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Diet of the blue shark, *Prionace glauca*, in the Northeast Atlantic

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Resumo

O tubarão azul, *Prionace glauca*, é uma das espécies de tubarão mais abundantes, tendo uma distribuição cosmopolita. No entanto, é muito procurado para o comércio das suas barbatanas e é frequentemente pescado como um produto acessório da pesca com palangre e redes. Sendo um predador de topo, este tubarão possui um papel fundamental na regulação das comunidades marinhas e o estudo da sua dieta e comportamento alimentar são fundamentais para obter informações relevantes sobre interacções predador-presa, mas também como indicadores de abundância de outras espécies. A utilização do índice IRI% para descrever a generalidade da dieta do tubarão azul no nordeste Atlântico demonstrou uma clara dominância dos items identificados como cefalópodes. Contudo, a grande variedade de items alimentares identificados, cefalópodes ou não, sugere um comportamento alimentar de natureza oportunista. A existência de espécies de profundidades consideráveis nos conteúdos estomacais deste tubarão, corrobora os resultados de vários estudos baseados em marcações e reforça a hipótese de que esta espécie se alimenta mesmo quando mergulha a maiores profundidades e que é capaz de executar mergulhos com mais amplitude do que se supunha. No que diz respeito à variação dos parâmetros da dieta, observaram-se diferenças entre as estações do ano, mas não se detectaram diferenças significativas entre sexos e estados de maturação. Não obstante das conclusões deste trabalho, são necessários mais estudos para que se consigam dados mais conclusivos no que respeita à dieta do tubarão azul e comportamento alimentar, mas também para que se possa compreender melhor o impacte que a remoção anual deste predator poderá ter sobre as comunidades marinhas.

Abstract

The blue shark, *Prionace glauca*, is among the most abundant and wide ranging sharks in the world. However, this species is highly targeted in the fin trade market and is frequently caught as a by-catch in the longline and gillnet fisheries. As a top predator, it plays a major role in the regulation of marine communities and the study of its diet and feeding behaviour may disclose valuable information about its biology but also about predator-prey interactions and may serve as a good indicator of local species abundance. The usage of the IRI% index to describe the overall diet of the blue shark in the northeast Atlantic revealed a clear dominance of cephalopod prey items in the stomach contents analyzsed. Nonetheless, the wide range of prey items identified, cephalopod or not, suggests an opportunist feeding behaviour for this species. The presence of deep water species in this shark's stomach contents is consistent with the findings of several tagging studies and reinforces the hypothesis that the blue shark may feed while diving at greater depths, and is capable of larger vertical incursions than expected. The analysis of variability of dietary parameters revealed that the most relevant differences were found between sampling seasons and no significant variation was found between sexes or maturity stages. Despite these findings, further investigation is required in order to gather more conclusive information about this shark's diet and to infer the impact of the annual removal of such a key predator in the marine communities.

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Chapter 1

Introduction

Sharks are among the top predators in the marine environment and play a major role in the regulation of marine communities (Pusineri *et al.*, 2008; Stevens *et al.*, 2000; Dulvy, 2008). Recent declines related with fishing pressure have been described for a number of shark species (Stevens *et al.*, 2000; Dulvy, 2008; Aires-da Silva *et al.*, 2008). Despite an increasing interest in their conservation and management there is still little quantitative information on their population genetics, growth rates, reproduction, diet and migratory behaviour.

The blue shark, *Prionace glauca* (*Linnaeus*, 1758) is a large carcharhinid which is considered one of the most common and widely distributed chondrichthyans, occurring worldwide, both in temperate and tropical waters (Compagno, 1984; Stevens, 1990). It is easily identified by its deep blue dorsal coloration and slender body, reaching four meters in length (Compagno, 1984). It is an oceanic pelagic shark, although it is often seen swimming slowly near the surface for prolonged periods of time with its first dorsal fin and terminal caudal lobe out of the water (Compagno, 1984; Carey & Scharold, 1990; Peter Klimley *et al.*, 2002). In the Atlantic Ocean, it is considered one of the most abundant species among the pelagic sharks ranging from Newfoundland to Argentina in the west and from Norway to South Africa in the east (including the Mediterranean Sea) and over the entire mid Atlantic (Compagno, 1984).

Despite being among the most productive shark species (Cortés, 2002) and considered a keystone predator in the Atlantic ocean (Pusineri *et al.*, 2008), the blue shark is highly targeted in shark's fin trade (Pusineri *et al.*, 2008) and is one of the shark species most frequently caught as a by-catch in the longline and gillnet fisheries (Gilman *et al.*, 2008; Mandelman *et al.*, 2008; Mejuto *et al.*, 2008). According to the International Union for

Conservation of Nature (IUCN), the reported landings of blue shark in the Atlantic ocean reached almost 80% of the landing estimates in 2007, approximately 45,087 ton (Camhi *et al.*, 2007). In some fisheries, blue sharks may even exceed the catch of the primary target species, such as in the longline and gillnet fisheries targeting the swordfish in the North and southwest Atlantic (Mejuto *et al.*, 2008; Hazin & Lessa, 2005; Campana *et al.*, 2009).

Even though the blue shark is currently listed as near threatened in the IUCN Red List (Stevens, 2009), there is a raising concern about their global exploitation rate and if it may exceed maximum sustainable yield (Clarke *et al.*, 2006). The resilience of this species, suggested by several authors, may be a misleading concept given the inconsistencies in the catch-rate trends and reports from different sources which may vary widely among studies, fishing gears and often within the same ocean basin over time (Campana *et al.*, 2009). Given the economical importance of this species and to the role of pelagic sharks in regulating marine ecosystems, further and more extensive studies are required in order to provide more accurate information useful for the design of adequate and realistic conservation plans and to give us some insight of the implications of the annual removal of large numbers of key predators on their environment and in their usual prey populations.

Most diet related studies focusing on this species are non-extensive and comprise small samples. This is most probably a consequence of the free-ranging behaviour of blue sharks, and because they live in a relatively inaccessible and concealing environment. The blue shark has been described several times as a large mesopelagic predator, predominantly diurnal (Pusineri *et al.*, 2008), which is suggested by the remarkably regular vertical oscillations, particularly during daylight hours, with an increasing amplitude of the dives and larger incursions in depth than the ones observed at night (Carey & Scharold, 1990; Queiroz *et al.*, 2005). This repetitive diving behaviour with an oscillatory vertical pattern, moving up and down in the water column, is frequently associated with feeding strategies. These movements are limited by the characteristics and structure of the water column which may also influence the spatial distribution and behaviour of prey items (N. Queiroz, *unpub. data.*, Carey & Scharold, 1990). The amplitude of these deep incursions may vary between -200 and -400 meters, but deeper dives (e.g., -620 m) have also been registered (Carey & Scharold, 1990). In recent studies using satellite tracking methods, the range of the dives recorded for several specimens confirmed the broad vertical occupation of the water column by the blue shark in the northeast Atlantic. Moreover, they extended the deepest range to -696 m, but additional reports suggest the occurrence of even deeper vertical incursions for this species (N. Queiroz, *unpub. data.*).

The study of the diet and feeding habits through the examination of stomach contents is a standard procedure in species with elusive behaviour such as the blue shark. Usage of this methodology may give us some insight into many aspects of the feeding habits of several marine species and may disclose valuable information on the structure of the marine ecosystem, predator-prey interactions, feeding behaviour, as well as the importance of each species in the food web (Cortés, 1997; Braccini *et al.*, 2005). The diet of the blue shark has already been described in several studies in the Atlantic Ocean (Table A1, Appendix). It consists mainly of cephalopods and pelagic fish. Between 1993 and 1994, Clarke *et al*. (1996) described the diet of the blue shark in Azorean waters. The analysis of 23 stomachs provided similar results to other diet related studies on this species, with the dominant occurrence of cephalopods in the stomach contents especially the following squid species: *Histioteuthis bonelli* and *Taonius pavo* and the octopod *Haliphron atlanticus*. Three teleost prey items were also predominant: *Capros aper*, *Macrorhamphosus scolapax* and *Lepidopus caudatus*. But the existing literature on the diet of this species reveals a much broader variety of prey items in their stomach contents, which varies according to the sampling area, suggesting an opportunistic feeding behaviour for this species (McCord & Campana, 2003; Cortés, 1999).

The present study aims to provide a more comprehensive and quantitative analysis of the overall diet of the blue shark in a larger sampling area of the North East Atlantic throughout a more extensive sampling period, to describe any seasonal variation of the diet composition of this species and to infer differences in the feeding behaviour between sexes and maturity condition of the specimens.

Chapter 2

Material and Methods

2.1 Study area

Blue shark stomachs were collected between 2005 and 2008 from sharks caught as by-catch in surface-drift longline fishery. The sampling area comprises the northeast Atlantic, roughly between 27-44ºN and 7-42ºW (Fig. 2.1). Samples were obtained in four different seasons: Spring (March), Summer (June-July), Autumn (October-November), and Winter (December-January). Each fishing trip lasted about 40 days.

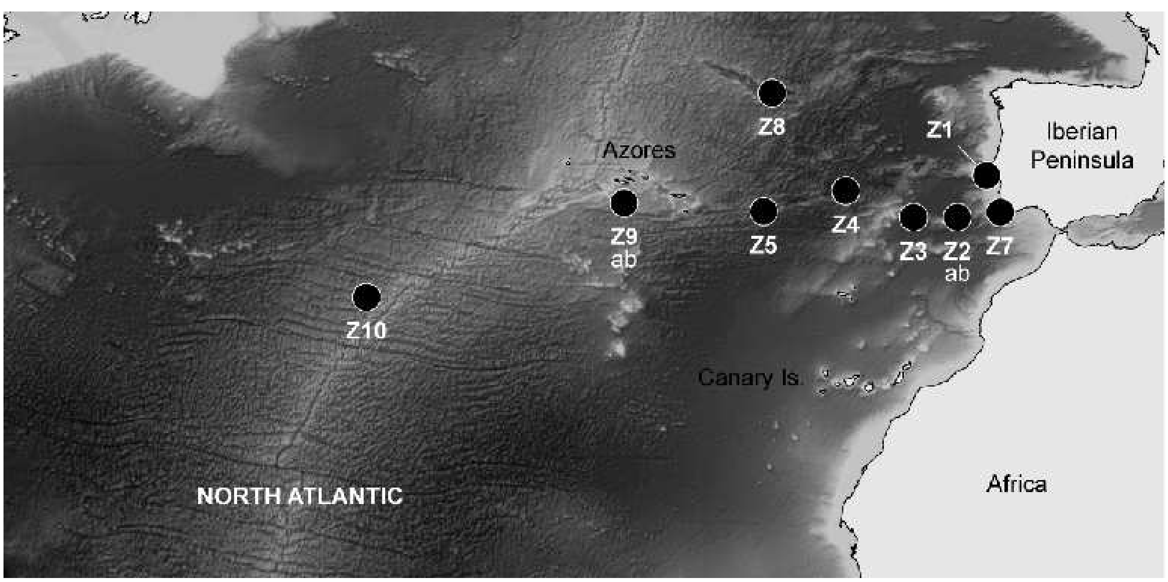

Figure 2.1: Longline fishery areas used as sampling sites in the Northeast Atlantic Ocean.

2.2 Sampling

All samples were pre-processed aboard fishing vessels. Upon capture sharks were measured (total length, T_L and fork length, F_L, according to Compagno, 1984), sexed and when possible the stage of development of the males was recorded according to Stehnann. (2002). All stomachs retrieved were felt by hand and whenever full or containing prey items were frozen for later laboratory examination. At laboratory, total stomach content and individual prey item weight and size were determined. All food items obtained were catalogued and then identified to the lowest possible taxonomic category. Prey items were grouped into several categories according to the prey type: Cephalopod, Teleost, Mammal. All unidentifiable items were considered 'Unknowns'.

All cephalopod parts and lower beaks retrieved from food containing stomachs were used for species identification by comparison with field and beak identification guides as well as personal cephalopod lower beak reference collections (Roper *et al.*, 1984; Lu & Ickeringill, 2002; Clarke, 1986). Whenever identification through morphological characteristics was impossible, lower beaks were catalogued for further identification and only used to quantify the overall diet of blue sharks. Measures of the lower hood length (LHL) and lower rostrum length (LRL) were used to reconstruct mantle length (M_L) and total mass (M_T) of cephalopods, following regression equations from Clarke (1986) and Lu & Ickeringill (2002). Stomachs containing only cephalopod beaks were excluded from the analysis, as the indigestibility of beaks can promote prolonged residency in the stomach and bias dietary estimates (Braccini *et al.*, 2005).

Whenever possible, all teleost items gathered were identified from sagittal otholits and morphological specific characteristics using reference material and published guides (Tuset *et al.*, 2008).

Stomach items identified as 'mammal' were identified by morphological characteristics. When identification was impossible, molecular techniques were used, through the amplification and sequentiation of the cytochrome *b* gene and applying specific cetacean primers (Leduc *et al.*, 1999). Sequences obtained were posteriorly compared with several databases (Ross *et al.*, 2003; Kumar *et al.*, 2004).

2.3 Diet analysis

In order to obtain a precise description of this species overall diet, it is important to assess sample sufficiency (Cortés, 1997). To do this, the cumulative number of randomly pooled stomachs was plotted against the cumulative diversity of the stomachs contents, using a pooled quadrat method based in the Brillouin Index of diversity (Pielou, 1966).

The overall diet composition was analysed using the index of relative importance (IRI) as described by Pinkas *et al.* (1971) and Cortés (1997). Three quantitative measures were obtained for every prey item: 1) the percentage of the total number of stomachs containing a specific prey item (O%), 2) the numerical composition (N%), that is the number of items of a specific category expressed as a percentage of the total number of prey items, and 3) the mass composition (W%), that is the wet mass of each specific prey group expressed as a percentage of the total wet mass of all specific prey items found. To minimize errors provided by each individual parameter, and for comparability purposes, all measures were incorporated in a single index, the Index of relative importance (IRI%), expressed as a percentage. Confidence intervals of the dietary parameters ($2.5th$ and $97.5th$ percentiles) of the previous estimates were computed using a bootstrap method with 1000 replicates (Haddon, 2001). In each replicate, individual stomachs were sampled with replacement and all dietary parameters were estimated. With 1000 replicates it was possible to obtain the distribution of each dietary parameter for each prey item.

The relationship between prey size and shark size was calculated using the Spearman's rank correlation coefficient (r). Only the mantle length of the cephalopod prey items was used in this analysis since most of the other prey items were too digested to be measured and the species' specific linear regressions were unavailable. In order to describe seasonal and sexual variation in dietary composition, a two-way non-parametric multivariate analysis of variance (PERMANOVA Anderson, 2005) with equal sample sizes ($n = 5$) and factors **Sex** (male or female) and **Season** (summer, autumn and winter) was conducted, using Bray-Curtis distances (Anderson, 2001). A similar analysis was performed to evaluate the effect of maturity condition and sexual variation in the diet of the sharks collected in this study considering as factors: sex (male, female) and size as a surrogate of maturity stage (FL>180 cm; FL<180 cm). Due to sampling constraints, samples collected in the spring were excluded from the analysis. If significant differences were found in the analysis, *a posteriori* pairwise comparisons were undertaken for the significant factors or interactions.

Chapter 3

Results

Of the 2,441 stomachs collected between 2005 and 2008 in the northeast Atlantic Ocean, only 137 (6%) contained food items, of which 28% contained a single prey item. The remnant stomachs had between two to 130 prey items. Stomachs with no information relative to size or sex were excluded in some of the analyses performed in this study. A total of 35 females were Included in the analyses, ranging from 79 cm to 223 cm (F_L), of which only five were considered adults. A total of 96 male sharks were caught in the longline surface drift fisheries, ranging in size from 89 cm to 258 cm (F_L), of which 23 were considered adults.

3.1 Overall diet

The cumulative prey diversity curve for the overall diet from the stomachs contents reached a stable level at about 120 stomachs, so this sample was large enough to accomplish the objectives defined for this study (Fig. 3.1).

Stomach contents analysis retrieved 58 different taxonomic prey item categories: 39 cephalopod species, representing 22 families, three mammal species from two families, and a total of 12 teleost species from 12 families were identified (Table A2, Appendix). Cephalopods were the dominant prey group in the stomach contents analysed, contributing to the overall diet with the highest values of W% (77%), O% (61%), N% (89%) and with an IRI% of 94%. The teleost contribution to the diet was very reduced with an IRI% value of 5% (W% = 10%; O% = 30%; N% = 9%), followed by mammal prey items with an even smaller contribution of IRI% = 1% (W% =14%; O% = 9%; N% = 2%). An item identified as belonging to a bird was found in one stomach but was not included in this analysis since

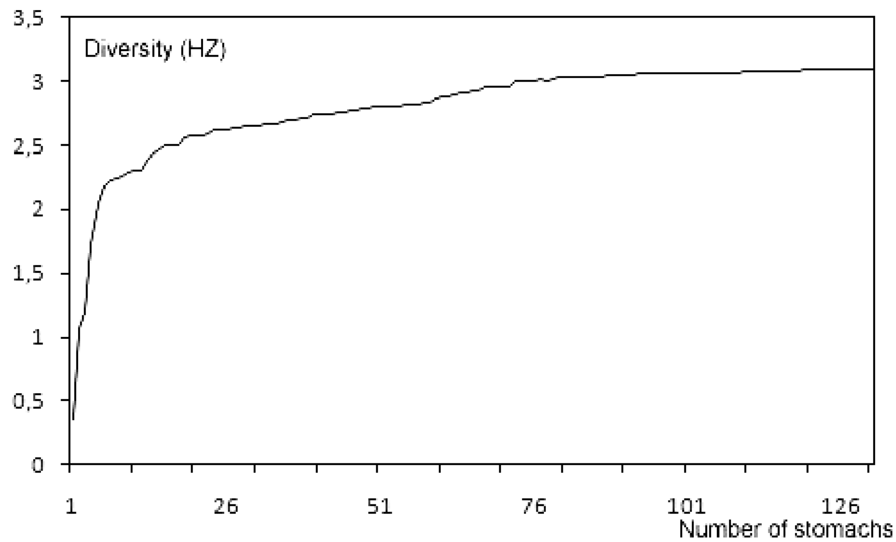

Figure 3.1: Cumulative diversity (HZ) curve of prey items for the overall diet of the blue shark, in the northeast Atlantic ocean.

it was the only item in the given stomach and no species, size or weight were possible to be determined from the residual parts (mostly feathers).

Histioteuthidae was the cephalopod family most frequently represented in the blue shark's diet (IRI%=48%; N%=23%; W%=32%; O%=17%) and *Histioteuthis arcturi* the predominant species in this group (IRI%=73%; N%=46%; W%=52%; O%=43%). Both Cranchiidae (N% = 7%; W% = 5%; O% = 10%) and Chiroteuthidae (N%=10%; W%=3%; O%=9%) families had similar importance in the diet (IRI%=6%). The Mastigoteuthidae family of cephalopods followed with an IRI% of 5% (N%=10%; W%=0, 10%; O%=9%). Onychoteuthidae (N%=5%; W%=4%; O%=6%), Allopsidae (N%=7%; W%=undetermined; O%=8%) and Ocythoidae (N%=4%; W%=5%; O%=7%) were also represented in the sampled stomach contents with an IRI% value of only 3%. Additionally, the Octopoteuthidae, *Taningia danae*, was the species which had the biggest contribution in terms of weight (N%=0.76%; W%=11%; O%=2%) despite its reduced frequency of occurrence in the stomachs when compared with other species from Histioteuthidae.

The remnant groups of cephalopod had a lighter contribution to the diet of the blue shark in this zone of the Atlantic, being considered rare species. The unidentified prey items of cephalopods had an important contribution to the overall diet of this species (IRI%=24%) but the higher susceptibility of cephalopod flesh to digestion and the damaged lower beaks hampered the conclusive identification of the unknown cephalopod prey items. The absence of linear regression equations in the literature for some of the cephalopod species limited the calculation of IRI% for the estimation of mantle length (M_L) and total mass (M_T) for some of the species: *Haliphron atlanticus*; *Grimalditeuthis bonplandi*; *Heteroteuthis dispar*; *Joubinoteuthis portieri*; *Lepidoteuthis grimaldii*; *Neoteuthis* sp. and *Vitreledonella richardi*.

Regarding the teleost groups identified, the major prey item groups belonged to the family Molidae – *Mola mola*, the ocean sunfish – with a contribution of IRI%=4% (N%=8%; W%=15%; O%=9%) and Alepisauridae (lancet fishes) with an IRI%=3% (N%=10%; W%=14%; O%=11%) relative to the total teleost items collected. The unidentified proportion of teleosts comprised 91% of the total teleost prey items mainly due to high levels digestion of the hard parts and flesh.

Mammal prey items contribution to the blue shark's diet was smaller when compared with the other prey groups. Delphinidae was the most represented mammal family in the blue shark's diet (IRI%=8%; N%=22%; W%=22%; O%=22%), followed by Phocidae with a smaller contribution, with a IRI% value of 0.36% (N%=6%; W%=2%; O%=6%). *Stenella coeruleoalba* (Stripped dolphin) was the most frequent mammal species present in the stomach contents (IRI%=95%; N%=75%; W%=98%; O%=75%), followed by *Tursiops truncatus* (bottlenose dolphin) with a much smaller importance (IRI%=5%; N%=25%; W%=2%; O%=25%). The major proportion of mammal items was categorized as unknown (IRI%= 91%; N%= 72%; W%=76%; O%=72%), given the advanced digestion levels of most items and untraceable morphological characteristics.

The overall diet analysis returned considerable variability around the point estimates of dietary items. Still, confidence intervals rarely exceed plus or minus 10% around each estimate and seldom overlapped with those of items belonging to the same category.

3.2 Predator-prey size relationship

The evaluation of the predator-prey relationship was only calculated for cephalopods since this was the group with more extensive information concerning prey item sizes, mostly because of the available information on the size/parts relationship in the literature. For this analysis sharks ranging from 89 cm to 239 cm at fork length (F_L), from both sexes were considered. Blue sharks examined consumed prey items of a wide range of estimated sizes, between 3.4 mm and 744.4 mm. Blue sharks analysed consumed cephalopod preys up to 55% of their F_L. A significant but very small correlation between predator F_L and M_L estimated for cephalopod species was found (r = -0.12; P < 0.05).

Table 3.1: PERMANOVA analysis for (A) temporal and sexual variation in diet composition and (B) variation of the overall diet given the sex and maturity stage.

A				B			
Factor	*d.f.*	*F*	*P*	Factor	*d.f.*	*F*	*P*
Season	2	2.5399	0.0010	Sex	1	1.2247	0.2341
Sex	1	10.666	0.3696	Size	1	1.4746	0.1065
Season×Sex	2	13.035	0.1661	Sex×size	1	0.9212	0.5214
Residual	24			Residual	16		

3.3 Variation in dietary composition

Prey diversity for sharks collected varied between sample season considerably: summer sampling season had 69% of prey diversity, followed by the winter (66%), the autumn (36%) and spring (29%). This numbers were corroborated by the significant differences found between seasons ($F = 2.5399$; $P < 0.05$) in the PERMANOVA analysis (Table 3.1 A). Despite differences between seasons no significant differences were found between males and females and no interaction was found in this analysis. The analysis between **Sex** and **Size** (maturity stage) revealed no differences in dietary composition of the sharks collected during this study (Table 3.1 B).

Chapter 4

Discussion

The impact of a predator on any particular trophic level may be understood by knowing the amount and diversity of the prey items it consumes and its stomach contents may be a good indicator of the marine species abundance in a given area and period of time. The study of the diet of a top predator, such as the blue shark, through the examination of stomach contents is hampered frequently by a high proportion of empty stomachs, reduced number of items per stomach and highly digested food items which suggests that the items spent prolonged periods of time in the stomach. Sharks have been frequently described as intermittent feeders, with small periods of frenetic active feeding and longer periods of time characterized by reduced predatory activity consequence of slow digestion rates and different feeding behaviour at different life stages (Simpfendorfer *et al.*, 2001; Wheterbee *et al.*, 1990). Some authors suggest that in some species, the pregnant female sharks cease feeding in nursery areas to prevent feeding on their young but this behaviour is not well documented (Wheterbee *et al.*, 1990). These feeding patterns may influence the number of sharks caught with food items in their stomachs. In addition, the fishing method used to catch the sharks might also play an important role in the selection of famine animals which may result in a large proportion of empty stomachs, as the one found in this study (94%).

The sex ratio of the specimens caught in this sampling was unbalanced, favouring males, in particular juveniles. Temporal and geographic patterns of size and sexual segregation have been described in several shark species (Costa *et al.*, 2005; Hulbert *et al.*, 2005; Mucientes *et al.*, 2009; Girard & Du Buit, 1999) and this has also been observed in the blue shark (Stevens, 1990; Queiroz *et al.*, 2005; Mucientes *et al.*, 2009; Kohler *et al.*, 2002; Pratt, 1979). Several studies carried out in the north and northeast Atlantic showed considerable sexual segregation in populations, with the females more abundant in higher latitudes than males (Stevens, 1990; Henderson *et al.*, 2001) and there are several reports of male clubs and kindergartens in the eastern Atlantic ocean (Litvinov, 2006). The Portuguese coast has been described as a preferential area for this species in the north-east Atlantic, with a population that consists primarily of immature males and immature or sub-adult females (Queiroz *et al.*, 2005; Casey, 1985; Kohler *et al.*, 1995). Adult females, frequently pregnant, were observed near the Canary Islands and North Africa, while mature males were localized further north off Portugal, along with juveniles and sub-adult females in the winter (Litvinov, 2006). Furthermore, catch rates of young-of-the-year blue sharks suggest that parturition occurs in nurseries off the Iberian Peninsula, particularly off Portugal, but also in the Bay of Biscay (Stevens, 1990; Litvinov, 2006). Several findings suggest that this area may be an important spring nursery ground for juvenile blue sharks (Stevens, 1990; Queiroz *et al.*, 2005; Kohler *et al.*, 2002; Litvinov, 2006). According to Silva *et al.* (Silva *et al.*, 1996), juvenile blue sharks comprise approximately 80% of the population in Azorean waters during the spring. Additionally, there are few records of juveniles in the western Atlantic (Casey, 1985), and as some authors suggest, smaller sharks remain within a confined area and do not participate in the longer migrations undertaken by the adults (Kohler *et al.*, 2002). This data corroborates the hypothesis of Litvinov (2006), who suggests that the northeast Atlantic, and in particular the Azorean waters, as areas of kindergartens. Hence, the unbalanced sex ratio of the catches in this study is also in agreement with the former hypothesis.

The usage of diversity curves to determine the sample size required for a sufficient description of the overall diet of sharks is recurrent and most studies reach stable levels of diversity at 200 stomachs (Bethea *et al.*, 2004; Morato *et al.*, 2003). In this study, the cumulative prey diversity curve stabilized at around 120 stomachs, suggesting that this is an appropriate sample to describe the overall diet of blue sharks in the northeast Atlantic Ocean.

The index of relative importance (IRI%) is a quantitative measure often used as a diet descriptor for comparative reasons and because it conjugates several quantitative parameters (W%; N%; O%) it tends to minimize the errors associated with their isolated interpretation. Yet, its usage is not consensual and several studies consider only raw weight or the frequency of the items (Cortés, 1997). However, when using this index to infer such parameters all variables must be taken into account since, as is the case of the blue shark, number, occurrence and weight of prey items revealed different patterns of importance. Moreover, the mandatory usage of linear regressions to estimate mantle length (M_L) and total mass (M_T) of cephalopods has its limitations, since for some species, such as *Haliphron atlanticus*, *Grimalditeuthis bonplandi*, *Heteroteuthis dispar*, *Joubinoteuthis portieri*, *Lepidoteuthis grimaldii*, *Neoteuthis* sp. and *Vitreledonella richardi*, no such equations exist in the literature. In such cases the relative importance of these species was clearly underestimated since the total mass of the prey item was not included in the IRI% calculation. A different problem arises in the case of species for which regression equations are available: estimates will always suffer from the error associated to the equations themselves plus the errors of measurement, often associated to poorly replicated items.

Blue sharks have been reported to feed mainly in cephalopods, which was also shown in the present results, with a relative importance of this group around 94%, in opposition to the smaller presence of teleosts (IRI%=5%) and mammals (IRI%=1%). Histioteuthidae was the most relevant family of cephalopods identified in the overall dietary analysis of the blue shark in the northeast Atlantic. Members of this family have been reported as important prey items for this species in previous studies, for the northeast Atlantic (Henderson *et al.*, 2001) and the northeast Pacific (Tricas, 1979). The Histioteuthidae family is composed mainly by weak muscled squids of moderate size, 33 cm in average, with a neutral buoyancy mechanism that are distributed at considerable depths (Roper *et al.*, 1984). The Dana octopus squid, *Taningia danae*, the single member of the family Octopoteuthidae identified in this study, was present in the blue shark's diet with a small but still considerable IRI% of 1%. This species is considered an epi-mesopelagic squid occurring as deep as -1,030 m (Santos *et al.*, 2001) and has been cited before by Clarke *et al.* (1996) as one of the predominant cephalopod species in this shark's diet together with the *Haliphron atlanticus* in Azores . Other deep water squids like *Vampyroteuthis infernalis* (IRI%=0,11%) and *Mastigoteuthis* sp. (IRI%=5%) were also present in blue shark's stomach contents. The occurrence of deep water species of cephalopods among the stomach contents of this species suggests that blue sharks may feed at considerable depths.

When compared to other top predators (such as marine mammals for instance), blue sharks have much lower energy requirements and are not restricted to the surface layer of the water column, thus being able to forage on deep living and lower energy species such as the cephalopods and other teleosts that they may find during their deep water incursions. Several tagging studies, have documented this repetitive diving behaviour, with vertical oscillatory movements (Carey & Scharold, 1990; Queiroz *et al.*, 2005) and differences registered between day and night diving behaviour are also probably associated with feeding strategies. Given the neutral buoyancy mechanism adopted by most of the pelagic and deep water cephalopod species (Voight *et al.*, 1994), the energy spent by the shark is reduced when compared with the chase of an active swimming prey item probably compensating the energy spent in the deep water incursion. The octopus *Haliphron atlanticus*, the only representative of the family Allopsidae (IRI%=2,71%), is also referred in other studies as being an important prey item for blue sharks (Henderson *et al.*, 2001; Clarke *et al.*, 1996).

This is a deep water octopus of considerable dimensions that migrates in the water column, up to -3,000 m in depth (Sierra, 1992). It is worth noticing that the weight of this particular species in the analysis was severely underestimated given the absence of regression lines to calculate their total weight. Almost 8% of the stomachs containing cephalopods had at least one beak of *H. atlanticus*, and several had 10 or more.

Another interesting finding was the identification of two batipelagic teleost species in the stomachs analysed in this study: *Argyropelecus gigas* (IRI%=0.05%) and *Chauliodus danae* (IRI%=0.03%) and the ocorrence of bethopelagic species in this species diet like the silver scabbardfish, *Lepidopus caudatus* (IRI% = 0,04%), john dory, *Zeus faber* (IRI% = 0,38%), atlantic pomfret, *Brama brama* (IRI% = 0,35%), longnose lancetfish, *Alepisaurus ferox* (IRI% = 3,24%) wreckfish, *Polyprion americanus* (IRI% = 0,18%), and boarfish *Capros aper* (IRI% = 0,03%), which are found at greater depths. Despite not being the most representative species of the blue shark's diet, their presence reinforces the hypothesis that these sharks may feed while diving at greater depths, as reported by Carey & Scharold (1990) and that they are capable of broader incursions than once thought.

As reported by several tagging studies and catch records, blue sharks also exhibit great migratory capacity with wide ranging seasonal migrations, which regularly include trans-Atlantic movements (up to 7176 Km long) (Queiroz *et al.*, 2005; Casey, 1985; Kohler *et al.*, 1998; Stevens, 1976) and trans-equatorial movements linking both northern and southern hemispheres of the Atlantic Ocean. In the Northeast Atlantic, this species undergoes an extensive north-south migration (Stevens, 1990; Carey & Scharold, 1990; Queiroz *et al.*, 2005; Casey, 1985; Stevens, 1976): in the early summer swimming northward to British and Irish waters, as stated by Henderson *et al.* (2001) and Stevens (1976) and a potential southward migration in late summer in response to seasonal cooling of the surface water in higher latitudes (N. Queiroz, *unpub. data*). According to the literature, water temperature influences the movement pattern of the blue sharks (Nakano, 1994), and the north-southward migration event corroborates this hypothesis (Queiroz *et al.*, 2005). Nonetheless, the blue shark has a wide range of temperature tolerance occurring frequently in relatively cool water between 7^{o}C and 16^{o}C, despite reports of larger temperature tolerance values for this species (N. Queiroz, *unpub. data.*). The resilience and dispersal capacity of this shark will ultimately influence its feeding behaviour. Nonetheless, the wide range of prey items present in its diet, either cephalopod or not, suggests an opportunistic feeding behaviour, as shown for several other elasmobranchs (McCord & Campana, 2003; Cortés, 1999; Wheterbee *et al.*, 1990). A fact that is supported by the presence of mammal prey items which reinforces the idea of the opportunistic feeding nature of this shark, feeding according to the availability of prey items at the actual location and moving on to the next best feeding site.

The IRI% has also been used in the literature to determine predator-prey main interactions and diet data is important to build ecosystem-based models, despite all problems related with sampling bias. Differences between item's importance in the diet, often associated with the opportunistic feeding behaviour of top predators might result in a high variability in the diet composition, such as in this study, and consequently inflate errors while inferring of predator-prey interactions. Hence, the main predatory interactions and attributes of this or other species feeding behaviour may be misleading through the unique analysis of IRI%. Predator-prey size dependent relations were found, with a significant negative correlation between prey size and predator size. The correlation value was, however, quite small (r=-0.12). Therefore, such contradictory finding might be related with the small number of replicas (stomachs with contents) and with the temporal and sexual segregation already discussed in this work (Stevens, 1990; Queiroz *et al.*, 2005; Mucientes *et al.*, 2009; Kohler *et al.*, 2002; Pratt, 1979). Moreover, for some common items in the diet of the blue shark (e.g., *Haliphron atlanticus*) it was not possible to estimate total mass given the absence of regression equations between mass and part size in the literature, rendering the correlation analysis less powerful. This problem also biased the IRI% calculation. Hence, a more robust analysis than the IRI% is required to predict and explain variability within dietary parameters. The most relevant differences observed in the multivariate analysis were found between seasons, which probably reflect, at least to some extent, seasonal and spatial variability of prey items. No relevant differences in diet composition were found between males or females or between different maturity stages. Lack of differences in dietary composition between sexes or maturity stages can be explained by the lack of power of statistical analysis given the low number of replicates. However, the same findings were already observed in other shark species (Braccini *et al.*, 2005).

Overall, the findings of the present work suggest the opportunistic feeding behaviour of this species, at least for the northeast Atlantic. Despite these results, further investigation of the diet of the blue shark is required and, given the high variability observed in prey items, larger samples are mandatory for a better understanding of this species feeding habits.

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Appendix A

Supplementary Material

Table A.1: Comparison of literature on the diet of the blue shark

Area	Prey Type	Prey Item	Source
Azores	Teleost	*Capros* sp.	
	Cephalopod	*Haliphron* sp. / *Taningia* sp.	Clarke *et al.* (1996)
Bay de Biscay	Teleost	-	
	Cephalopod	Cranchiidae	Clarke & Stevens (1974)
English Channel	Teleost	-	
	Cephalopod	Sepiidae	Clarke & Stevens (1974)
Southwest Atlantic	Teleost	*Alepisaurus* sp.	
	Cephalopod	-	Clarke & Stevens (1974)
California	Teleost	*Engraulis* sp.	
	Cephalopod	*Loligo* sp.	Hazin & Lessa (2005)
California	Teleost	*Engraulis* sp.	
	Cephalopod	*Histioteuthis* sp. / *Loligo* sp.	Harvey (1989)
Gulf of Alaska	Teleost	Salmon	
	Cephalopod	-	Tricas (1979)
Northeast Atlantic	Teleost	*Thunnus* sp.	
	Cephalopod	*Histioteuthis* sp./ *Haliphron* sp.	Le Brasseur (1964)
Canada	Teleost		
	Cephalopod	*Scomber* sp.	Henderson *et al.* (2001)

Table A.2: IRI% table with confidence intervals at 95% for every prey category

	N%	W%	O%	IRI%
Cephalopod	89.18%	76.62%	60.89%	93.55%
	0.8394-0.9282	0.6549-0.8564	0.5598-0.6615	0.8900-0.9633
Onychoteuthidae	5.06%	3.75%	5.80%	2.54%
	0.0280-0.0829	0.0201-0.0638	0.0380-0.0781	0.0097-0.0507
Ancistrocheirus lesueuri	5.00%	11.50%	9.09%	1.16%
	0.0000-0.1364	0.0000-0.3382	0.0000-0.2222	0.0000-0.0958
Moroteuthis aequatorialis	10.00%	0.16%	18.18%	1.43%
	0.0227-0.2143	0.0003-0.0038	0.0455-0.3529	0.0007-0.0789
Onychoteuthis banskii	85.00%	88.34%	72.73%	97.41%
	0.7059-0.9516	0.6604-0.9989	0.5500-0.8947	0.8678-0.9970
Cranchiidae	7.33%	5.23%	9.57%	5.98%
	0.0485-0.1093	0.0326-0.0833	0.0720-0.1199	0.0315-0.0993
Bathotauma lyromma	1.72%	0.00%	2.56%	0.03%
	0.0000-0.0545	0.0000-0.0000	0.0000-0.0833	0.0000-0.0038
Cranchia scabra	1.72%	0.30%	2.56%	0.04%
	0.0000-0.0600	0.0000-0.0108	0.0000-0.0857	0.0000-0.0052
Liocranchia reinhardtii	10.34%	0.13%	15.38%	1.24%
	0.0323-0.1818	0.0004-0.0025	0.0541-0.2619	0.0011-0.0412
Phasmotopsis cymoctypus	5.17%	3.50%	7.69%	0.52%
	0.0000-0.1129	0.0000-0.0815	0.0000-0.1538	0.0000-0.0262
Taonius pavo	81.03%	96.07%	71.79%	98.17%
	0.7091-0.8958	0.9130-0.9960	0.5952-0.8333	0.9420-0.9942
Chiroteuthidae	9.61%	3.28%	8.70%	5.58%
	0.0690-0.1302	0.0208-0.0513	0.0668-0.1067	0.0285-0.0904
Chiroteuthis sp1	2.63%	12.13%	4.88%	1.06%
	0.0000-0.0746	0.0000-0.3073	0.0000-0.1250	0.0000-0.0791
Chiroteuthis sp.	15.79%	16.56%	19.51%	9.29%
	0.0652-0.2667	0.0627-0.2866	0.0938-0.3030	0.0155-0.2493
Chiroteuthis veranyi	47.37%	71.31%	41.46%	72.45%
	0.3488-0.6000	0.5283-0.8832	0.3000-0.5429	0.4897-0.8670
Valbyteuthis sp.	34.21%	0%	34.15%	17.20%
	0.2188-0.4651	0.0000-0.0000	0.2250-0.4545	0.0622-0.3268

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Table A.2: IRI% table with confidence intervals at 95% for every prey category

	N%	**W%**	**O%**	**IRI%**
Ctenopterygidae	0.38%	0.03%	0.29%	0.01%
	0.0000-0.0095	0.0000-0.0008	0.0000-0.0091	0.0000-0.0006
Ctenopteryx_sicula	100%	100%	100%	100%
	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000
Cycloteuthidae	0.76%	4.48%	1.74%	0.45%
	0.0023-0.0159	0.0096-0.0932	0.0058-0.0319	0.0003-0.0158
Cycloteuthis akimushkini	83.33%	100.00%	83.33%	98.21%
	0.5000-1.0000	1.0000-1.0000	0.5000-1.0000	0.7500-1.0000
Discoteuthis laciniosa	16.67%	0%	16.67%	1.79%
	0.0000-0.5000	0.0000-0.0000	0.0000-0.5000	0.0000-0.2500
Gonatidae	6.19%	11.08%	1.45%	1.25%
	0.0034-0.1372	0.0060-0.2418	0.0033-0.0262	0.0001-0.0504
Gonatus steenstrupi	100%	100%	100%	100%
	1.0000-1.0000	1.0000-1.0000	1.0000-1.0000	1.0000-1.0000
Grimalditeuthidae	0.13%	0%	0.29%	0.00%
	0.0000-0.0036	0.0000-0.0000	0.0000-0.0089	0.0000-0.0001
Grimalditeuthis bonplandi	100%	0%	100%	100%
	0.0000-1.0000	0.0000-0.0000	0.0000-1.0000	0.0000-1.0000
Allopsidae	6.95%	0%	7.83%	2.71%
	0.0371-0.1067	0.0000-0.0000	0.0534-0.1067	0.0109-0.0494
Haliphron atlanticus	100%	0%	100%	100%
	1.0000-1.0000	0.0000-0.0000	1.0000-1.0000	1.0000-1.0000
Sepiolidae	0.63%	0%	0.58%	0.02%
	0.0000-0.0181	0.0000-0.0000	0.0000-0.0145	0.0000-0.0013
Heteroteuthis dispar	100%	0%	100%	100%
	0.0000-1.0000	0.0000-0.0000	0.0000-1.0000	0.0000-1.0000
Histioteuthidae	23.26%	31.92%	17.39%	47.78%
	0.1638-0.3185	0.2035-0.4656	0.1454-0.2061	0.3256-0.6034
Histioteuthis sp. A	16.85%	21.70%	27.50%	18.58%
	0.0854-0.3158	0.1124-0.3815	0.1739-0.3816	0.0577-0.4095
Histioteuthis arcturi	45.65%	51.66%	42.50%	72.50%
	0.3721-0.5648	0.3970-0.6226	0.3375-0.5263	0.5202-0.8486
Histioteuthis bonnellii	3.80%	13.84%	5.00%	1.55%

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Table A.2: IRI% table with confidence intervals at 95% for every prey category

	N%	W%	O%	IRI%
	0.0063-0.0667	0.0136-0.2305	0.0119-0.0978	0.0005-0.0507
Histioteuthis corona	0.54%	0.90%	1.25%	0.03%
	0.0000-0.0222	0.0000-0.0351	0.0000-0.0429	0.0000-0.0043
Histioteuthis meleanogroteuthis	9.24%	5.55%	13.75%	3.56%
	0.0447-0.1712	0.0190-0.1209	0.0694-0.2027	0.0075-0.0939
Histioteuthis reversa	22.83%	5.13%	7.50%	3.68%
	0.0288-0.3458	0.0086-0.0865	0.0274-0.1268	0.0022-0.0898
Histioteuthis sp.	1.09%	1.22%	2.50%	0.10%
	0.0000-0.0315	0.0000-0.0353	0.0000-0.0588	0.0000-0.0069
Ommastrephidae	0.25%	1.53%	0.58%	0.05%
	0.0000-0.0061	0.0000-0.0495	0.0000-0.0142	0.0000-0.0032
Illex coindeti	50%	2.78%	50%	26.39%
	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000
Ommastrephes bartramii	50%	97.22%	50%	73.61%
	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000
Joubiniteuthidae	0.38%	0%	0.87%	0.02%
	0.0000-0.0090	0.0000-0.0000	0.0000-0.0195	0.0000-0.0008
Joubinoteuthis portieri	100%	0%	100%	100%
	0.0000-1.0000	0.0000-0.0000	0.0000-1.0000	0.0000-1.0000
Lepidoteuthidae	0.25%	0%	0.58%	0.01%
	0.0000-0.0062	0.0000-0.0000	0.0000-0.0142	0.0000-0.0004
Lepidoteuthis grimaldii	100%	0%	100%	100%
	0.0000-1.0000	0.0000-0.0000	0.0000-1.0000	0.0000-1.0000
Mastigoteuthidae	9.86%	0.10%	8.99%	4.46%
	0.0628-0.1498	0.0006-0.0016	0.0690-0.1106	0.0245-0.0716
Mastigoteuthis sp.	100%	100%	100%	100%
	1.0000-1.0000	1.0000-1.0000	1.0000-1.0000	1.0000-1.0000
Neoteuthidae	1.52%	0%	2.03%	0.15%
	0.0038-0.0318	0.0000-0.0000	0.0066-0.0344	0.0002-0.0047
Neoteuthis sp.	100%	0%	100%	100%
	1.0000-1.0000	0.0000-0.0000	1.0000-1.0000	1.0000-1.0000
Ocythoidae	3.79%	5.32%	6.67%	3.03%
	0.0242-0.0569	0.0232-0.0835	0.0445-0.0904	0.0113-0.0603

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Table A.2: IRI% table with confidence intervals at 95% for every prey category

	N%	**W%**	**O%**	**IRI%**
Ocythoe tuberculata	100%	100%	100%	100%
	1.0000-1.0000	1.0000-1.0000	1.0000-1.0000	1.0000-1.0000
Pholidoteuthidae	0.13%	0.74%	0.29%	0.01%
	0.0000-0.0046	0.0000-0.0268	0.0000-0.0098	0.0000-0.0015
Pholidoteuthis adami	100%	100%	100%	100%
	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000
Octopoteuthidae	0.76%	10.96%	1.74%	1.01%
	0.0026-0.0149	0.0113-0.2501	0.0058-0.0307	0.0005-0.0358
Taningia danae	100%	100%	100%	100%
	1.0000-1.0000	1.0000-1.0000	1.0000-1.0000	1.0000-1.0000
Teuthoidea	7.46%	4.29%	1.16%	0.68%
	0.0014-0.1649	0.0001-0.0961	0.0026-0.0231	0.0000-0.0317
Teuthoidea	1.69%	0.13%	25%	0.31%
	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000
Teuthowenia megalops	98.31%	99.87%	75%	99.69%
	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000
Thysanoteuthidae	0.13%	4.29%	0.29%	0.06%
	0.0000-0.0042	0.0000-0.1316	0.0000-0.0090	0.0000-0.0062
Thysanoteuthis rhombus	100%	100%	100%	100%
	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000
Vampyroteuthidae	0.51%	2.03%	0.87%	0.11%
	0.0000-0.0132	0.0000-0.0534	0.0000-0.0201	0.0000-0.0064
Vampyroteuthis infernalis	100%	100%	100%	100%
	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000
Vitreledonellidae	1.64%	0%	2.32%	0.19%
	0.0047-0.0348	0.0000-0.0000	0.0090-0.0401	0.0002-0.0063
Vitreledonella richardi	100%	0%	100%	100%
	1.0000-1.0000	0.0000-0.0000	1.0000-1.0000	1.0000-1.0000
Unknown cephalopod	13.02%	10.98%	20%	23.90%
	0.0825-0.1970	0.0562-0.1951	0.1671-0.2350	0.1433-0.3665
Mammal	2.03%	13.80%	8.91%	1.31%
	0.0110-0.0330	0.0606-0.2271	0.0526-0.1298	0.0038-0.0316

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Table A.2: IRI% table with confidence intervals at 95% for every prey category

	N%	**W%**	**O%**	**IRI%**
Phocidae	5.56%	2.03%	5.56%	0.36%
	0.0000-0.2000	0.0000-0.0869	0.0000-0.2000	0.0000-0.0659
Pagophilus groenlandicus	100%	100%	100%	100%
	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000
Delphinidae	22.22%	22.03%	22.22%	8.39%
	0.0476-0.4286	0.0029-0.5404	0.0476-0.4286	0.0016-0.4120
Stenella coeruleoalba	75%	97.81%	75%	95.02%
	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000
Tursiops truncatus	25%	2.19%	25%	4.98%
	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000
Unknown mammal	72.22%	75.94%	72.22%	91.25%
	0.5000-0.9286	0.4256-0.9916	0.5000-0.9286	0.5540-0.9962
Teleost	8.79%	9.58%	30.20%	5.14%
	0.0568-0.1327	0.0546-0.1608	0.2462-0.3487	0.0265-0.0929
Alepisauridae	7.69%	15.13%	8.96%	3.24%
	0.0235-0.1429	0.0246-0.3291	0.0282-0.1613	0.0020-0.1180
Alepisaurus ferox	100%	100%	100%	100%
	1.0000-1.0000	1.0000-1.0000	1.0000-1.0000	1.0000-1.0000
Sternoptychinae	1.28%	0.82%	1.49%	0.05%
	0.0000-0.0411	0.0000-0.0304	0.0000-0.0469	0.0000-0.0058
Argyropelecus gigas	100%	100%	100%	100%
	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000
Belonidae	3.85%	0.64%	4.48%	0.32%
	0.0000-0.0875	0.0000-0.0175	0.0000-0.1017	0.0000-0.0176
Belone belone	100%	100%	100%	100%
	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000
Bramidae	2.56%	4.83%	2.99%	0.35%
	0.0000-0.0690	0.0000-0.1479	0.0000-0.0781	0.0000-0.0243
Brama brama	100%	100%	100%	100%
	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000
Caproidae	1.28%	0.02%	1.49%	0.03%
	0.0000-0.0455	0.0000-0.0007	0.0000-0.0500	0.0000-0.0041

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Table A.2: IRI% table with confidence intervals at 95% for every prey category

	N%	W%	O%	IRI%
Capros aper	100%	100%	100%	100%
	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000
Stomiidae	1.28%	0.18%	1.49%	0.03%
	0.0000-0.0411	0.0000-0.0067	0.0000-0.0469	0.0000-0.0041
Chauliodus danae	100%	100%	100%	100%
	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000
Trichiuridae	1.28%	0.61%	1.49%	0.04%
	0.0000-0.0500	0.0000-0.0255	0.0000-0.0580	0.0000-0.0075
Lepidopus caudatus	100%	100%	100%	100%
	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000
Zeidae	2.56%	5.40%	2.99%	0.38%
	0.0000-0.0674	0.0000-0.1537	0.0000-0.0769	0.0000-0.0263
Zeus faber	100%	100%	100%	100%
	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000
Molidae		14.21%	10.45%	4.06%
	0.0333-0.1884	0.0420-0.2757	0.0357-0.1846	0.0043-0.1398
Mola mola	100%	100%	100%	100%
	1.0000-1.0000	1.0000-1.0000	1.0000-1.0000	1.0000-1.0000
Ophidiidae	1.28%	16.03%	1.49%	0.41%
	0.0000-0.0460	0.0000-0.4187	0.0000-0.0526	0.0000-0.0419
Polyprionidae	1.28%	6.25%	1.49%	0.18%
	0.0000-0.0429	0.0000-0.2053	0.0000-0.0492	0.0000-0.0199
Polyprion americanus	100%	100%	100%	100%
	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000
Carangidae	1.28%	4.20%	1.49%	0.13%
	0.0000-0.0455	0.0000-0.1445	0.0000-0.0500	0.0000-0.0167
Tranchurus sp.	100%	100%	100%	100%
	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000	0.0000-1.0000
Unknown teleost	64.10%	31.67%	59.70%	90.77%
	0.5128-0.7561	0.1734-0.5236	0.4844-0.7121	0.7646-0.9585