


Cephalopods in the diet of Risso's dolphin (*Grampus griseus*) from the Mediterranean Sea: A review

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Abstract

The Risso's dolphin, *Grampus griseus*, is a deep-sea cetacean with a predominantly teuthophagous diet. Its distribution in the northwest Mediterranean is generally in deeper waters, but there is little information on diet or feeding areas. To extend knowledge of the diet of *G. griseus*, the stomach contents of six stranded Risso's dolphins in the Mediterranean Sea were analyzed. A total of 578 cephalopod beaks (166 uppers and 392 lowers) were found, identified as 386 individuals from 19 different species of Coleoidea cephalopods, one Sepiolida, eight Octopoda, and ten species belonging to the Order Oegopsida. This adds six species of cephalopods to those previously recorded in the Mediterranean Sea: *Rondeletiola minor*, *Eledone moschata*, *Scaevurgus unicolor*, *Bathypolypus sponsalis*, *Pteroctopus tetracirrus* and *Taonius pavo*. In this study the most abundant prey family was Histioteuthidae. In addition, based on the available literature, the diet of 39 Risso's dolphins was reviewed in Mediterranean waters. The abundance of cephalopod species in the diet of these specimens was compared according to genus, geographical area, season, and age. The habitat of the prey of *G. griseus* was reviewed, suggesting a teuthophagous diet in this area. This study helps to identify both the prey species and the areas where prey are available in the northwest Mediterranean, which

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are key factors in establishing the limits and regulations of the “Northwest Mediterranean Sea, Slope and Canyon IMMA System” (Important Areas for Marine Mammals) proposed by the Working Group on Marine Mammal Protected Areas (MMPATF - IUCN).

KEYWORDS

Cephalopoda, cetacean stranding, *Grampus griseus*, NW Mediterranean Sea, stomach contents

1 | INTRODUCTION

The Risso's dolphin (*G. griseus*, Cuvier, 1812), the smallest member of the subfamily Globicephalinae (Delphinidae), is a common odontocete in the Mediterranean Sea; however, it is one of the lesser-known species because of its patchy distribution (Podestà & Meotti, 1991) and its low stranding frequency (Hartman, 2018). This cosmopolitan species lives in temperate and tropical waters throughout the world (Baird, 2009; Leatherwood et al., 1980; Riccialdelli et al., 2012), roughly between 64°N and 46°S (Jefferson et al., 2013). Although *G. griseus* occurs in coastal to oceanic habitats, it shows a strong preference for mid-temperate waters warmer than 12°C and it does not occur in polar regions (Hartman, 2018; Jefferson et al., 2013). It has been sighted in deep offshore waters (200–1,200 m depth; Jefferson et al., 2013; Pereira, 2008). Its distribution is concentrated on the upper continental slope and around steep shelf-edge areas (Jefferson et al., 2013; Notarbartolo di Sciara, 2002), often near the slope edge (Cañadas et al., 2002; Fabbri et al., 1992; Kenney & Winn, 1986), around strong bathymetric features such as submarine canyons and seamounts (Chicote et al., 2013; Gazo et al., 2004; Kenney & Winn, 1987; Waring, 1993), and oceanic trenches (Chicote et al. 2015; Toledano, 2003). It has been found to have a closer association with submarine canyons than other species (Chicote et al. 2015); however, long distance movements have been reported within NW Mediterranean waters (Lanfredi et al., 2018). This may be due to its preferred prey, cephalopods, and their particular ecological requirements (Notarbartolo di Sciara et al., 1993). Shallower occurrences are less frequent, and Risso's dolphins seem to favor areas where the shelf is narrow, such as near islands (Notarbartolo di Sciara et al., 1993; Palacios, 2003; Shane, 1995). Inshore movements and site fidelity have been documented off the United Kingdom and in the Mediterranean Sea (Jefferson et al., 2013). This cetacean inhabits most European coasts from Norway to Greece (Frantzis & Herzing, 2002; Jefferson et al., 2013; Raga et al., 1985) and can be found around all Macaronesian Archipelagos (Fernández et al., 2009; Freitas et al., 2012; Pereira, 2008; Reiner et al., 1996).

The species is distributed throughout the Mediterranean and has been reported in the Alborán Sea (Cañadas et al., 2002; Gannier, 2005; García-Polo et al., 2014), Ligurian Sea (Azzellino et al., 2008, 2012; Di Méglia et al., 1999; Gannier, 2005; Moulins et al., 2008; Notarbartolo di Sciara et al., 1993), Tyrrhenian Sea (Campana et al., 2015; Marini et al., 1996), Adriatic Sea (Azzellino et al., 2016), Ionian Sea (Dimatteo et al., 2011; Frantzis et al., 2003), and Aegean Sea (Frantzis et al., 2003).

Very few Risso's dolphins have been stranded in the Mediterranean in a good enough condition to conduct full necropsies, and therefore little is known about their diet in the region [Podestà & Mettoni (1991), Würtz et al. (1992), and Orsi Relini et al. (1997) in the Ligurian Sea; Bello & Bentivegna (1996), Carlini et al. (1992), and Maio (1998) in the Tyrrhenian Sea; Bello (1992, 1996) in the Adriatic Sea; Blanco et al. (2006, Valencia Gulf), García-Polo et al. (2014, Alborán Sea), Pedà et al. (2015, Tuscany), and the present study (Catalan Maresme) in the western Mediterranean; Öztürk et al. (2007, Turkish waters) and Milani et al. (2017, Greek waters) in the eastern Mediterranean]. Moreover, not many individuals have been taken as bycatch (Öztürk et al., 2007).

Cephalopods are a key component of marine food-webs worldwide (Boyle & Rodhouse, 2005; Hunsicker et al., 2010). It is known that many odontocetes feed on commercially exploited and unexploited cephalopods (Clarke, 1996). Risso's dolphins have a clear teuthophagous diet (Bello, 1992, 1996; Bello & Bentivegna, 1996; Blanco et al., 2006; Clarke, 1996; Clarke & Pascoe, 1985; García-Polo et al., 2014; Milani et al., 2017; Öztürk et al., 2007; Pedà et al., 2015; Podestà & Meotti, 1991; Würtz et al., 1992), with a preference for deep-sea squids (Benoit-Bird et al., 2019). Benoit-Bird et al. (2019) showed that Risso's dolphins dive to depths exceeding 500 m both during the day and night, switching frequently throughout the day from being more generalist predators near the surface to specializing on larger squids at deeper depths. By analyzing cephalopod prey composition in teuthophagous cetaceans it is possible to determine details of the predator's trophic habitat and behavior, as well as gain information about the cephalopod prey in the dietary ecology of the cetaceans (Clarke, 1996; Pedà et al., 2015; Santos et al., 2001).

Data about the diet of many predators, such as sperm whales *Physeter macrocephalus* Linnaeus, 1758 (Clarke, 1977) and other cetaceans, seals (Clarke & Trillmich, 1980), albatrosses (Clarke et al., 1981), tuna (Downes et al., 2017), and swordfish *Xiphias gladius* Linnaeus, 1758 (Bello, 1991), can be effectively used to determine the biology and relative ecological importance of mesopelagic prey, such as cephalopods, which would otherwise be difficult to sample from open ocean marine ecosystems (Clarke & Kristensen, 1980; Downes et al., 2017). Until recently, stomach content analysis was the main method used for diet studies. Lower beaks of cephalopod species have proven to be extremely valuable for identifying the cephalopods in the predator's diet due to their resistance to digestive juices (Cherel, 2006; Clarke, 1986, 1996; Clarke & Kristensen, 1980).

The Mediterranean subpopulation of *G. griseus* is still classified as "Data Deficient" on the International Union for the Conservation of Nature (IUCN) Red List (Gaspari & Natoli, 2012). The Mediterranean *Grampus* Project 2.0 report (Lanfredi et al., 2018) highlighted the necessity to include the species in the EU Habitats Directive and to reassess the IUCN assessment status for the Mediterranean subpopulation. Aligned with the specific situation of *G. griseus* in the western Mediterranean, the establishment of "the North West Mediterranean Sea, Slope and Canyon System IMMA," (Important Marine Mammal Areas, IMMAs) was proposed by The Marine Mammal Protected Areas Task Force (MMPATF - IUCN). This study aims to make a valuable contribution by determining both the prey species in the diet and prey availability areas, key factors for establishing boundaries and regulations to implement marine protected areas for teuthophagous species.

The present study adds new information from the stomach contents of six Risso's dolphins and conducts a comparative analysis of all available information on the diet of *G. griseus* in the Mediterranean, thus increasing understanding of the ecology of *G. griseus* in the area. This study enlarges the list of cephalopod prey captured by this species in the Mediterranean.

2 | MATERIAL AND METHODS

2.1 | Sampling and stomach contents

Between December 2012 and April 2016, six Risso's dolphins were stranded on the central Catalan coast in a good enough conservation state to conduct a full necropsy. The cetaceans were recovered by the Servei de Biodiversitat i Protecció dels Animals (Departament d'Agricultura, Ramaderia, Pesca, Alimentació i Medi Natural. Generalitat de Catalunya) and the necropsy was conducted by the Servei de Diagnòstic de Patologia Veterinària (Universitat Autònoma de Barcelona). G1 was an adult female (309 cm length) found floating near the Castelldefels coast (Barcelona, December 2012), with no external evidence of human interaction. G2 was an adult male (316 cm) that was stranded in Calafell (Tarragona, August 20, 2013). It was beached alive but died during the rescue attempt. G3 was an adult female (290 cm) that also beached alive in El Vendrell (Tarragona, February 11, 2016) and was euthanized on that same beach. G4 was an adult male (310 cm) found stranded on the beach of Buda Island (Ebro Delta)

in Tarragona (April 10, 2016). G5 was a malnourished adult male (310 cm) with a seemingly poor body condition that was found stranded in the Ebro Delta on March 14, 2016, but died shortly after. G6 was an adult female (290 cm) found alive on San Salvador Beach (El Vendrell, February 11, 2016) and died shortly after. The stomach contents were frozen (-20°C) to temporarily fix the tissues until they were analyzed later in the laboratory. After specimens had been extracted and cleaned, they were preserved in 70% ethanol. Cephalopod beaks found in the stomachs were used to determine the taxonomy of the specimens following the specific method developed mainly by Clarke (1986) and Pérez-Gándaras (1986), and also by using the reference collection in the Instituto de Ciencias del Mar (CSIC). The standard way of counting the number of individuals is to study only the lower beaks, which are more distinctive and characteristic than upper beaks (Clarke, 1986). It is assumed that the number of upper and lower beaks will be the same in predator diet samples, and more effort has been made to create keys for the lower beaks (Xavier et al., 2011). G1 was a seemingly healthy animal. G2, G3, and G6 had not ingested food recently, and were parasitized by nematodes (*Crassicauda grampicola*). G4 had not ingested food recently either, but seemed healthy and well-fed. G5 was a malnourished animal with a seemingly poor body condition. The list of cephalopod species recovered from the stomachs is shown in Appendix S1.

2.2 | Data analysis

We conducted a thorough review of the studies on the diet of *G. griseus* from the Mediterranean Sea (35 specimens) and determined the relationship between our results and those of other similar works (Bello, 1992, 1996; Blanco et al., 2006; Milani et al., 2017; Öztürk et al., 2007; Appendix S2).

Prior to analyses, *Teuthida* A, B, C, and D (Milani et al., 2017) were included as a single taxon. *Histioteuthis* Type A (Öztürk et al., 2007) is considered a valid species. Statistical analyses were conducted on cephalopod abundance in the contents of each stomach. We used the PRIMER statistical software to perform multivariate analyses of the species prey data (Clarke & Warwick, 1994). A cluster analysis using the Bray–Curtis similarity index was carried out with double square root transformed data, and dendrograms were made using the group average clustering method. The resulting similarity matrices were then used to perform nonmetric multidimensional scaling (MDS). The cephalopod species in the work of Blanco et al., 2006 were not differentiated by individual dolphin; therefore, this work is not included in the dendrogram. The analyses aimed to determine diet differences between sex, age, geographical area, and season variables between all specimens studied (both the specimens necropsied and those found in the literature). The work by García-Polo et al. (2014) did not include data on age or sex, and therefore is not included in the MDS diagrams.

The maximum length of subadults of *G. griseus* was difficult to determine with complete certainty because there are practically no data on this in the specialized literature. According to Evans (2008, 2013) the calves reach a maximum length of 135 cm, and the adults have a maximum length of 300–400 cm. Hartman et al. (2008), in a study based in Azores waters, define calves as individuals that are a maximum of 75% of adult size and are accompanied by adults. The sizes used in the present study for *G. griseus* were subadult (135–278 cm) and adult (278–380/400 cm).

3 | RESULTS

3.1 | New information about the diet of *G. griseus*

Entire prey, beaks and cephalopod eyeballs were found in the six analyzed stomachs. In G1 there were three semi-digested octopods (with the beak still attached), 73 single beaks (40 uppers and 33 lowers), six cephalopod eyeballs and other semidigested unidentifiable remains. The beaks of the half-digested cephalopod bodies were removed and

studied. In G2 there was only one upper beak (*Ommastrephes caroli*) and a cephalopod eyeball, as well as some very digested and unidentifiable remains. G3 had 269 beaks (122 uppers and 147 lower) and an additional 20 beaks that were too damaged to be identified. In G4 there were 151 lower beaks. G5 contained 44 lower beaks, and in G6 there were only 14 lower beaks and some cephalopod eyeballs. The results of the new information about the six Risso's dolphins' diets are shown in Table 1 and Appendix S1.

In total, 578 beaks were recovered from the stomachs. A total of 21 cephalopod species were recorded, without counting the unidentified specimens and those only determined to family level. Two beaks, upper and lower of similar height, were counted as the same individual, similarly to the *Argonauta argo* case (Table 1). *Histioteuthis bonnellii* represented 51.7% of all the cephalopod beaks found in the stomach of the six Risso's dolphins, followed by *Eledone cirrhosa* (15.7%), *Histioteuthis reversa* (11.8%), and *Octopoteuthis sicula* (5.6%). Each of the other prey species made up less than 4% of the diet. Table 1 and Figure 1 show the species that were identified in this work and their abundance per stomach.

3.2 | Data analysis

All the cases were stranded adults or subadults. Of the 39 specimens from the Mediterranean Sea, 12 were adult females, seven adult males, five subadult females, and six subadult males. The sex and size of the specimens of Orsi Relini et al. (1997; six specimens) and García-Polo (2014; three specimens) were unknown.

Figure 2 shows the mean depth range of species found in the stomachs of *G. griseus* depending on whether they are benthic or pelagic species.

The results of the cluster analysis and the MDS (Figures 3–6) failed to find significant differences for sex, age, season, or geographical zone. The model associates the individuals based on the similarity of their diet. Although no pattern can be seen in the cluster analysis, some specimens show great similarity between them. For example, G7 (female, adult, Central Catalan Coast, spring) and G33 (female, adult, Tuscany, spring) have in common that they have eaten *H. bonnellii* but not *H. reversa*; G3 (female, adult, Central Catalan Coast, winter) and G4 (male, adult, Central Catalan Coast, spring) are the only ones that have eaten *O. sicula*; G5 (male, adult, Central Catalan Coast, winter) and G6 (female, adult, Central Catalan Coast, winter) have eaten almost the same cephalopod species and in very similar amounts. However, other specimens have very different stomach contents from the rest of the analyzed samples. Individuals G2 (male, adult, Central Catalan Coast, summer) and G8 (female, adult, Tyrrhenian, winter), completely separated from the rest, had only eaten one cephalopod species.

4 | DISCUSSION

4.1 | New insights into the diet of *G. griseus*

Figure 3 clearly shows most specimens of the family Histioteuthidae in the stomachs of G3 and G5, as well as *Eledone cirrhosa* in G1 and *Pteroctopus tetracirrhus* in G5. The most abundant species was *H. bonnellii*, with 91 records in G3, 89 in G4, 13 in G5, 4 in G6, and 1 in G1 (this stomach only had this beak), similar to other Mediterranean studies (Bello, 1992, 1996; Milani et al., 2017; Podestà & Mettioni, 1991). Six cephalopod species not previously recorded in the stomachs of Mediterranean specimens included: *Rondeletiola minor*, *Eledone moschata*, *Scaevurgus unicolor*, *Bathypolypus sponsalis*, *P. tetracirrhus*, and *Taonius pavo*.

There are probably fewer than 60 cephalopod species that are a regular part of the diet of cetaceans (Clarke, 1996). The latest studies added some species to Bearzi et al.'s (2011) review of the ecology of *G. griseus* in the Mediterranean Sea (Appendix S2). The list was extended to a total of 50 identified taxa in the diet of this

TABLE 1 Species found in the analyzed Risso's dolphins.

| Species | N | % of the N total | Stomach |
|---|-----|------------------|--------------------------------------|
| Order Sepioidea | | | |
| Family Sepiolidae | | | |
| <i>Rondeletiola minor</i> (Naef, 1912) | 16 | 2.8 | G3(1), G4(7), G5(5), G6(3) |
| Order Oegopsida | | | |
| Family Brachioteuthidae | | | |
| <i>Brachioteuthis riisei</i> (Steenstrup, 1882) | 12 | 2.1 | G3(6), G4(6) |
| Family Chiroteuthidae | | | |
| <i>Chiroteuthis veranii</i> (Férussac, 1834) | 8 | 1.4 | G3(1), G4(3), G5(1), G6(1) |
| <i>Chiroteuthis</i> sp. | 1 | 0.2 | G4(1) |
| Family Cranchiidae | | | |
| <i>Taonius pavo</i> (Lesueur, 1821) | 1 | 0.2 | G3(1) |
| <i>Taonius</i> sp. | 1 | 0.2 | G4(1) |
| Family Histioteuthidae | | | |
| <i>Histioteuthis bonnellii</i> (Férussac, 1834) | 198 | 34.2 | G1(1), G3(91), G4(89), G5(13), G6(4) |
| <i>Histioteuthis reversa</i> (Verrill, 1880) | 48 | 8.3 | G3(21), G4(22), G5(4), G6(1) |
| Family Octopoteuthidae | | | |
| <i>Octopoteuthis sicula</i> (Rüppell, 1844) | 20 | 3.5 | G3(1), G4(10) |
| Family Ommastrephidae | | | |
| <i>Illex coindetii</i> (Vérany, 1839) | 2 | 0.4 | G3(1), G4(1) |
| <i>Ommastrephes caroli</i> (Furtado, 1887) | 1 | 0.2 | G2(1) |
| <i>Todarodes sagittatus</i> (Lamarck, 1798) | 23 | 4 | G1(1), G3(5), G4(9), G5(5), G6(3) |
| <i>Todarodes</i> sp. (Steenstrup, 1880) | 1 | 0.2 | G3(1) |
| Order Octopoda | | | |
| Family Argonautidae | | | |
| <i>Argonauta argo</i> (Linnaeus, 1758) | 1 | 0.2 | G1(1) |
| Family Bathypolypodinae | | | |
| <i>Bathypolypus sponsalis</i> | 1 | 0.2 | G4(1) |
| Family Eledonidae | | | |
| <i>Eledone cirrhosa</i> (Lamarck, 1798) | 29 | 5 | G1(28), G5(1) |
| <i>Eledone moschata</i> (Lamarck, 1798) | 1 | 0.2 | G1(1) |
| Family Octopodidae | | | |
| <i>Octopus vulgaris</i> (Cuvier, 1797) | 3 | 0.6 | G1(3) |
| <i>Pteroctopus tetracirrhus</i> | 16 | 2.8 | G5(14), G6(2) |
| <i>Scaergus unicirrhus</i> (delle Chiaje, 1841) | 1 | 0.2 | G1(1) |
| Family Tremoctopodidae | | | |
| <i>Tremoctopus violaceus</i> (delle Chiaje, 1830) | 2 | 0.4 | G3(1), G4(1) |
| Total | 578 | | |

Note: N, number of specimens for this species; Stomach, individuals in which the beaks were found; in parentheses, number of specimens for each stomach. The percentages are in reference to the total number of beaks; G1–6: *G. griseus* stomachs.

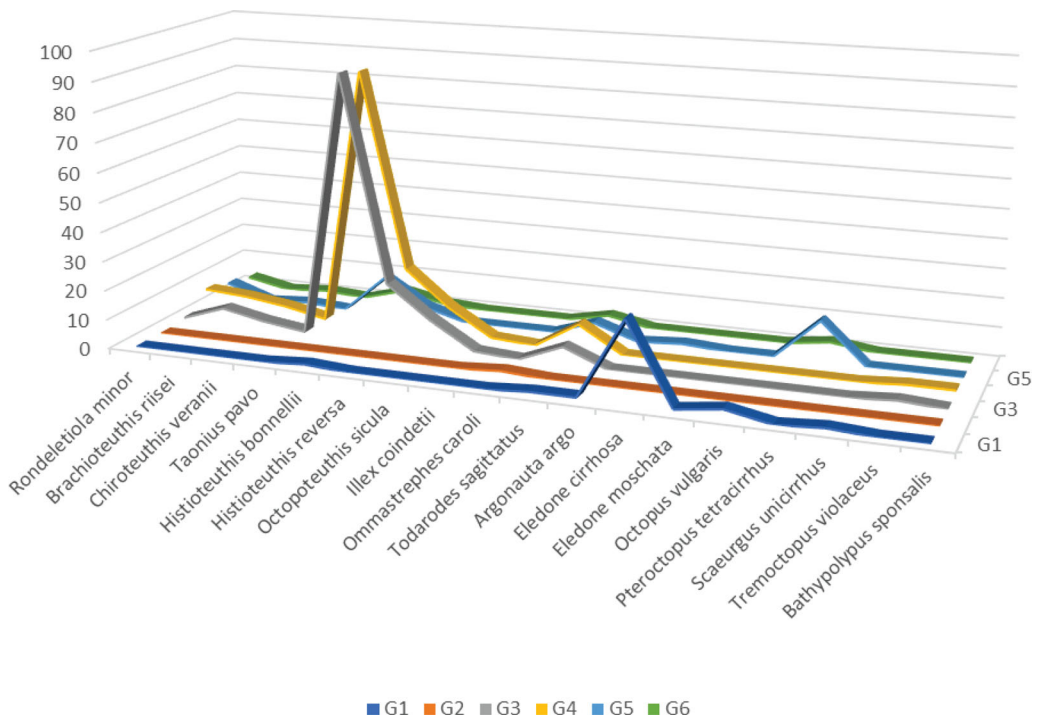


FIGURE 1 Number of individuals of each cephalopod species per stomach.

cetacean in this area, 39 of which were identified to species level. With a review of the *G. griseus* diet literature, the list now includes the sepiolid *R. minor*, the squid *T. pavo*, *Tewthowenia* sp., *P. margaritifera*, and the octopuses *B. sponsalis*, *P. tetracirrhus*, *O. tuberculata*, *S. unicolor*, *E. moschata*, and *T. violaceus*.

The poor condition (very digested and fragmented) of most of the beaks in the collection indicate that they had been in contact with gastric juices for some time. However, it is impossible to determine exactly how long the beaks had been in the stomachs (Xavier et al., 2007).

4.2 | Comparison of the different studies on the diet of *G. griseus* in the Mediterranean Sea

Except for the studies of Bello & Bentivegna (1996), Maio (1998), and Pedà et al. (2015), the rest of the articles find Histiotteuthidae to be among the most abundant families, and the majority state that this family represents the largest number of individuals. These papers generally have a small sample size, and therefore their statistical results must be seen as preliminary.

In the Mediterranean Sea, the following authors found species in common with the 18 species found in the present study (Appendix S2): Podestà & Meotti (1991) had two cephalopod species in common: *H. bonnellii* and *E. cirrhosa*. Carlini et al. (1992) had six (or seven) species in common: *T. sagittatus*, *I. coindetii*, *H. bonnellii*, *A. argo*, and *Eledone* sp. (this specimen could be either *E. cirrhosa* or *E. moschata*; finally, *E. cirrhosa* was chosen because of its greater abundance compared with *E. moschata*, but it could not be confirmed with the existing data). Würtz et al. (1992) had three species in common: *T. sagittatus*, *H. reversa* and *H. bonnellii*. Öztürk et al. (2007) had seven species: *B. riisei*, *C. veranii*, *T. pavo*, *O. sicula*, *T. sagittatus*, *I. coindetii*, *H. bonnellii*, *H. reversa*, *O. caroli*. Bello (1992, 1996) had six matching species: *C. veranii*, *T. sagittatus*, *H. bonnellii*, *H. reversa*, *A. argo*. Bello & Bentivegna (1996) and

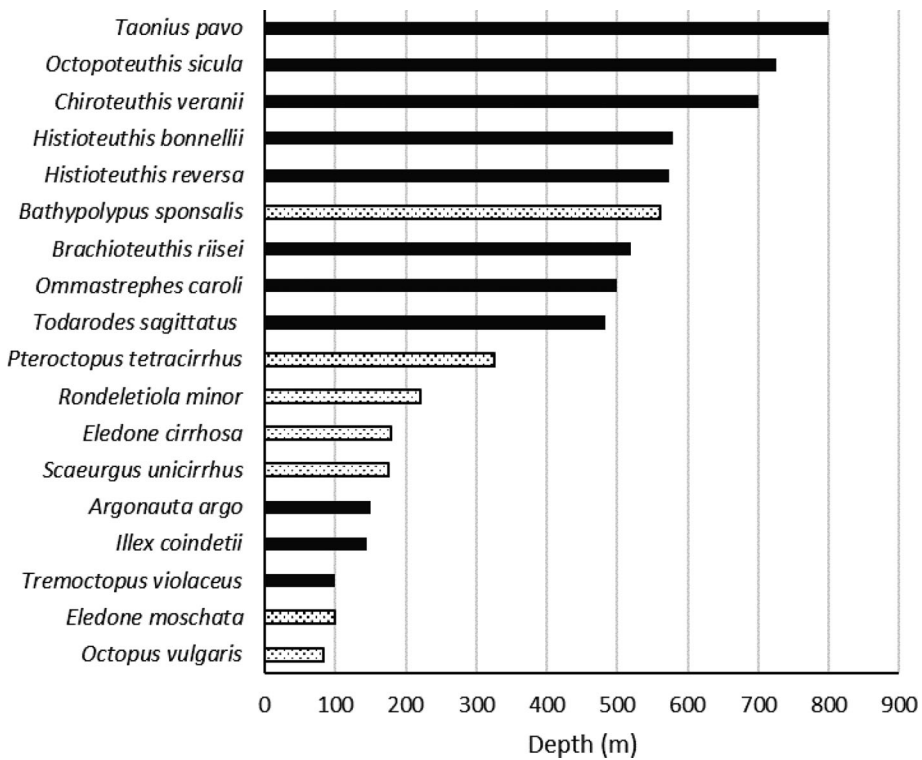


FIGURE 2 Mean depth range of benthic and pelagic species found in stomachs of *G. griseus*.

Maio (1998) only had one species in common with the present study: *T. sagittatus*. Orsi Relini et al. (1997) also found *H. bonnellii* and *H. reversa* in common with the present study. Blanco et al. (2006) found nine prey that coincide with this work: *Brachioeuthis riisei*, *C. veranii*, *T. sagittatus*, *I. coindetii*, *O. caroli*, *H. bonnellii*, *H. reversa*, *A. argo*, *E. cirrhosa*, *O. vulgaris*. García-Polo et al. (2014) had three species in common: *H. bonnellii*, *H. reversa*, *T. sagittatus*, and *O. vulgaris*. Pedà et al. (2015) had three cephalopod species in common: *C. veranii*, *H. bonnellii*, and *T. violaceus*. Finally, there were three matching species in the work of Milani et al. (2017) and the present study: *H. bonnellii*, *H. reversa*, and *A. argo*.

4.3 | Cephalopod families

The most abundant families found in the present study were Histiotteuthidae (246 beaks, 42.5% of the total beaks), Eledonidae (29 beaks, 5%), and Ommastrephidae (27 beaks, 4.7%). These results confirm the information gained from previous studies; that is, in Mediterranean waters, *G. griseus* feeds primarily on the Histiotteuthidae family (Appendix S2).

Clarke (1996) reported that *G. griseus* generally eats both oceanic and neritic cephalopods from 14 families (Ommastrephidae, Onychoteuthidae, Enoploteuthidae, Ancistrocheiridae, Octopoteuthidae, Histiotteuthidae, Loliginidae, Sepiidae, Sepiolidae, Octopodidae, and others) with Histiotteuthidae as the most important family in the Mediterranean. According to Clarke, the most important families of cephalopods in cetacean diets are by far the oceanic Ommastrephidae, Histiotteuthidae, and Cranchiidae, with the neritic Loliginidae being the most abundant on the continental shelves (Clarke, 1996).

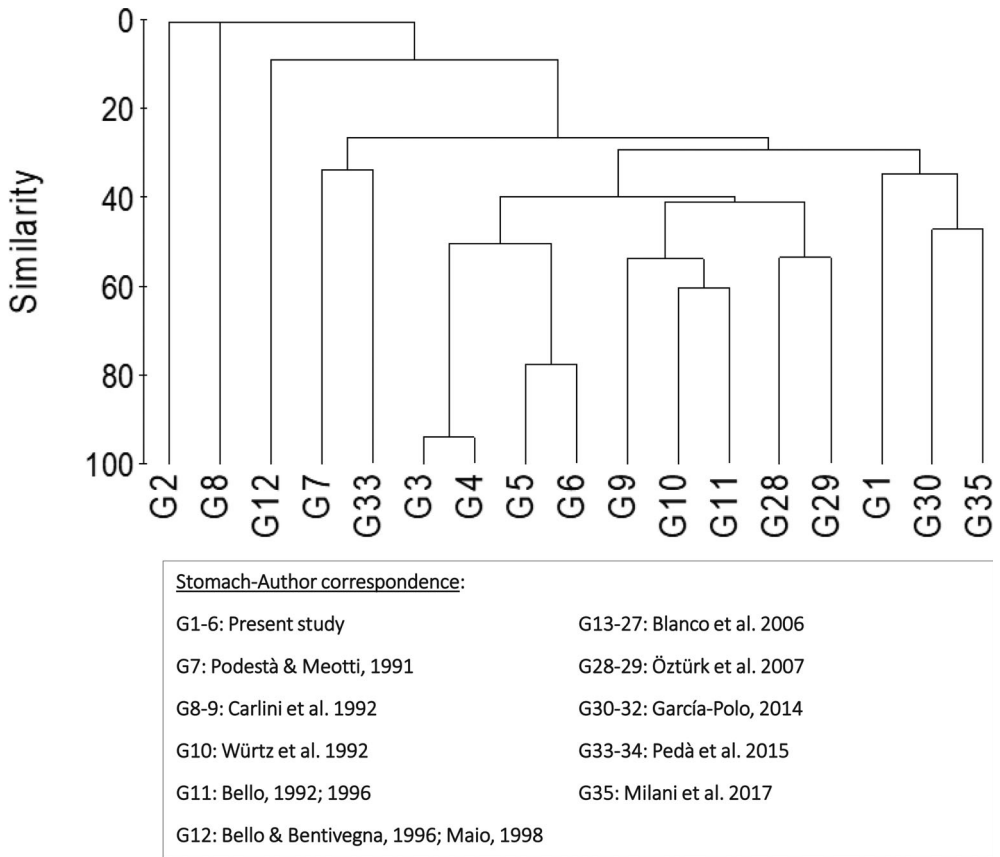


FIGURE 3 Dendrogram of abundance of cephalopod prey captured by *G. griseus* in the Mediterranean Sea based on Bray-Curtis distance.

4.4 | Bathymetric distribution of the prey

Like other teuthophagous cetaceans, *G. griseus* finds prey both in pelagic waters and in benthic areas of the continental slope, which they probably reach by long deep dives (Carlini et al., 1992; Clarke & Pascoe, 1985). As Baumgartner (1997) hypothesized, it is possible that Risso's dolphins take advantage of a wide variety of cephalopod prey, since the upper continental slope and shelf break region is a transition zone between two distinct ecosystems: the continental shelf and oceanic waters. Subsequent studies are needed to determine whether *G. griseus* dives to these depths to obtain food or whether it feeds in shallower depths, because *Grampus* are believed to forage on neritic and mesopelagic oceanic cephalopods that make diel vertical migrations to surface waters at night (Riccialdelli et al., 2012; Soldevilla et al., 2010). However, according to Würtz et al., 1992, whether Risso's dolphin preys on the diel migrators (*Eledone* sp. in our case) in midwater or on the bottom depends on time of day/night day. Benoit-Bird et al. (2019) show that Risso's dolphins dive to depths exceeding 500 m during both the day and night. The cosmopolitan habitat of these oceanic cephalopods and of the Risso's dolphin must be taken into consideration, as well as the scarce data on their bathymetry. The studies of Azzellino et al. (2008), Cañadas et al. (2002), Casacci & Gannier (2000), Gannier (2005), and Moulins et al. (2008) all describe that Risso's dolphins prefer steep gradients and submarine canyons. *Grampus* typically inhabits oceanic waters associated with slope break boundaries (400–1,000 m depth; Baumgartner, 1997; Olavarría et al., 2001), but normally dives to depths of <50 m with maximum dive times of 10–30 min (Cañadas et al., 2002; Riccialdelli et al., 2012; Wells et al., 2009). Beyond this, however, no references

to possible bathymetric preferences have been found. Their oceanic distribution limits the possibilities for systematically studying their movements and dive patterns (Wells et al., 2009). Furthermore, considering the cosmopolitan distribution of *Grampus*, it is possible that their feeding area could be larger than the Mediterranean Sea and they could travel sporadically and find prey in nearby areas.

According to Baumgartner (1997), a physical mechanism that may explain the diet of *G. griseus* is the shelf/oceanic water exchange at the upper continental slope and shelf break because the currents or physical features, such as the boundary between shelf and oceanic waters, could be a strategic location for a Risso's dolphin to take advantage of cephalopod aggregations.

The data presented are useful for understanding the ecology of *G. griseus* better, as well as for determining cephalopod assemblages in the Mediterranean. It must be emphasized that there are three main cephalopod communities in the Mediterranean Sea (González & Sánchez, 2002; Quetglas et al., 2000; Sánchez et al., 1998): the shelf community (<150 m, with *Alloteuthis media* as indicator species), the middle slope community (>480 m, with *T. sagittatus* as indicator species of this group) and the transitional zone community (ecotone; Margalef, 1974), as well as a group of cephalopods that are distributed more abundantly on the lower continental shelf-upper slope (150–480 m; with *E. cirrhosa* and *O. vulgaris* as indicator species) with overlapping species of the two previous communities. This phenomenon is due to the combination of changes in environmental and biological factors along the depth gradient and their interaction (Abelló et al., 1988; González & Sánchez, 2002; Moranta et al., 1998; Sardà et al., 1994).

In the present study, there are species belonging to the three assemblages, in agreement with the data collected in trawl surveys along the west Mediterranean coast (González & Sánchez, 2002; Quetglas et al., 2000): *R. minor*, overlaps with the shelf and middle slope group; *E. moschata* is in the lower continental shelf-upper slope group; *H. reversa* is in the middle slope community; *I. coindetti* and *O. vulgaris* overlap with shelf and lower continental shelf-upper slope groups; *T. sagittatus* and *H. bonnellii* overlap with lower continental shelf-upper slope and middle slope communities; and *E. cirrhosa* overlaps with the three groups.

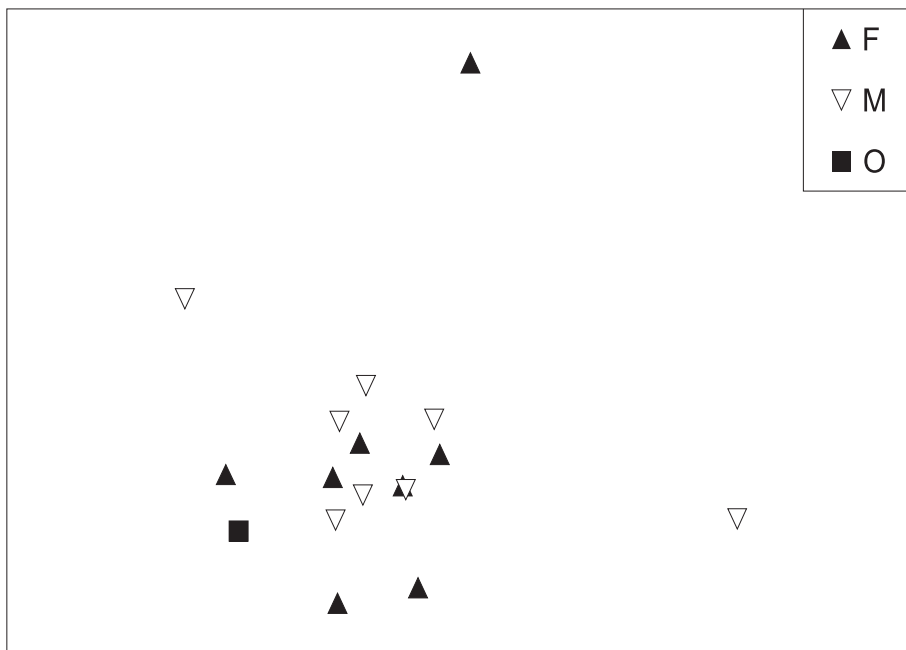


FIGURE 4 MDS diagram of abundance of cephalopod prey captured in relation to *G. griseus* sex in the Mediterranean Sea. F, female; M, male; O, unknown. Analysis carried out with stress of 0.9.

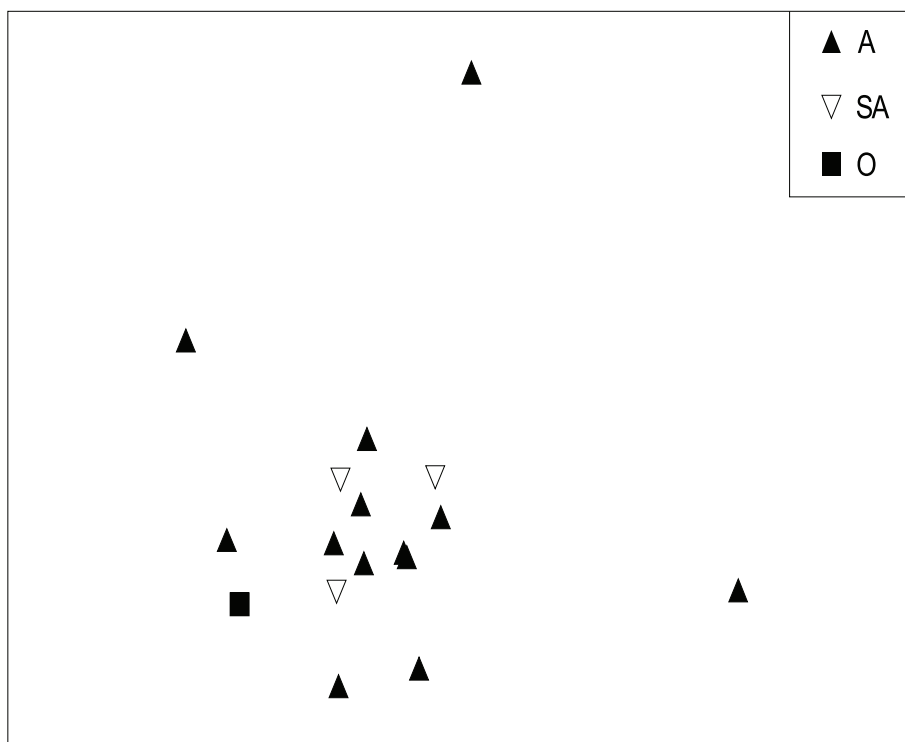


FIGURE 5 MDS diagram of abundance of cephalopod prey captured in relation to *G. griseus* age class in the Mediterranean Sea. A, adult; SA, subadult; O, unknown. Analysis carried out with stress of 0.9.

It is interesting to note that *E. cirrhosa*, the curled octopus, was one of the main prey types found in Risso's dolphins stranded in the U.K. (Clarke & Pascoe, 1985; 16 specimens, 38%). In the present study, *E. cirrhosa* represents 5% of the total cephalopod species (76% of one of the stomachs studied), but in the rest of the Mediterranean studies, it is not a very common species.

The bathymetric distribution of the species found in the present study includes a wide range of depths (Appendix S2). The mean depth range of species found in *G. griseus* stomachs depending on whether they are benthic or pelagic species (Figure 2) suggest that this cetacean has a teuthophagous diet in this area and that in the Mediterranean it not only feeds on the middle continental slope, as previously thought (Blanco et al., 2006), but also on the continental shelf. There are benthic animals (*Eledone* sp., *O. vulgaris*, *S. unicolor*, *B. sponsalis*, *P. tetracirrus*) that live on the continental shelf and on the middle slope as deep as 770–800 m, in the case of *E. cirrhosa*, *P. tetracirrus*, and *S. unicolor*, which reach deeper depths in their life cycle. In addition, there is a deep-sea species, *B. sponsalis*, which inhabits depths from 200 to 2,300 m depth. We also found oceanic species (*H. bonnellii*, *A. ago*, *B. riisei*, *T. pavo*, *O. sicula*), whose maximum depth reaches bathyal or abyssal zones, and they are able to move around the shelf. The available data about the Mediterranean deep-sea teuthofauna are fragmentary and limited to studies on a small number of captured individuals (Bello, 1985; Quetglas et al., 2000; Roper, 1974; Villanueva, 1992) or information from indirect data from stomach content analyses of cephalopod predators (Bello, 1991, 1992, 1996; Milani et al., 2017; Würtz et al., 1992). Therefore, this information improves our knowledge of this fauna. The present study shows (Table 2) that the majority of both species and specimens found in the stomachs are pelagic: 18 species (61.1% of the species) and 386 specimens (82.6% of the total number of specimens). This is supported by other works such as Blanco et al. (2006) and Benoit-Bird et al. (2019). It seems clear that *G. griseus* prefers pelagic cephalopods. Bello (1992, 1996), Öztürk (2007), and Podestà and Meotti (1991) also showed oceanic preferences in their studies.

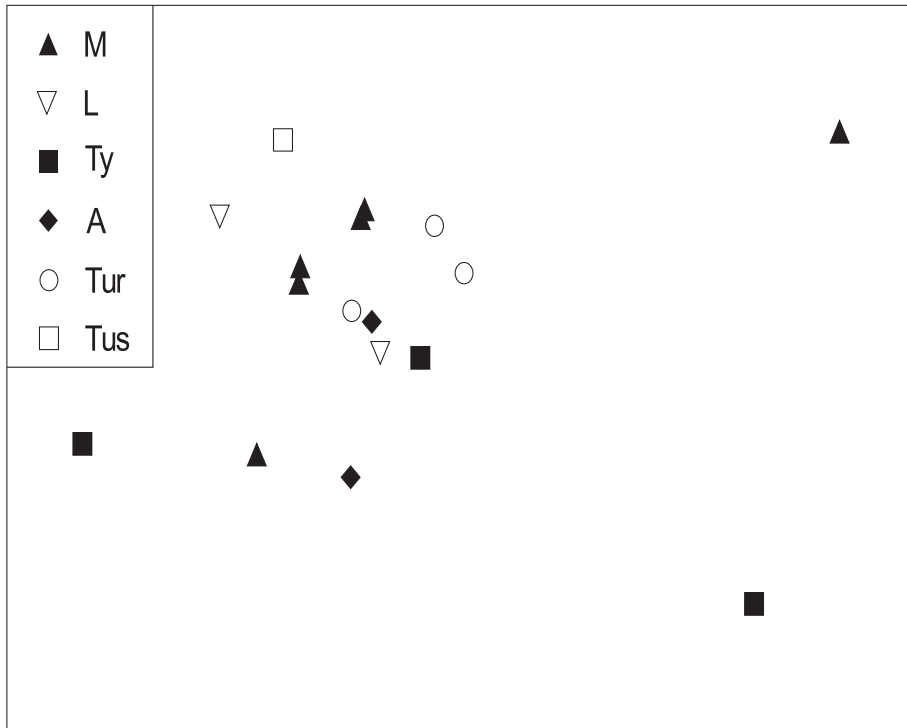


FIGURE 6 MDS diagram of abundance of cephalopod prey captured in relation to *G. griseus* from different geographical areas in the Mediterranean Sea. M, Central Catalan Coast (present study); L, Liguria; Ty, Tyrrhenian; A, Adriatic; Tur, Turkey; Tus, Tuscany. Analysis carried out with stress of 0.9.

TABLE 2 Number of cephalopod species and specimens according to whether they are pelagic.

| | Total | Pelagic | Benthic | % benthic |
|-----------|-------|---------|---------|-----------|
| Species | 18 | 11 | 7 | 38.9 |
| Specimens | 386 | 319 | 67 | 17.4 |

However, the information available is rather limited and fragmentary because most cephalopods are active swift swimmers and can avoid all types of nets, and because sampling at such great depths is difficult. Therefore, to increase the data on this fauna, different information sources, such as scientific surveys, data from the commercial fleet and stomach content studies of teuthophagous species, must be explored.

4.5 | Final remarks

In cephalopods, seasonality is related to their short life span, rapid population turnover, and reproductive behavior (Sánchez & Martín, 1993). Moreover, large aggregations of *G. griseus* can occur in response to abundant but ephemeral pulses of productivity related to oceanographic fronts that attract their primary prey, squid (Bearzi et al. 2011; Davis et al. 2002; Riccialdelli et al., 2012). Because *G. griseus* can exploit a wide variety of prey, depending on their availability, it is possible that the species is an opportunistic feeder on seasonal blooms of cephalopods. The case of G1 is consistent with this hypothesis. The most abundant species in this adult female was the benthic octopod

E. cirrhosa (nearly 85% of its stomach content), making up more than 30% of the total species found in the stomachs. The hypothesis is supported by the study of Clarke and Pascoe (1985) carried out on a *G. griseus* stranded on the British coast, and the work of González et al. (1994) in Galician waters (northwestern Spanish Atlantic coast).

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AUTHOR CONTRIBUTIONS

Amanda Luna: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; software; visualization; writing – original draft. **Pilar Sánchez:** Data curation; formal analysis; resources; software; supervision; validation; visualization; writing – review and editing. **Carla Chicote:** Resources. **Manel Gazo:** Conceptualization; resources; supervision.

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