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The diet of deep-water sharks

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ABSTRACT

548 shark species were considered in this paper. They were classified in function of their depth of occurrence: 218 deep, 114 transitory and 210 shallow. The diets of the 332 deep and transitory species are reviewed. 10 prey categories are recognized here: Chondrichthyes, Teleosts, Cephalopods, Crustaceans, Marine mammals, Annelids, Ctenophores, Egg of Chondrichthyes, Siphonophores, and Bivalves. There is a complete lack of data for 210 species, and 59 have only a limited amount of information available. In general, teleosts, crustaceans, and cephalopods were the main prey found in deep-water sharks. However, some species have a specialized diet. A simple index of dietary knowledge has been developed to highlight the current state of knowledge on the subject, further illustrating the lack of information. The proportion of empty and regurgitated stomachs varies significantly between species and studies. Most data on deep and transitory sharks come from stomach content analysis. Stable isotope analysis provides additional insight into their trophic ecology. Fatty acid profiling and DNA metabarcoding can also add important information, but their use is currently limited with deep-water sharks. The most important conclusion from this synthesis is the lack or scarcity of information for most deep and transitory species.

1. Introduction

Numerous shark species (clade: Selachii) are considered apex predators or mesopredators. Most species are relatively large and have an important top-down impact on their trophic network (Cortés, 1999; Heupel et al., 2014). The current decline of shark populations can thus significantly impact ecosystems, with important cascading effects (Ferretti et al., 2010). The idea of sharks being top predators is further enhanced by the low number of other taxa able to prey on them, at least at their adult stage, with young individuals being most susceptible to predation (Heupel and Simpfendorfer, 2011). Nevertheless, *Orcinus orca*, the killer whale or Orca, is known to feed on large sharks (Sonnino Sorisio et al., 2006), while large shark species are the main predators of smaller ones (Ferretti et al., 2010).

Sharks feed on a large array of prey, and many species have an adaptive feeding behavior, targeting the most abundant prey item (Motta and Wilga, 2001). Some species have a more specialized diet, like the whale shark, *Rhincodon typus*, feeding mainly on zooplankton and small fishes (Rohner et al., 2013), or the prickly dogfish feeding mostly on elasmobranch eggs and embryos (Finucci et al., 2016). Specialization in larger prey size categories often happens with increasing size and gape size in older individuals (Heupel et al., 2014). Some species may also vary their diet with the time of the year or place where they forage (Joyce et al., 2002; McElroy et al., 2006). Several species undertake long horizontal migrations during their life, like the great white shark *Carcharodon carcharias* or the tiger shark *Galeocerdo cuvier* (Jorgensen et al., 2010; Holmes et al., 2014).

Numerous shark species, especially deep-water ones, undergo vertical migrations (Shipley et al., 2017). Such behavior is only inferred in many species based on indirect observations or taxonomic criteria. Some go up the water column at night and back down during the day in a diel pattern that might involve foraging near the sea surface (Nelson et al., 1997; Comfort and Weng, 2015; Rodríguez-Cabello et al., 2016). However, the diet, trophic role and interactions of deep-water species are still poorly known compared to shallower species. Indeed, they *(i)* live at a depth where samples are hard to obtain, *(ii)* are elusive species, *(iii)* are hard to observe directly and *(iv)* may have a high percentage of empty or regurgitated stomachs when fished (Pethybridge et al., 2011). In addition to that, a lot of deep-water shark species rarely grow beyond a meter long, making their supposed position of apex or mesopredator less obvious.

The lack of knowledge on the ecology of deep-water sharks reflects the lack of data in deep water. Moreover, this ecosystem is amongst the least well-known on Earth (Shipley et al., 2017). However, human

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pressures are increasing in deep parts of the seas, mostly with fisheries (Clark et al., 2015) and deep-water mining (Pinheiro et al., 2021). Impacts on shark populations have already been observed in several locations, raising concerns about their conservation and the consequences of their decline (Simpfendorfer and Kyne, 2009). Increasing knowledge of their trophic ecology is thus necessary to understand the role they play in deep-water ecosystems.

The most common method to obtain data about the diet of marine organisms is stomach content analysis. It is particularly relevant for the deep waters as direct observations are scarce (Shipley et al., 2017). However, stomach contents analysis only provides information about the recent diet and is biased toward digestion-resistant prey items because they stay longer in the stomach, with soft tissues being rapidly digested (Churchill et al., 2015). The retention of digestion-resistant structures, like cephalopod beaks or teleost otoliths, in the stomachs allows the use of keys to identify various prey items. Nevertheless, many specimens are needed to characterize the diet because of the high proportion of empty or regurgitated stomachs (Pethybridge et al., 2011).

Recently, DNA metabarcoding has provided a tool to obtain additional information on prey items digested in the stomachs of deep-water sharks (Finucci et al., 2016). The use of this method allows the identification of already decomposed prey items but relies on the amplification of various DNA sequences from a single sample, which might incur better amplification of more represented sequences. Estimating prey importance with this method is complex and, if not done correctly, can lead to erroneous results. Finally, DNA metabarcoding relies on already existing databases, especially if a high taxonomic resolution is desired, rendering it hard to apply in some areas of the oceans (Sousa et al., 2019). Other methods are increasingly used to assess the ecological importance of deep-water sharks. Stable Isotope Analysis (SIA) and Fatty Acid Profiling (FAP) provides ecologically relevant data over a more prolonged period than stomach content analysis (about one year for SIA and weeks to months for FAP) (Shipley et al., 2017; Meyer et al., 2019).

SIA relies on different ratios (expressed in ‰) of heavy to light stable isotopes inside the organism's tissues. These ratios depend directly on an individual's diet and are transferred in a relatively predictable manner from primary producers or prey to consumers (Fry, 2006). The most common isotope ratios in marine biology are $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$. The chemical characteristics of these isotopes help answer different ecological questions. The primary production sources at the base of the food web can be determined using the isotope ratios of carbon ($\delta^{13}C$) and sulfur ($\delta^{34}S$), although the last one is less precise. The isotope ratio of nitrogen ($\delta^{15}N$) is commonly employed to calculate trophic levels (Fry, 2006; Shipley et al., 2017). The combination of these isotopic ratios can also highlight the existence of ontogenic diet shifts, as well as the presence of migratory behavior (Shipley et al., 2017) and analysis of the isotopic niche and its metrics gives insight into the trophic niche (Layman et al., 2007; Jackson et al., 2011).

FAP is a method relying on the inability of vertebrates to produce a series of key-function fatty acids. Thus, many fatty acids retain the structure from dietary sources. By looking at the fatty acids present in a consumer, it is then possible to make inferences on their ecology. The mix of fatty acids found in the consumer will depend of its diet and of the biological characteristics of the predator itself because different species of consumers can synthesize different fatty acids, and must take others directly from their prey. It is then critical to have a good understanding of the physiology of the consumer when using this method (Meyer et al., 2019).

The present review summarizes the available information on the diet of deep-water sharks worldwide based on taxon-specific, places-specific, or methods-specific reviews (see Barnett et al., 2012; Stevens et al., 2011; Shipley et al., 2017). Because of the large number of prey species that vary in time and space, we only considered relatively high taxonomic levels for the different prey categories: chondrichthyes, teleosts, cephalopods, crustaceans, marine mammals, annelids, ctenophores, egg of chondrichthyes, siphonophores, and bivalves (see Annex 1). Higher taxonomic resolution is available in the corresponding papers. We address the definition of deep-water sharks and provide data on the proportion of deep-water species. We collate the available published information on stomach content analysis, metabarcoding, SIA, and FAP. We analyze the diet per family to reveal trends and give precision on species when available. Additional information on each reference used for each species is presented in Annex 1.

2. General data

2.1. Deep-water shark definition

Firstly, defining what a deep-water shark is critical. We refer here to the species included in the Selachii clade presented in Table 1. They are separated into two super-orders: Squalimorphii and Galeomorphii. The first contains five orders with 11 families, and the second one has four orders with 26 families.

To avoid the problem of various definitions according to authors or

Table 1
Taxonomic classification of the super-orders, orders and families of the Selachii. The number of species in each family is indicated next to it. Based on Pollerspöck and Straube (2021).

Selachii		
Super-order	Order	Family
Galeomorphii		
	Carcharhiniformes	
		Carcharhinidae (55)
		Galeocerdonidae (1)
		Hemigaleidae (8)
		Leptochariidae (1)
		Pentanchidae (112)
		Proscylliidae (6)
		Pseudotriakidae (5)
		Scyliorhinidae (50)
		Sphyrnidae (9)
		Triakidae (46)
	Heterodontiformes	
		Heterodontidae (9)
	Lamniformes	
		Alopiidae (3)
		Carchariidae (1)
		Cetorhinidae (1)
		Lamnidae (5)
		Megachasmidae (1)
		Mitsukurinidae (1)
		Odontaspididae (2)
		Pseudocarchariidae (1)
	Orectolobiformes	
		Brachaeluridae (2)
		Ginglymostomatidae (4)
		Hemiscylliidae (17)
		Orectolobidae (12)
		Parascylliidae (8)
		Rhincodontidae (1)
		Stegostomatidae (1)
Squalimorphii		
	Echinorhiniformes	
		Echinorhinidae (2)
	Hexanchiformes	
		Chlamydoselachidae (2)
		Hexanchidae (5)
	Pristiophoriformes	
		Pristiophoridae (10)
	Squaliformes	
		Centrophoridae (17)
		Dalatiidae (10)
		Etmopteridae (53)
		Oxynotidae (5)
		Somniosidae (17)
		Squalidae (41)
	Squatiniformes	
		Squatinidae (24)

fields of study, in this review, we will take the traditional definition of the deep-water as the part of the ocean located below 200m depths, approximately at the depth the continental shelf breaks (Gage and Tyler, 1991) and where photosynthesis becomes impossible due to light depletion (Antoine et al., 2006). Considering this, Cotton and Grubbs (2015) and Kyne and Simpfendorfer (2010) distinguished two categories of sharks: deep-water sharks that spend most of their time below 200m and shallow-water species that spend most of their time above 200m.

However, some species do not fit in either of these two categories for different reasons: (i) their depth range might extend both above and

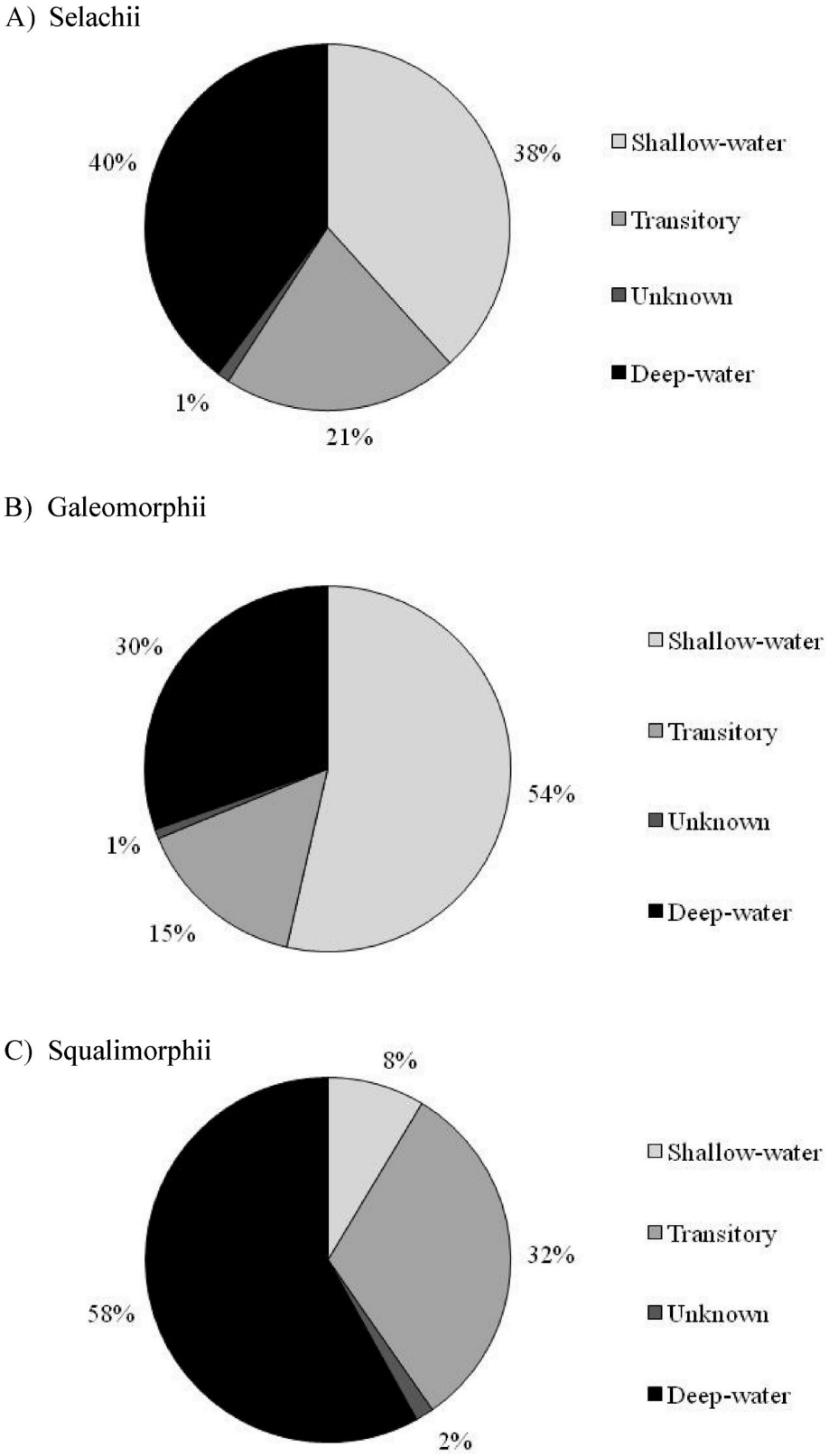

Fig. 1. Proportions of shark species classified as shallow-water, transitory, unknown and deep-water. A) Selachii, B) Squalimorphii and C) Galeomorphii.

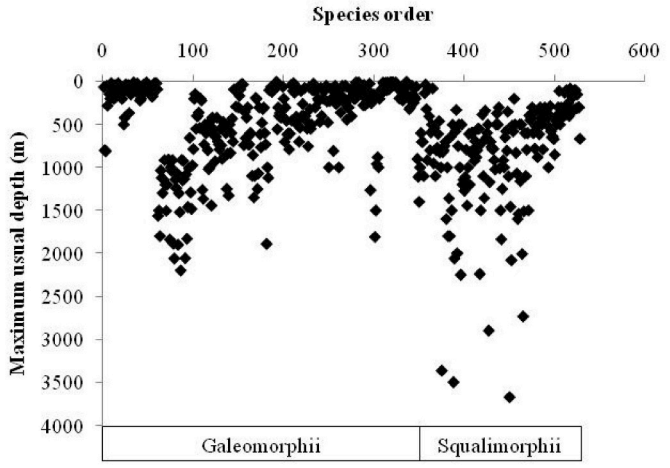

Fig. 2. Maximum usual depth for the different Selachii species. The species were classified following the taxonomic order in Table 1 then assigned a number from 1 to 548 following the classification.

below 200m, or there is a lack of data on their depth distribution, and it is not known if they spend most of their time above or below 200m; (ii) some species live at different depths depending on the season or geographical location, for example, *Squalus acanthias* is found primarily above 200m in the Mediterranean Sea (Yigin and I., 2013) and below 200m in New Zealand (Roberts et al., 2015). These uncertainties lead us to suggest a new class of transitory shark species. Similar classifications have been suggested by Heymans et al. (2011) with an "intermediate" depth class and by O'Hea et al. (2020) with a "slope" depth class. Both their definitions do not correspond precisely to the separation proposed here, and thus, we propose the term "transitory" for species with a usual depth of occurrence starting above 200m and extending below this limit (See Annex 2). A few species have been described from collection specimens or fish markets, and the depth of capture is unknown. For example, *Squalus formosus* is known from specimens collected in fish markets, but the depth of capture is unknown (White and Iglésias, 2011). We classified these as unknown in terms of living depth.

Depth ranges were obtained from scientific literature and the databases shark-reference (Pollerspöck and Straube, 2022) and IUCN red list (IUCN, 2021). When available, the usual depth range of a species is used as it is where it is expected to spend most of its time. Some species are known from a restricted number of individuals, or their biology is poorly known and their classification might change with increasing knowledge.

Of the 548 extant shark species currently recognized (see Annex 2), 218 (40%) are classified here as deep-water, 210 (38%) as shallow-water species, 114 (21%) as transitory and 6 (1%) as unknown (Fig. 1A). When considering the super-orders, Galeomorphii have a higher proportion of shallow-water species (52%) and a lower proportion of transitory (15%) and deep-water ones (30%) (Fig. 1B). Squalimorphii show the opposite trend, with a lower proportion of shallow-water species (8%) and higher proportions of transitory (32%) and

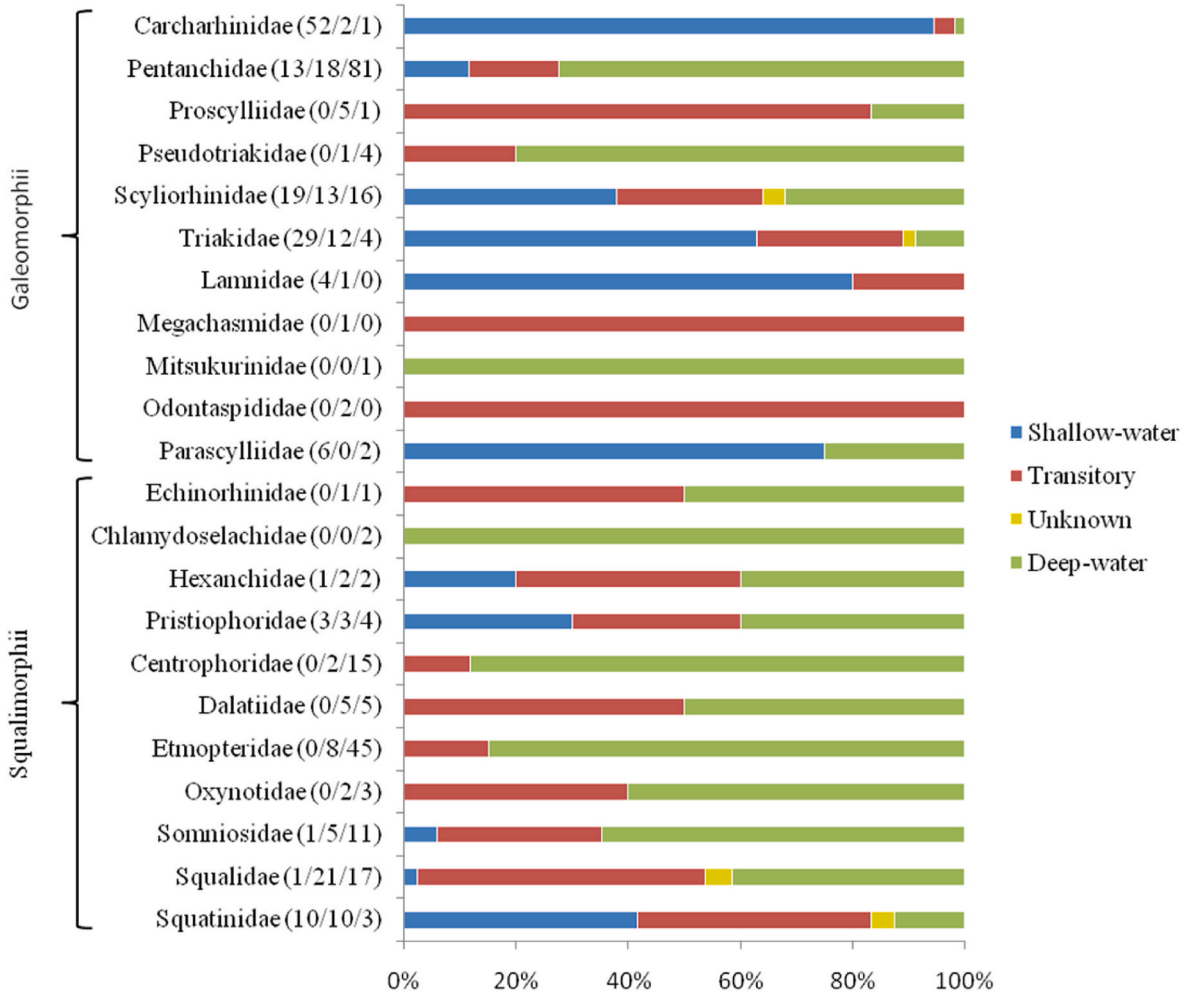

Fig. 3. (COLOR): Proportion of shallow-water, transitory, deep-water and unknown shark species per family. The families containing only shallow-water species are not included. The numbers next to each family are the number of shallow, transitory and deep species in this family.

deep-water species (58%) (Fig. 1C). Squalimorphii also go deeper than Galeomorphii, with a few species going below 2300 m (Fig. 2). However, most of the Squalimorphii do not go below the mesopelagic layer. A similar situation is found in the Galeomorphii, found from the surface to the mesopelagic zone but not below. Likely, most of the Selachii do not go deeper than 1300 m.

When considering the division between shallow, transitory and deep-water by family, half families (19 out of the 37) belong to only one category, either shallow, transitory or deep-water species (Fig. 3). Transitory species are always present in families with both shallow and deep-water species representatives. We consider only deep-water and transitory sharks in the following parts of this paper.

2.2. Diet knowledge and stomach fullness

In order to assess the current state of knowledge on the diet of the 332 transitory and deep-water sharks, we developed an index of diet knowledge and assigned a score to each deep-water and transitory species. The index values vary between 0 and 6. Table 2 describes the criteria for each score. The diet knowledge index aims to give a broad view of the literature, highlighting the strength and weaknesses of various species.

The number of species for each score is presented in Fig. 4. The vast majority of the species (210) entirely lack diet data hence being categorized as 0, while for 59 species, the diet is known only from a few stomachs, often taken opportunistically or in descriptive papers (scores 1 and 2). The third most important score corresponds to 37 species with one complete study (score 3). It illustrates a tendency in deep-water shark diet studies for analyses from a single set of samples, such as from a fishery survey campaign. Finally, good to complete diet knowledge is available for only 28 species (scores 4 to 6). Thus, the diet composition of deep-water and transitory shark species is currently poorly known.

When studying the stomach content of deep-water sharks, the proportion of empty or regurgitated stomachs is relatively high (Pethybridge et al., 2011). However, the proportion of stomachs with content varies significantly between studies, as shown in Fig. 5. Out of 229 records made in 179 studies, half of them described diet items in more than 70% of the stomachs examined.

Some shark families tend to be collected with more stomachs filled with prey (Fig. 6). It is the case for the families of the order Carcharhiniformes (Pentanchidae, Triakidae, Pseudotriakidae, Proscylliidae and Scyliorhinidae), which have, on average more than 70% stomachs with content. The only exception is the family Carcharhinidae, with an average of 40% of stomachs with content. Squaliformes (Centrophoridae, Etmopteridae, Oxynotidae, Squalidae, Dalatiidae and Somniosidae) seem to have a higher proportion of empty or regurgitated stomachs as they have, on average, between 40 and 70% stomachs with content. However, the proportion of empty stomachs is highly variable between studies, even in these orders. The relatively low number of studies on other families makes it hard to draw conclusions.

The differences between families might also be related to the methodology used during the different studies. It might vary if only the stomach is examined or the gut is also considered. Filtering the stomach contents to retain and closely examine small items, or making a coarse examination onboard a ship, might also lead to respectively fewer or more stomachs being classified as empty. Other factors could explain the results presented here, such as the time of the year, location, or capture method.

Table 2
Criteria and scores of the diet knowledge index.

Index score	Criteria
0	No data in the literature.
1	Information comes from less than 10 filled stomachs.
2	Information comes from incomplete studies. That is studies with 10–40 filled stomachs or studies considering only juveniles or one particular aspect of the diet.
3	Information comes from one complete study. That is a study with more than 40 filled stomachs considered.
4	Information comes from at least one complete study with ontogeny considered
5	Information comes from at least one complete study with ontogeny considered and comparing different geographical locations in the species range OR comparing different years and seasons without ontogeny considerations.
6	Information comes from at least one complete study with ontogeny considered and comparing different geographical locations in the species range AND comparing different years and seasons without ontogeny considerations.

3. Stomach content per families

3.1. Carcharhiniformes

3.1.1. Carcharhinidae

Among the 55 Carcharhinidae species, one is deep-water, and two are transitory (index 0 to 4, see annex 1). There is only sparse information on *Carcharhinus obscurus*. *Carcharhinus signatus* seems to feed mainly on teleost fishes supplemented by cephalopods (Júnior et al., 2009). *Carcharhinus obscurus* also feeds mainly on teleost fishes. Elasmobranchs often appear as secondary prey, having higher importance in larger individuals (Smale, 1991; Gelsleichter et al., 1999; Dudley et al., 2005). Cephalopods have also been reported as important prey (Simpfendorfer et al., 2001).

3.1.2. Pentanchidae

Out of the 112 species in the Pentanchidae family, 81 are deep-water and 18 transitory (index 0 to 6, see annex 1). There is a lack of data for 76 species (see annex one for the species list). Scarce data are available on the diet of *Apristurus aphyodes*, *Apristurus kampae*, Apristurus nakayai, Apristurus saldanha, Figaro boardmani, Galeus area, Galeus murinus *and* Halaelurus quagga. Teleosts were found in *A. nakayai* (Iglésias, 2012), cephalopods in *F. boardmani* (Pethybridge et al., 2011), shrimps in *A. kampae* (Taylor, 1972), *G. area* (Kiraly et al., 2003) and *H. quagga* (Akhilesh et al., 2011), a mix of teleosts and cephalopods in *A. saldanha*, with myctophids being the only teleost found in this case (Ebert et al., 1996), and finally crustaceans, squids and bony fishes in *A. aphyodes* (Moore et al., 2013) and *G. murinus* (Mauchline and Gordon, 1983).

Parmaturus xaniurus seems to feed mainly on crustaceans (Cross, 1988) and Apristurus japonicus on myctophids (Ando et al., 2002). Many species of this family seem to be generalist feeders, with teleosts, cephalopods, and crustaceans as the main prey in their stomachs. It is the case for *Apristurus brunneus* (Cross, 1988), Apristurus fedorovi (Ando et al., 2002), Apristurus microps (Ebert et al., 1996), Bythaelurus canescens (Acuña and Villarroel, 2010; Lopez et al., 2013), Bythaelurus dawsoni (Francis, 2006), Bythaelurus hispidus (Nair and Appukuttan, 1973; Appukuttan and Nair, 1988; Akhilesh et al., 2013), Bythaelurus stewarti (Weigmann et al., 2018), *Galeus atlanticus* (Ordines et al., 2021), Galeus eastmani (Horie and Tanaka, 2000), Galeus nipponensis (Horie and Tanaka, 2000), Galeus polli (Macpherson and Roel, 1987) and Holohalaelurus regani (Macpherson, 1989; Ebert et al., 1996; Richardson et al., 2000; van der Heever et al., 2020). Diets of Galeus eastmani and Galeus nipponensis showed seasonal, geographical, and sexual variations (Horie and Tanaka, 2000), while Bythaelurus hispidus and Holohalaelurus regani diets revealed ontogenic variations (Appukuttan and Nair, 1988).

The diet of *Galeus melastomus* is one of the most studied ones in deep-water sharks. The species is a broad generalist in its adult stage and feeds on what it finds, its diet shifting with seasons and supposedly with available prey (Mattson, 1981; Carrassón et al., 1992; Olaso et al., 2004; Fanelli et al., 2009; Preciado et al., 2009; Valls et al., 2011;

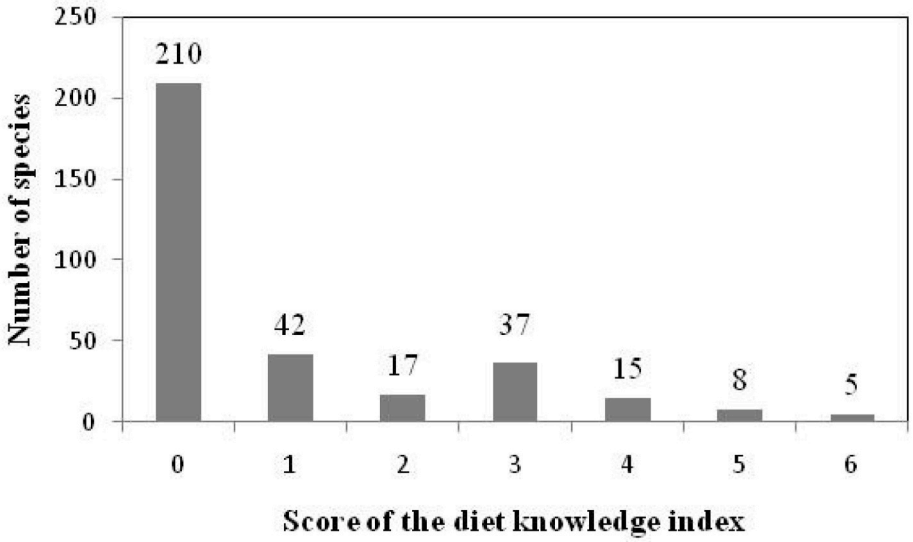

Fig. 4. Number of species for each score of the diet knowledge index.

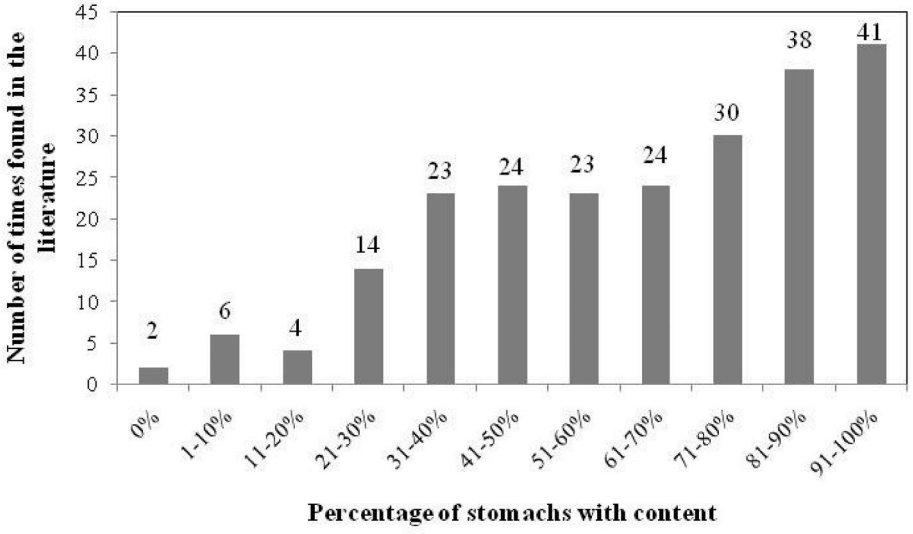

Fig. 5. Number of times a percentage of stomachs with content was reported in 179 studies with at least 10 stomachs examined per study. Studies with fewer examined stomachs were not considered here.

Anastasopoulou et al., 2013; Albo-Puigserver et al., 2015; Bengil et al., 2019; D'Iglio et al., 2021). The presence of pieces of prey too large compared to the shark's size made Carrassón et al. (1992) hypothesize that this species might hunt in groups in its adult stage. Moreover, Carrassón et al. (1992) suggested that it is an occasional scavenger. The species present ontogenic changes (Carrassón et al., 1992; Olaso et al., 2004; Fanelli et al., 2009; Preciado et al., 2009; Valls et al., 2011), with the immature stage feeding on different prey according to the various studies. It suggests that immatures are also generalists on prey organisms adapted to their size. The difference between life stages might also reflect the presence of depth segregation depending on size, with the mature individuals living closer to the bottom and hunting more benthic prey than the immature individuals staying closer to the surface and in the water column (Carrassón et al., 1992; Fanelli et al., 2009; Preciado et al., 2009; Valls et al., 2011).

In general, Pentanchidae feed on teleosts, cephalopods and crustaceans without preferences. Most species with substantial data appear to be broad generalists. *P. xaniurus* and *A. japonicus* seem to target more specific taxa, with crustaceans for the first and myctophids for the second.

3.2. *Proscylliidae*

Out of the 6 Proscylliidae species, one is deep-water, and five are transitory (index 0 to 3, see annex 1). *Ctenacis fehlmani*, *Eridacnis barbouri, Eridacnis sinuans*, *Proscyllium habereri* and *Proscyllium magnificum* have no reported data. *Eridacnis radcliffei* is the only deep-water species with information on the diet available: fishes (especially myctophids) are the most significant part of the diet, followed by crustaceans (mainly shrimps) and then squids (Nair and Appukuttan, 1973; Appukuttan and Nair, 1988; Akhilesh et al., 2012; Viji et al. 2017).

3.2.1. *Pseudotriakidae*

In the Pseudotriakidae family, four species are deep-water living, and one is transitory (index 0 to 3, see annex 1). Three of the five species have no published information on their diet: *Gollum suluensis*, *Planonasus indicus,* and *Planonasus parini*. The available data on *Pseudotriakis microdon* relies on a low number of stomachs containing teleosts, Squalidae, cephalopods, and shrimps (Yano and Musick, 1992; Crow et al., 1996). Stomach contents of *Gollum attenuatus* include mainly fishes (especially myctophids), followed by decapod crustaceans, then

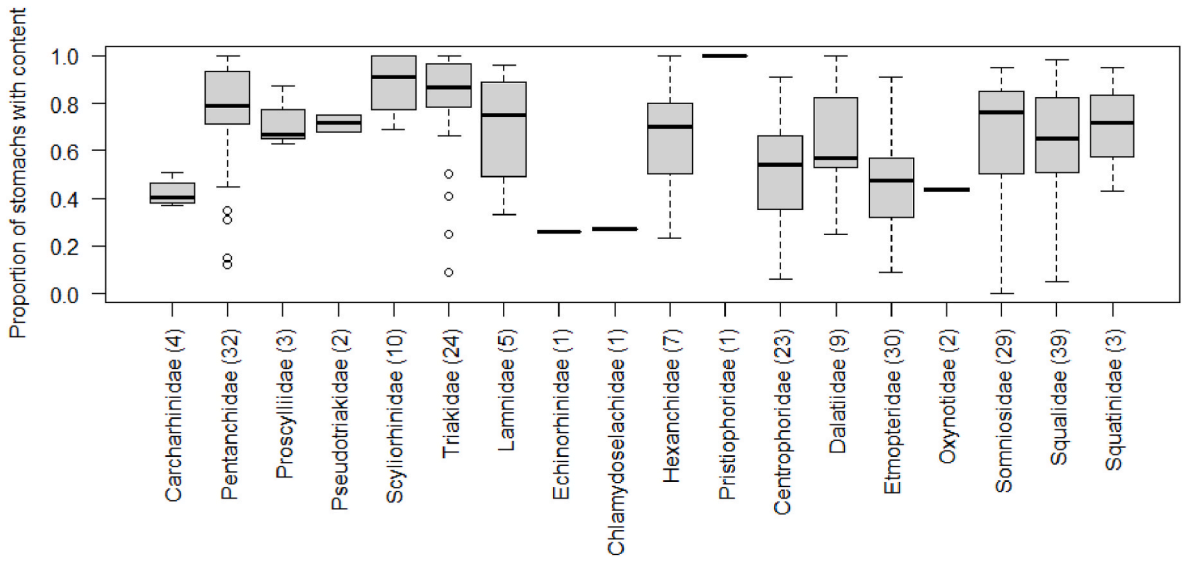

Fig. 6. Mean proportion of stomachs with content per family for deep and transitory shark species. Only the studies with at least 10 stomachs examined were considered. The number of replicates is indicated next to the family name. Error bars are standard errors.

cephalopods. However, slight differences depending on the sampling locations and the size category of the specimen studied exist (Yano, 1993).

3.2.2. Scyliorhinidae

Out of the 50 Scyliorhinidae species, 16 are deep-water and 13 transitory (index 0 to 5, see annex 1). 18 of these species lack published data (see annex one for species list). For Schroederichthys tenuis, Scyliorhinus cabofriensis, *Scyliorhinus torrei* and Scyliorhinus ugoi, limited information is available based on the description papers, but they rely on a low number of individuals with teleosts and cephalopods reported in their stomachs (Gomes and de Carvalho, 1995; Kiraly et al., 2003; Soares et al., 2015; Soares et al., 2016). Schroederichthys saurisqualus seems to feed mainly on cephalopods, but the data come mainly from juveniles (Sêga et al., 2020). For Scyliorhinus haeckelii, 11 stomach contents contained a mixed diet of polychaetes, crustaceans, and fishes (Belleggia et al., 2019). *Cephaloscyllium umbratile* has been reported to feed on bony fishes supplemented by cephalopods and cartilaginous fishes (Taniuchi, 1988). In Scyliorhinus meadi, stomach contents provided cephalopod beaks, egg cases, and euphausids (Burgess et al., 1979; Parsons, 1985). Teleosts, crustaceans, cephalopods and annelids have been reported in *Scyliorhinus retifer* (Bowman, 2000; Kiraly et al., 2003). Scyliorhinus capensis is known to feed on teleosts, cephalopods, and crustaceans. The importance of these three taxa varies between studies and suggests a generalist diet (Macpherson, 1989; Ebert et al., 1996; van der Heever et al., 2020). The diet of *Scyliorhinus torazame* also varies between studies, with crustaceans reported as the main prey by Huh et al. (2010) and teleost fishes and polychaetes by Park et al. (2019), both in the southern sea of South Korea. Crustaceans and teleosts mainly represented the diet of Cephaloscyllium isabellum. The smaller specimens ate more small crustaceans, while the larger ones ate more teleost, cephalopods, and mantis shrimp. This species is probably using a mix of ambush and active searching at night (Horn, 2016).

In general, teleosts, crustaceans, and cephalopods have been found to make most of the diet of deep-water Scyliorhinidae. The importance of these taxa varies widely between species and studies for the same species. Annelids also appear as important prey items in *S. haeckelii*, *S. rotifer*, and *S. torazame*.

3.2.3. Triakidae

In the family Triakidae, 16 of 46 species are deep-water and transitory (index 0 to 6, see annex 1). No data are available on the diet of 7 of these species: *Hemitriakis abdita*, *Iago garricki*, *Mustelus albipinnis*, *Mustelus mangalorensis*, *Mustelus mosis*, *Mustelus ravidus* and *Mustelus stevensi*. Of the nine remaining species, one is classified here as deep-water, the others being transitory species.

Mustelus canis, *Mustelus lenticulatus*, *Mustelus manazo*, *Mustelus palumbes* and *Mustelus punctulatus* feed mainly on crustaceans with small teleosts and cephalopods also present as secondary prey (Moss, 1972; Taniuchi et al., 1983; King and Clark, 1984; Rountree and Able, 1996; Smale and Compagno, 1997; Gelsleichter et al., 1999; Vianna et al., 2000; Yamaguchi and Taniuchi, 2000; Jardas et al., 2007; Lipej et al., 2011; Montemarano et al., 2016; Di Lorenzo et al., 2020; Park et al., 2020). An ontogenic shift is described for *M. canis*, *M. manazo* and *M. palumbes*, where young specimens feed on natant decapods while adults feed more on benthic crustaceans like crabs and mantis shrimps (Smale and Compagno, 1997; Vianna et al., 2000; Yamaguchi and Taniuchi, 2000; Park et al., 2020). In *Mustelus punctulatus*, cephalopods gain importance with increasing size (Lipej et al., 2011; Di Lorenzo et al., 2020). *Mustelus griseus* feeds mainly on crustaceans (Kamura and Hashimoto, 2004). *Iago omanensis* is a more generalist feeder with a variable mix of cephalopods, teleosts and crustaceans found in its stomach (Nair and Appukuttan, 1973; Waller and Baranes, 1994; Goldshmidt et al., 1996).

Galeorhinus galeus feeds mainly on teleosts with a variable occurrence of cephalopods, the importance of this last taxon being higher in adults without overcoming the importance of teleosts (Freer, 1992; Bulman et al., 2001; Morato et al., 2003; Lucifora et al., 2006; Dunn et al., 2010). A higher rate of filled stomachs containing more numerous prey items was observed in juveniles by Lucifora et al. (2006), possibly because younger individuals feed more often on anything they can catch to meet the dietary requirements for their growth. A similar diet has been reported in *Hypogaleus hyugaensis* (Simpfendorfer et al., 2002).

In general, deep-water Triakidae feed mainly on crustaceans. *I. omanensis* appear to be more generalist, and *G. galeus* and *H. hyugaensis* focus more on teleosts.

3.3. Lamniformes

3.3.1. Lamnidae

There is only one transitory species in the Lamnidae family: Lamna nasus (index 5, see annex 1). Over its wide geographic distribution, it feeds mainly on teleost fishes, with cephalopods often reported as secondary prey (Yatsu, 1995; Joyce et al., 2002; Horn et al., 2013; Belleggia

et al., 2021).

3.3.2. Megachasmidae

M. pelagios (index 1, see annex 1) is known to perform vertical migration, coming up in shallow waters at night to feed on euphausiids and other zooplanktonic species (Nelson et al., 1997). It is one of the three shark species that filter feed, the other two being the basking shark (Cetorhinus maximus) and the whale shark (Rhincodon typus). Nakaya et al. (2008) suggest that it has an engulfment feeding method similar to humpback whales based on oral morphology and jaw articulations. The hypothesis that the particular white band protruding on the upper lip might be bioluminescent and attract prey close to the mouth (Taylor et al., 1983) was challenged by a recent paper not finding any bioluminescent structure in this species (Duchatelet et al., 2020) supporting the hypothesis this white band could attract prey by reflecting light or would serve in intraspecific communication.

3.3.3. Mitsukurinidae

Mitsukurina owstoni is the only known species of this deep-water family (index 2, see annex 1). It presents a particular jaw morphology allowing it to protrude its jaw forward a considerable distance to capture prey (Nakaya et al., 2016). So far, it seems to feed primarily on bony fishes, but most of the data come from immature specimens caught in Japan (Yano et al., 2007b) while the species is reported worldwide (Orlov et al., 2017).

3.3.4. Odontaspididae

The two deep-water species of this group are Odontaspis ferox and Odontaspis noronhai *(index 1, see annex 1)*. Their diet is known only from scarce stomach contents examination as they are both elusive species. O. ferox feeds on sharks, bony fishes, squid, and shrimps (Bass et al., 1975; Seigel and Compagno, 1986; Kiraly et al., 2003; Fergusson et al., 2008). Only one specimen of O. noronhai provided stomach content with the remains of teleosts and a squid (Branstetter and McEachran, 1986).

3.4. Orectolobiformes

3.4.1. Parascylliidae

The only two deep-water species of the 8 in this family, *Cirrhoscyllium japonicum* and *Parascyllium sparsimaculatum*, are poorly known, and no dietary information is currently available in the literature (index 0, see annex 1).

3.5. Echinorhiniformes

3.5.1. Echinorhinidae

There are two species in this family, one deep and one transitory: *Echinorhinus brucus* and *Echinorhinus cookei* (index 1 and 4, see annex 1). The available data on their diet are scarce. For *Echinorhinus cookei*, stomach content revealed the presence of sharks (including young sixgills), teleosts, and cephalopods (Compagno, 1984; Crow et al., 1996). For *Echinorhinus brucus*, authors report teleosts, small sharks and crabs being part of its diet (Musick and McEachran, 1969; Silas and Selvaraj, 1972; Appukuttan and Nair, 1988; Kiraly et al., 2003). The most comprehensive study was made by Akhilesh et al. (2013) on 431 *Echinorhinus brucus* fished southwest of India. One hundred thirteen stomachs contained identifiable prey, most of them crustaceans and teleosts. Elasmobranchs and cephalopods were also present. The smaller *E. brucus* fed exclusively on crustaceans.

3.6. Hexanchifores

3.6.1. Chlamydoselachidae

The family Chlamydoselachidae contains only two species, both of which live in deep-water: *Chlamydoselachus africana* and *Chlamydoselachus anguineus* (index 1 and 2, see annex 1). *Chlamydoselachus africana* lives off the southern coasts of Africa (Ebert and Compagno, 2009), and the second one has a wide distribution worldwide (Kubota et al., 1991). Dietary information for *C. africana* is only available from the stomachs of five specimens in the species description paper (Ebert and Compagno, 2009). The only prey types found were small Chondrichthyes (scyliorhinid shark species). *C. anguineus* also feeds on other sharks (Taniuchi, 1987; Ebert and Compagno, 2009), but a study made by Kubota et al. (1991) on 37 stomachs with content from Suruga Bay, Japan, found mostly squids (frequency of occurrence of 60.5%) with a smaller proportion of bony fishes (frequency of occurrence of 10.5%). Fast swimming epipelagic squids were part of the prey, and Kubota et al. (1991) suggest that they are captured while being injured or exhausted after spawning because *C. anguineus* does not have good swimming capabilities. However, Ebert and Compagno (2009) suggest that Chlamydoselachidae slowly approach their prey and then make a sudden lunge to capture them. They also hypothesize that they are specialized for grasping and engulfing large prey items based on their body shape, teeth morphology, highly distensible jaw and large buccal cavity and the presence of food items in stomachs up to ½ the size of the sharks. The two Chlamydoselachidae species are commonly caught in midwater trawls and thus migrate vertically, potentially to capture prey (Ebert and Compagno, 2009).

The low number of stomachs examined for *C. africana* and the scarcity of dietary information outside Suruga Bay for *C. anguineus* call for more observations of both species' stomach content to describe their diet accurately.

3.6.2. Hexanchidae

The family Hexanchidae contains five species, out of which two are deep-water ones and two others are transitory (index 1 to 5, see annex 1). Studies on their feeding habits are scarce; a large part of the information comes from opportunistically collected stomachs. For the species *Hexanchus nakamurai* and *Hexanchus vitulus*, it is the only kind of data available (Barnett et al., 2012). The stomachs of *H. nakamurai* contained teleosts with the rare occurrence of octopus, elasmobranch and crustacean (Barnett et al., 2012). For *H. vitulus*, to our knowledge, only one stomach content has been reported by Forster et al. (1970), containing one pelagic teleost. However, this species, described by Springer and Waller in 1969, has been considered a subspecies of *H. nakamurai* following Ebert (1989) and Taniuchi and Tachikawa (1991). It had only been redescribed by Daly-Engel et al. in 2018. It could explain the lack of dietary information for *H. vitulus*, and its stomach contents assigned to *H. nakamurai*. Given the former taxonomic confusion, new studies could provide specific dietary requirements.

The diet of *H. griseus* contains a wide array of different prey types. An extensive study on stomach contents was made by Ebert (1994), who found ontogenic changes with size in southern Africa. Individuals of less than 120 cm eat mostly cephalopods and teleosts, with some chondrichthyans occurring in the diet, while individuals between 120 and 200 cm eat mostly teleosts, chondrichthyans and cephalopods. Marine mammal remains are also found in the stomachs of this size category but are less important. Individuals of more than 200 cm have a high incidence of marine mammals and large teleosts, with cephalopods and chondrichthyans of secondary importance. Chondrichthyans and teleosts have also been reported as main prey items in other studies (Ebert, 1986a, 1986b; Kabasakal, 2004; Celona et al., 2005), but Celona et al. (2005) noticed that the diet of individuals from central Mediterranea consists of mainly small with some large species of teleosts, despite the presence of numerous small chondrichthyan species in the same habitat. They suggest that the diet of *H. griseus* varies with location. This shark is known to perform vertical migration and feeds on shallow-water species, sometimes fast-swimming ones, while *H. griseus* is rather sluggish (Ebert, 1994). It may be that this shark hunts using camouflage to approach its prey (Ebert, 1994). It is also known that *H. griseus* feeds on marine animals trapped in human fishing gear (Celona et al., 2005) and

scavenges carrions (Aguzzi et al., 2018).

Heptranchias perlo seems to have a more specialized diet than *H. griseus*, mainly feeding on deep-water teleosts (Capapé, 1980; Braccini, 2008), except at meteor seamount where cephalopods have as much importance as teleosts in diet (Frentzel-Beyme and Köster, 2002). Crustaceans and chondrichthyans can also be found in stomach contents but are of minor importance (Capapé, 1980; Frentzel-Beyme and Köster, 2002; Braccini, 2008). Braccini (2008) found an ontogenic shift in diet, small (48.5–90 cm) and large (90–136.5 mm) individuals, both preying mainly on teleost species but the latter ones preying on larger prey. The relatively high incidence of empty stomachs in this study (24%) led the authors to qualify *H. perlo* as an intermittent feeder.

3.7. Pristiophoriformes

3.7.1. Pristiophoridae

Four of the 10 Pristiophoridae species are deep-water, and three are transitory (index 0 to 2, see annex 1). Diet information is only available for two of them: Pliotrema warreni and Pristiophorus nancyae. The stomach contents of 32 P. warreni consisted mainly of bony fish remains (Foor, 2016). On the other hand, only shrimp remains were identified in the stomachs of the eight specimens used for the original description of P. nancyae (Ebert and Cailliet, 2011). The typical rostrum of the Pristiophoridae serves for predation through prey sensing and capture with a secondary utility in defense when needed (Nevatte et al., 2017).

3.8. Squaliformes

3.8.1. Centrophoridae

The family Centrophoridae contains 17 species (2 transitory and 15 deep), of which 8 have no available dietary information (index 0 to 4, see annex 1). *Centrophorus moluccensis* and *Centrophorus zeehaani* have been observed to feed mainly on teleost fishes and cephalopods (Daley et al., 2002; Graham and Daley, 2011; Pethybridge et al., 2011), with crustaceans being also important in the diet of *C. zeehaani* (Graham and Daley, 2011). However, these data come from a restricted number of stomachs with content and thus must be viewed with some reserve, even if they might indicate the actual diet.

More complete information on the feeding habits of the remaining seven species can be found in the literature: *Centrophorus granulosus*, *Centrophorus harrissoni*, *Centrophorus squamosus*, *Centrophorus uyato*, *Deania calcea*, *Deania profundorum* and *Deania quadrispinosa*. Teleost fishes appear to be the main prey in these species, with cephalopods often being of secondary importance and sometimes crustaceans (Forster et al., 1970; Mauchline and Gordon, 1983; Blaber and Bulman, 1987; Ebert et al., 1992; Saldanha et al., 1995; Bulman et al., 2002; Daley et al., 2002; Capapé et al., 2003; Megalofonou and Chatzispyrou, 2006; Preciado et al., 2009; Dunn et al., 2010; Pethybridge et al., 2011; Dunn et al., 2013; Churchill et al., 2015). Myctophids appear to be the teleost taxa mainly found in stomach contents, and Centrophoridae species are qualified as piscivores (Blaber and Bulman, 1987; Bulman et al., 2002; Megalofonou and Chatzispyrou, 2006; Dunn et al., 2013).

3.8.2. Dalatiidae

In the Dalatiidae family, five species are deep-water living, and five are transitory (index 0 to 5, see annex 1). 6 out of 10 species lack data on their diet: *Euprotomicroides zantedeschia*, *Heteroscymnoides marleyi*, *Isistius plutodus*, *Mollisquama mississippiensis*, *Mollisquama parini*, and *Squaliolus aliae*. Few data are available on *Euprotomicrus bispinatus*. Hubbs et al. (1967) caught this species in surface water but found mostly deep-water squids and teleosts in the stomachs, suggesting that *E. bispinatus* undergo vertical migrations possibly to follow its prey. *Squaliolus laticaudus* is one of the smallest shark species, with squids and teleosts reported in its stomach (Seigel, 1978; Driggers et al., 2010).

Dalatias licha feeds on teleosts, cephalopods, and decapods crustaceans (Matallanas, 1982; Dunn et al., 2010; Navarro et al., 2014), teleosts being the most important prey item in most cases (Matallanas, 1982; Dunn et al., 2010; Navarro et al., 2014). *D. licha* is also known to feed on other deep-water sharks (Matallanas, 1982; Kabasakal and Kabasakal, 2002; Dunn et al., 2010; Pethybridge et al., 2011; Navarro et al., 2014; Barría et al., 2015). Navarro et al. (2014) describe this species as a true shark predator, but other authors report sharks as secondary prey (Matallanas, 1982). *D. licha* has a high lipid content in the liver compared to other species (Lewis, 1969), and Navarro et al. (2014) suggest that it obtains these lipids by eating other sharks.

Isistius brasiliensis is known for its particular predatory behavior. Its jaw morphology allows it to cut pieces of much larger prey (Strasburg, 1963). Large teleosts, sharks, cetaceans, and seals have been found with bite marks attributed to the cookie-cutter shark (Jones, 1971; Taylor et al., 1983; Le Boeuf et al., 1987; Muñoz-Chápuli et al., 1988; Hiruki et al., 1993; Gasparini and Sazima, 1996; Evans et al., 2002; McSweeney et al., 2007; Papastamatiou et al., 2010; Hoyos-Padilla et al., 2013). Contents of cookie-cutter stomachs revealed the presence of large chunks of teleosts, squids and cetaceans swallowed whole (Strasburg, 1963; Jahn and Haedrich, 1988; Murakami et al., 2018). The depth range of these prey extends from the surface to deep-water habitats, which agrees with *I. brasiliensis* large diurnal vertical migration from 3600 m to 0 (Kiraly et al., 2003). The species also presents a particular pattern of bioluminescence, with a black band located just behind the jaw potentially serving as a lure for large organisms to get close and bite off a piece of the approaching prey (Widder, 1998). Carlisle et al. (2021) highlighted the presence of different teleost taxa in the guts of *I. brasiliensis* using DNA metabarcoding.

In general, Dalatiidae seem to have a widely different diet between species. The larger *Dalatias licha* feeds on teleosts, cephalopods, crustaceans, and other sharks, while the smaller *E. bispinatus* and *S. aliae* seem to focus more on squids and teleosts. *I. brasiliensis* has a unique feeding behavior with the capacity to cut pieces of much larger prey and target a large diversity of prey.

3.9. Etmopteridae

The family Etmopteridae contains 45 deep-water species and eight transitory, of which 32 have no available dietary information (index 0 to 5, see annex 1). Among the 21 remaining species, nine species revealed a weak number of data available, making the dietary information indicative and should not be considered complete. In these cases, cephalopods and crustaceans have been reported as the main items in the stomachs of *Centroscyllium kamoharai* (Daley et al., 2002) and *Etmopterus bullisi* (McEachran and Fechhelm, 1998). *Etmopterus bigelowi* has been found to feed on squids and small fishes (Kiraly et al., 2003), while *Etmopterus schultzi*, *Etmopterus splendidus* and *Etmopterus virens* had cephalopods in their stomachs (Yano, 1988; Compagno, 2002). The presence of myctophids, euphausiids and squids has been reported by (Straube et al., 2011) in the stomachs of *Etmopterus viator*. Euphausiids and teleosts have been reported in *Centroscyllium ritteri* (Baba et al., 1987), myctophids, squids and crustaceans in *Etmopterus villosus* (Dolganov, 2019), and teleost remains in *Centroscyllium excelsum* (Shirai and Nakaya, 1990).

The diet of *Aculeola nigra*, *Centroscyllium fabricii*, *Etmopterus granulosus*, *Etmopterus brachyurus*, *Etmopterus compagnoi*, *Etmopterus lucifer*, *Etmopterus princeps*, *Etmopterus pusillus*, *Etmopterus spinax*, *Etmopterus unicolor* and *Trigonognathus kabeyai* is better known. All these species seem to feed opportunistically on teleosts (mostly myctophids), cephalopods and crustaceans (mostly shrimps), with the importance of these three taxa varying between studies (Mauchline and Gordon, 1983; Ebert et al., 1992; Saldanha et al., 1995; Punzón and Herrera, 2000; Jakobsdóttir, 2001; Santos and Borges, 2001; Bergstad et al., 2003; Capapé et al., 2003; Neiva et al., 2006; Jones, 2008; Fanelli et al., 2009; Acuña and Villarroel, 2010; Hallett and Daley, 2011; Pethybridge et al., 2011; Valls et al., 2011; Dunn et al., 2013; Isbert et al., 2014; Galland, 2015; Bengil et al., 2019; Dolganov, 2019) except for *T. kabeyaii*,

E. pusillus and *E. lucifer*, where the few extensive studies on stomach contents have found mostly teleosts for the first two (Santos and Borges, 2001; Yano et al., 2003; Xavier et al., 2012) and squids for the third (Baba et al., 1987). Interestingly, for *E. granulosus*, *E. lucifer*, and *E. spinax*, chunks of large teleost species found in the stomach lead some authors to suggest that it might come from organisms caught in the same net or scavenging (Galland, 2015; Bulman et al., 2002). Others suggest that they represent pieces taken on large living prey thanks to schooling behavior hence possible group hunting (Clark et al., 1989; Daley et al., 2002; Jones, 2008; Bello, 1998; Neiva et al., 2006; Finucci et al., 2018; Pinte et al., 2020). Ontogenic changes in diet have been reported in *A. nigra*, *C. fabricii*, *E. granulosus*, *E. lucifer*, *E. princeps*, *E. pusillus*, *E. spinax* and *T. kabeyai* (Mauchline and Gordon, 1983; Baba et al., 1987; Punzón and Herrera, 2000; Jakobsdóttir, 2001; Bergstad et al., 2003; Capapé et al., 2003; Yano et al., 2003; Neiva et al., 2006; Jones, 2008; Fanelli et al., 2009; Acuña and Villarroel, 2010; Hallett and Daley, 2011; Xavier et al., 2012; Isbert et al., 2014; Bengil et al., 2019).

Offals from fishing have been found for *C. fabricii* as the most important food items found by Punzón and Herrera (2000), but their data collection occurred on a large commercial fishing vessel. Ontogenic changes in diet are commonly found in Etmopteridae species, with larger individuals switching to larger prey, and the different taxa's importance might also change. Such changes are found in *C. fabricii* (Punzón and Herrera, 2000), *E. granuslosus* (Hallett and Daley, 2011), *E. pusillus* (Xavier et al., 2012) and *E. spinax* (Mauchline and Gordon, 1983; Bergstad et al., 2003; Capapé et al., 2003; Neiva et al., 2006; Fanelli et al., 2009; Isbert et al., 2014).

Etmopteridae seem to feed on a mix of myctophids, squids, and shrimps. The last one appears less important in *T. kabeyaii*, *E. pusillus*, and *E. lucifer*. Relatively large pieces of prey have been found in the stomachs of several species, leading to hypotheses of net feeding, scavenging, or group hunting.

3.10. Oxynotidae

The family Oxynotidae contains five species, three being deep ones and two transitory (index 0 to 3, see annex 1). They present a particular morphology with a triangular body shape. The diets of *Oxynotus caribbaeus*, *Oxynotus japonicus*, and *Oxynotus paradoxus* are unknown. In New Zealand, *Oxynotus bruniensis* is known to feed on elasmobranch eggs and embryos and, more specifically, on the ones of chimaeras (Finucci et al., 2016). *Oxynotus centrina* diet contains a significant part of polychaetes, with, to a lesser extent, sipunculids, crustaceans, and teleost fishes (Capapé, 1975, 2008; Barría et al., 2015). However, Barrull and Mate (2001) found yolk sacs and embryos of *Scyliorhinus canicula* in the stomachs of two individuals in the Mediterranean Sea. In addition, Guallart et al. (2015) managed to maintain a specimen in an aquarium for two years. The individual did not feed on polychaetes but only on various elasmobranch eggs, piercing them and sucking the content. From these observations and the known dietary items of *O. bruniensis*, *O. centrina* possibly feeds primarily on elasmobranch eggs, ingesting other organisms on the capsules and/or supplementing its diet with the reported taxa. Other studies might have missed yolk contents in the stomachs as it appears similar to digested material and might go through the digestive tract relatively rapidly.

3.11. Somniosidae

Eleven species of the Somniosidae family are deep-water ones, and five are transitory (index 0 to 4, see annex 1). The diet is unknown for 5 of these 16 species: *Scymnodalatias albicauda*, *Scymnodalatias garricki*, *Scymnodon ichiharai*, *Somniosus longus* and *Scymnodon ringens*. The data available for *Zameus squamulosus* are very scarce as Ebert et al. (1992) found only empty stomachs, and Kiraly et al. (2003) reported the presence of fishes and bottom invertebrates. Squid beaks and eye lenses have been found in the stomachs of *Scymnodalatias scherwoodi* by Dolganov (2019). For *Scymnodon ringens*, fish bones and crustacean remains have been found in one stomach with content (Mauchline and Gordon, 1983). *Somniosus antarcticus* seems to feed on cephalopods, teleosts, mammals and birds in that order (Yano et al., 2007a), while squids have been found in the stomachs of *Somniosus rostratus* (Golani, 1986; Barría et al., 2015).

Centroscymnus coelolepis, *Centroscymnus owstonii* and *Centroselachus crepidater* have been reported to feed mainly either on cephalopods or on teleost fishes, myctophids being the most important in *C. crepidater* (Mauchline and Gordon, 1983; Yano and Tanaka, 1984; Carrassón et al., 1992; Ebert et al., 1992; Bulman et al., 2002; Carrassón and Cartes, 2002; Daley et al., 2002; Dunn et al., 2010; Pethybridge et al., 2011, 2012). Decapod crustaceans are important only in young *C. coelolepis* (Carrassón et al., 1992). Moreover, in *C. coelolepis*, pieces of cetaceans have been reported (Mauchline and Gordon, 1983; Ebert et al., 1992; Bulman et al., 2002; Daley et al., 2002). The authors hypothesize that these pieces come from scavenging. *Scymnodon macracanthus* seems to feed mainly on teleost fishes, but other sharks (especially Etmopteridae) and cetacean pieces have often been reported too (Daley et al., 2002; Dunn et al., 2010).

Somniosus microcephalus and *Somniosus pacificus* have received a significant focus on their diet; they are opportunistic and feed on a large array of prey. Teleosts make a large part of their diet (Ebert, 1987; Yang and Page, 1999; Sigler et al., 2006; Yano et al., 2007a; McMeans et al., 2010; Nielsen et al., 2014; McMeans et al., 2015; Nielsen et al., 2019). An ontogenic shift has been described, with cephalopods being predominant in smaller individuals while in larger ones, marine mammals form an important part of the diet, especially whale carrions and seals. Findings of fresh seals' flesh in stomachs suggest that they are hunted and not scavenged on, despite the apparent sluggish movements and slow speed of the two Somniosus species (Ridoux et al., 1998; Sigler et al., 2006; Yano et al., 2007a; McMeans et al., 2010, 2015; Nielsen et al., 2014). Nielsen et al. (2019) suggested that *S. microcephalus* catches seals when they are sleeping. Likewise, Ebert et al. (1987) mentioned, in the stomachs of S. pacificus, the presence of fast-swimming teleosts supposedly eaten while resting, but another hunting method like an ambush or high burst speed might be present. *S. microcephalus* has been reported to feed on fishing offals (Beck and Mansfield, 1969; Leclerc et al., 2011).

In general, cephalopods and teleost fishes seem to be the primary prey of Somniosidae. Marine mammals, especially seals and whale carrions, appear important for *S. microcephalus* and *S. pacificus*.

3.12. Squalidae

The Squalidae comprise 41 species, and on the 21 deep and 17 transitory (index 0 to 6, see annex 1), the diet of 32 species is currently unknown (see annex 1 for the list of these species). Little information is available for *Cirrhigaleus asper* and *Squalus cubensis*, the first seemingly feeding on squids and teleosts (Kiraly et al., 2003) and the second on teleosts (Churchill et al., 2015).

The diet of *Squalus blainville* is known from numerous articles. Teleosts are the main prey of this species (Quignard, 1971; Capapé, 1975; Kousteni et al., 2017; Anastasopoulou et al., 2018; Bonnici et al., 2018; Bengil et al., 2019; Yemisken et al., 2019), crustaceans being more critical only in the study of Martinho et al. (2012) in Portugal and one population of the Aegean Sea in Kousteni et al. (2017). Cephalopods have been found as the main prey by Bonnici et al. (2018), but both cephalopods and crustaceans are otherwise secondary prey. *S. blainville* is qualified as a generalist opportunistic predator (Quignard, 1971; Martinho et al., 2012; Kousteni et al., 2017; Bonnici et al., 2018). *Squalus megalops* has been found to feed mainly on cephalopods in Australia, with teleosts being secondary prey items (Braccini et al., 2005) and on teleosts (especially myctophids) in South Africa with cephalopods being secondary prey items (Ebert et al., 1992; Huh et al., 2010). *Squalus mitsukurii* has been found to feed on teleosts, cephalopods

and crustaceans, with the importance of these three taxa varying with locations (Ebert et al., 1992; Wilson and Seki, 1994; Daley et al., 2002; Churchill et al., 2015).

The information provided here must be taken with caution concerning the three species S. blainville, S. megalops and S. mitsukurii. Indeed, there are identification concerns about *S. blainville* being confused with *S. mitsukurii* and *S. megalops*. In addition, *S. megalops* and *S. mitsukurii* belong to a complex of similar species. Several species have been described from individuals associated with *S. mitsukurii*, and more are expected to be described (Cavanagh and Lisney, 2003; Cavanagh et al., 2009; Ebert et al., 2009).

The species *Squalus acanthias* is one of the best-known species. It is a worldwide spread species considered to feed on various taxa, presenting an opportunistic feeding behavior. Throughout the different studies, teleost fishes are the main prey most of the time, with squids and crustaceans often found as secondary prey (Graham, 1938; Holden, 1966; Nammack, 1982; Ebert et al., 1992; Ellis et al., 1996; Avsar, 2001; Laptikhovsky et al., 2001; Henderson et al., 2002; Demirhan and Seyhan, 2007; Dunn et al., 2013; Gračan et al., 2017; Pitchford et al., 2020; Gül and Demirel, 2021). Ontogenic changes in diet are well-reported, with adults gaining access to more prey with increasing size (Jones and Geen, 1977; Nammack, 1982; Hanchet, 1991; Ellis et al., 1996; Laptikhovsky et al., 2001; Koen Alonso et al., 2002; Dunn et al., 2013). Cannibalism has been observed (Hanchet, 1991). Belleggia et al. (2012) saw a change from teleosts to squids as the main prey in Argentina over an important period. They hypothesize that the regional fishing pressure might have forced *S. acanthias* to switch their primary prey. Pitchford et al. (2020) used real-time PCR TaqMan on specimens of *Squalus acanthias* to unravel a predator-prey relationship with cods which was never discovered by conventional stomach examination.

In general, deep-water Squalidae feed on teleosts, cephalopods, and crustaceans. The importance of these taxa varies between studies of the same species and between locations. Thus, the species of this family might feed on abundant prey in their environment.

3.13. Squatiniformes

3.13.1. Squatinidae

Among the 24 Squatinidae species, three are qualified as deep-water and ten as transitory (index 0 to 4, see annex 1). On the ten transitory species, information is available for only four of them: *Squatina aculeata*, *Squatina africana*, *Squatina argentina*, and *Squatina armata*. No complete diet study has been done for the first of the four species, but squid, shrimp, small shark, and teleost remains have been reported from its stomach contents (Compagno, 1984; Corsini and Zava, 2007). Concerning *S. africana*, its diet comprised teleosts and cephalopods with very few occurrences of other items (Bass et al., 1975; Shelmerdine and Cliff, 2006). Only one stomach of *Squatina argentina* contained the remains of a *Merluccius hubbsi* (Belleggia et al., 2019). *Squatina armata* feeds mainly on teleost fishes and crustaceans (Velázquez-Chiquito et al., 2021). On the three deep-water species, information is available for only *Squatina tergocellata*. Bridge et al. (1999) found stomach contents of *S. tergocellata* that were highly similar to *S. africana*, with only squid and teleosts present.

In general, few studies on the diet of Squatinidae have found teleosts and squids as the most important items, with crustaceans also being important in *S. armata* only. Most Squatinidae are ambush predators, lying motionless on the seafloor, sometimes buried in the sand, until prey comes close enough (Fouts and Nelson, 1999), a behavior not yet described in all the species despite their similar morphology.

4. Additional information on trophic ecology

An illustration of the general trends in the deep-water shark diets shows the relative importance of prey taxa consumed in various families (Fig. 7). For each family, the number of species ($N_{s,i}$) within which each prey category (i) occurred was counted. Only studies with at least 10 filled stomachs and diet analyses were included. The relative occurrence of each prey category per family ($R_{family,i}$) was then calculated as:

$$R_{family,i} = N_{s,i} \Big/ \sum_{i=1}^{i=10} N_{s,i}$$

The calculation is shown in Annex 1. Many deep-water sharks seem to be generalists that feed on available prey in the environment. The most common taxa are teleost fishes, crustaceans and cephalopods. Usually, the size of the prey species found in stomach contents depends on the shark's size. However, group hunting on large prey is reported in Etmopteridae (Bello, 1998; Neiva et al., 2006) and Pentanchidae (Carrassón et al., 1992). Chlamydoselachidae are also believed to hunt large prey relative to their size (Ebert and Compagno, 2009). More specialized diets are also present in deep and transitory sharks. Some families have all species specialized, like the Oxynotidae, but in others, species show specialization different from other closely related species (e.g., *Isistius brasiliensis* or *Galeorhinus galeus*).

To further look at the differences between families in more detail, a Multiple Correspondence Analysis (MCA) was conducted comparing the diet composition of species per order, family and depth of occurrence. The presence or absence of a prey category for each species was determined using papers with at least ten filled stomachs analyzed. The prey categories were the same as the ones used in annex one. The analysis was performed using R version 3.4.3. There was no separation of diet composition with depth at the considered taxonomic scale. The only order separating from the others was the Hexanchiformes because they consumed Chondrichthyes. The other species consuming Chondrichthyes did not drive the separation of their orders at this scale.

When considering the families, more differences appeared. The vast majority of the families did not separate from each other and the different prey categories, illustrating the generalist tendency found in deep-water sharks with teleost fishes, cephalopods and crustaceans being the main prey categories. Four families are separated from the others in different dimensions. Oxynotidae were separated by their consumption of Chondrichthyes eggs and embryos (Fig. 8A), Hexanchidae and Chlamydoselachidae by their consumtion of Chondrichthyes (Fig. 8B) and Somniosidae by their consumption of marine mammals (Fig. 8C). The clustering analysis of the MCA was best represented with three clusters (Fig. 8D). The Oxynotidae formed a cluster alone. The species with teleosts and another prey category but without crustaceans as main prey were clustered together, corresponding to the families Chlamydoselachidae, Hexanchidae and Somniosidae and the species *Isistius brasiliensis* and *Dalatias licha*. The presence of these last two species in this cluster shows their particular diet inside their families. Again, the vast majority of the other species were clustered together.

Stable isotope analysis, fatty-acid profiling and DNA-metabarcoding have the advantage that they cover relatively long periods, are integrative of all prey consumed by the sharks and require a relatively low number of individuals to provide useful information. Of these three methods, stable isotope analysis is currently the most used in deep-water sharks study and provides interesting insight into their trophic ecology (Shipley et al., 2017).

The use of stable isotope analyses to study the trophic ecology of deep-water sharks is currently increasing. A recent review by Shipley et al. (2017) focused on the discoveries, methodological challenges, and interpretation difficulties for stable isotope analysis in deep-water chondrichthyans. In the present section, we will summarize Shipley's main ecological findings on deep-water sharks' trophic ecology, and we will complete these pieces of information with the more recent literature.

Ecological inferences obtained on deep-water sharks through stable isotope analysis have been defined into four categories: (i) source of primary production; (ii) size-based enrichment, i.e., changes in stable

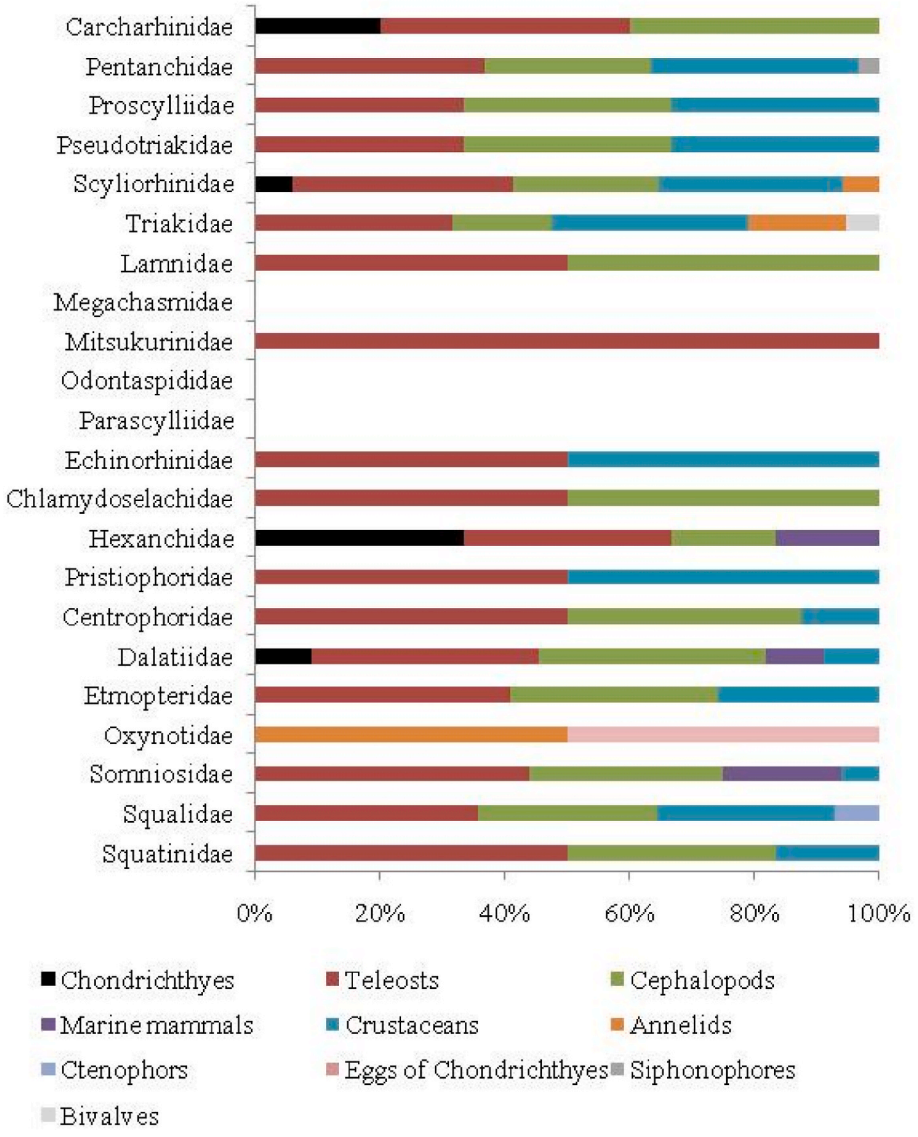

Fig. 7. Relative diet composition of deep and transitory shark families. Only the studies with an analysis of the diet and at least ten filled stomachs examined have been summarized here. The families without bars are the ones lacking data.

isotope ratios with ontogeny; (iii) the effect of depth; and (iv) trophic level and isotopic niche width (Shipley et al., 2017).

According to Shipley's review, three sources of primary production were described by different authors: pelagic phytoplankton, geothermal activity, and coastal source. In a more recent study, Bird et al. (2018), in their consequent analysis of deep and shallow-water oceanic sharks, suggested that pelagic phytoplankton might represent the common source of primary production they found. This result supports Shipley's review, but the authors noted that the general trend might differ in other places since most of their data on deep-water species come from the Atlantic.

Although Churchill et al. (2015) found different variations of enrichment of $\delta^{15}N$ and $\delta^{13}C$ values during ontogeny in 5 out of 8 species of sharks from the Gulf of Mexico, Shipley suggested a need for more sampling. Recent studies described changes in stable isotope ratios with ontogeny for two species. Isotopic enrichment in both $\delta^{13}C$ and $\delta^{15}N$ values was detected in a *Squalus* sp. for specimens up to 60–70 cm (Matich et al., 2019). In *Somniosus microcephalus*, an increase of $\delta^{13}C$ and $\delta^{15}N$ values were detected between individuals of less than 200 cm that feed mainly on cephalopods and individuals of more than 200 cm that eat at higher trophic levels, i.e., large teleosts and mammals (Nielsen et al., 2019).

In general, the effect of depth on isotopic ratio values appears as an increase in $\delta^{15}N$ values with depth, while the depth effect on $\delta^{13}C$ values is more variable, possibly due to different sources of primary production at different depth layers. Churchill et al. (2015) found a significant relationship for three species of sharks for $\delta^{13}C$ and associated it with changing sources of the food web production or dietary switches to specific prey items. Again, more data are required to characterize the depth effect on the stable isotope ratio of deep-water sharks.

In terms of trophic level, deep-water sharks occupy a similar position to pelagic and coastal species. Churchill et al. (2015) highlighted a relatively high percentage of unique isotopic niche space occupied by four deep-water shark species, potentially associated with vertical migration and, thus, a more extensive range of potential prey, with the possibility to prey on species with restricted depth distribution along the water columns, together with species vertically migrating like the predator. Pethybridge et al. (2012) found ontogenic variability in the trophic niche in *Etmopterus granulosus* and *Centroselachus crepidater*. Iitembu and Richoux (2015) observed that *Centrophorus squamosus* separates from *Deania calcea* and *Deania profundorum* in Namibia, the two last having a similar diet and lower trophic level than *C. squamosus*.

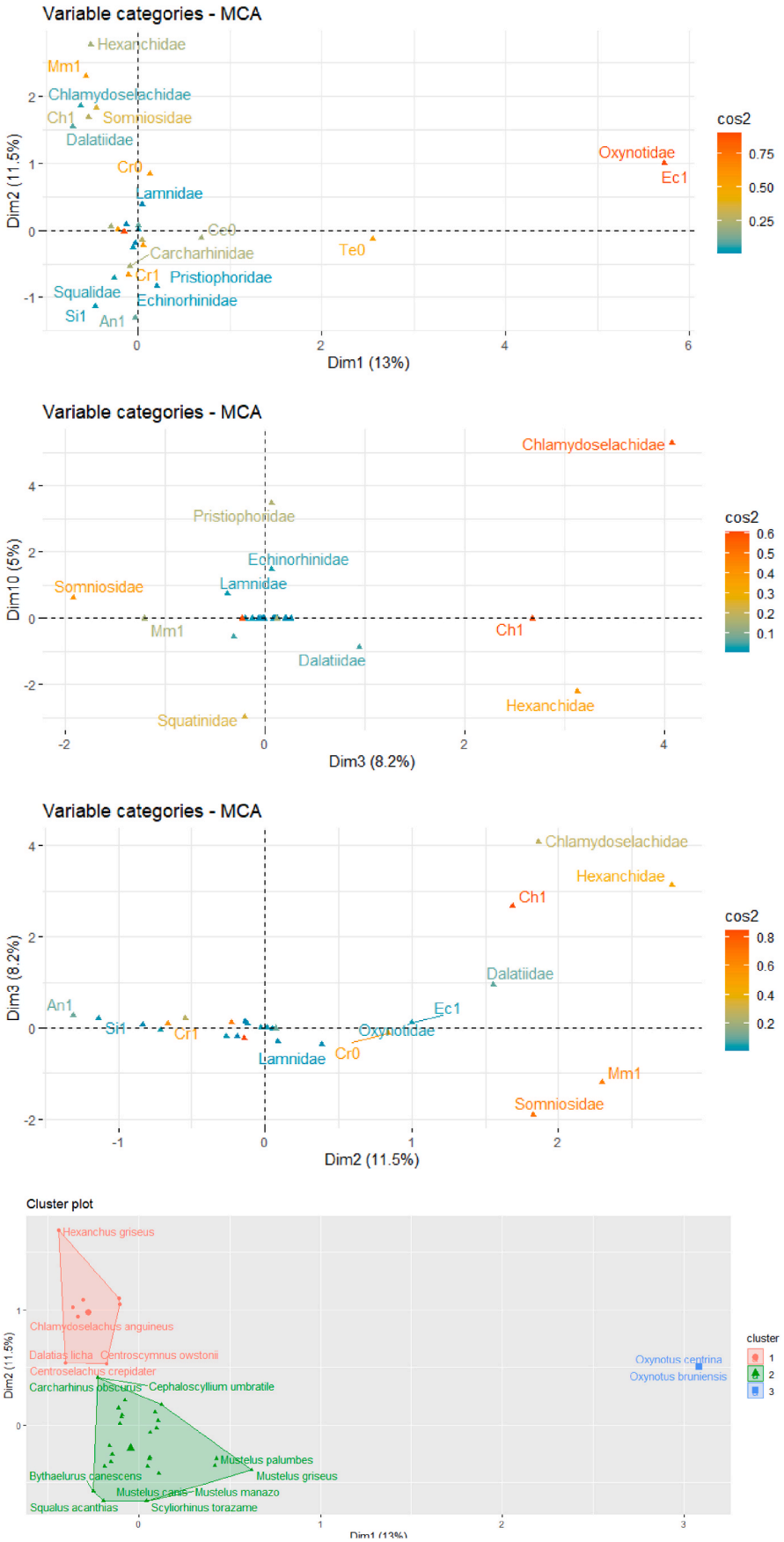

Fig. 8. (COLOR): Results of the MCA analysis for A) dimensions 1 and 2 B) dimensions 3 and 10 C) dimensions 2 and 3 D) clustering. Colors in A, B and C indicate the correctness of the representation for each variable. Only the well-represented variables are analyzed in each graphic.

Valls et al. (2017) found a low trophic overlap between *Etmopterus spinax* and *Galeus melastomus*, with *E. spinax* presenting a higher trophic diversity. Barría et al. (2018) compared niches of four species: *Dalatias licha*, *Etmopterus spinax*, *Galeus melastomus*, and *Scyliorhinus canicula*. *D. licha* has a well-separated niche and higher trophic level, possibly explained by its diet composed of other sharks. *E. spinax*, the smallest of the four species, had a lower trophic level due to its size and inability to capture larger prey. *G. melastomus* and *S. canicula* had overlapping niches, and the authors suggest different foraging depths to avoid competition. Yemisken et al. (2019) also compared five species: *Squalus blainville*, *Galeus melastomus*, *Scyliorhinus canicula*, *Mustelus mustelus*, and *Scyliorhinus stellaris*. *S. blainville* had a lower isotopic niche width and higher trophic level. *G. melastom*us and *S. blainville* had low trophic niche widths, indicating a more specialized diet, while *M. mustelus* and *S. canicula* were qualified as generalists. The trophic niches for *M. mustelus* overlapped with *G. melastomus* and *S. stellaris*, and the authors suggest different habitats and foraging depths to avoid competition. Reum et al. (2020) qualified subadults *Hexanchus griseus* of generalist feeders using mixing models. Carlisle et al. (2021) found *I. brasiliensis* to rely on mesopelagic prey in the short-term and mesopelagic and diel-vertical migrating prey in the long term, challenging the common idea that this species feeds mainly on large epipelagic species.

The different results found by authors using stable isotopes confirm what can be found in stomach contents. It also add information by highlighting differences in trophic niche which are not always visible from stomach contents, and might depend on other factors than the prey species, like habitat separation for example.

Two studies have examined the trophic ecology of deep-water sharks using fatty-acid profiling. Pethybridge et al. (2011) examined 16 chondrichthyan species. They were able to highlight taxonomical differences between their species. They classified medium-sized dogfish as consumers of mid-trophic fishes and squids, catsharks as cephalopod predators and deeper-living dogfishes as predators of bathypelagic fishes, squids and higher orders organisms such as cetaceans and seals. Their results were consistent with the stomach contents they examined. Carlisle et al. (2021) used fatty-acid profiling on *Isistius brasiliensis* and found a potential relationship with the consumption of mesopelagic teleosts and marine mammals. These studies indicate that fatty acid profiling is a valuable tool, especially when sample numbers are low, such with hard-to-obtain deep species, and should be considered more in the future in such cases (Meyer et al., 2019).

5. Concluding remarks

The present work provides an overview of the diet of deep-water and transitory shark species and reveals some important trends in this study field. First, the general lack of data on the subject is the most critical aspect. 269 of the 332 deep-water and transitory shark species present poor to no information on the diet, with index scores of 0–2. Improvements in information on diet change during development and cross-analyses between geographical locations should lead to a rapid increase in the number of species with higher scores in the index. We also found that the common idea that deep-water sharks have a high proportion of empty and regurgitated stomachs is not always accurate. Indeed, the proportion of empty stomachs is highly variable in deep-water sharks. It might have ecological relevance or be due to the different fishing methods and stomach examination.

In general, teleosts, crustaceans, and cephalopods were the main prey found in deep-water sharks. However, there is a vast diversity of species with different ecological roles in each of these taxa. The scale considered in this review does not take this diversity into account, and greater differences between shark species will certainly appear when looking at a finer taxonomic scale. The point of view presented here gives a general idea of what can be found in deep-water sharks, and readers should have a global idea of the diet of these animals by reading the present paper. Still, even at this level, differences are already observable between the "generalist" concept of species eating different proportions of teleosts, crustaceans, and cephalopods and more "specialized" exceptions. Entire families can differ from the others, such as the Oxynotidae feeding on egg cases or the Hexanchidae preying on other elasmobranchs. Single species can also differ from their closely related kin inside the same family, such as *I. brasiliensis* with its particular jaw and hunting behavior (during which it comes close to organisms larger than itself to remove a piece of flesh) or *D. licha* targeting other sharks.

Because most of the information comes from stomach contents, biases inherent to this method might influence the results of the studies presented here: only the recent diet is present, digestion-resistant prey items are more represented, and a high number of stomachs is often necessary to fully describe the diet (Pethybridge et al., 2011; Churchill et al., 2015). Thus, studies with a low number of stomachs with content might be misleading on the actual diet of a species, especially if a higher taxonomic resolution is used. In addition, distinguishing between scavenged and captured items can be difficult and might lead to an underestimation of the importance of scavenging in the diet of deep-water sharks. In the same way, net feeding can be hard to detect.

The increasing use of alternative methods to study deep-water shark trophic ecology brings valuable insights, especially stable isotope analysis, which is the most highly developed method after stomach content. Fatty acid profiling and DNA metabarcoding are promising, especially when dealing with small sample size. The first allows making interesting ecological inferences, and the second to identify prey species from a restricted number of stomachs. But these methods are currently less used. Although the cost of these analyses might be a limiting factor, the development of both methods is relatively recent in this field of research, and methodological challenges are still to be addressed (Pethybridge et al., 2011; Shipley et al., 2017). The use of alternative methods should not replace the conventional stomach analysis but rather be complementary to it, taking advantage of the strengths of the different methods together.

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Declaration of competing interest

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Data availability

The data are available in Annex 1

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2022.103898.

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