 5 days, and then frozen. A sub-sample of devil ray and zooplankton tissues was divided in half, with one half being frozen and the other stored in ethanol. For devil ray tissue there was no significant difference between samples stored in ethanol or frozen (*t*-test, $P > 0.05$). For zooplankton, there was a significant difference between samples frozen and those kept in ethanol (*t*-test, $P < 0.05$). We therefore calculated a correction factor for the effects of ethanol on $\delta^{13}C$ and $\delta^{15}N$ values for each zooplankton group, which was later used to correct the isotopic values for the remaining samples.

Isotopic analysis

Muscle samples were dried for 48 hours in an oven at 58°C; lipids were extracted by placing the samples in 20 ml of 1:1 chloroform:methanol solution for 20 minutes in a microwave (MARS5 FALCON). Zooplankton samples were dried for 24 hours in an oven at 58°C. All samples were ground to a fine powder with a mortar and pestle; 0.001 g were weighed and packed in 3.3 × 5 mm tin cups. Stable isotope ratios were determined at the stable isotope facility of the University of California at Davis (USA) using a PDZ Europa Hydra 20/20 continuous flow isotope ratio mass spectrometer (PDZ Europa Ltd, Norwich, UK). Stable isotope ratios are given using the conventional δ notation where $\delta^{13}C$ or $\delta^{15}N = (R_{sample}/R_{standard} - 1) \times 1000$ and R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The standard used for $\delta^{13}C$ was Vienna Pee Dee Belemnite (VPDB) and for $\delta^{15}N$ atmospheric nitrogen. Analytical precision was 0.19‰ estimated from standards analysed with the samples.

Data analysis

The size distribution and sex of sampled rays were used to infer the composition of the population sampled. Individuals of *M. thurstoni* measuring <150 cm disc width (DW) and individuals of *M. japanica* measuring <205 cm DW were considered to be immature (Notarbartolo-di-Sciara, 1988). We determined isotopic composition at different times of the year in order to compare isotopic values to oceanographic conditions in the area.

For zooplankton isotopic data, the difference in the values obtained after freezing and after storage in ethanol was used as a correction factor. Legget *et al.* (1999) and Kaehler & Pakhomov (2001) found that while storage in ethanol acted as a solvent and lipid extractor, resulting in more positive $\delta^{13}C$ values, $\delta^{15}N$ values were not significantly affected.

The Shapiro–Wilk test was used to analyse isotopic data of devil rays and zooplankton (all tests used Statistica 6 software, StatSoft Inc. 2004). Since the original data were not normal, we removed 2 outliers, thereby achieving normality. We used *t*-tests to compare isotopic values between devil ray species, between sexes, between juveniles and adults, and between samples frozen and samples stored in ethanol. ANOVA was used to compare isotopic variability between *N. simplex* and devil rays.

We calculated the trophic fractionation and trophic position of devil rays and zooplankton using published values and equations (Vander Zanden & Rasmussen, 2001; McCutchan *et al.*, 2003).

RESULTS

Isotopic values

DEVIL RAYS

We obtained 32 *Mobula thurstoni* and 6 *Mobula japanica* muscle samples (Figure 2). The size of organisms sampled ranged from 86 to 210 cm for *M. thurstoni* and from 96 to 240 cm for *M. japanica*. Twelve *M. thurstoni* were immature (<150 cm DW), 19 were mature (>150 cm DW) and 1 undetermined, while five of the six *M. japanica* individuals were immature (<205 cm DW) (Notarbartolo-di-Sciara, 1988; White *et al.*, 2006). We found no significant differences in stable isotope (SI) values between mature and immature individuals or between males and females (*t*-test, $P > 0.05$).

Stable isotope values for *M. thurstoni* (all values given as average ± standard deviation) ranged from -17.14 ± 0.13‰ to -16.29 ± 0.31‰ for $\delta^{13}C$ and from 17.51 ± 0.58‰ to 18.66 ± 0.72‰ for $\delta^{15}N$. Samples from August showed the most depleted $\delta^{15}N$ and $\delta^{13}C$ values, and samples from January had the most enriched values.

For *M. japanica* SI values ranged from -17.10 ± 0.20‰ to -16.32‰ for $\delta^{13}C$ and from 17.39‰ to 18.29‰ for $\delta^{15}N$. Samples from June had the most depleted $\delta^{13}C$ values, and samples from August had the most depleted $\delta^{15}N$ values. The most enriched values for $\delta^{13}C$ and $\delta^{15}N$ were obtained in July. These monthly values, however, were not significantly different from each other for either species (*t*-test, $P > 0.05$). There were no significant differences in isotopic values between *M. thurstoni* and *M. japanica* (ANOVA, $P > 0.05$).

ZOOPLANKTON

Eleven zooplankton samples were obtained for March, April, May, June, August, September and November 2006. Storage in ethanol affected zooplankton isotopic values significantly (ANOVA, $P < 0.05$), resulting in an increase of $\delta^{15}N$ values of 0.72 ± 0.37‰ on average, and an increase of $\delta^{13}C$ values of 2.00 ± 0.64‰ on average. The increase of $\delta^{13}C$ values in these samples was probably due to an extraction of lipids, which are depleted in ^{13}C (Post, 2002). Since ethanol acts as a solvent, removing lipids from the sample (Leggett *et al.*, 1999), the isotopic value of samples stored frozen were corrected for lipid content. This allowed us to compare all samples across trophic levels. The $\delta^{13}C$ values ranged from −20.66‰ (for herbivores) to −15.11‰ (for decapods) and $\delta^{15}N$ values ranged from 10.97‰ (for herbivores) to 16.53‰ (for decapods) (Table 1). There were no significant differences in isotopic values between samples that were collected during day or night (ANOVA, $P > 0.05$).

Trophic fractionation

Variability in the isotope signal (indicated by the standard deviation in Figure 3) was significantly higher in zooplankton than in devil rays (ANOVA, $P < 0.05$). Zooplankton was depleted in ^{13}C and ^{15}N compared with devil rays (annual averages for total zooplankton −18.36‰ $\delta^{13}C$ and 13.95‰ $\delta^{15}N$; *M. thurstoni* −16.74‰ $\delta^{13}C$ and 18.00‰ $\delta^{15}N$; *M. japanica* −16.78‰ $\delta^{13}C$ and 17.85‰ $\delta^{15}N$). From the annual isotopic averages we calculated the trophic fractionation between devil rays and zooplankton (Table 2). The trophic fractionation between devil rays and *N. simplex* was 3.17‰ for $\delta^{15}N$ and 1.50‰ for $\delta^{13}C$ on average.

Several authors have provided differing values of the isotopic fractionation occurring between a consumer and its prey, ranging from 0.3 ± 0.6‰ to 0.8 ± 1.2‰ for $\delta^{13}C$ and from 1.3‰ to 3.4 ± 1.8‰ for $\delta^{15}N$ (Minagawa & Wada, 1984; Vander Zanden & Rasmussen, 2001; Sherwood & Rose, 2005). The Minagawa & Wada (1984) study included a range of animals from freshwater and saltwater environments; Vander Zanden & Rasmussen (2001) studied freshwater lakes; and although Sherwood & Rose (2005) studied an oceanic ecosystem, their samples were not lipid-extracted. We selected the study by McCutchan *et al.* (2003) as our benchmark for comparison, since it was carried out on muscle of marine organisms on which lipid extraction had been performed, corresponding to the circumstances of the present study.

We additionally calculated the trophic fractionation between zooplankton groups known to exhibit different feeding strategies (herbivores, omnivores and carnivores) and the devil rays. Devil rays probably did not feed on any of these groups, since the fractionation values for $\delta^{13}C$ and/or $\delta^{15}N$ fell outside the range of expected values between predators and prey (Table 2).

Regarding temporal variation in isotopic values, during 2006 we found that *M. thurstoni* reflected *N. simplex* SI values with a 2 month delay for $\delta^{15}N$ and a 1 month delay for $\delta^{13}C$. For *M. japanica* the small sample size prevented determination of a SI trend that could be compared to *N. simplex* SI values (Figure 4).

Calculated trophic positions

Trophic position was calculated following the equation proposed by Vander Zanden & Rasmussen (2001):

$$TL_{consumer} = (\delta^{15}N_{consumer} - \delta^{15}N_{baseline})/3.4 + 2$$

This equation takes as $\delta^{15}N_{baseline}$ a primary consumer, since there seems to be less variability in their isotopic values than lower down the food chain, at the phytoplankton

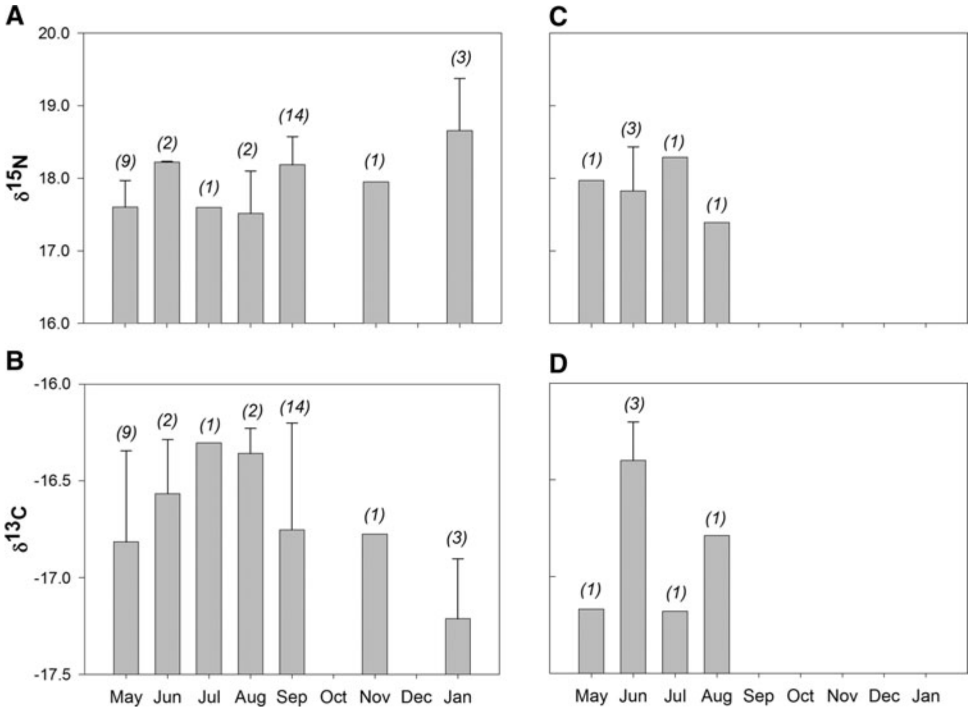

Fig. 2. $\delta^{15}N$ and $\delta^{13}C$ values for *Mobula thurstoni* (A and B) and *Mobula japanica* (C and D) from May 2006 to January 2007 in the south-west Gulf of California. Number of samples in parentheses. Black lines indicate 1 standard deviation.

trophic level (Vander Zanden & Rasmussen, 2001). In this study $\delta^{15}N_{baseline}$ was given by herbivorous zooplankton (calyptope larvae of *N. simplex* and copepods of the genus *Acrocalanus*). We obtained trophic positions of 3.48 for *M. thurstoni*, 3.43 for *M. japanica* and 2.52 for *N. simplex*.

DISCUSSION

Stable isotope analysis, through the comparison of bentfin and spinetail devil ray (*Mobula thurstoni* and *Mobula japanica*) SI values with those of their potential prey, allowed us to determine a predator–prey relationship between the devil rays and the euphausiid *Nyctiphanes simplex* in the south-west Gulf of California. This confirmed the results previously found through stomach contents analysis by Notarbartolo-di-Sciara (1988).

The low variability in the isotopic values of devil ray tissues was indicative of a highly specialized diet (Sweeting *et al.*, 2005). We obtained five whole specimens of devil ray during 2006, all of which contained only remains of euphausiids in the gut. *Nyctiphanes simplex* is an important component of the south-west Gulf of California food web, as it is preyed on by birds, blue whales (*Balaenoptera musculus*), Bryde's whales (*B. edeni*) and fin whales (*B. physalus*) (Gendron, 1992). It is also the most abundant euphausiid in neritic waters of the Gulf of California (Gómez-Gutiérrez *et al.*, 2009), and its swarming behaviour (Gendron, 1992) potentially makes it an easy prey for filter-feeding predators such as devil rays. Within the study area, *N. simplex* represents the main component of zooplankton samples, accounting for more than 98% of euphausiid larval abundance and from 27‰ to 99.7‰ of euphausiid adult abundance (De Silva-Dávila & Palomares-García, 2002).

Basking sharks are highly specialized filter-feeding elasmobranchs, feeding mostly on one species of copepod. Sims & Merrett (1997) found that basking sharks spent most of their feeding time in areas where large copepods *Calanus helgonlandicus* were predominant. The results of the present study concur with the results of the only previous account

Table 1. Monthly isotopic values ($\delta^{13}C$ and $\delta^{15}N$, in ‰) for zooplankton groups analysed in the south-west Gulf of California during 2006.

Month	Herbivores		Carnivores		Decapods		Chaetognaths		*Nyctiphanes simplex*	
	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
*March	−19.61	13.03	−19.24	14.12	−15.11	16.53	−17.87	13.81	−19.04	14.30
*April	−19.10	14.16	−18.69	15.66	−16.59	14.60	−16.97	16.29	−18.13	15.88
*+May	−17.31	13.09	−19.19	14.73	−17.97	14.29	−17.93	14.80	−18.27	15.47
+June	−19.09	12.26	−20.35	14.62	−18.20	12.89	−18.57	14.50	−18.36	14.89
+August			−18.81	15.12	−16.51	13.26	−20.11	12.22		
+September	−20.66	14.37	−18.61	14.56	−17.52	12.91	−17.10	13.97	−17.28	13.33
+November	−19.04	10.97	−18.50	12.10	−16.81	11.13	−17.57	12.57	−17.65	14.39

*, samples stored frozen; +, samples stored in ethanol. Correction factor has been applied to values shown in table.

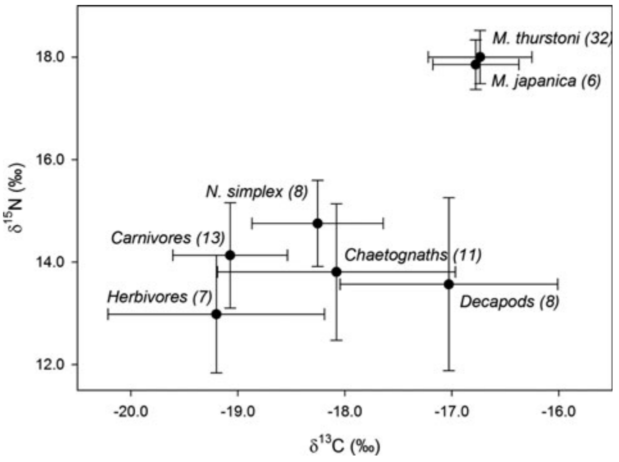

Fig. 3. Annual isotopic values of δ^{13}C and δ^{15}N for mobulids and zooplankton in the south-west Gulf of California in 2006–2007. Number of samples in parentheses.

of mobulid diet (Notarbartolo-di-Sciara, 1988), which reported an index of relative importance for *N. simplex* of 97.90% in stomachs of *M. thurstoni* and 99.62% in *M. japanica*.

The fractionation values obtained in this study between devil rays and their prey fit within the values proposed by McCutchan *et al.* (2003) (3.2 ± 0.43 ‰ for δ^{15}N and 1.8 ± 0.29 ‰ for δ^{13}C) for one trophic level. Fractionation factors obtained between devil rays and the other zooplanktonic groups analysed were outside the range of proposed values, confirming the fact that devil rays did not feed on those groups.

As expected, SI variability was greater in zooplankton than in devil rays; zooplankters tend to have more variable SI values, since these reflect changes in the environment over a period of days, whereas larger organisms such as rays integrate isotopic signals over a period of several months (O'Reilly *et al.*, 2002). We detected variations in the isotopic signal of *N. simplex* of up to 2.55‰ for δ^{15}N and 1.76‰ for δ^{13}C, whereas the signal for the devil rays varied only up to 1.14‰ for δ^{15}N and 0.91‰ for δ^{13}C. Sampling for prey during several months provided a shifting isotopic baseline, which was compared with the isotopic values from the tissues of the devil rays. Harvey *et al.* (2002) have pointed out the importance of taking into account seasonal variations in isotopic signals. Small zooplanktonic prey reflect baseline SI changes much faster than larger animals, so sampling prey over a longer period of time gives a better estimate of the isotopic signals that the predators are reflecting (MacNeil *et al.*, 2005).

Table 2. Mean trophic fractionation between devil rays and zooplankton in 2006.

	$\Delta\delta^{15}$N	$\Delta\delta^{13}$C
M. thurstoni–*N. simplex*	3.25	1.52
M. thurstoni–carnivores	3.87	2.34
M. thurstoni–chaetognaths	4.19	1.34
M. thurstoni–decapods	4.43	0.29
M. thurstoni–herbivores	5.02	2.47
M. japanica–*N. simplex*	3.10	1.48
M. japanica–carnivores	3.72	2.30
M. japanica–chaetognaths	4.04	1.30
M. japanica–decapods	4.29	0.25
M. japanica–herbivores	4.87	2.43

$\Delta\delta$, isotopic fractionation for nitrogen and carbon respectively; *M. thurstoni*, *Mobula thurstoni*; *N. simplex*, *Nyctiphanes simplex*; *M. japanica*; *Mobula japanica*.

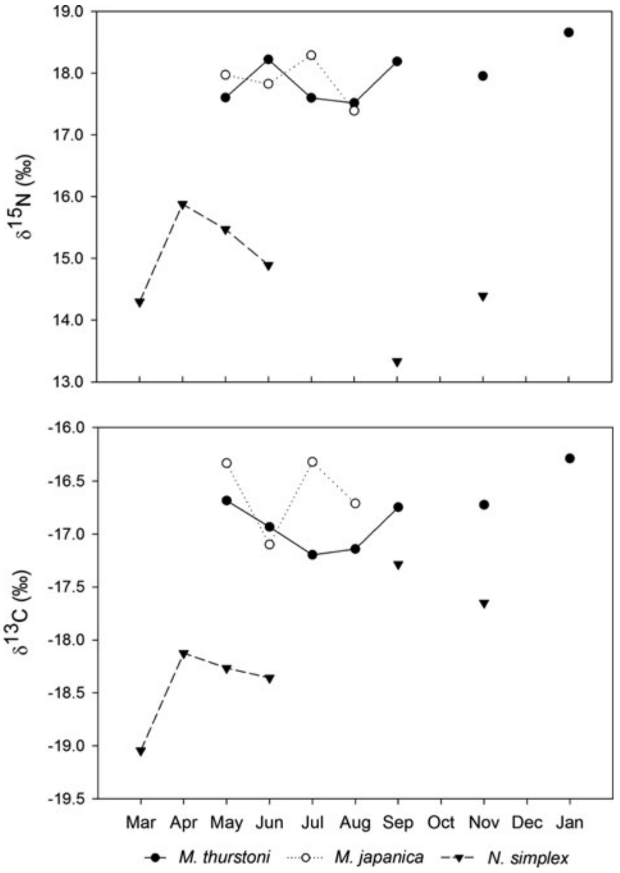

Fig. 4. δ^{13}C and δ^{15}N monthly values for *Mobula thurstoni*, *Mobula japanica* and *Nyctiphanes simplex* during 2006–2007 in the south-west Gulf of California.

The values obtained for devil rays were slightly higher than the value of 3.2 calculated by Estrada *et al.* (2003) for the filter-feeding basking shark *Cetorhinus maximus*, which consumes mainly copepods (Sims *et al.*, 2005). The organisms selected as the baseline δ^{15}N (calyptope stage *N. simplex* and *Acrocalanus* copepods) were deemed appropriate to represent trophic level 2 of this food chain as their diets consist mostly of phytoplankton and/or detritus (Suh, 1989; Suh *et al.*, 1991). Most zooplanktonic organisms are not purely herbivores or carnivores, but ingest a range of food items depending on availability (Kleppel, 1993; Zhang *et al.*, 2006). The overlapping SI values observed in all the zooplanktonic groups analysed here reflect their changing feeding strategies as well as changes in nutrient origin during the study period.

Mobula thurstoni isotopic values were most enriched in January. Notarbartolo-di-Sciara (1988) suggested that this species switches to a diet consisting mainly of mysids during the winter. In this study we collected only one mysid sample (14.37‰ δ^{15}N and −17.68‰ for δ^{13}C) and we did not collect zooplankton samples in the winter months. We therefore do not have a good estimate of mysid isotopic values and could not compare *M. thurstoni* values with those of mysids to determine whether the more enriched values observed in

January are indicative of a mysid diet. The *M. thurstoni* samples collected that month were obtained at El Mogote, which is close to the city of La Paz, and the higher $\delta^{15}N$ values obtained could be reflecting nitrogen runoff from the city (Hansson *et al.*, 1997).

The most depleted isotopic values for *M. thurstoni* were obtained in August. This could be explained by the oceanographic conditions in the Gulf of California in the summer, when the entry of Pacific Ocean water could bring into the gulf different water masses with a distinctive isotopic signature (Altabet *et al.*, 1999).

We did not collect as many *M. japanica* ($N = 6$) as *M. thurstoni* samples ($N = 32$), making it difficult to infer the diet of the former species. Sample numbers, however, do not necessarily reflect the true abundance of these species in the area. Because of former overexploitation of devil rays in Mexico, their capture, trade, and consumption are now considered illegal according to Mexican regulations (NOM-029-PESC (2004)). As the samples were obtained from fishing camps where these species were incidentally caught, sample abundance reflects the willingness of the local fishermen to cooperate. *Mobula japanica* is locally known to be more abundant during the summer months (Notarbartolo-di-Sciara, 1988). In the present study samples for this devil ray could not be obtained after August 2006.

Local fishermen report that *M. japanica* moves out of the south-west Gulf of California at the end of the summer, and Notarbartolo-di-Sciara (1988) mentioned that large individuals of this species were locally rare in winter. Studies of a variety of marine animals (sea turtles, whales, seabirds and seals) have used stable isotopes in order to investigate migration patterns by comparing tissue SI values with values of prey in certain areas, or based on tissue growth (Hobson, 1999). If *Mobula japanica* feeds outside the south-west Gulf of California in winter, the isotopic signature it presents in the spring might be reflecting the isotopic signal of a different food chain. Tissue turnover rate refers to the replacement of old tissue with new, and results in the detection of new prey items in the isotopic signature of the consumer (Sweeting *et al.*, 2005). Large migrating animals have slow tissue turnover rates; if they consume prey with different isotopic signals, their SI values could be reflecting the isotopic signal of food consumed at a previous location (Schmidt *et al.*, 2003; Carmichael *et al.*, 2004). *Mobula thurstoni* samples were obtained from May to January, indicating that this species probably remains in the study area all year round.

Sweeting *et al.* (2005) found that after about 7 months of being fed a new diet, European sea bass (*Dicentrarchus labrax*) <1 year old had equilibrated with their diet. If *M. japanica* enters the study area in May and leaves in October, its tissues would probably not be completely in equilibrium with the local prey. If *M. thurstoni* fed in the study area all year, it would be reflecting the SI values of the local prey, with a time delay dependent on tissue turnover rates. The delay found in the present study was 2 months for $\delta^{15}N$ and 1 month for $\delta^{13}C$.

The data obtained, however, suggest that overall *M. thurstoni* and *M. japanica* have very similar diets, as their $\delta^{13}C$ and $\delta^{15}N$ values as well as their standard deviation, were very similar (t-test, $P > 0.05$). Mobulids have a very specialized diet. As filter feeding animals they might have evolved to follow euphausiid swarms. Sims & Merrett *et al.* (1997) suggest that basking sharks *Cetorhinus maximus* feed in areas where their preferred prey are located, and do not feed indiscriminately. This supports the suggestion that mobulids would tend to favour areas where there are aggregations of *N. simplex* and therefore integrate the signal of this prey as opposed to other prey that might be found in the area. To our knowledge this is the first stable isotope study of devil rays, and the first time the stable isotope values of devil rays have been linked to their prey.

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