

The role of fish in the diet of swordfish (*Xiphias gladius*) in the Strait of Gibraltar

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*To study the diet of the swordfish (*Xiphias gladius*) in the Strait of Gibraltar, a total of 176 stomachs were examined from the Moroccan artisanal fishery targeting this species, from April to September 2015. The frequency of occurrence (FO), percentage in number and in weight of prey as well as the per cent index of relative importance of prey (%IRI) were calculated to assess the diet preferences of swordfish in relation to its body size, sex and month. Our findings confirm the opportunistic feeding behaviour of swordfish. The prey items consist primarily of fish (54.6% in number and 82.7% in weight), followed by cephalopod (43.36% in number and 17.25% in weight). The Atlantic horse mackerel (*Trachurus trachurus*) and the southern shortfin squid (*Illex coindetii*) are the most important prey, with a % IRI of 47.54 and 35.04%, respectively. The results revealed that there are no significant differences in the diet preferences among sexes and size classes. However, diet composition varied significantly among months. A significant correlation was found between the body length of predator and prey size. The remarkable decrease in the fullness index (fi) from June to August suggests that swordfish were in a spawning condition, with reduced feeding.*

Keywords: Swordfish, diet, size, sex, season, Strait of Gibraltar, fullness index

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INTRODUCTION

Swordfish is a cosmopolitan species found in tropical and temperate waters of all the oceans between 45°N and 45°S, including the Mediterranean, Black Sea and the Marmara Sea (Palko *et al.*, 1981).

Most research results based on genetic studies have shown that the Mediterranean swordfish constitutes a single stock, separated from the North Atlantic and South Atlantic stocks (Kotoulas *et al.*, 2003; Smith *et al.*, 2015). Recent research suggests that there is genetic differentiation among the Mediterranean swordfish population (Viñas *et al.*, 2010).

Although there is incomplete information on the mixture and boundaries between stocks, it is generally accepted that Mediterranean population swordfish extends beyond the current management boundary at the Strait of Gibraltar to ~10°W. Mixing between the North Atlantic and Mediterranean populations is low with the Strait of Gibraltar as a mixing zone (Smith *et al.*, 2015).

Swordfish perform vertical excursions, reaching depths up to 800 m during daylight and remaining near the surface at night when they stay in the superficial layer between 0 and 10 m; however, their diel vertical excursions are usually discontinuous and frequently interrupted by vertical rises (Carey & Robinson, 1981; Carey, 1990; Matsumoto *et al.*, 2003; Canese *et al.*, 2008). Past studies showed that billfishes

such as swordfish use an unusual method of catching the prey, by using the bill as shown by the prey status (Tibbo *et al.*, 1961; Stillwell & Kohler, 1985; Romeo *et al.*, 2009).

In general, stomach content analysis is an important tool to study ecology and fisheries biology (Clarke, 1966). In that sense, several studies on the swordfish diet were previously conducted. In the Atlantic, the diet of swordfish was studied, analysing the frequency of occurrence and the percentages of prey in number and/or in weight (Stillwell & Kohler, 1985; Moreira, 1990, Guerra *et al.*, 1993; Hernández-García, 1995; Chancollon *et al.*, 2006; Castillo *et al.*, 2007). In the Mediterranean Sea, Bello (1991), Peristeraki *et al.* (2005) and Romeo *et al.* (2009, 2011) studied prey preferences of swordfish, using the frequency of occurrence and the percentage in weight and in number of food items as diet indicators.

Nevertheless, information on the diet of the species in the Strait of Gibraltar has remained limited to the study published by Hernández-García (1995). In addition, very few studies have analysed changes in swordfish diet composition in relation to season, sex and body size (Stillwell & Kohler, 1985; Ibáñez *et al.*, 2004).

The specific purpose of the present study was to assess the diet preferences and improve knowledge on feeding behaviour and ecology of swordfish in the Strait of Gibraltar. It also aimed to examine for the first time the diet variability of the species in relation to season, sex and body size. The analysis utilizes biological and fisheries data obtained from the Moroccan artisanal longline fishery operating in the Strait of Gibraltar.

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MATERIALS AND METHODS

Data collection and laboratory analysis

To study the diet of swordfish in the Strait of Gibraltar (Figure 1), a total of 176 stomachs of which 57% were females (100), were collected from the Moroccan commercial artisanal longline fleet landings at the port of Tangier for contents examination. The samples covered a size range from 110 to 237 cm lower jaw–fork length (LJFL) and eviscerated weight from 17 to 243 kg. Sampling took place on a monthly basis during the main swordfish fishing season in the area, from April to September 2015, except for the month of July when there was no fishing activity due to the absence of the species in the study area.

For each sampled stomach, the following information was recorded: date of catch, sex, size (LJFL) and eviscerated weight of fish. The sex of fish was determined visually by examining the gonads of fish. The collected samples were frozen at -20°C to halt any further digestive process (Ferraton, 2007).

In the laboratory, for each examined stomach, the prey were sorted by species, counted and weighed, using an electronic balance with an accuracy of 0.01 g. Given their low level of digestion, most of the prey were macroscopically identified to the species level, using published identification guides for fish, cephalopods and crustaceans (Lagardère, 1971; Lloris & Rucabado, 1998). One hundred and eighty cephalopod beaks were identified using the guide developed by Clarke (1986); these beaks were also compared with those from

entire cephalopods found in the stomachs. The cephalopod weight was estimated by multiplying the total number of beaks by the mean individual weight of whole individuals of the same species found in the corresponding samples (Hyslop, 1980).

To analyse the monthly evolution of the catch per unit effort (CPUE), as a relative abundance index of the main prey species of swordfish in the study area, daily catch and effort data from the Moroccan purseiners operating in the Strait of Gibraltar during 2015, were obtained from the fish market at the port of Tangier.

Statistical analysis

The diet of swordfish was characterized by calculating and analysing the following indices (Hureau, 1970; Hyslop, 1980):

Fullness index: $fi = W/We$

W: total weight of the various prey

We: eviscerated weight of fish

Frequency of occurrence index: $FO = Ni/Np$, where

Np: Total number of full stomachs

Ni: Number of stomachs containing prey *i*

Percentage in number: $Cni = Pi \times 100/P$

Pi: Number of observations of the prey *i*

P: Number of various preys

Percentage in weight: $Cpi = Wi \times 100/W$

Wi: total weight of the prey *i*

W: total weight of the various prey

Index of relative importance: IRI

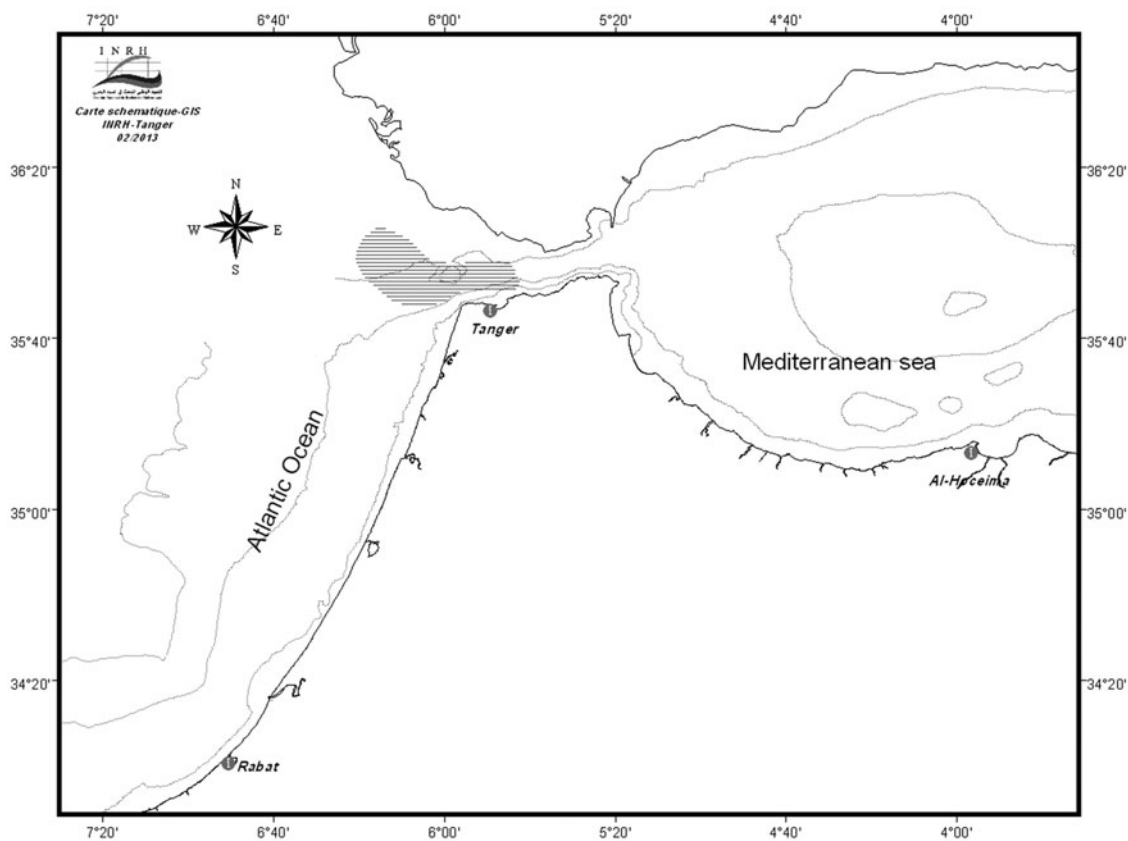


Fig. 1. A map showing the study area. Shaded area indicates the fishing grounds of the Moroccan artisanal longline fleet targeting swordfish.

This index combines both the frequency of occurrence of prey, its percentage in number (*Cni*) and its percentage in weight (*Cpi*). Thus, it gives a more accurate picture of the diet than that obtained by using a single index, and minimizing the biases caused by each of these percentages (Pinkas *et al.*, 1971). It is expressed as follows:

$$IRI = FO \times (Cni + Cpi)$$

Per cent index of relative importance: %IRI

It is the ratio between the index value (IRI) of each prey and the sum of all index values (ΣIRI).

$$IRI\% = IRI / \Sigma IRI$$

This index allows classification of prey items as preferential ($\%IRI > 50\%$), secondary ($10 \leq \%IRI \leq 50\%$), complementary ($1 \leq \%IRI \leq 10\%$) and accidental ($\%IRI < 1\%$) (Pinkas *et al.*, 1971).

To compare the swordfish diet by size class, sex and month, we used the χ^2 statistical test on contingency tables (percentage of prey in number), with rows representing the prey groups/species and columns the levels of different variables (size, sex and month) (Zar, 1984). In addition, a linear discriminant analysis was performed employing as the dependent variable the percentage (in terms of weight) of each prey species and as explanatory variables the size classes, sex and month of capture (Quinn & Keough, 2002).

The *F* test of ANOVA analysis was used to evaluate if there is any linear correlation between the body size of swordfish (LJFL) and the mean individual weight of prey, and between sex of fish and the mean individual weight of prey (Zar, 1984). All statistical analyses were performed using the statistical program XLStat-Pro. 7.5. All statistical inference was based on the 95% significance level.

RESULTS

Fullness index

The mean fullness index values (*fi*) decreased from April to August, reaching a minimum value of 0.67 in August, and increased in September. The differences among months were statistically significant ($F = 27.34$, $P < 0.01$). However, the differences in mean values of this index were not statistically significant between males and females ($F = 0.799$, $P = 0.373$) and between individuals of different size classes ($F = 0.421$, $P = 0.657$) (Figure 2A–C).

Diet composition

Except for some fragments of unidentified fish that represented about 5% of the total food items in number, all prey items found in the examined stomachs were identified.

In general, the diet of the swordfish caught in the Strait of Gibraltar was quite diverse. It consisted of 13 species of which nine species were fish, two species were cephalopods and two species were crustaceans, belonging to 12 families (Table 1).

The analysis of per cent index of relative importance (%IRI), for the whole fishing season, showed that there was no preferential prey species for swordfish caught in the Strait of Gibraltar (%IRI for all prey items were $< 50\%$) (Table 1).

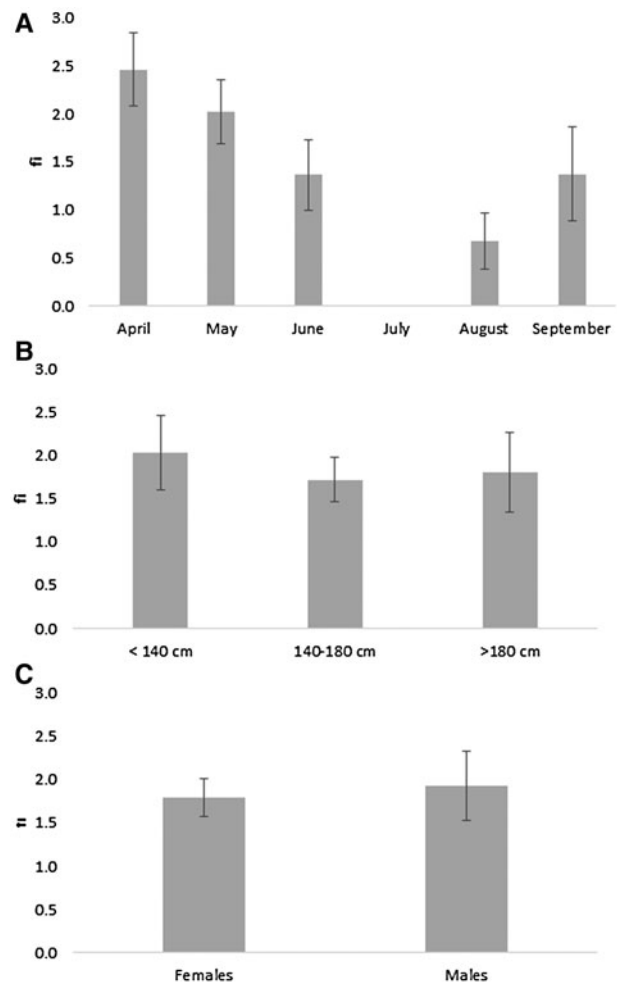


Fig. 2. Evolution of the mean fullness index values (*fi*) by month (A); size class (B); by sex (C) for swordfish caught in the Strait of Gibraltar (bars represent confidence interval at 95%).

Analysis of the diet according to the size of predator

The analysis of per cent index of relative importance (%IRI) by size classes showed that there was no preferential prey for any given size class ($\%IRI < 50$). From the values of this index, the Atlantic horse mackerel (*Trachurus trachurus*), the southern shortfin squid (*Illex coindetii*) and the silver scabbard fish (*Lepidopus caudatus*) were all secondary prey for the three size classes considered ($10 < \%IRI < 50\%$) (Figure 3).

The percentage by number of prey groups (fish, cephalopods and crustaceans) in the diet varied significantly among the three size classes for crustaceans ($\chi^2 = 9488$, $P = 0.002$). Indeed, the percentage of kangaroo shrimp (*Glyphus marsupialis*) that essentially made up this group was relatively higher (6.9%) in individuals less than 140 cm LJFL compared with fish larger than this size ($< 0.1\%$). However the differences in the percentages by number of the main prey species were not statistically significant among size classes at 5% ($\chi^2 = 9488$, $P = 0.062$) (Figure 4).

Table 1. The frequency occurrence, the percentage in number, the percentage in weight and the %IRI of each prey species in swordfish stomachs.

Taxon	Frequency	%	Number	%	Weight (g)	%	%IRI
FISHES				54.56		82.73	
Belonidae							
<i>Belone belone</i>	1	0.63	1	0.11	80.00	0.04	0.00
Bramidae							
<i>Brama brama</i>	1	0.63	1	0.11	396.00	0.19	0.00
Carangidae							
<i>Trachurus trachurus</i>	95	60.13	297	32.60	99919.13	49.00	47.54
Clupeidae							
<i>Sardina pilchardus</i>	5	3.16	11	1.21	1285.00	0.63	0.06
Mullidae							
<i>Mullus surmuletus</i>	1	0.63	1	0.11	308.00	0.15	0.00
Scombridae							
<i>Scomber scombrus</i>	6	3.80	16	1.76	2252.30	1.10	0.11
<i>Auxis thazard</i>	1	0.63	1	0.11	1190.00	0.58	0.00
Sparidae							
<i>Pagellus bogaraveo</i>	1	0.63	3	0.33	2345.00	1.15	0.01
Trichiuridae							
<i>Lepidopus caudatus</i>	62	39.24	137	15.04	60749.75	29.79	17.04
Fish remains	8	5.06	29	3.18	152.72	0.07	0.16
CEPHALOPODS				43.36		17.25	
<i>Illex coindetii</i>	95	60.13	393	43.14	34685.15	17.01	35.04
<i>Sepia officinalis</i>	2	1.27	2	0.22	493.00	0.24	0.01
CRUSTACEANS				2.09		0.02	
<i>Glyphus marsupialis</i>	3	1.90	18	1.98	34.69	0.02	0.04
<i>Aristeus varidans</i>	1	0.63	1	0.11	7.20	0.00	0.00
Total			911	100	203897.94	100	100

The results of the linear discriminant analysis confirmed those based on the %IRI and the percentage by number of each prey species. Indeed, according to the results of this analysis, it was not possible to discriminate among individuals of the three size classes considered based on the percentage by weight of their prey species ($F = 2.147$, $P = 0.152$).

The F test result showed that there is a significant linear correlation between the size of swordfish and the mean individual weight of prey ($F = 11.82$, $P = 0.00069$). Thus, the size of prey tends to increase with the size of predator (Figure 5).

Analysis of the diet according to the sex of predator

The prey species ingested by swordfish remain generally similar between males and females. The analysis of the percent index of relative importance (%IRI) by sex indicated that Atlantic horse mackerel (*T. trachurus*) and the southern shortfin squid (*I. coindetii*) were secondary prey for both sexes, while the silver scabbard fish (*L. caudatus*) is secondary prey for females (%IRI = 24.07%), but only a complementary prey for males (%IRI = 6.36%). It seems that females consume

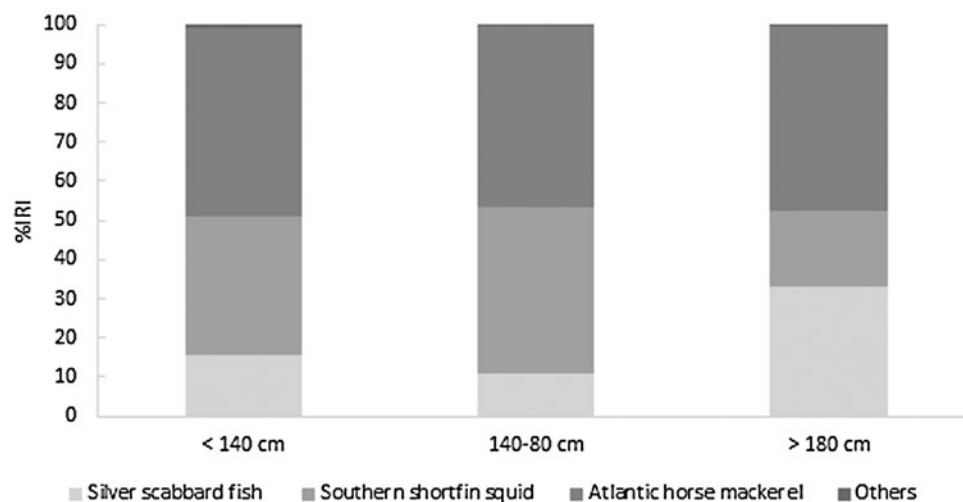


Fig. 3. Per cent index of relative importance (%IRI) by size class for the main prey species of swordfish caught in the Strait of Gibraltar.

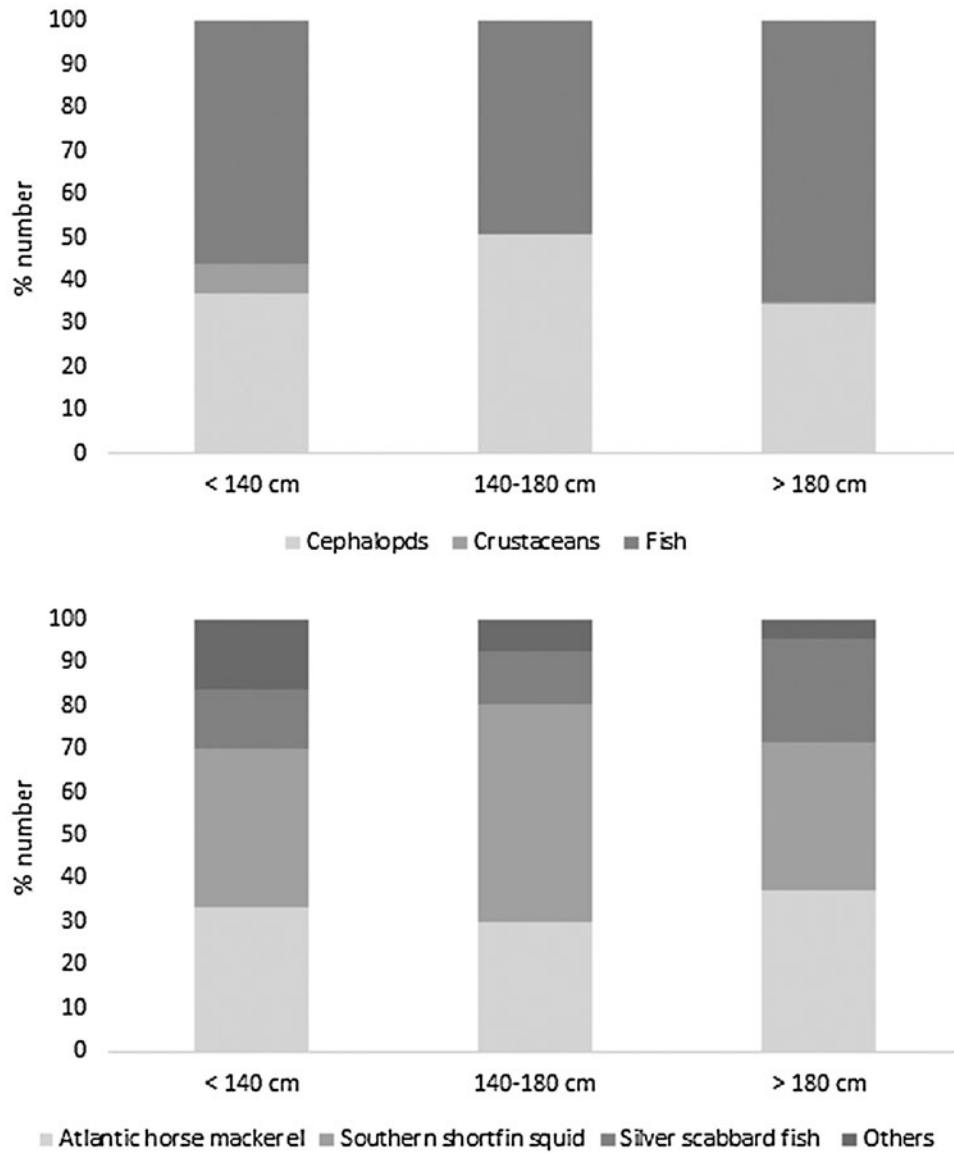


Fig. 4. Percentage in number by size class of the main prey groups and prey species of swordfish caught in the Strait of Gibraltar.

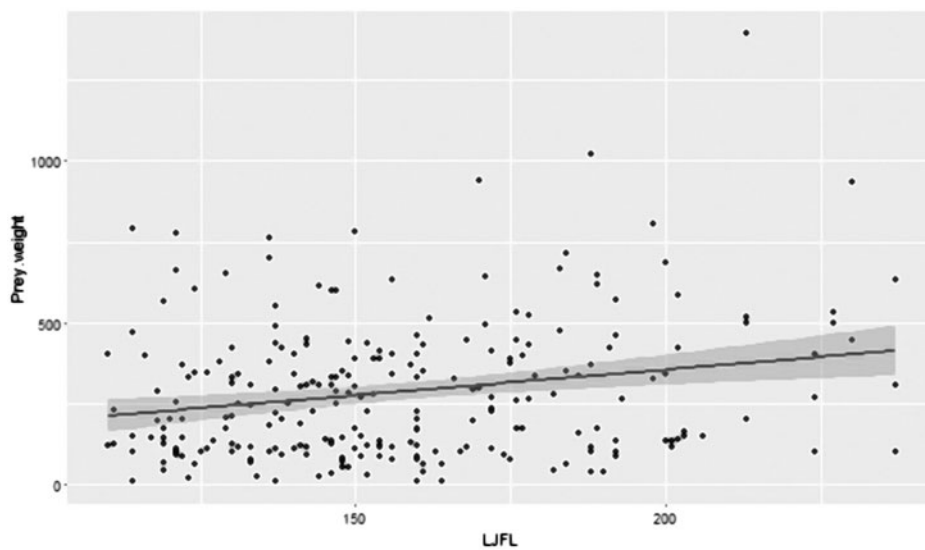


Fig. 5. Relationship between the size of swordfish and individual mean weight of prey species.

more silver scabbardfish than males, while the latter consume more shortfin squid than females (Figure 6).

Statistical analysis showed that individual mean weight of prey species varies significantly among sexes ($F = 10.79$, $P = 0.00115$). It seems that females tend to feed on larger prey size species than males (Figure 7).

The differences in percentage by number of prey groups were not statistically significant between males and females ($\chi^2 = 5.991$, $P = 0.067$). Neither are the differences in percentage by number of the main prey species ($\chi^2 = 7.81$, $P = 0.054$) (Figure 8).

The results of linear discriminant analysis showed also that there were no significant differences in the percentages by weight of the main prey species between males and females ($F = 1.390$, $P = 0.248$).

Analysis of the diet according to the month

The monthly analysis of per cent index of relative importance (%IRI) revealed that the Atlantic horse mackerel (*T. trachurus*) is the preferential prey of swordfish during the months of April and May, with a %IRI of 73.30% and 60.80%, respectively, while the silver scabbard fish (*L. caudatus*) and the southern shortfin squid (*I. coindetii*) are only secondary prey. The situation was reversed during August–September where the shortfin squid clearly became the preferential food of swordfish (%IRI = 92%), while the Atlantic horse mackerel and silver scabbard fish were only complementary prey of the predator with a %IRI of 2.96% and 2.01%, respectively.

It should be noted that sardine (*Sardina pichardus*) was also a complementary prey of swordfish in June with a %IRI of 2.37%. It is the same for the Kangaroo shrimp (*G. marsupialis*) during the month of August (%IRI = 1.32%) (Figure 9).

The differences in the percentages by number of prey groups are statistically significant between months ($\chi^2 = 15.5$, $P < 0.0001$). It is the same for the percentages by number of the main prey species ($\chi^2 = 31.41$, $P < 0.0001$). As shown by %IRI analysis, there was a slight supremacy of Atlantic horse mackerel in April–May in number (51%),

however the southern shortfin squid became the dominating prey during the period August–September (71%) (Figure 10).

The results of the discriminant analysis confirmed the previous analyses results, showing that the differences in the percentages by weight of prey species are statistically significant among months ($F = 1.59$, $P < 0.0001$). The southern shortfin squid and the Atlantic horse mackerel were the two species that essentially discriminate the diet of swordfish by months (Figure 11).

DISCUSSION

The findings of the present study confirmed the predominance of teleost fish in the diet of swordfish in the Strait of Gibraltar, as previously reported by Hernández-García (1995). Similar results were also found in the Eastern Atlantic and in the Mediterranean Sea (Moreira, 1990; Salman, 2004; Romeo *et al.*, 2009). On the contrary, many authors clearly highlighted the importance of cephalopods in the diet of the species in the Atlantic (Toll & Hess, 1981; Guerra *et al.*, 1993; Hernández-García, 1995; Chancollon *et al.*, 2006) as well as in the Mediterranean Sea (Bello, 1991; Peristeraki *et al.*, 2005).

The differences in the diet composition of swordfish among different geographic areas, confirm the opportunistic feeding behaviour of the species, foraging a wide range of abundant prey in their distribution area (Stillwell & Kohler, 1985; Guerra *et al.*, 1993; Velasco & Quintans, 2000; Chancollon *et al.*, 2006; Young *et al.*, 2006). The variations in the swordfish diet seem to be due to the proximity to the coast (longitudinal variation) rather than to latitudinal variation, since all prey species whose abundance varies from one area to another, have a wide geographic distribution. Thus, Hernández-García (1995), Chancollon *et al.* (2006) and Young *et al.* (2006) found different patterns of predation in swordfish between neritic and oceanic areas. Indeed, in neritic areas, as is the case in our study, these authors found that the diet of swordfish was primarily based on pelagic and benthic fish and squid, while in the oceanic areas, this species feeds mainly on cephalopods.



Fig. 6. Per cent index of relative importance (%IRI) by sex for the main prey species of swordfish caught in the Strait of Gibraltar.

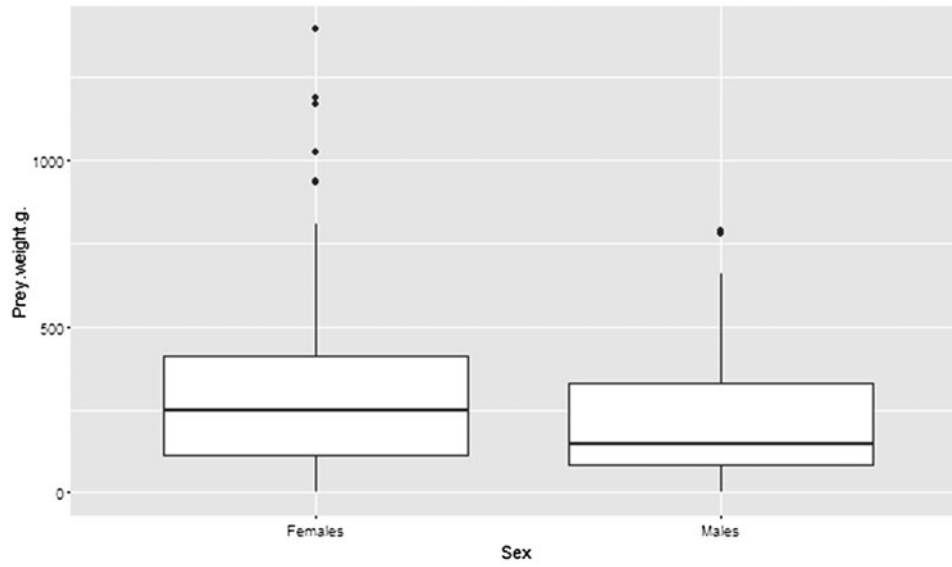


Fig. 7. Individual mean weight distribution of prey species in male and female swordfish caught in the Strait of Gibraltar.

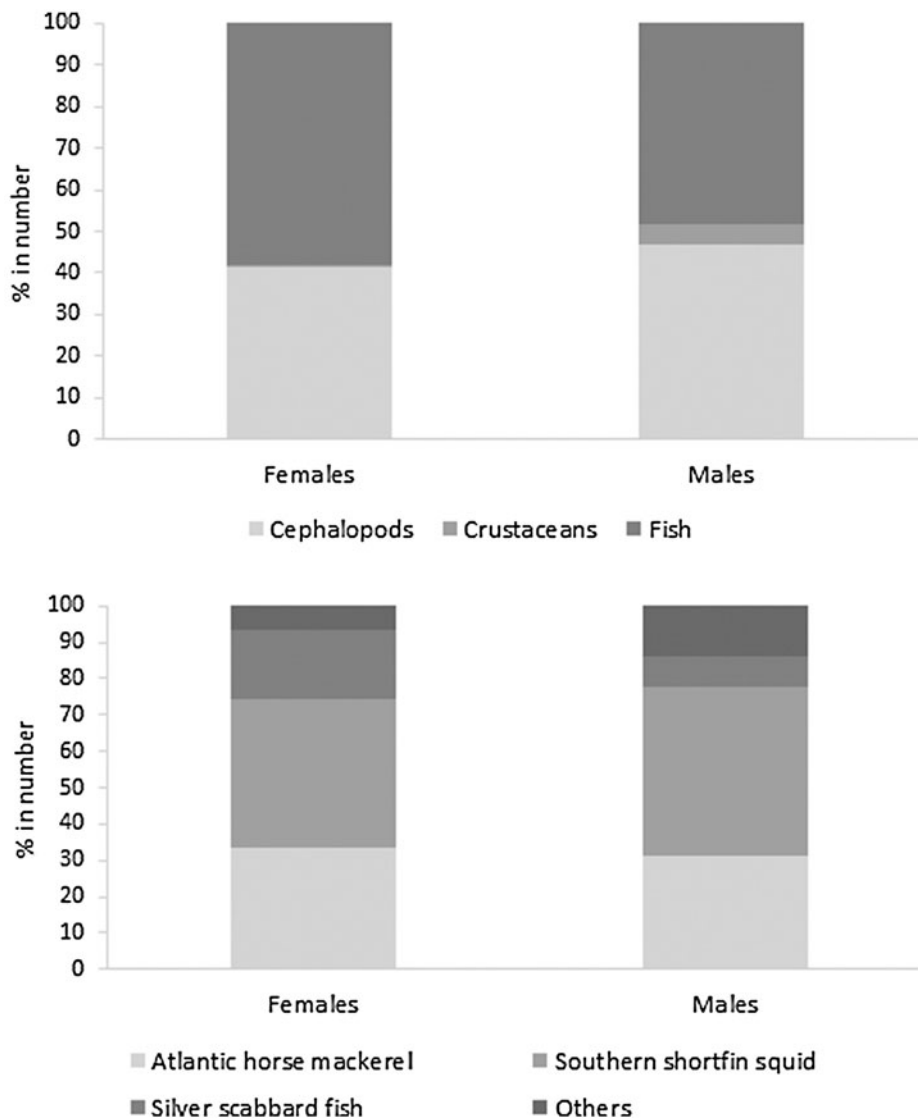


Fig. 8. Percentage in number by sex of the main prey groups and prey species of swordfish caught in the Strait of Gibraltar.

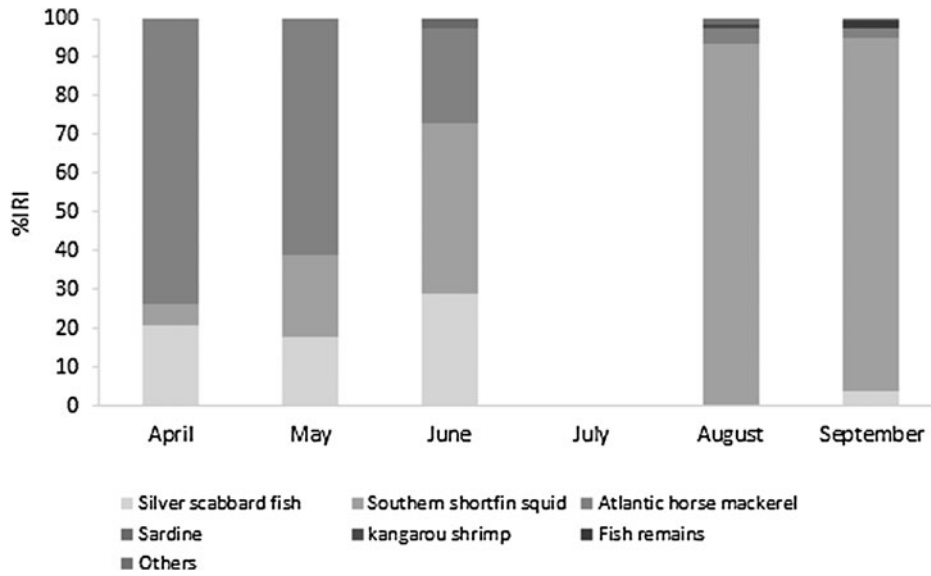


Fig. 9. Per cent index of relative importance (%IRI) by month of the prey species of swordfish caught in the Strait of Gibraltar.

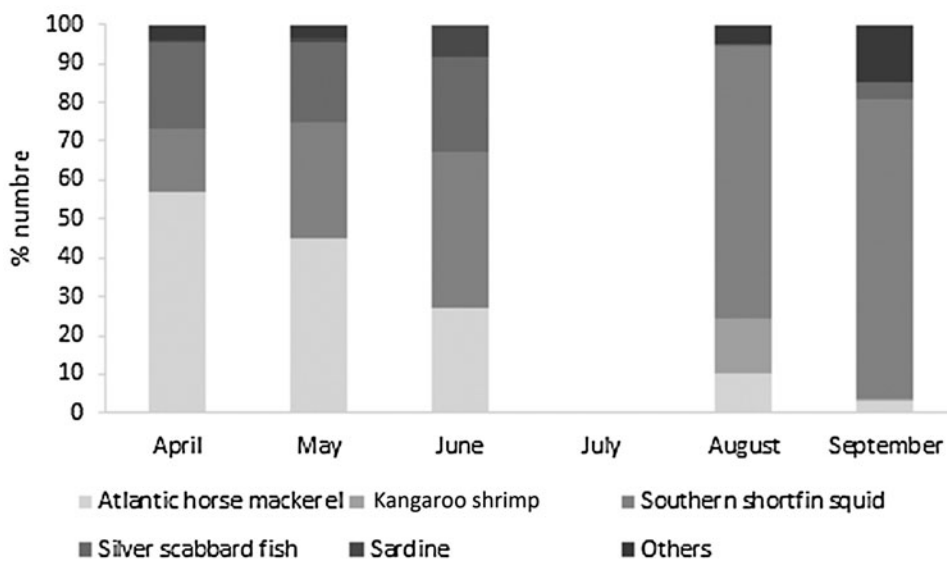
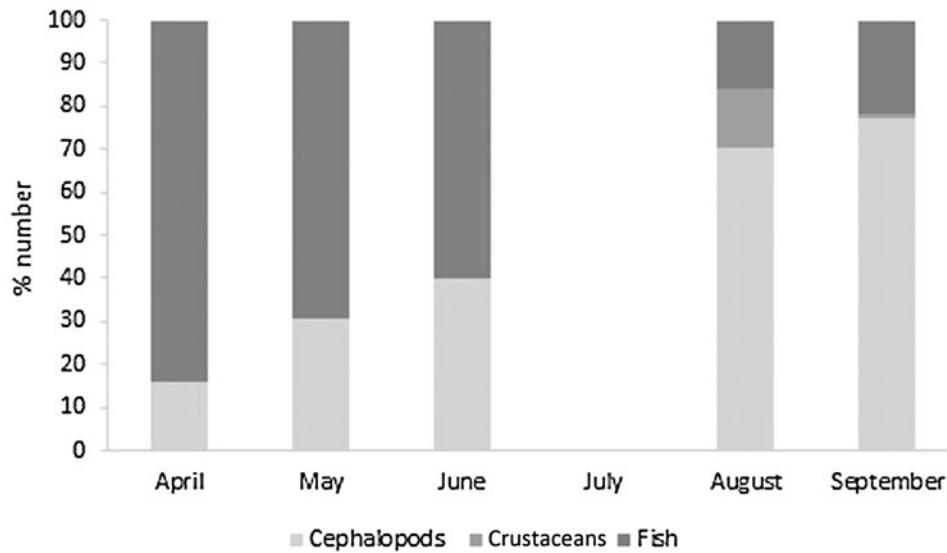


Fig. 10. Percentage in number by month of the main prey groups and species of swordfish caught in the Strait of Gibraltar.

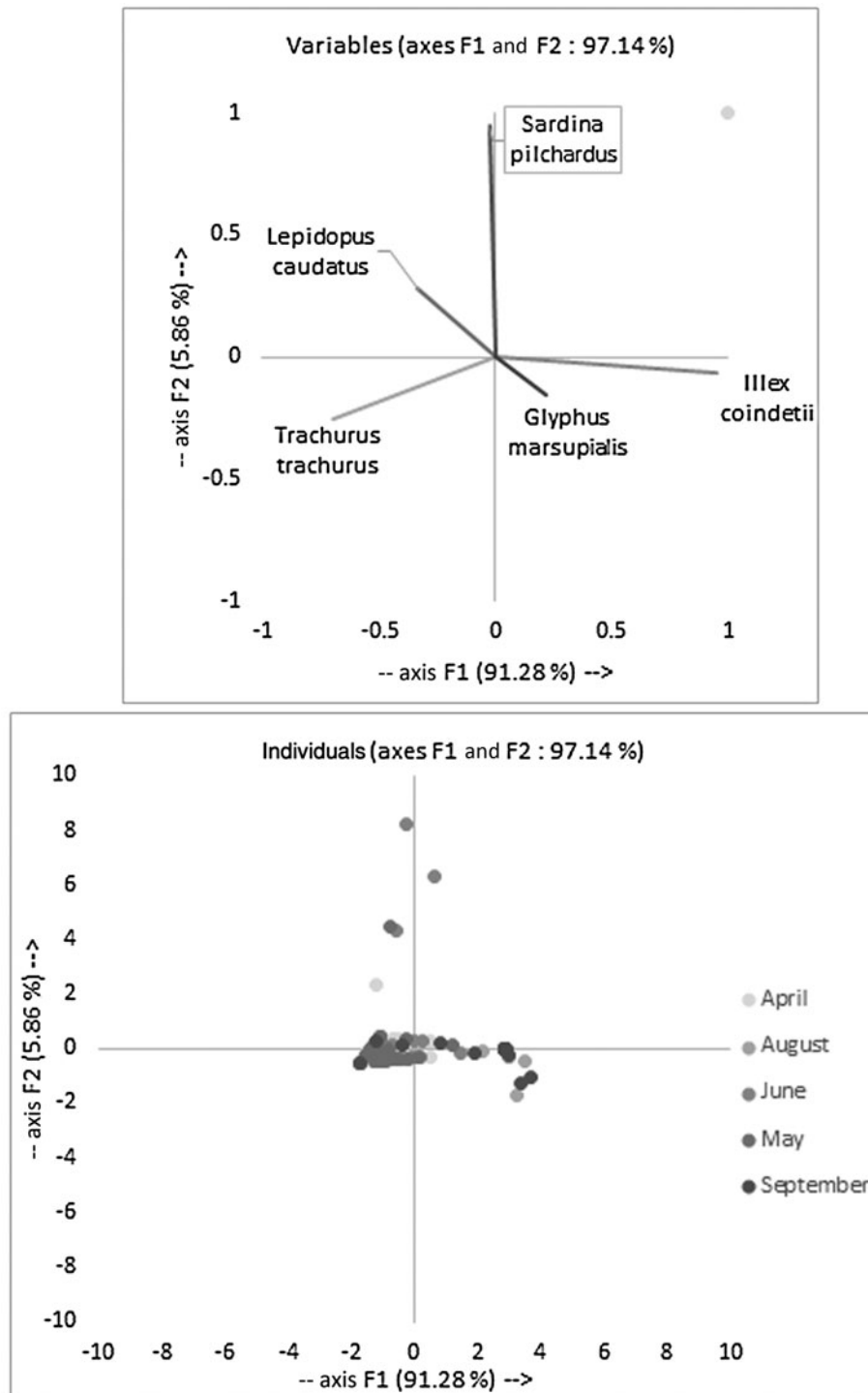


Fig. 11. Results of the discriminant analysis based on the percentage in weight of the main prey species of swordfish caught in Strait of Gibraltar.

In the Strait of Gibraltar, the diet composition of swordfish determined by this study (13 species) is quite diverse. It is comparable to that obtained by Toll & Hess (1981) from the Florida Straits (15 species); Moreira (1990) off the Portuguese coast (14 species); and Peristeraki *et al.* (2005) in the southern Aegean Sea (11 species). However, this figure is lower than that found by Stillwell & Kohler (1985) in the north-western Atlantic Ocean (36 species), Hernández-García (1995) in the central-east Atlantic (38 species), Salman (2004) in the Aegean Sea (34 species) and Romeo

et al. (2009) in the Central Mediterranean Sea (40 species). The differences in number of prey species ingested by swordfish are related to their abundance and availability in a given area (Stillwell & Kohler, 1985). It is generally accepted that large predators such as swordfish eat all that is abundant in their immediate environment (Palko *et al.*, 1981).

In addition, it should be noted that the number of cephalopod species identified by the present study (two species) is lower than that reported by Hernández-García (1995) in the Strait of Gibraltar (13 species), Salman (2004) in the Aegean

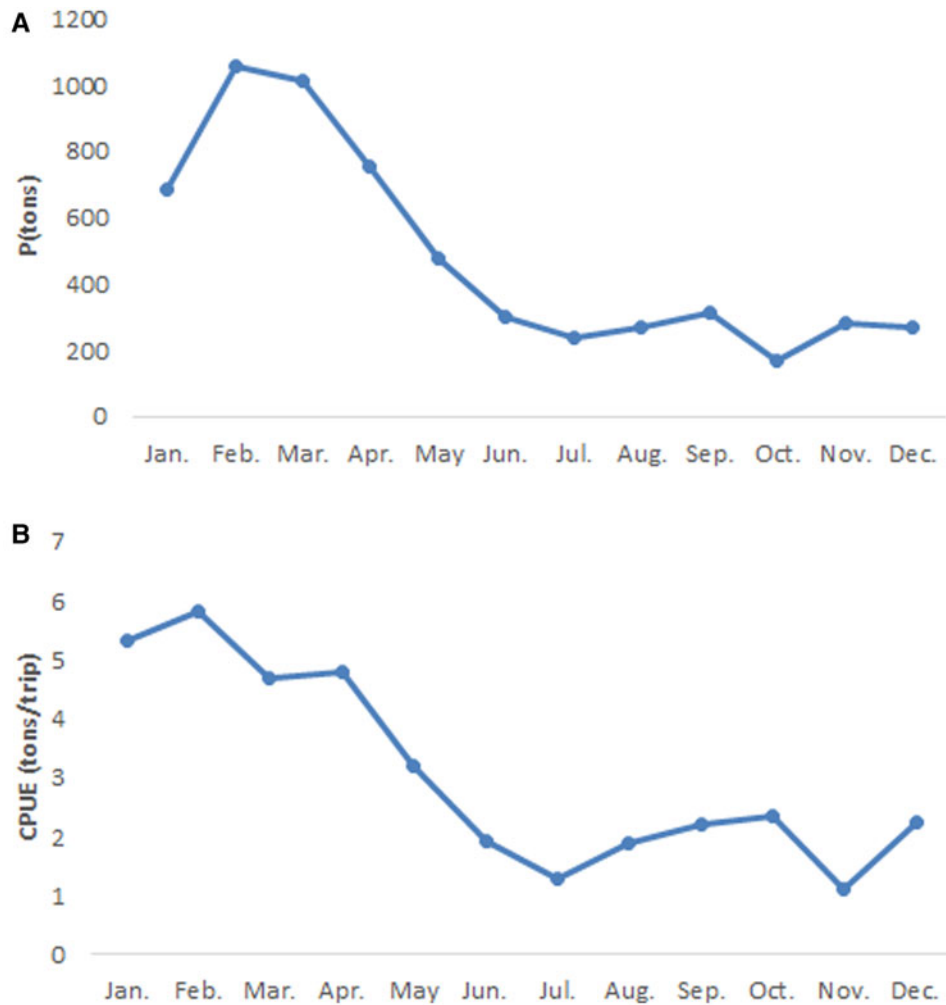


Fig. 12. Monthly evolution of the catches (A) and the CPUE (B) for *Trachurus trachurus* caught by Moroccan purseiners in the Strait of Gibraltar.

Sea (19 species) and Romeo *et al.* (2011) in the central Mediterranean Sea (20 species). These discrepancies could be explained by the fact that in the study area, the Moroccan artisanal longline fleet targets swordfish in surface waters at depths not exceeding generally 30 m, where the few abundant epipelagic squid prey such as *I. coindetii* are available to swordfish at night when these cephalopods rise near the surface to feed. In contrast, in the Mediterranean Sea, large longliners fished for swordfish in deeper waters (10–100 m) (García-Barcelona *et al.*, 2010; Cambie *et al.*, 2013). The mesopelagic longliners can even target large swordfish at depths ranging between 100 and 500 m (Cambie *et al.*, 2013), which could explain the higher number of cephalopod species found in the swordfish stomachs contents. Furthermore, a recent study conducted in the central western Mediterranean Sea showed that the presence of cephalopods in the diet of large pelagics is strictly related to the water layer where the predator usually feeds (Romeo *et al.*, 2011). Unfortunately, the rocky aspect and the irregular bottom topography of the Strait of Gibraltar, make it difficult to assess the cephalopod biodiversity in this particular area by means of bottom trawl surveys (Sánchez-Garrido *et al.*, 2011).

The results from this study confirm that cephalopods, especially the ommastrephidae, play an important role in the diet of swordfish in the Strait of Gibraltar, contributing 43.36% of

total prey in number. This fact was previously highlighted by several authors (Stillwell & Kohler, 1985; Bello, 1991; Guerra *et al.*, 1993; Clarke *et al.*, 1995; Hernández-García, 1995; Velasco & Quintans, 2000; Young *et al.*, 2006; Romeo *et al.*, 2009, 2011). Moreover, it is well known that these muscular, fast-swimming squids are high-speed, growing and active predators, which efficiently convert prey into biomass (Clarke, 1996).

The analysis of the depth distribution of prey species showed that in the Strait of Gibraltar swordfish feeds primarily on pelagic species such as the Atlantic horse mackerel (*T. trachurus*), but also on some demersal species like the southern shortfin squid (*I. coindetii*) and silver scabbard fish (*L. caudatus*). It can even occasionally forage some deep crustacean species such as the striped red shrimp (*Aristeus varidans*) (300–1134 m) (Holthuis, 1980) and kangaroo shrimp (*G. marsupialis*) (500–1100 m) (Fischer *et al.*, 1981). The last two prey species have been reported for the first time by the present study. The presence of these two crustacean species in the swordfish stomachs confirms that swordfishes are able to dive during the day to depths reaching up to 800 m (Takahashi *et al.*, 2003; Matsumoto *et al.*, 2003; Canese *et al.*, 2008). This can also be justified by the bathymetric characteristics of the study area, in which the maximum depth reaches up to 900 m (Malanotte-Rizzoli & Robinson, 1994).

The wide bathymetric distribution of prey species, and the presence of entire food items in swordfish stomachs, indicate that swordfish feeds throughout the water column, especially at night when some species, such as the southern shortfin squid and silver scabbard fish, rise near the surface in search of prey (Roper & Young, 1975). Moreover, the presence in the majority of examined stomachs of many individuals belonging to the same prey species and with similar size confirms that swordfish prefers chasing schools of fish and cephalopods on which to feed (Tibbo *et al.*, 1961; Carey & Robinson, 1981).

The findings from this study revealed that swordfish of both sexes feed generally on the same prey species. Similarly, the percentages of the main prey groups and species (both in number and in weight) did not vary significantly according to the sex and the size of predator. Our results are in agreement with those found by Stillwell & Kohler (1985) and Ibáñez *et al.* (2004).

Our results showed for the first time that there are significant differences in the diet composition of swordfish between months, depending on the abundance of prey species in the study area. In fact, the high proportion of Atlantic horse mackerel in the stomach contents in April, suggests their abundance in the area, as shown by the monthly evolution of catches and abundance index of this species from the Moroccan purse seiners operating in the Strait of Gibraltar (Figure 12A, B). The high relative abundance of *T. trachurus* in the Strait of Gibraltar from January to May could be due to the fact that this species spawns during that period in the study area. Indeed, previous studies showed that in the Moroccan Atlantic coast adjacent to the Strait of Gibraltar, Atlantic horse mackerel spawns from January to May (Sedletskaia, 1971).

The predominance of small size shortfin squid (average weight of about 107 g) in the swordfish stomachs during August–September is worth noting. Results from the most recent bottom trawl surveys in the Atlantic area adjacent to the Strait of Gibraltar showed that the southern shortfin squid was the most abundant species of cephalopod in the area during that period (Benchoucha *et al.*, unpublished).

The results from this study revealed also that there is a significant linear correlation between the body length of the predator and the size of its prey species. This means that large swordfish tend to feed on larger prey than small ones. These results are in agreement with those obtained by other authors (Velasco & Quintans, 2000; Chancollon *et al.*, 2006).

The remarkable decrease in the fullness index (*fi*) from June to August may indicate that this period corresponds to the spawning season of swordfish caught in the area. Thus, the observed decline in the fullness index would be associated with a change in the physiological state of the fish owing to the process of gonad maturation (Berg, 1979). This hypothesis is supported by previous studies suggesting that swordfish spawns in the Mediterranean Sea in the summer time (Tserpes *et al.*, 2001). Furthermore, a more recent growth study suggests that a fraction of swordfish catches in the Strait of Gibraltar would be of Mediterranean origin (Abid *et al.*, 2013), supporting results of the most recent genetic studies that showed that the Mediterranean swordfish population extends beyond the current management boundary at the Strait of Gibraltar to ~10°W (Smith *et al.*, 2015).

In the light of current results and given that the diet of swordfish depends considerably on the abundance of prey species in their distribution area, more studies will be

needed in the future to depict any changes in the prey species composition due to fishing activities and environmental factors. Indeed, research has shown that variations in the abundance of marine organisms depend on the combined effect of the sea surface temperature and fishing (Ware, 1995; O'Brien *et al.*, 2000). The sea temperature can also have a direct effect on spawning and survival of larvae and juveniles as well as on fish growth, by acting on physiological processes. It also affects the biological production rate, thus food availability in the ocean, which is a powerful regulator of fish abundance and distribution (Lehodey *et al.*, 1997).

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