



ARTICLE

Diet of striped dolphins (*Stenella coeruleoalba*) in southern Spanish waters

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Abstract

Identifiable food remains were analyzed from 46 stomachs of striped dolphins (*Stenella coeruleoalba*) stranded in southern Spain between 2007 and 2014. Results suggest that the species feeds mainly on mesopelagic and neritic fish, but also on oceanic squids. Fish species of the family Myctophidae were

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the main prey in terms of numerical importance and reconstructed prey weight (62% N and 29% W), followed by squids of the family Ommastrephidae (20% W) and bogue (*Boops boops*) (15% W). The most important prey taxa according to the General Importance Index (GII) were *C. maderensis*, Ommastrephidae gen. spp., *Notoscopelus* spp., and *M. punctatum*. Higher number of mesopelagic myctophids were found in dolphins from the Mediterranean (73% vs. 29% N), while more demersal gobiids and European hake (*Merluccius merluccius*) were found in those from the Atlantic (44% vs. 1% and 8% vs. <1% N), where a more varied diet was also observed. Differences were also seen in the seasonal importance of some prey, as well as between years, sexes, and maturity states. The diet composition suggests that most of feeding occurred in oceanic regions, during twilight and night hours, while the observed dietary variation may reflect differences in topography, and changes in the prey availability.

KEYWORDS

Alboran Sea, cetaceans, diet, Gulf of Cadiz, Spain, *Stenella coeruleoalba*, strandings, striped dolphin

1 | INTRODUCTION

The striped dolphin (*Stenella coeruleoalba*) is widely distributed in temperate, subtropical, and tropical seas. It is mainly recorded from offshore waters and, even when found close to shore, is usually seen in deep waters (Cañadas et al., 2002; Perrin, 2017; Reeves & Notarbartolo di Siciara, 2006). There are two distinct subpopulations in European waters, one in the Mediterranean and another in the Atlantic, with a very low gene flow between them through the Strait of Gibraltar (Bourret et al., 2007; Calzada & Aguilar, 1995; García-Martínez et al., 1995; Gaspari, 2004). The Mediterranean subpopulation is currently listed as “Least Concern” by the IUCN (Lauriano, 2021), but it was previously classified as “Vulnerable” (Aguilar & Gaspari, 2012) due to a suspected reduction in population size of over 30% over the last three generations (~60 years), among other criteria (Braulik, 2019). In addition to high levels of fishery bycatch (e.g., Rogan & Mackey, 2007; Silvani et al., 1999), the population suffered two massive die-offs (from 1990 to 1992 and in 2006–2007) linked to an infection by cetacean morbillivirus (Aguilar & Raga, 1993; Keck et al., 2010; Raga et al., 2008). High contaminant loads (Aguilar & Borrell, 2005; Troisi et al., 2001), but also prey depletion caused by overfishing (Bearzi et al., 2006; Jusufovski et al., 2019), have been proposed as factors that could have prompted the morbillivirus outbreaks (Aguilar, 2000). Thus, the study of striped dolphin diet is of interest to monitor changes in the diet and life habits of these populations, to identify possible factors that may affect their health status.

The diet of Mediterranean striped dolphins has been studied through analysis of stomach contents of stranded and bycaught individuals (e.g., Aznar et al., 2017; Desportes, 1985; Spitz et al., 2006; Würtz & Marrale, 1993) and based on stable isotope analysis (e.g., Gómez-Campos et al., 2011; Meissner et al., 2012). Results of such studies

indicate that the diet consists mostly of small, pelagic, and mesopelagic schooling fish, followed by cephalopods, with few records of crustaceans in the diet.

There has been only one previous study on the diet of striped dolphins based on the analysis of stomach contents in the south of the Iberian Peninsula, but this included only strandings in Portugal (Marçalo et al., 2021). In the Portuguese waters, the diet of striped dolphins is based mainly on sardine (*Sardina pilchardus*) and blue whiting (*Micromesistius poutassou*) (Marçalo et al., 2021). However, it is unknown if their diet is maintained along the Spanish Gulf of Cadiz and on the other side of the Strait of Gibraltar, in the Alboran Sea, which present different oceanographic characteristics and topography. Stomach content analysis, by providing a quantification of the diet, can shed light on the composition of the diet of striped dolphins in the area, allowing the identification of possible longitudinal variations in the diet composition in the south of the Iberian Peninsula and/or food overlap with other species, which may be relevant for the management of this species.

We analyzed the stomach contents of striped dolphins stranded south of the Iberian Peninsula, comprising the Spanish coast of the Gulf of Cadiz (Atlantic Ocean) and the Alboran Sea (Mediterranean Sea), during 2007–2014, to describe, quantify, and investigate which factors could explain dietary variability. These results are intended to contribute to the knowledge of the trophic ecology of this species in an area characterized by a topographical, oceanographic, and biological discontinuity. Conventional stomach analysis methods have been applied, while a method based on bootstrap simulations has been used for descriptive analyses and comparisons.

2 | MATERIALS AND METHODS

2.1 | Study area

The stomachs analyzed came from animals stranded along the Spanish coasts of the Gulf of Cadiz and the Alboran Sea (see Figure 1). The Gulf of Cadiz is a highly productive area characterized by a wide continental platform with a maximum width of 30 km in the central part of the basin (Sobrinho et al., 1994); while the Alboran Sea, located in the

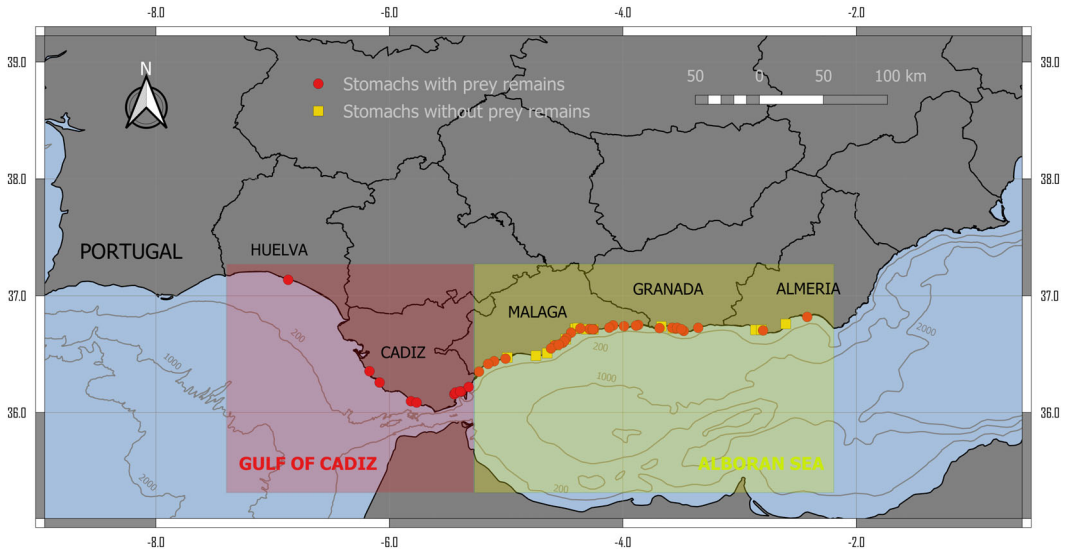


FIGURE 1 Map of the study area showing the locations of the stranded striped dolphins which stomach contents have been collected, both with (red dots) and without (yellow dots) prey remains. The two regions in which the study area was divided, Gulf of Cadiz and Alboran Sea, are shaded in red and yellow, respectively.

westernmost basin of the Mediterranean Sea, has a very narrow continental platform. The Alboran Sea is highly influenced by the Atlantic Ocean through the Strait of Gibraltar, which limits its western border, while its eastern border is located in the Almeria-Oran front, the main oceanographic barrier between the Atlantic Ocean and the Mediterranean Sea. This semi-permanent boundary acts as a gene flow barrier for various species (Patarnello et al., 2007).

2.2 | Collection and processing of samples

Stomachs of 63 striped dolphins stranded in southern Spain were examined from 2007 to 2014 (Figure 1). Stranded cetaceans were attended by experienced personnel from several organizations (Centro de Gestión del Medio Marino, CEGMA; Centro de Recuperación de Especies Marinas Amenazadas, CREMA; and Estación Biológica de Doñana, EBD-CSIC) that participate in the Andalusian stranding network, coordinated by the Agencia de Medio Ambiente y Agua de Andalucía from the Andalusian Regional Government. When the condition of the carcass allowed it, the species, sex, and cause of death were determined, standard measurements taken, and the stomachs and other samples collected. The methodology for data and sample collection from the carcasses followed the European Cetacean Society protocols (Kuiken & Hartmann, 1991).

Stomachs were removed and stored frozen for later examination in the laboratory, or their contents were first fixed with 70% formalin and then transferred to 70% ethanol until they were processed in the laboratory, depending on the accessibility of the carcasses. Once in the laboratory, frozen stomachs were thawed, the three stomach compartments were opened, and their contents washed through nested sieves (from 1 mm to 0.355 mm diameter). Stomach contents that had been transferred to 70% ethanol were similarly washed through nested sieves.

Prey remains consisted mainly of hard parts (i.e., fish otoliths, bones, cephalopod mandibles, and eye lenses) which were cleaned, sorted, and stored. Fish otoliths and bones were kept dry, while cephalopod mandibles (beaks) and eye lenses of both fish and cephalopods were kept in 70% ethanol.

2.3 | Prey identification and quantification

Prey remains were identified using our own reference collections and published guides (e.g., Campana, 2004; Clarke, 1986; Härkönen, 1986; Lombarte et al., 2006; Tuset et al., 2008; Xavier & Cherer, 2009). Otoliths were used for fish identification, while cephalopods were identified by their mandibles (beaks). Hard structures were measured with a binocular microscope fitted with an eyepiece reticule. For stomachs in which one fish species was represented by >30 otoliths, a random sample of 30 otoliths was measured and extrapolated to the total sample.

Fish length and weight were back-calculated using published regressions (e.g., Giménez et al., 2016; Härkönen, 1986; Santos et al., 2001) as well as cephalopod dorsal mantle length and weight (e.g., Clarke, 1986; see Table S1). Regressions were applied to the fish otolith length (OL) or otolith width (OW) measurements. For cephalopods, rostral (LRL) and hood (LHL) lengths of the lower beaks were used. Prey were identified to species level when possible, and species-specific regressions were used to estimate their size/weight, when available. When species-specific regressions were not available, or remains were not identified to species level, regressions for genus, family, or other groupings were used. These new regressions were built based on combined data for species in that group. Remains not identified were grouped into species level. For otoliths or beaks that were eroded, fragmented, or not identifiable, the mean weight of all the identified fish or cephalopod species in all stomachs was applied (see Table S1 for details of the regressions used).

To reconstruct total prey weight, each otolith was considered to correspond to a “half fish,” while each lower beak was assumed to represent one cephalopod (except if the number of upper beaks was greater, in which case the measurements taken from the lower beaks were extrapolated to the total number of upper beaks).

The importance of each prey taxon in each stomach was assessed in terms of presence/absence, number of individual prey taxon, and summed reconstructed prey weight. For overall diet, we also used five standard indices to estimate the relative importance of each prey taxon.

(1) Percentage of number of prey taxon:

$$\%N = \left(\frac{\sum N_i}{\sum N_t} \right) \times 100,$$

where N_i is the number of individuals of the prey taxon i and N_t the total number of all individuals of all prey species, in both cases, summed across all the stomachs.

(2) Percentage of reconstructed prey weight:

$$\%W = \left(\frac{\sum W_i}{\sum W_t} \right) \times 100,$$

where W_i is the summed weight of the individuals of the prey taxon i and W_t is the total weight of all individuals of all prey species, again in both cases summed across all the stomachs.

(3) Percentage of frequency of occurrence:

$$\%F = (F_i/F_t) \times 100,$$

where F_i is the number of striped dolphin stomachs containing prey taxon i and F_t is the total number of stomachs containing any prey taxon.

(4) General Importance Index (GII; Assis, 1996):

$$GII = (\%N + \%W + \%F) / \sqrt{3},$$

where $\%N$ is the percentage of number of prey taxon, $\%W$ is the percentage of reconstructed prey weight, and $\%F$ is the percentage of frequency of occurrence of a given prey taxon.

(5) Index of Relative Importance (IRI; Hart et al., 2002):

$$IRI = (\%N + \%W) \times \%F$$

where $\%N$ is the percentage of number of prey taxon, $\%W$ is the percentage of reconstructed prey weight, and $\%F$ is the percentage of frequency of occurrence of a given prey taxon. Although the IRI has not been used for the comparisons between groups of samples, it has been calculated to facilitate comparison with other similar studies.

2.4 | Confidence limits for diet composition

Confidence intervals (CI) for the indices of diet composition were calculated with the R package *boot* (Canty & Ripley, 2019), following Santos et al. (2014). One thousand runs were performed for each index of interest using a random sample of n values with replacement (where n is the number of nonempty stomachs analyzed). Once the 1,000 runs were available, the median and 95% CI were calculated separately for each prey category by sorting the 1,000 measures for that prey category, and identifying the 26th, 500th, and 975th values in the sorted sequence.

2.5 | Pairwise comparisons

Samples were grouped to examine differences in diet between regions (i.e., Atlantic and Mediterranean coasts), years (grouped in periods of two years to increase sample size), quarters, sexes, and maturity states (Table 1). Because maturity information was not available, it was assumed that dolphins larger than 190 cm total length were mature, both for males and females, following Meissner (2012) and Calzada et al. (1996, 1997). To overcome potential issues with the distributions of the response variables we used bootstrap methods to compare groups of samples. 1,000 bootstrap simulations (combinations with repetition) of GII values of the four most important prey taxa, were used to compare the diet of the dolphin subgroups, and for each replicate it was noted in which subgroup GII was higher. If the GII value in subgroup *a* was higher than the GII value in subgroup *b* in more than 95% of replicates, we argue that the prey taxon is significantly more important in the diet of subgroup *a* than in the diet of subgroup *b*. Since GII is based on percentages, there is nonindependence between prey taxa within a given subgroup of samples (i.e., a higher value for one prey taxon will tend to lead

TABLE 1 Strandings of striped dolphins (*Stenella coeruleoalba*) along the coasts of southern Spain from 2007 to 2014 which stomach contents have been analyzed in the present study. Strandings grouped by region, year, quarter, sex, and maturity.

	N
Region	
Gulf of Cadiz	12
Alboran Sea	31
Unknown	3
Year	
2007–2008	13
2009–2010	10
2011–2012	13
2013–2014	7
Unknown	3
Quarter	
January–March	11
April–June	9
July–September	10
October–December	13
Unknown	3
Sex	
Male	21
Female	20
Unknown	5
Maturity	
Immature	23
Mature	18
Unknown	5
Total	46

to lower values for other prey taxa). Therefore, comparisons across prey in a subgroup of samples are not appropriate, thus the comparisons were made only across subgroups of samples for a given prey. A total of 15 comparisons was made for each of the four most important prey taxa in terms of GII, (i.e., 60 comparisons in total). These are effectively 60 separate hypotheses so that it is not necessary to apply corrections for multiple comparisons.

3 | RESULTS

3.1 | Sample composition

Of the 64 stomachs of striped dolphins stranded on the coasts of Andalusia during the period 2007–2014, 46 contained identifiable food remains. Table 1 summarizes the number of dolphin stomachs with food remains grouped by region, year, quarter, sex, and maturity state. Most animals (67%) were recovered from the Mediterranean region (Alboran Sea). Similar numbers of strandings (22%–28%) were recorded in three out of the four time periods considered (2007–2008, 2009–2010, and 2011–2012). In the last period (2013–2014), only 15% of the total number of strandings was recorded. Most strandings (28%) took place in the fourth quarter of the year (October to December), followed by the first (24%) and third quarters (22%). Of the 41 animals for which sex was determined, 21 were males and 20 females. Half of the animals were considered immature and almost 40% mature, where the remaining were undetermined since length was not available.

3.2 | Diet description and quantification

Food remains consisted mostly of fish otoliths and cephalopod mandibles (beaks) with very little soft material found. Remains of 11,962 fish belonging to 12 taxa were found together with remains of 203 individual cephalopods belonging to 11 different taxa. Myctophids, composed of *Ceratoscopelus maderensis* (34% N), *Myctophum punctatum* (12% N), *Benthosema glaciale* (10% N), and *Notoscopelus* spp. (6% N), were the most abundant prey in terms of numerical importance and reconstructed prey weight (62% N) (Table 2). Another abundant prey was the silvery lanternfish (*Maurolicus muelleri*), which made up 12% N of the total number of prey taxa. These five species were also found in a high proportion of stomachs, but they contributed only 30% W of the total reconstructed weight of all prey, due to their small size. However, it is worth noting that the regressions available for these species have large biases, mainly at the extremes of their size ranges (with the weight of the smallest sizes of *M. muelleri*, considered to be substantially underestimated when using the available regression; Battaglia et al., 2010). Values obtained for GII and IRI also highlight the importance of these prey species in the diet. Both myctophids and lanternfishes are mesopelagic fish, but neritic species are also found, such as bogue (*Boops boops*) (1% N; 15% W), European hake (*Merluccius merluccius*) (1% N; 5% W), or gobiids (5% N; 5% W).

In the case of cephalopods, although remains of this group were found in many stomachs, only those of the family Ommastrephidae were important in the diet, being identified in almost half of the stomach analyzed, representing 20% of the total reconstructed prey weight. The importance of this taxon was also apparent from the GII and IRI indices (Table 2). Other cephalopod prey identified were oceanic squids of the families Brachioteuthidae, Chiroteuthidae, Enoploteuthidae, and Histioteuthidae. In addition, we also identified neritic species such as *Alloteuthis* spp. and sepiolids.

The CI obtained were generally narrow for most prey categories and most indices of prey importance. Indices of prey importance are also provided separately in Tables S2 and S3 for dolphins stranded in the Spanish Gulf of Cadiz and Alboran Sea, respectively.

TABLE 2 Importance of prey species identified in the stomach contents of striped dolphins (*Stenella coeruleoalba*) stranded in southern Spain from 2007 to 2014 ($n = 46$). Prey importance is given as: N (total number of individual prey species identified), W (reconstructed prey weight, grams), F (number of stomachs with each prey category), GII (General Importance Index), IRI (Index of Relative Importance). All indices are also expressed as percentages. 95% confidence intervals are provided between brackets. Note that figures are provided without decimals for easy reading, so zero values may represent a value lower than 0.5 and not strictly zero.

Prey species	N	%N	W	%W	F	%F	GII	%GII	IRI	%IRI
Clupeiformes										
Clupeidae gen. spp.	4	<1 [0, 1]	62	1 [0, 2]	1	2 [0, 7]	2 [0, 5]	1 [0, 3]	1 [0, 16]	<1 [0, 1]
Gadiformes										
Gadidae										
<i>Gadiculus argenteus</i>	909	7 [0, 21]	32	<1 [0, 1]	7	15 [7, 26]	13 [4, 26]	8 [2, 15]	118 [2, 481]	2 [0, 8]
Merlucciidae										
<i>Merluccius merluccius</i>	109	1 [0, 2]	561	5 [0, 11]	7	15 [4, 26]	12 [4, 21]	7 [2, 12]	97 [1, 289]	2 [0, 5]
Myctophiformes										
Myctophidae										
<i>Benthoosema glaciale</i>	1,244	10 [0, 28]	143	1 [0, 5]	5	11 [2, 22]	13 [3, 28]	8 [1, 16]	126 [0, 533]	2 [0, 9]
<i>Ceratoscopelus maderensis</i>	4,135	34 [13, 56]	582	6 [1, 15]	18	39 [26, 54]	46 [27, 66]	26 [16, 38]	1,553 [471, 3,174]	25 [8, 52]
<i>Myctophum punctatum</i>	1,405	12 [3, 27]	240	2 [0, 8]	14	30 [17, 43]	26 [14, 40]	15 [8, 23]	423 [74, 1,188]	7 [1, 20]
<i>Notoscopelus</i> spp.	764	6 [1, 14]	2017	20 [2, 36]	17	37 [24, 52]	36 [20, 53]	21 [11, 30]	960 [125, 2,045]	16 [2, 34]
Ophidiiformes										
Ophidiidae										
<i>Ophidion barbatum</i>	2	<1 [0, 1]	3	<1 [0, 1]	1	2 [0, 7]	1 [0, 4]	1 [0, 2]	<1 [0, 1]	<1 [0, 1]
Perciformes										
Carangidae										
<i>Trachurus trachurus</i>	2	<1 [0, 1]	3	<1 [0, 1]	2	4 [0, 11]	3 [0, 6]	1 [0, 4]	<1 [0, 2]	<1 [0, 1]
Gobiidae gen. Spp.	600	5 [0, 16]	508	5 [0, 10]	2	4 [0, 11]	8 [0, 20]	5 [0, 12]	43 [0, 260]	1 [0, 4]
Sparidae										
<i>Boops boops</i>	139	1 [0, 3]	1551	15 [3, 22]	5	11 [2, 20]	16 [4, 25]	9 [2, 14]	177 [10, 450]	3 [0, 7]

TABLE 2 (Continued)

Prey species	N	%N	W	%W	F	%F	GII	%GII	IRI	%IRI
Stomiformes										
Sternoptychidae										
<i>Maurollicus muelleri</i>	1,493	12 [2, 25]	31	<1 [0, 1]	10	22 [11, 35]	20 [9, 32]	11 [5, 19]	273 [34, 748]	4 [1, 12]
Unidentified fish	1,156	10 [6, 15]	1721	17 [12, 28]	23	50 [35, 63]	44 [33, 56]	25 [19, 33]	1,316 [731, 2,173]	22 [12, 36]
Mollusca										
Cephalopoda										
Octopoda										
Ocythoidea										
<i>Ocythoe tuberculata</i>	1	<1 [0, 1]	2	<1 [0, 1]	1	2 [0, 7]	1 [0, 4]	1 [0, 2]	<1 [0, 1]	<1 [0, 1]
Sepiida										
Sepiidae gen. spp.	12	<1 [0, 1]	91	1 [0, 4]	2	4 [0, 11]	3 [0, 8]	2 [0, 4]	4 [0, 32]	<1 [0, 1]
Sepioidae gen. spp.	52	<1 [0, 1]	127	1 [0, 2]	10	22 [11, 35]	14 [7, 22]	8 [4, 13]	36 [6, 98]	1 [0, 2]
Teuthida										
Myopsida										
Loliginidae gen. spp.										
<i>Alloteuthis</i> spp.	2	<1 [0, 1]	13	<1 [0, 1]	2	4 [0, 11]	3 [0, 7]	2 [0, 4]	1 [0, 5]	<1 [0, 1]
Oegopsida	8	<1 [0, 1]	39	<1 [0, 1]	4	9 [2, 17]	5 [1, 10]	3 [1, 6]	4 [0, 13]	<1 [0, 1]
Ancistrocheiridae gen. Spp.	1	<1 [0, 1]	24	<1 [0, 1]	1	2 [0, 7]	1 [0, 4]	1 [0, 3]	1 [0, 7]	<1 [0, 1]
Brachioteuthidae										
<i>Brachioteuthis</i> spp.	33	<1 [0, 1]	101	1 [0, 2]	11	24 [13, 37]	15 [8, 22]	8 [5, 13]	30 [8, 93]	<1 [0, 2]
Chiroteuthidae gen. spp.	14	<1 [0, 1]	159	2 [0, 5]	5	11 [2, 22]	7 [2, 14]	4 [1, 8]	18 [0, 92]	<1 [0, 2]
Enoploteuthidae gen. spp.	10	<1 [0, 1]	32	<1 [0, 1]	3	7 [0, 15]	4 [0, 9]	2 [0, 5]	3 [0, 15]	<1 [0, 1]
Histiototeuthidae										
<i>Histiototeuthis</i> spp.	3	<1 [0, 1]	30	<1 [0, 1]	2	4 [0, 11]	3 [0, 7]	2 [0, 4]	1 [0, 12]	<1 [0, 1]
Ommastrephidae gen. spp.	60	<1 [0, 1]	2056	20 [10, 39]	20	43 [30, 59]	37 [26, 51]	21 [15, 30]	895 [381, 1,867]	15 [6, 31]
Unidentified cephalopod	6	<1 [0, 1]	108	1 [0, 3]	4	9 [2, 17]	6 [1, 11]	3 [1, 7]	10 [0, 42]	<1 [0, 1]

(Continues)

TABLE 3 The “Pairwise comparison test” described in section 2.5 was applied to perform pairwise comparisons using the General Importance Index (GII) by Region, Year, Quarter, and Sex of the four most important prey categories (*Ceratoscopelus maderensis*, Ommastrephidae gen. spp., *Notoscopelus* spp., and *Myctophum punctatum*), selected attending to the GII values (without considering unidentified species). Significant results are highlighted in bold.

GII		<i>Ceratoscopelus maderensis</i>	Ommastrephidae gen. spp.	<i>Notoscopelus</i> spp.	<i>Myctophum punctatum</i>
Region	Gulf of Cadiz (a)	a > b = 18.6%	a > b = 28.6%	a > b = 16.3%	a > b = 2.3%
	Alboran Sea (b)	a < b = 81.4%	a < b = 71.4%	a < b = 83.6%	a < b = 97.7%
Year	2007–2008 (a)	a > b = 1.2%	a > b = 94.2%	a > b = 44.2%	a > b = 53.1%
	2009–2010 (b)	a < b = 98.8%	a < b = 5.8%	a < b = 55.8%	a < b = 46.9%
	2007–2008 (a)	a > c = 5.5%	a > c = 61.1%	a > c = 68.8%	a > c = 93.7%
	2011–2012 (c)	a < c = 94.5%	a < c = 38.9%	a < c = 31.2%	a < c = 6.3%
	2007–2008 (a)	a > d = 11.9%	a > d = 66.8%	a > d = 78.1%	a > d = 90.1%
	2013–2014 (d)	a < d = 87.9%	a < d = 33.2%	a < d = 21.9%	a < d = 9.9%
	2009–2010 (b)	b > d = 68.5%	b > d = 19.7%	b > d = 58.5%	b > d = 72.1%
	2011–2012 (c)	b < d = 31.5%	b < d = 80.2%	b < d = 41.2%	b < d = 27.7%
	2009–2010 (b)	b > d = 38.6%	b > d = 25.1%	b > d = 63.7%	b > d = 69.4%
	2013–2014 (d)	b < d = 61.4%	b < d = 74.9%	b < d = 36%	b < d = 29.6%
	2011–2012 (c)	c > d = 28.1%	c > d = 54.5%	c > d = 59.4%	c > d = 43%
	2013–2014 (d)	c < d = 71.9%	c < d = 45.5%	c < d = 40.5%	c < d = 56.7%
Quarter	Jan–Mar (a)	a > b = 2.8%	a > b = 70.2%	a > b = 94.7%	a > b = 74.5%
	Apr–Jun (b)	a < b = 97.2%	a < b = 29.7%	a < b = 5.3%	a < b = 25.5%
	Jan–Mar (a)	a > c = 0%	a > c = 72.1%	a > c = 98%	a > c = 80.4%
	Jul–Sep (c)	a < c = 100%	a < c = 27.9%	a < c = 2%	a < c = 19.5%
	Jan–Mar (a)	a > d = 26.5%	a > d = 48.5%	a > d = 67%	a > d = 67.5%
	Oct–Dec (d)	a < d = 72.9%	a < d = 51.5%	a < d = 33%	a < d = 32.4%
	Apr–Jun (b)	b > d = 2.9%	b > d = 52.2%	b > d = 75.6%	b > d = 59.5%
	Jul–Sep (c)	b < d = 97.1%	b < d = 47.8%	b < d = 24.3%	b < d = 40.3%
	Apr–Jun (b)	b > d = 91.9%	b > d = 29.6%	b > d = 11.9%	b > d = 34.7%
	Oct–Dec (d)	b < d = 8.1%	b < d = 70.4%	b < d = 88.1%	b < d = 65.3%
	Jul–Sep (c)	c > d = 99.6%	c > d = 29%	c > d = 3.9%	c > d = 26.3%
	Oct–Dec (d)	c < d = 0.4%	c < d = 70.9%	c < d = 96.1%	c < d = 73.6%
Sex	Male (a)	a > b = 53.3%	a > b = 66.4%	a > b = 37.7%	a > b = 98.5%
	Female (b)	a < b = 46.7%	a < b = 33.6%	a < b = 62.3%	a < b = 1.5%
Maturity	Immature (a)	a > b = 26.3%	a > b = 24.2%	a > b = 93.8%	a > b = 95.6%
	Mature (b)	a < b = 73.7%	a < b = 75.7%	a < b = 6.2%	a < b = 4.4%

3.3 | Dietary variation

Pairwise comparisons performed using the GII of the four most important prey taxa (*C. maderensis*, Ommastrephidae gen. spp., *Notoscopelus* spp., and *M. punctatum*) showed that striped dolphins that stranded on the Spanish coasts of the Alboran Sea have higher GII values for these four prey categories than individuals that stranded on the Spanish coasts of the Gulf of Cadiz, although only in the case of *M. punctatum* was this difference significant (see Table 3 and Figure 2).

The GII values for *C. maderensis* were significantly lower in the first 2 years of the series (2007–2008) when compared with 2009–2010. None of the remaining GII comparisons by group of years showed significant differences (see Table 3 and Figure 2).

By quarter, results of the pairwise comparisons showed that there were significant differences in the GII values of *C. maderensis*, with the highest importance in the third quarter (\approx summer), followed by the second (\approx spring)

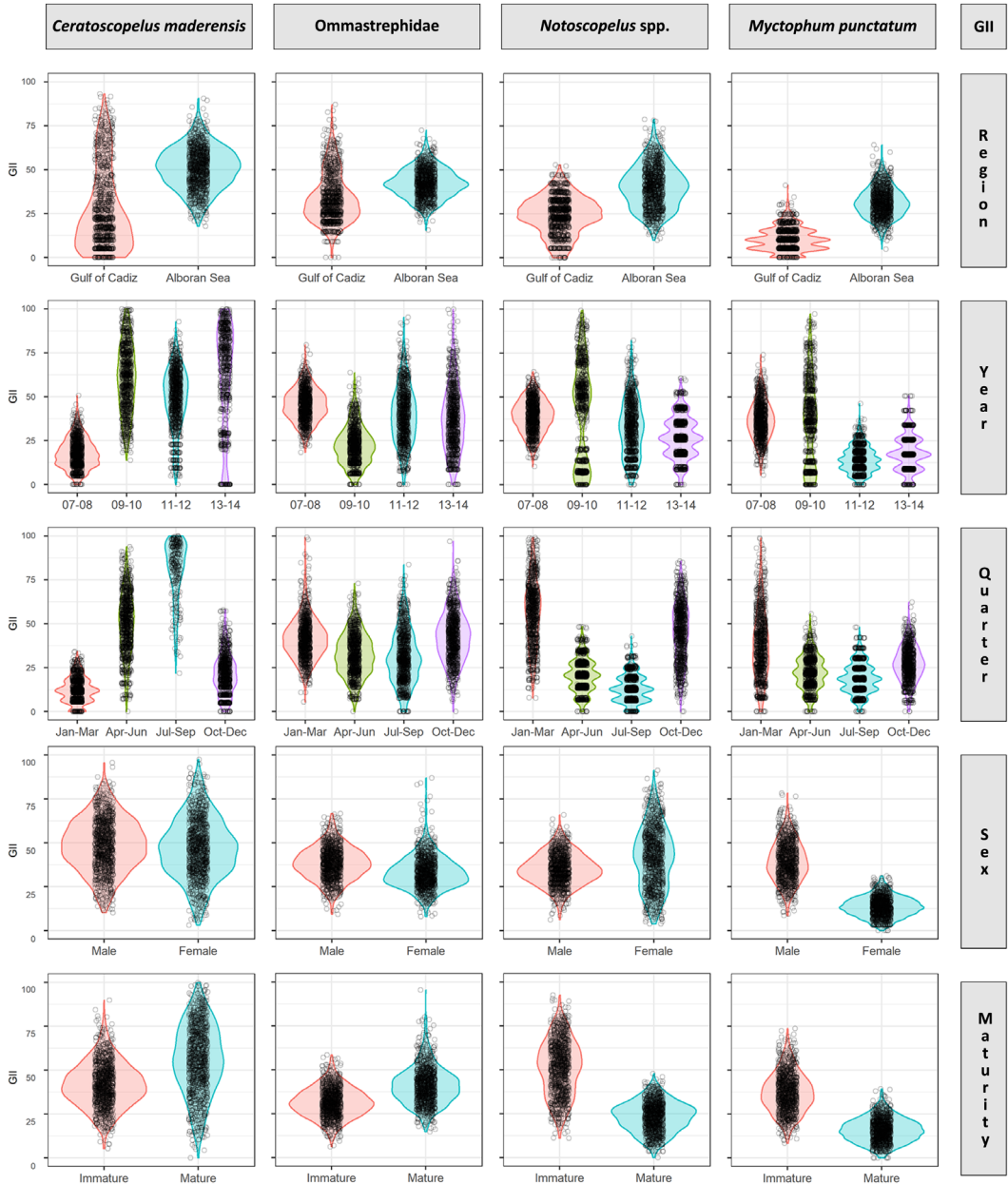


FIGURE 2 Plots of the General Importance Index (GII) of the main prey taxa (*Ceratoscopelus maderensis*, Ommastrephidae, *Notoscopelus* spp., and *Myctophum punctatum*) identified in the stomach contents of striped dolphins stranded on the Andalusian coast by region, year, quarter, sex, and maturity.

(see Table 3 and Figure 2). Differences were also significant for *Notoscapelus* spp. which showed an opposite pattern, with the highest importance in the first (\approx winter) and fourth (\approx autumn) quarters.

Male striped dolphins showed significantly higher values of GII for *M. punctatum* than females, but there were no significant differences between the GII values for other most important species, although ommastrephids seemed to be more important in the diet of males than that of females (see Table 3 and Figure 2).

Finally, immature striped dolphins showed significantly higher values of GII for *M. punctatum* than mature dolphins. Ommastrephids seemed to be more important for mature than for immature dolphins while the opposite was true for *Notoscapelus* spp. (see Table 3 and Figure 2).

4 | DISCUSSION

The diet of the striped dolphins inhabiting the vicinity of the Strait of Gibraltar has been characterized for the first time. The convergence of the Atlantic Ocean and Mediterranean Sea in this area makes it important for many species (Patarnello et al., 2007). Topographical and oceanographic differences between these areas cause changes and discontinuities in biological communities. In the case of the striped dolphin, two different subpopulations have been distinguished, the Atlantic and the Mediterranean (Bourret et al., 2007; Calzada & Aguilar, 1995; García-Martínez et al., 1995; Gaspari, 2004). Although there may be some movements between both regions, physical and chemical characteristics vary substantially, which leads to differences in the behavior and habits of the dolphins that inhabit them (Aguilar & Gaspari, 2012).

The contents of 46 stomachs, with identifiable food remains, of striped dolphins stranded on the Spanish coasts of the Gulf of Cadiz (Atlantic Ocean) and the Alboran Sea (Mediterranean Sea), between 2007 and 2014, have been analyzed. Results indicate that individuals that inhabit these regions are mainly piscivorous, and to a lesser extent teuthophagous (about a quarter of the weight of the diet), consistent with what has been reported in other Atlantic areas (Desportes, 1985; Marçalo et al., 2021; Spitz et al., 2006), but contrary to what has been reported in other regions of the Mediterranean (Bello, 1993; Blanco et al., 1995; Dede et al., 2016; Öztürk et al., 2007; Würtz & Marrale, 1993). Their diet in the study area consisted mainly of mesopelagic and neritic fish species, but also of oceanic squids. This diet indicates mainly oceanic habits, but also reflects incursions into the neritic region (Aznar et al., 2017; Marçalo et al., 2021; Spitz et al., 2006; Würtz & Marrale, 1993), where striped dolphins feed on species with a pelagic but also a demersal neritic distribution. In the sample as a whole, myctophids, together with the silvery lanternfish, were the most represented in number (74% N) and in weight, despite their small size (30% W), followed by ommastrephid cephalopods (20% W), and by various fish (e.g., bogue 15% W, European hake 5% W, and gobiids 5% W), and other cephalopods. Surprisingly, we did not find blue whiting, as were found in adjacent waters (Marçalo et al., 2021), and the number of clupeids was very low (probably due to the rapid degradation of these otoliths). When we separated the sample geographically, we observed that higher number of myctophids were found in dolphins from the Mediterranean (73% vs. 29% N) while more gobiids and European hake were found in those from the Atlantic (44% vs. 1% and 8% vs. <1% N). Furthermore, the diet in the Atlantic region was more varied, while in the Alboran Sea it was mainly circumscribed to oceanic species. These results are consistent with the topography of the areas. In the Gulf of Cadiz, with a wide continental shelf, striped dolphins are expected to consume a greater variety of pelagic and demersal neritic species (Marçalo et al., 2021), contrary to what one might hypothesize for the Alboran Sea. However, the individuals stranded in the Gulf of Cadiz and the Alboran Sea do not necessarily belong to the Atlantic and Mediterranean subpopulations, respectively, since certain displacement of individuals between both sides of the Strait is assumed, and there could be also a mixture of individuals that feed in one area and end up stranding in the other due to the drift of the carcasses. In this case, it is expected that the main transport of dead individuals will occur from the Atlantic to the Mediterranean, because the predominant surface current is the one entering the Mediterranean (Lacombe & Richez, 1982). In any case, these differences in diet, whether due to

separate populations or to individuals from the same population traveling between regions, seem to indicate a high degree of plasticity to explore and feed both in oceanic and coastal habitats (Aznar et al., 2017; Spitz et al., 2006).

The four prey taxa with the highest GII values (i.e., *C. maderensis*, Ommastrephidae gen. spp., *Notoscopelus* spp., and *M. punctatum*) seemed to be more important in the overall diet in the Alboran Sea than in the Atlantic, although only the differences in *M. punctatum* were significant. This again supports the predominance of a more varied diet in the Gulf of Cadiz, while in the Alboran Sea a few (pelagic) species predominate with greater impact on the diet. There were hardly any annual differences in the relative importance of these four prey taxa in the diet. There was only a slight increase in the importance of *C. maderensis*, to the detriment of the rest, but it was only significant in first years of the series. The seasonal differences were somewhat more evident. A greater importance of *C. maderensis* was observed in summer months, while *Notoscopelus* spp. (and even of *M. punctatum*, although not significant) in winter months, which may indicate a certain seasonality of these species. Regarding sex and maturity, the only significant difference was a greater importance of *M. punctatum* in immature males, which could reflect some age differences in trophic habits. It should be noted that the comparisons all considered single explanatory variables and it is not possible to account for partial effects or interactions given the small sample size.

Finally, it should be noted that stable isotope analysis of striped and common dolphins (*Delphinus delphis*) in the Alboran sea showed high isotopic overlap (Giménez et al., 2017). Our data demonstrate that these two species share some of their main prey, such as *C. maderensis* or bogue, which may be one reason for the isotopic overlap found by Giménez et al. (2017).

The data presented here are the first for the species in the area, and although limited, they show that the diet of this species can vary substantially, both temporally and spatially, even between contiguous regions, adapting to oceanographic characteristics and availability of prey.

AUTHOR CONTRIBUTIONS

Camilo Saavedra: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; software; visualization; writing – original draft; writing – review and editing. **Manuel García-Polo:** Conceptualization; data curation; formal analysis; methodology; writing – review and editing. **Joan Giménez:** Conceptualization; formal analysis; investigation; methodology; writing – original draft; writing – review and editing. **José Luis Mons:** Funding acquisition; writing – review and editing. **Juan José Castillo:** Data curation; methodology; writing – review and editing. **Carolina Fernández-Maldonado:** Data curation; resources; writing – review and editing. **Renaud de Stephanis:** Conceptualization; funding acquisition; supervision; writing – review and editing. **Graham John Pierce:** Conceptualization; investigation; methodology; supervision; writing – review and editing. **María Begoña Santos:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; supervision; writing – original draft; writing – review and editing.

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