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# Temporal and geographical changes in the intestinal helminth fauna of striped dolphins, *Stenella coeruleoalba*, in the western Mediterranean: a long-term analysis (1982 - 2016)

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Temporal and geographical changes in the infections of intestinal helminths of striped dolphins, *Stenella coeruleoalba* were investigated in waters off the Spanish Mediterranean coast based on a sample of 233 dolphins stranded during 1982–2016. The influence of host-related factors (length and sex) and seasonality was also examined. Four helminth species had a prevalence > 5%, including adults of three cestodes, i.e., *Trigonocotyle globicephalae* (prevalence: 5.2%), *Tetrabothrius forsteri* (94.4%) and *Strobilocephalus triangularis* (18%); and juveniles of an acanthocephalan of the genus *Bolbosoma* (15.9%), identified as *B. capitatum* using molecular techniques. One immature specimen of *Diphyllobothrium* sp. (Cestoda) was also found in a single dolphin, and two juveniles of *Bolbosoma balaenae* in two dolphins. *Trigonocotyle globicephalae* seems to have low specificity for striped dolphins and was only found sporadically. *Tetrabothrius forsteri* and *S. triangularis* experienced a slight vs. a strong decrease, followed by a recovery, in infection levels throughout the study period, which are compatible with a reduction in the striped dolphin population caused by the Dolphin Morbillivirus outbreak in 1990. Infections of *B. capitatum*, a parasite typical from pilot whales, suddenly increased in 1990, then vanished. This rapid increase and following decrease are puzzling and can hardly be explained by a single factor. Infections of any helminth species were apparently uncorrelated to geographic origin, dolphin sex or season, but parasite load decreased with dolphin length in the case of *T. forsteri* and *S. triangularis*. To our knowledge, this study represents the first investigation of multi-decadal changes in cetacean parasites.

## KEYWORDS

trophically transmitted parasites, *Stenella coeruleoalba*, cetaceans, long-term trends, geographical variation, western Mediterranean

## 1 Introduction

Long-term studies on animal populations are essential to monitor ecosystem changes, especially in the global change scenario we have been facing during the last century (Luo et al., 2011). In the marine environment, this type of studies are relatively common for free-living species, particularly those of commercial interest (e.g. Kovach et al., 2015; Pershing et al., 2015; Pang et al., 2018). In contrast, long-term surveys of marine parasite populations are very scarce. This is unfortunate because parasites represent an integral part of ecosystems that influence, *inter alia*, trophic web dynamics and population sizes of their hosts (Hudson et al., 1998; Lafferty et al., 2008). In particular, there is evidence suggesting that trophically-transmitted metazoan parasites (TTPs) can alter several food-web properties. TTPs can increase interaction strength through the modification of their hosts behaviour, enhancing predation on infected prey hosts (Lafferty and Morris, 1996; Moore, 2002). Similarly, they may facilitate new trophic interactions, thus increasing food-web connectivity (Lafferty et al., 2006); modulate the flow of energy along certain trophic links (Morand and Harvey, 2000; Wood et al., 2007), and decrease food-web stability (Otto et al., 2007). On the other hand, parasites can reduce the fitness of their hosts, through increased mortality, reduced fecundity, altered behaviour and/or reduced growth, among others (Kuris, 2003; Miura et al., 2006; Hasik and Siepielski, 2022). These interactions may become surprisingly complex when other environmental stressors (i.e., pollution, fisheries impacts) are also at stake (e.g., Wood et al., 2010; Sures et al., 2017). For instance, parasite diversity (and their potential associated effects) are significantly lower in fished than unfished areas (Wood and Lafferty, 2015).

There are few studies that have monitored populations of marine parasites for at least two decades, and those available deal with species of human health concern, e.g. *Anisakis* spp., or with host species in the life-cycle that have commercial interest or are more easily accessible for sampling, e.g. fish (Mackenzie, 1987; Fiorenza et al., 2020; Welicky et al., 2021; Diez et al., 2022; Wood et al., 2023). To our knowledge, none of these studies have focused on infections in marine top predator species.

Cetaceans are ubiquitous marine top-predators that exert significant non-linear effects on trophic webs and, therefore, represent excellent sentinels of marine ecosystem changes (Heithaus et al., 2008; Estes et al., 2016). These mammals harbour a rather diverse fauna of TTPs including digeneans, cestodes, nematodes and acanthocephalans (Fraija-Fernández et al., 2016). The life-cycle of these parasites also involves invertebrates (crustaceans, molluscs) as intermediate hosts, and a number of fish and/or cephalopods as paratenic (transport) hosts that can expand infections throughout the whole trophic web through predator-prey interactions (Raga et al., 2009). These features could make the TTPs of cetaceans particularly useful to trace trophic interactions and to monitor long-term ecosystem trends. Unfortunately, the specific identity of the intermediate and paratenic hosts of these parasites is, for the most part, unknown (Mateu et al., 2015). Therefore, this part of the cycle must currently be treated as a 'black-box' for interpretation purposes.

To date, surveys on TTPs of cetaceans have usually been based on small, opportunistic samples (e.g. Berón-Vera et al., 2001; Romero et al., 2014; Terracciano et al., 2020). Furthermore, with a few exceptions (Aznar et al., 1995; Mead and Potter, 1995; Herrerias et al., 1997), hosts have typically been pooled for analysis, disregarding potential geographic effects on the composition and abundance of TTPs (Dailey and Perrin, 1973; Van Waerebeek et al., 1993; Dans et al., 1999; Lehnert et al., 2017). In this study, we take advantage of a well-established stranding network to investigate spatial and temporal changes (i.e. through several decades) in the infections of TTPs of a cetacean species. The striped dolphin, *Stenella coeruleoalba* is the most abundant cetacean species in waters off the Spanish Mediterranean coast [hereafter referred to as western Mediterranean for brevity] (Gómez de Segura et al., 2006). In 1990, this population suffered a severe epizootic outbreak caused by the Dolphin Morbillivirus (DMV), currently known as a strain of the Cetacean Morbillivirus (CeMV) (see Van Bresseem et al., 2014), which presumably resulted in the death of several thousand individuals (Aguilar and Raga, 1993). Subsequent DMV outbreaks occurred in 2007 (Raga et al., 2008) and, perhaps, 2011 (Rubio-Guerri et al., 2013), but in the latter the death toll was much lower and concentrated in the Valencian Community only. On the other hand, there is evidence that this striped dolphin population has progressively shifted its diet throughout the study period, from one dominated by oceanic prey (chiefly mesopelagic squids) towards one based on neritic, demersal prey (particularly hake, *Merluccius merluccius*) (Gomez-Campos et al., 2011; Aznar et al., 2017).

In this study, we addressed two research questions. First, we compared the intestinal helminth fauna of striped dolphins stranded in different regions along the Spanish Mediterranean coast. The sample was composed of animals that were killed by the DMV in the summer and autumn of 1990, which minimized the confounding effects of time upon spatial variability. This geographical analysis was exploratory as we did not know whether striped dolphins in the Western Mediterranean belong to one or several population units (Gaspari et al., 2019). Second, we investigated the potential effects of mortality outbreaks in the dolphins and the dietary shift on the infection dynamics of TTPs during the last three decades. With regard to the effect of the die-offs, we expected a general decrease of infections with time because of the reduction of the striped dolphin population.

## 2 Materials and methods

### 2.1 Data collection

Intestinal helminths were collected from a total of 233 striped dolphins stranded along the east coast of Spain between 1982 and 2016. Permission to collect stranded dolphins was given by the wildlife services of the regional governments, which are the official institutions in charge of managing and protecting wildlife. During the 1990 epizootic, the geographic coverage included the coasts of Catalonia, Valencian Community, Murcia and eastern Andalusia; in the remaining years, sampling was restricted to the Valencian

Community (Figure 1). The sample included the 52 animals examined by Mateu et al. (2014), as well as 6 of the 13 dolphins examined by Raga and Carbonell (1985), for which at least information on occurrence of all intestinal helminths was available. The remaining 175 dolphins were examined in this study, and included dolphins from every year within the time series, in order to avoid significant gaps that could affect the results. All dolphins in the final sample were > 100 cm long to exclude calves that had consumed milk only.

Before necropsy, total body length was measured and sex was determined for all animals. Intestines were removed and stored at -20°C. After thawing, intestines were weighed, measured and divided into 20 sections of equal length. Each section was opened and washed over a 0.02 mm sieve using tap water. The solid content was collected in a Petri dish and examined under a stereomicroscope. The intestinal wall was also thoroughly examined for attached helminths. Acanthocephalans were left in tap water for 24 hours at 4°C to allow the proboscis to evert. All parasites were washed in saline (9 g/l), fixed and preserved in 70% ethanol, and later identified to the lowest taxonomic level possible. Cestodes were stained with iron acetocarmine (Georgiev, 1986) and identified following Delyamure (1955) and Raga, (1985). Acanthocephalans were cleared in lactophenol, drawn using a light microscope

connected to a drawing tube, and identified following Petrochenko (1958); Amin and Margolis (1998) and Costa et al. (2000). All parasites were counted except in 12 dolphins stranded before 1988, for which only presence/absence data were recorded. ‘Small’ and ‘large’ plerocercoids of tetraphyllidean cestodes were not considered members of the intestinal assemblage and were not included in this study (see Aznar et al., 2007).

## 2.2 Molecular identification of *Bolbosoma vasculosum*

All individuals identified as *B. vasculosum* based on morphologic traits were juveniles (see the Results section), thus raising the possibility that they actually represent immature forms of other *Bolbosoma* species. We investigated this possibility using molecular barcoding. Two species of *Bolbosoma* have been recorded as adults in the Mediterranean, i.e., *Bolbosoma balaenae* in fin whales, *Balaenoptera physalus*, and *Bolbosoma capitatum* in long-finned pilot whales, *Globicephala melas* (Delyamure, 1955; Yamaguti, 1963; Raga and Balbuena, 1993; Santoro et al., 2021). We sequenced a partial (479 bp) region of the mitochondrial cytochrome *c* oxidase subunit I (*cox1*) of (i) 5 specimens of *B. vasculosum* from our sample (DNA extraction

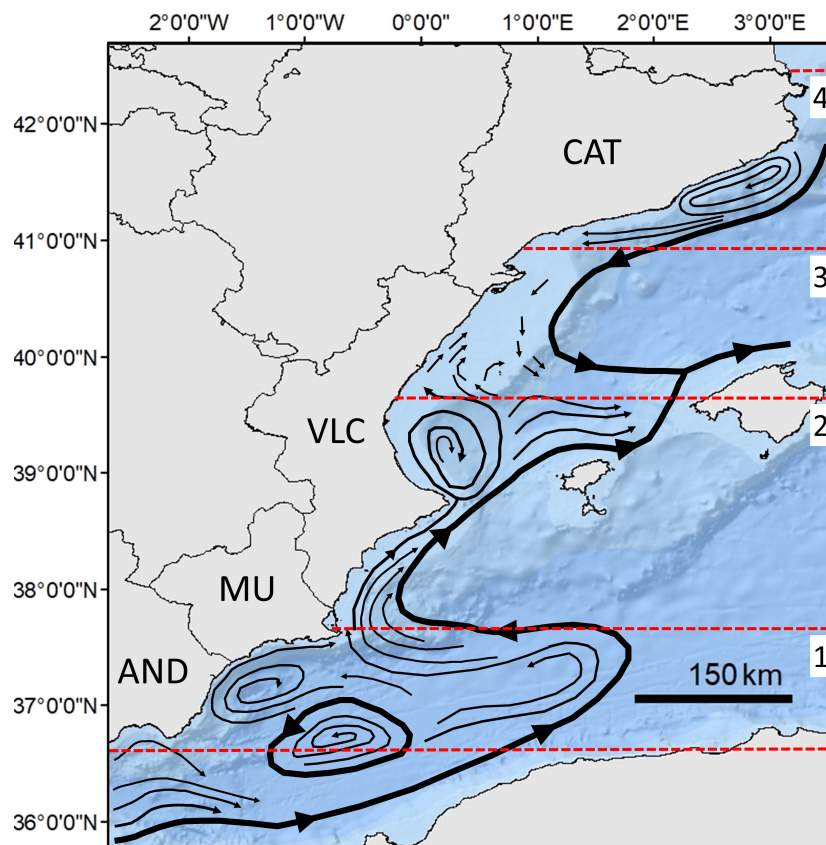


FIGURE 1

Map of the study area showing major water currents and the extent of the continental shelf in the Spanish Mediterranean. Red dashed lines indicate the four regions (numbered from 1 to 4) in which the coast was divided for the latitudinal comparison of helminth fauna of striped dolphins, *Stenella coeruleoalba*. Autonomous Communities are abbreviated as follows: Cat, Catalonia; VLC, Valencian Community; MU, Murcia; and AND, Andalusia. The map was created using ArcGIS Desktop version 10.8 (ESRI, 2011), and water currents were redrawn from Martínez et al. (2022).

was attempted on a number of additional specimens, but it was unsuccessful due to poor preservation); (ii) two juvenile specimens of putative *B. balaenae* also collected from our sample of striped dolphins, and (iii) one adult specimen of *B. capitatum* from a long-finned pilot whale, *Globicephala melas* sampled in the study area, which was available at the collection of the Marine Zoology Department of the University of Valencia, Spain (voucher specimen ID: 13653). Available *cox1* sequences from GenBank from adults of *B. balaenae* infecting Mediterranean fin whales, as well as from two other *Bolbosoma* species, were also used for comparison (Table 1).

Total genomic DNA was extracted from specimens using the DNeasy Blood and Tissue Kit (Qiagen), following manufacturer's instructions. The *cox1* region was amplified using primers forward LCO1490F (5'-GGTCAACAAATCATAAAGATATTGG-3') and reverse HC02198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Folmer et al., 1994). The concentration and quality of the extracted DNA was measured using a NanoDrop™ One (Thermo Scientific). PCR amplification reactions were performed in a total volume of 20 µL, including 1.6 µL of both forward and reverse primers (final concentration of 5 µM), 2 µL of template DNA, 4.8 µL of PCR water and 10 µL of MyFi™ DNA Polymerase (BioLine, Meridian Life Science Inc., Taunton, MA, USA). Cycling conditions were 94°C for 5 min for an initial denaturation, then 38 cycles of 94°C for 45 s, 48°C for 45 s, and 72°C for 80 s, followed by a final extension at 72°C for 7 min. Positive and negative (no template DNA) controls were used in each PCR reaction. PCR products were purified using the Nucleospin® PCR and Gel Purification Clean-up kit (Machery-Nagel, Düren, Germany). Purified amplicons were sent to MacroGen Europe (Amsterdam, The Netherlands) for sequencing with the same primers used in the PCR amplifications.

Nucleotide sequences from both strands were used to assemble consensus sequences using Geneious R7 (<https://www.geneious.com>). The identity of the assembled sequences was verified using the NCBI Basic Local Alignment Search Tool (BLAST). The obtained *cox1* sequences, together with all *cox1* sequences of *Bolbosoma* available in GenBank, were aligned and trimmed using Geneious R7. The accuracy of the alignment was inspected by checking the amino acid translation, using the invertebrate mitochondrial code. The total number of sequences included in the final alignment was 23. Pairwise genetic distances were calculated using the Maximum Composite Likelihood model (Tamura et al., 2004) in MEGA v.11 (Tamura et al., 2021).

## 2.3 Infection parameters

Ecological terms follow Bush et al. (1997). Infection parameters were determined using the online software Quantitative Parasitology 1.0.15 (Reiczigel et al., 2019). Prevalence is the percentage of hosts that are infected by a specific helminth species, mean abundance is the average number of individuals of a helminth species per examined host, and mean intensity is the average number of individuals of a helminth species per infected

TABLE 1 Data on host, locality and GenBank accession number for *cox1* sequences of *Bolbosoma* spp. used for molecular barcoding of *Bolbosoma vasculosum*.

Species	Host	Locality	Acc. no.
<i>B. vasculosum</i>	<i>Stenella coeruleoalba</i>	Western Mediterranean	OR601512*
<i>B. vasculosum</i>	<i>Stenella coeruleoalba</i>	Western Mediterranean	OR601513*
<i>B. vasculosum</i>	<i>Stenella coeruleoalba</i>	Western Mediterranean	OR601514*
<i>B. vasculosum</i>	<i>Stenella coeruleoalba</i>	Western Mediterranean	MZ357085*
<i>B. vasculosum</i>	<i>Stenella coeruleoalba</i>	Western Mediterranean	MZ357087*
<i>B. capitatum</i>	<i>Globicephala melas</i>	Western Mediterranean	OR601511*
<i>B. balaenae</i>	<i>Stenella coeruleoalba</i>	Western Mediterranean	OR601515*
<i>B. balaenae</i>	<i>Stenella coeruleoalba</i>	Western Mediterranean	MZ357084*
<i>B. balaenae</i>	<i>Balaenoptera physalus</i>	Capri Island (Med. Sea)	MZ047272
<i>B. balaenae</i>	<i>Balaenoptera physalus</i>	Capri Island (Med. Sea)	MZ047273
<i>B. balaenae</i>	<i>Balaenoptera physalus</i>	Capri Island (Med. Sea)	MZ047274
<i>B. balaenae</i>	<i>Balaenoptera physalus</i>	Capri Island (Med. Sea)	MZ047275
<i>B. balaenae</i>	<i>Balaenoptera physalus</i>	Capri Island (Med. Sea)	MZ047276
<i>B. balaenae</i>	<i>Balaenoptera physalus</i>	Capri Island (Med. Sea)	MZ047277
<i>B. balaenae</i>	<i>Balaenoptera physalus</i>	Capri Island (Med. Sea)	MZ047278
<i>B. balaenae</i>	<i>Balaenoptera physalus</i>	Capri Island (Med. Sea)	MZ047279
<i>B. balaenae</i>	<i>Balaenoptera physalus</i>	Capri Island (Med. Sea)	MZ047280
<i>B. balaenae</i>	<i>Balaenoptera physalus</i>	Capri Island (Med. Sea)	MZ047281
<i>B. turbinella</i>	<i>Eschrichtius robustus</i>	Monterrey Bay (North Pacific)	JX442189
<i>B. turbinella</i>	<i>Paralichthys isosceles</i>	South Atlantic	KU314821
<i>B. turbinella</i>	<i>Paralichthys isosceles</i>	South Atlantic	KU314823
<i>B. nipponicum</i>	<i>Callorhinus ursinus</i>	St. Paul Island (Bering Sea)	ON359908
<i>B. nipponicum</i>	<i>Callorhinus ursinus</i>	St. Paul Island (Bering Sea)	ON359909

Sequences marked with an asterisk were obtained in this study.



host. The 95% confidence interval (CI) for prevalence was calculated with Sterne's exact method (Reiczigel, 2003). The 95% CI for mean abundance and mean intensity of each helminth species were obtained with the bias-corrected and accelerated bootstrap method using 10000 replications (Rózsa et al., 2000).

## 2.4 Representativeness of the host sample

Our dolphin sample was not a random sample of the wild striped dolphin population, but a subset of stranded animals that died from varied causes. Thus, a pertinent question is to what extent our sample could be biased regarding helminth infections if, e.g. it is enriched with heavily parasitized dolphins. We carried out a preliminary exploration of this question based on the comparison of two dolphin subsamples collected in the same period (2010-2015) for which the putative cause of death could reliably be determined based on a thorough veterinary analysis. The first one ( $N = 10$ ) was composed of striped dolphins that were killed by common bottlenose dolphins, *Tursiops truncatus* or as a result of fisheries interactions (Crespo-Picazo et al., 2021; Izquierdo-Serrano et al., 2022). In principle, these causes of death are not related with the health condition of dolphins and should be little influenced by the infections of intestinal helminths, which were light (see the Results section). In fact, veterinary analyses indicated good body condition and no pathologies were detected. The second subsample ( $N = 20$ ) included dolphins that died from diverse infectious syndromes (Unpub. data). Therefore, we hypothesized that these animals would be more prone to concomitant recruitment of TTPs due to a compromised immune response. Potential differences in abundance of each helminth species between the two subsamples were tested with Mann-Whitney tests.

## 2.5 Geographical analysis

The geographic analysis was carried out using 74 dolphins that died during the DMV outbreak in the summer and autumn of 1990 and stranded along the coast from Andalusia to Catalonia (Figure 1). This subsample was considered suitable for three reasons. First, it was the only sample of dolphins collected across a wide geographical range; in other years (including 2007, when the second DMV epizootic occurred), sampling was restricted to the Valencian Community; second, it was composed of animals that died from the same disease; and third, it was temporally restricted, thus reducing potential confounding seasonal or inter-annual effects.

We used two approaches to investigate latitudinal variability in helminth infections in the stranded dolphins. First, the coast was divided into four regions based on latitude, distance from coastline to continental slope, and current circulation schemes (Martínez et al., 2022) (Figure 1). The numbers of dolphins from regions 1 to 4 were 9, 33, 16 and 16, respectively (Figure 1). Differences in prevalence of each helminth species among regions were tested with exact Chi squared tests. Differences in helminth community structure were investigated using PERMANCOVA with the software PERMANOVA + for PRIMER (Anderson et al., 2008).

Abundances of parasites were firstly fourth-root transformed and a Bray-Curtis similarity matrix was obtained. The full model included 'Region' (fixed factor) and two relevant predictors associated with individual dolphins, i.e. 'Sex' (fixed factor) and 'Length' (fixed covariate), as well as their interactions. Pseudo-F statistics under a true null hypothesis were obtained by using 20,000 permutations. Akaike Information Criterion (AIC) values were used to compare competing models with different numbers of parameters. The model with minimum AIC for small sample sizes ( $AIC_c$ ) was considered the best model, and the rest of the models were ranked according to increasing  $AIC_c$  values (Johnson and Omland, 2004; Anderson et al., 2008; Aho et al., 2014). Models with values of  $\Delta AIC_c \leq 2$  with respect to the best model were considered to have substantial empirical support, whereas those with  $\Delta AIC_c > 4$  were considered to have considerably less support (Anderson and Burnham, 2004). Akaike weights ( $w_i$ ) were calculated according to Anderson and Burnham (2004). It was assumed that models with  $w_i \leq 0.05$  were unlikely to be the 'true' models (Anderson and Burnham, 2004).

Second, we used Generalised Additive Models (GAMs) (Zuur et al., 2009; Wood, 2017) to explore non-linear patterns in the abundance, or likelihood of occurrence, of each helminth taxon with latitude of stranding. Abundance and occurrence (presence/absence) of each parasite species were used as the response variable for each type of model, respectively, and 'Latitude', 'Dolphin sex' and 'Dolphin length' as the explanatory variables. For abundance data, negative binomial GAMs were fitted using a log link function; for occurrence data, binomial GAMs were fitted using a clog-log link function, which is recommended when there are considerably more zeros than ones or *vice versa* (Zuur et al., 2009). Model selection followed the same criteria used for the PERMANCOVA models. Collinearity between variables was checked by calculating the Variance Inflation Factor (VIF); values in between 1 and 5 were considered to indicate low collinearity (Goldstein, 1993). We further ensured the lack of dependency between covariates and factors ('Sex') with Mann-Whitney tests, and between the two covariates with Spearman correlation. Models were validated following Zuur et al. (2009), i.e., checking normality, homogeneity of variance, autocorrelation and over-dispersion of residuals.

## 2.6 Temporal analysis

GAMs were also used to investigate long-term infection changes of each helminth species. The initial models included two alternative response variables (helminth abundance or occurrence) and five predictors, i.e. 'Group' (with two levels, i.e., epizootic and non-epizootic), 'Dolphin sex' and 'Season' as fixed factors; and 'Year' and 'Dolphin length' as covariates for which smoothers were applied. Alternative models excluding dolphins affected by the DMV, or using 'Julian day' instead of 'Year', were also fitted, but the results were nearly identical to those of the models described above and are not shown. Note that 'Latitude' was not included in the temporal analysis because, in years other than 1990, all stranded dolphins were collected on the coasts of the Valencian Community (Figure 1).

For abundance data, negative binomial GAMs were fitted using a log link function; for occurrence data, binomial GAMs were fitted using a clog-log link function. Model selection and validation, as well as collinearity analysis between predictors, were carried out as indicated in the previous section. However, AIC was not corrected for small samples in this case because sample size ( $n$ ) was large compared with the number of parameters ( $k$ ), i.e.  $n/k > 40$  (Anderson and Burnham, 2004). The lack of dependency between factors was further examined with Chi Squared tests; between covariates and factors with Kruskal-Wallis ('Season') or Mann-Whitney ('Group', 'Sex') tests, and between the two covariates with Spearman correlation.

All GAM models were fitted using the *mgcv* package (Wood, 2011) available in R version 4.2.2 (R Core Team, 2022).

## 3 Results

### 3.1 Infection parameters

Six helminth species were found in the intestine of the striped dolphins analysed. Three tetrabothriid cestodes included adult specimens, i.e. *Trigonocotyle globicephalae*, *Tetrabothrius forsteri* and *Strobilocephalus triangularis*, but only the two latter exhibited a prevalence  $> 10\%$  and mean intensity  $> 10$  individuals/dolphin (Table 2). A single juvenile cestode belonging to the genus *Diphyllobothrium* was detected in a dolphin from 1987, but

identification at species level was not possible due to poor preservation (Table 2). Finally, two species of acanthocephalan were found as juvenile forms. *Bolbosoma vasculosum* showed an overall prevalence  $> 15\%$ , whereas single specimens of *B. balaenae* were found in two dolphins from 2011 and 2013, respectively (Table 2).

### 3.2 Molecular affiliation of *Bolbosoma vasculosum*

The ranges of intraspecific genetic distances of *Bolbosoma* spp. based on *cox1* sequences were as follows: 0.006 - 0.024 (*B. vasculosum*); 0 - 0.017 (*B. balaenae*); 0.004 - 0.109 (*B. turbinella*) and 0.004 (*B. nipponicum*) (Table S1). At interspecific level, specimens of *B. vasculosum* were indistinguishable from the specimen of *B. capitatum* (range: 0.006 - 0.024), showing higher distances with respect to other *Bolbosoma* spp. (minimum distance: 0.194) (Table S1).

### 3.3 Representativeness of the host sample

Infection parameters of helminths from striped dolphins that were killed by interactions with bottlenose dolphins or fisheries were closely similar to those from dolphins that died from infectious diseases (Table 3). In fact, we did not find significant differences in abundance for any of the helminth species (Mann-Whitney tests, all  $p \gg 0.680$ ).

TABLE 2 Infection parameters (with 95% confidence intervals in parentheses and ranges in brackets) of intestinal helminths found in striped dolphins, *Stenella coeruleoalba* from the western Mediterranean.

Species	Prevalence		Mean intensity	Mean abundance
	1982-2016	1987-2016		
<b>Cestoda</b>				
<b>Tetrabothriidae</b>				
<i>Tetrabothrius forsteri</i>	94.4 (90.6 - 96.9)	95.5 (91.9 - 97.6)	44.3 (36.6 - 55.8) [1 - 518]	42.3 (34.6 - 53.2)
<i>Strobilocephalus triangularis</i>	18 (13.5 - 23.6)	15.8 (11.5 - 21.2)	13.0 (8.4 - 20.8) [1 - 81]	2.1 (1.2 - 3.7)
<i>Trigonocotyle globicephalae</i>	5.2 (2.9 - 8.7)	5.4 (3.1 - 9.2)	2.8 (1.8 - 3.9) [1 - 6]	0.1 (0.1 - 0.3)
<b>Diphyllobothriidae</b>				
<i>Diphyllobothrium</i> sp.	0.4 (0 - 2.5)	0.5 (0 - 2.6)	1	0.005 (0 - 0.014)
<b>Acanthocephala</b>				
<b>Polymorphidae</b>				
<i>Bolbosoma vasculosum</i>	15.9 (11.5 - 21.2)	16.3 (11.9 - 21.9)	2.3 (1.8-3) [1-7]	0.4 (0.3 - 0.4)
<i>Bolbosoma balaenae</i>	0.9 (0.2 - 3.1)	0.9 (0.2 - 3.3)	1	0.009 (0 - 0.023)

Host sampling covers the period 1987-2016 (221 dolphins), but additional data on occurrence were obtained from 12 dolphins during the period 1982-1986, hence two sets of values are shown for prevalence.

TABLE 3 Infection parameters (with 95% confidence intervals in parentheses and ranges in brackets) of intestinal helminths found in two samples of striped dolphins, *Stenella coeruleoalba* from the western Mediterranean collected during the period 2010–2015, and for which the cause of death was determined.

Species	Prevalence	Mean intensity	Mean abundance
<i>Tetrabothrius forsteri</i>	95.0 (75.6 - 99.7)	29.4 (18.4 - 48.0) [3 - 119]	27.9 (17.5 - 46.7)
	100 (70.9 - 100)	37.1 (14.4 - 101.5) [2 - 213]	37.1 (14.4 - 101.5)
<i>Strobilocephalus triangularis</i>	20.0 (7.1 - 42.4)	13.8 (1.0 - 34.0) [1 - 48]	2.8 (0.2 - 11.7)
	20.0 (3.7 - 55.4)	22.5 [18 - 27]	4.5 (0.0 - 10.8)
<i>Trigonocotyle globicephalae</i>	5.0 (0.3 - 24.4)	1	0.05 (0.0 - 0.2)
	0.0 (0.0 - 29.1)	–	–
<i>Bolbosoma balaenae</i>	10.0 (1.8 - 32.0)	1	0.1 (0.0 - 0.2)
	0.0 (0.0 - 29.1)	–	–

For each helminth species, infection parameters are given considering dolphins that died from infectious diseases (N = 20, upper row) or that were killed by interspecific competition or fisheries interactions (N = 10, lower row).

### 3.4 Geographical analysis

Of the four species found in 1990, *T. forsteri*, *S. triangularis* and *B. vasculosum* were detected throughout the whole study area, whereas *Tri. globicephalae* was apparently restricted to its southern part (Figure 2). However, we failed to detect differences in prevalence of this species between regions (exact Chi-Squared,  $\chi^2 = 2.308$ , 3 df,  $p = 0.538$ ), nor a significant latitudinal trend ( $\chi^2 = 1.934$ , 1 df,  $p = 0.121$ ).

There were four PERMANCOVA models that had substantial empirical support ( $\Delta AIC_c \leq 2$ ), and two that had less support ( $2 < \Delta AIC_c < 4$ ). Among them, the simplest and with highest  $w_i$  value included the intercept only (Table 4). In the rest of the models, none of the individual predictors was found to be significant (Table 4).

GAMs could be fitted for *T. forsteri*, *S. triangularis* and *B. vasculosum*. In the case of *T. forsteri*, the model with lowest  $AIC_c$ , highest  $w_i$  and lowest number of predictors included 'Latitude' only. There was a significant but modest positive effect of this variable on the abundance of *T. forsteri* (deviance explained = 13.3%, edf = 3.071,  $p = 0.0154$ ) (Figure 3). Three additional negative-binomial GAMs also had substantial empirical support ( $\Delta AIC_c \leq 2$ ), namely, those including 'Latitude' and 'Dolphin length' ( $\Delta AIC_c = 0.385$ ), 'Latitude' and 'Dolphin Sex' ( $\Delta AIC_c = 1.321$ ) or the three predictors ( $\Delta AIC_c = 1.501$ ). In all of them, the only significant variable was 'Latitude' ( $p < 0.03$ ). In the GAMs for the abundance of *S. triangularis* and *B. vasculosum*, none of the predictors were found to be significant, and the same occurred in the models involving occurrence data (data not shown).

### 3.5 Temporal analysis

The cestodes *T. forsteri*, *S. triangularis* and *Tri. globicephalae* were detected throughout the whole study period, but the acanthocephalan *B. vasculosum* was almost exclusively found in 1990; only two additional individuals were found in 1989 and 1997, respectively (Figure 4).

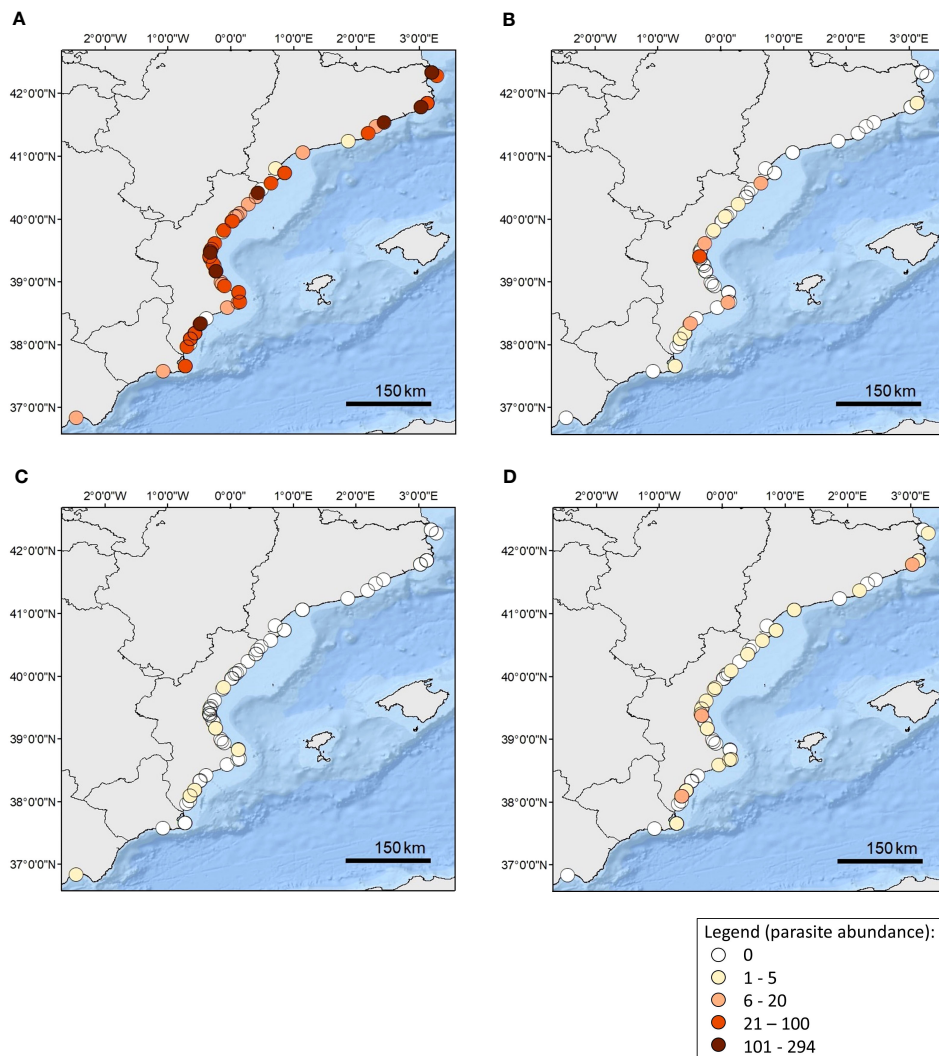
Long-term trends could be investigated with GAMs in the case of *T. forsteri* and *S. triangularis*. Binomial GAMs could not meaningfully be fitted for *T. forsteri* due to its high prevalence ( $> 94\%$ ). There were four negative-binomial GAMs for abundance with substantial empirical support ( $\Delta AIC \leq 2$ ) and two with less support ( $2 < \Delta AIC < 4$ ) (Table 5). The two simplest models included two predictors (Table 5). Among them, the one with the highest  $w_i$  value explained  $< 10\%$  of deviance and included the predictors 'Year' and 'Dolphin length' (Table 5). In this model, the effect of 'Dolphin length' was highly significant, and that of 'Year' just marginally so (Table 5). The abundance of *T. forsteri* experienced a slight decrease with a subsequent recovery throughout the study period (Figure 5A), and peaked at dolphin lengths between 130 and 150 cm, then decreased (Figure 5B). All the other competing models included 'Length' as a highly significant predictor; 'Year', 'Group (epizootic vs. non-epizootic)' or 'Dolphin sex' were included in some models, but their effects were only marginally significant, or not significant (Table 5).

In the case of Binomial GAMs accounting for the occurrence of *S. triangularis* in striped dolphins, there were three models with substantial empirical support ( $\Delta AIC \leq 2$ ) and two with less support ( $2 < \Delta AIC < 4$ ) (Table 6). The model with the highest  $w_i$  value included the predictors 'Year', 'Dolphin length' and 'Dolphin sex', while the simplest model included 'Year' and 'Dolphin length' (Table 6). The deviance explained for these models was 12.5% and 10.6%, respectively (Table 6). The effects of 'Year' and 'Dolphin length' were statistically significant in both models (Table 6). The likelihood of occurrence of *S. triangularis* strongly decreased from ca. 1990 (note the wide 95% CI in previous years) to 1997–1999, then increased, but without reaching the initial levels of the time series (Figure 5C). The likelihood of occurrence also decreased monotonically at increasing dolphin length (Figure 5D). In the other models; 'Year' and 'Dolphin length' remained as significant predictors; 'Group (epizootic vs. non-epizootic)', 'Dolphin sex' and 'Season' were included only in some models, having just marginally significant, or not significant effects (Table 6). None of the negative binomial GAMs for the abundance of *S. triangularis* had a suitable fit according to model validation plots, thus they are not considered further.

## 4 Discussion

### 4.1 Representativeness of the dolphin sample

The sample used in this study is composed of stranded dolphins, thus a potential concern is whether they represent an unbiased subset of animals from the wild population. First, the DMV that caused the epizootics in 1990 and 2007 is known to



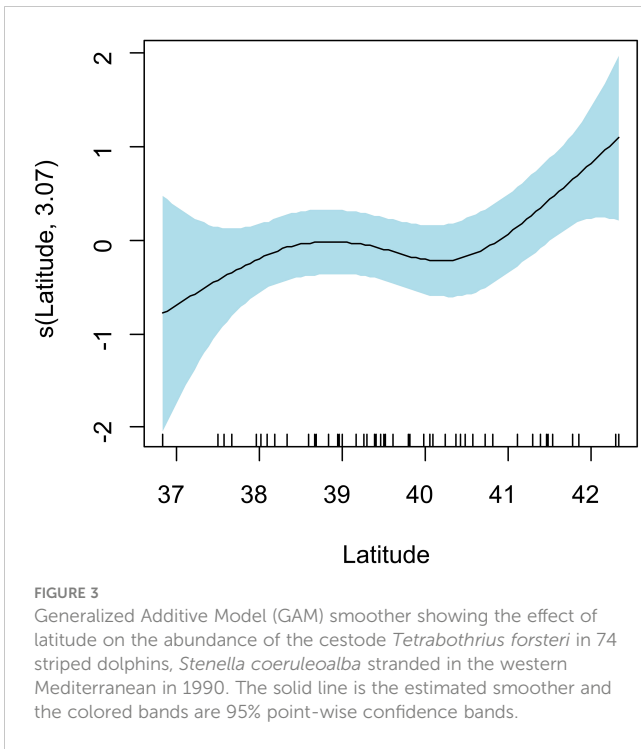
**FIGURE 2** Maps showing the localities where 74 striped dolphins, *Stenella coeruleoalba* were found stranded along the Mediterranean coast of Spain in 1990. Colors indicate the abundance of intestinal helminths, when present. (A) *Tetrabothrius forsteri*. (B) *Strobilocephalus triangularis*, (C) *Trigonocotyle globicephalae* and (D) *Bolbosoma vasculosum*.

**TABLE 4** Permutational Multivariate Analysis of Covariance (PERMANCOVA) accounting for the effect of region, dolphin length, dolphin sex, and their interactions, on the abundance of four intestinal helminth species found in 74 striped dolphins, *Stenella coeruleoalba*, stranded in the western Mediterranean in 1990.

Model	$\Delta AIC_c$	$w_i$	Predictor	F	df	p
Intercept	0	0.343				
Intercept + Region	0.790	0.231	Region	0.981	3, 73	0.462
Intercept + Sex	1.922	0.131	Sex	0.431	1, 73	0.743
Intercept + Length	1.992	0.127	Length	0.272	1, 73	0.816
Intercept + Region + Sex	2.725	0.088	Region	0.974	3, 69	0.463
			Sex	0.514	1, 69	0.686
Intercept + Region + Length	2.873	0.081	Region	0.944	3, 69	0.486
			Length	0.272	1, 69	0.814

Models are arranged by increase of the Akaike Information Criterion for small samples ( $AIC_c$ ) and decrease of Akaike weight ( $w_i$ ). Models with  $\Delta AIC_c > 4$  with respect to the best model are not included. Probability values for individual predictors are also shown.





impair the host’s immune system (Bossart et al., 2011; Van Bressesem et al., 2014). Although this effect could facilitate the establishment of parasites, thus abnormally increasing their loads (Aznar et al., 1994; Aznar et al., 2005), this is unlikely to occur in the case of TTPs. Mammals affected by other morbillivirus diseases have been reported to die between 8 hours and 2 weeks after the first clinical symptoms (Harder et al., 1990; Evermann et al., 2001; Mahy and Van Regenmortel, 2008). If the disease caused by DMV also runs its course quickly (Kennedy, 1998), the temporal window for recruitment or senescence of the helminths infecting striped dolphins would be too narrow to generate significant alterations of previous parasite loads (Mateu et al., 2014).

Second, the cause of stranding for other dolphins was not always easy to assess but included, *inter alia*, by-catch (Cuvertoret-Sanz et al., 2020; Izquierdo-Serrano et al., 2022), deadly interactions with bottlenose dolphins (Crespo-Picazo et al., 2021) and infectious diseases (Isidoro-Ayza et al., 2014; Cuvertoret-Sanz et al., 2020). Our results indicate that infection parameters were closely similar for ill vs. non-ill dolphins. One could wonder whether the striped dolphins belonging to the latter category exhibited non-lethal pathological conditions that made them prone to accidental catch or aggression by bottlenose dolphins; however, no such conditions were detected in any of them during the necropsies. Besides, none of the intestinal

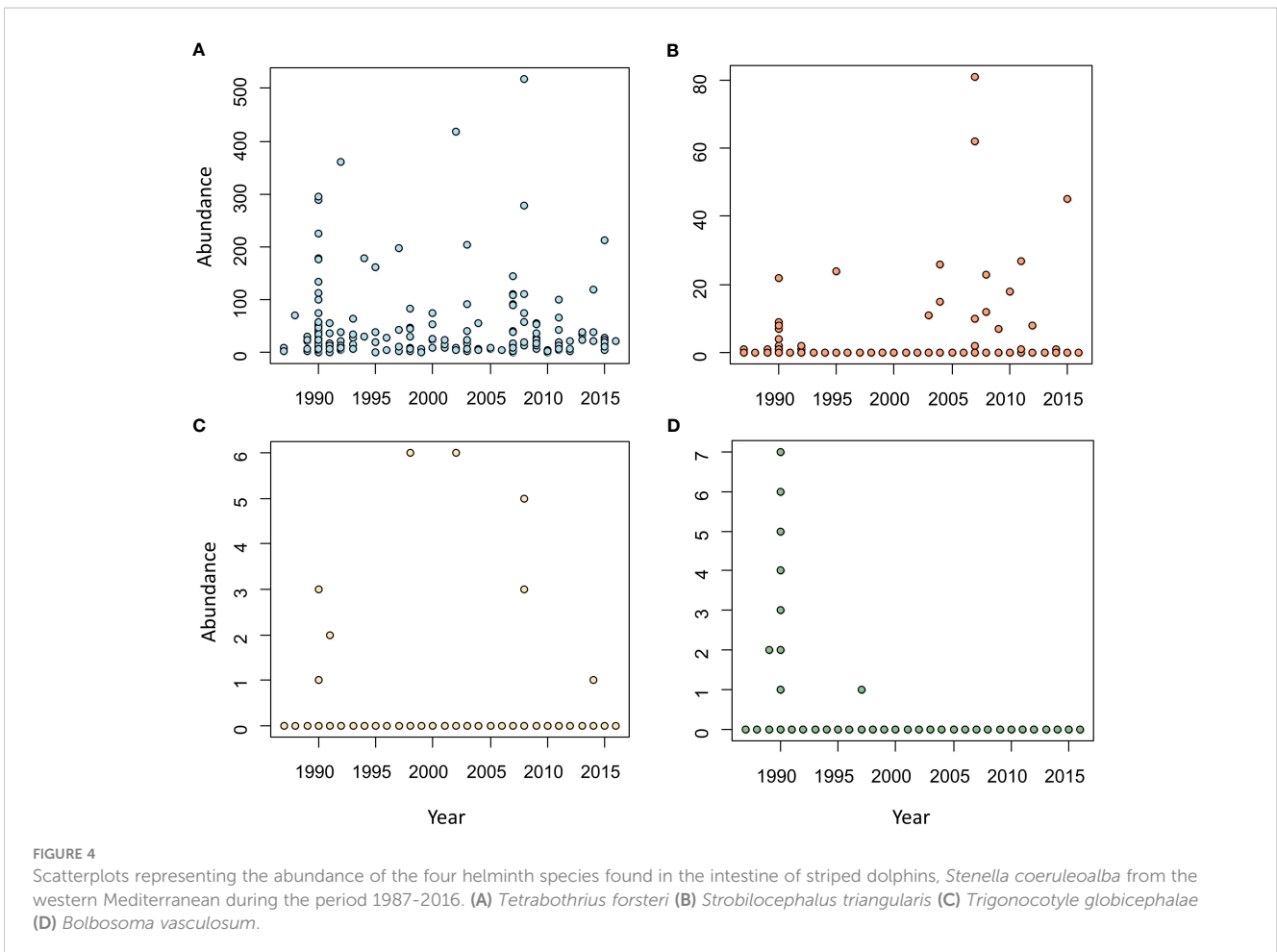


TABLE 5 Negative binomial Generalized Additive Models (GAMs) assessing the effect of year, dolphin length, group (epizootic vs. non-epizootic), dolphin sex and season on the abundance of the cestode *Tetrabothrius forsteri* in striped dolphins, *Stenella coeruleoalba*, from the western Mediterranean during the period 1987-2016 (N = 221).

Model	Predictors	$\Delta$ AIC	$w_i$	Deviance explained (%)	Predictor	df/edf	p value
1	Length + Year	0	0.309	9.64	Length	4.555	< 0.0001
					Year	1.949	0.037
2	Length + Group	0.651	0.223	8.38	Length	4.136	< 0.0005
					Group	1	0.046
3	Length + Year + Group	1.319	0.160	9.66	Length	4.418	< 0.0001
					Year	1.777	0.264
					Group	1	0.256
4	Length + Year + Sex	1.979	0.115	9.63	Length	4.533	< 0.0001
					Year	1.950	0.037
					Sex	1	0.914
5	Length	2.043	0.111	7.40	Length	4.501	0.003
6	Length + Group + Sex	2.638	0.083	8.37	Length	4.117	< 0.0005
					Group	1	0.047
					Sex	1	0.961

Models are arranged by increase of the Akaike Information Criterion (AIC) and decrease of Akaike weight ( $w_i$ ). Models with  $\Delta$ AIC > 4 with respect to the best model are not included. The percentage of deviance explained by each model, and the degrees of freedom/effective degrees of freedom (df/edf) and probability associated to the effect of each variable are also given. Statistically significant p-values are in bold.

parasites found, except perhaps *Diphyllobothrium* sp., have pathological significance (Geraci and St. Aubin, 1987; Cuvertoret-Sanz et al., 2020), thus they were unlikely to be involved in dolphin stranding. In addition, post-mortem infection is not a possibility, since TTPs are transferred to dolphins through the consumption of infected prey. Accordingly, the load of intestinal helminths in our dolphin sample is not expected to be significantly higher than that of the wild population.

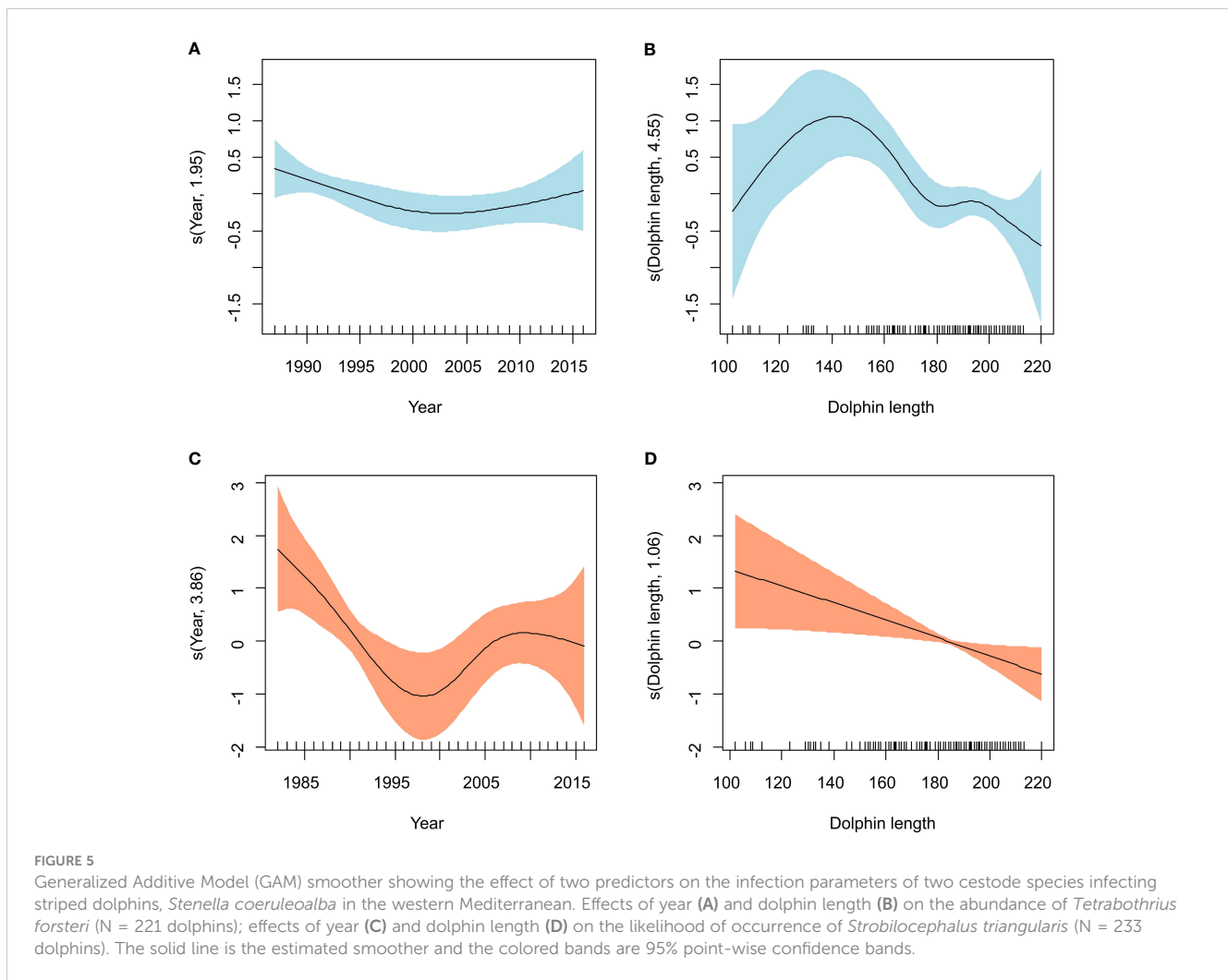
## 4.2 Intestinal helminths collected

Out of the 6 helminth species found, 4, i.e., *T. forsteri*, *Tri. globicephalae*, *S. triangularis* and *B. vasculosum*, had previously been reported by Mateu et al. (2014) based on a subset of 52 striped dolphins from 1990, now included in the present study. Mateu et al. (2014) identified the juvenile specimens of *Bolbosoma* as *B. vasculosum*, as we do here, based on the most detailed descriptions of this taxon (Van Cleave, 1953; Costa et al., 2000). However, the absence of adults in a large sample of worms ( $n = 84$ , collected from 37 dolphins), which agrees with previous reports in cetaceans (Van Cleave, 1953; Fernández et al., 2004; Fraija-Fernández et al., 2016), indicates that these specimens must be juveniles of another *Bolbosoma* species. We cannot rule out the possibility that they belong to a new species associated with striped dolphins, but the absence of adults rather suggests that they correspond to an existing species present in other cetacean hosts. In the western

Mediterranean, the only two additional species of *Bolbosoma* are *B. balaenae* and *B. capitatum* (Raga and Balbuena, 1993; Santoro et al., 2021). Molecular barcoding showed that our specimens of *B. vasculosum* were indistinguishable from *B. capitatum*. Nevertheless, further research using a higher number of markers and *Bolbosoma* specimens should be conducted to confirm our results. Since morphological similarities are also apparent between both species (Amin and Margolis, 1998; Costa et al., 2000), a taxonomic re-analysis of the concept of *B. vasculosum* is warranted.

*Bolbosoma balaenae* and *Diphyllobothrium* sp., were not detected by Mateu et al. (2014) and constitute exceptional records in the present survey. The former species typically infects baleen whales worldwide (Fraija-Fernández et al., 2016), with only two previous records in *Stenella* spp. (Dailey and Perrin, 1973). In the Mediterranean Sea, adults of *B. balaenae* have been reported in the only baleen whale species regularly present in this area, the fin whale *Balaenoptera physalus* (Santoro et al., 2021). The occurrence of juvenile specimens in striped dolphins could be interpreted as an accidental infection through shared prey.

With regard to *Diphyllobothrium* sp., a single immature specimen was found in our sample. The only previous record of species of *Diphyllobothrium* in striped dolphins corresponds to an adult of an unidentified species in the Atlantic Ocean (Jaber et al., 2006). In the study area, there are records of adults of an unidentified species of *Diphyllobothrium* in common bottlenose dolphins *Tursiops truncatus* (Raga, 1985; Quiñones et al., 2013). Since at least 7 species of this genus have been reported in



odontocetes (Fraija-Fernández et al., 2016), further molecular studies are needed to determine the identity of the species occurring in our study area.

### 4.3 Effects of host size on parasite infections

Mateu et al. (2014) did not detect a significant effect of host body length or sex on the abundance of any intestinal helminth taxa. Using now a larger sample size, we neither detected a sex effect, nor seasonal changes in infections, but we did find a significant effect of dolphin length on the abundance of *T. forsteri* and the prevalence of *S. triangularis*. Admittedly, the current sample also covers a large number of years and, therefore, inferences are more prone to confounding effects of time. However, there are also contrasting differences in the host length composition between samples that could readily explain the difference. Only 4 of 52 dolphins (7.7%) from the sample analysed by Mateu et al. (2014) could be considered sexually immature (<180 cm long, see Calzada et al., 1997), vs. 72 of 233 (30.9%) in the present study. Thus, it is likely that host length effects on parasite infections are now being

detected because there is a suitable representation of small dolphins; among adult dolphins, infection parameters would vary individually regardless of host's body length (Mateu et al., 2014).

The occurrence of *S. triangularis* was found to be negatively related with host length, whereas the abundance of *T. forsteri* peaked at ca. 140 cm, then decreased in larger dolphins. Interestingly, comparable trends appear to exist for the same parasites in other *Stenella* spp. Dailey and Perrin (1973) reported raw data on the abundance of *T. forsteri* and the occurrence of *S. triangularis* in a sample of pantropical spotted dolphins, *S. attenuata* from the eastern tropical Pacific. When we examined the relationship of both variables with host length (excluding calves), it was negative and significant, as expected (*T. forsteri*: Spearman correlation,  $r_s = -0.235$ ,  $n = 75$ , one-tailed  $p < 0.021$ ; *S. triangularis*: logistic regression,  $b = -3.561$ , 1 df, one-tailed  $p = 0.025$ ).

The factor(s) accounting for such trends are difficult to ascertain. In theory, larger (older) dolphins have more chances to get infected because they are exposed to infected prey for longer and/or consume more infected prey due to their higher metabolic demands (Mateu et al., 2014; Pool et al., 2020). Since this does not occur in the striped dolphins of our study, one could argue that smaller (younger) dolphins have a weaker immune system (thus

TABLE 6 Binomial Generalized Additive Models (GAMs) assessing the effect of year, dolphin length, group (epizootic vs. non-epizootic), dolphin sex and season on the likelihood of occurrence of the cestode *Strobilocephalus triangularis* in striped dolphins, *Stenella coeruleoalba*, from the western Mediterranean during the period 1982–2016 (N = 233).

Model	Predictors	$\Delta$ AIC	$w_i$	Deviance explained (%)	Predictor	df/edf	p value
1	Length + Year + Sex	0	0.401	12.5	Length	1.060	<b>0.013</b>
					Year	3.860	<b>0.007</b>
					Sex	1	0.051
2	Length + Year + Group + Sex	0.778	0.271	12.3	Length	1.114	<b>0.011</b>
					Year	2.984	<b>0.006</b>
					Group	1	0.253
					Sex	1	<b>0.046</b>
3	Length + Year	1.957	0.151	10.6	Length	1	<b>0.014</b>
					Year	3.839	<b>0.005</b>
4	Length + Year + Group	2.853	0.096	10.4	Length	1	<b>0.012</b>
					Year	3.048	<b>0.004</b>
					Group	1	0.281
5	Length + Year + Season + Sex	3.188	0.081	13.4	Length	1	<b>0.009</b>
					Year	3.569	<b>0.019</b>
					Season	3	0.427
					Sex	1	0.070

Models are arranged by increase of the Akaike Information Criterion (AIC) and decrease of Akaike weight ( $w_i$ ). Models with  $\Delta$ AIC > 4 with respect to the best model are not included. The percentage of deviance explained by each model, and the degrees of freedom/effective degrees of freedom (df/edf) and probability associated to the effect of each variable are also given. Statistically significant p-values are in bold.

they offer more opportunities for parasite establishment) and/or feed more on specific prey that serve as intermediate hosts for *T. forsteri* and *S. triangularis*. The latter possibility opens future avenues to pinpoint relevant prey taxa for the transmission of these cestodes.

#### 4.4 Spatial patterns

At a spatial scale of ca. 800 km (from the highest to the lowest latitude), we did not detect obvious geographical differences in the intestinal helminth assemblages of striped dolphins, except for a modest positive effect of latitude on the abundance of *T. forsteri*. The dolphins used for this analysis were collected in a narrow time window (summer and autumn, 1990) that minimises confounding time effects, but these animals were ill and could have performed unusual movements or suffered post-mortem transport by currents prior to stranding. However, it seems unlikely that such movements occurred at the spatial scale of the study as we compared regions ca. 200 km long on average.

Differences in helminth infection levels between localities have been observed when cetacean populations are sedentary within the spatial scale covered by the surveys (e.g., Aznar et al., 1995; Mead and Potter, 1995). In contrast, it is likely that, in the study area, striped dolphins perform large-scale movements, perhaps facilitated by the lack of obvious physical or oceanographic barriers, and this would tend to homogenise infections across the defined regions.

Currently, there are no precise data on movements of striped dolphins based on satellite tagging, but evidence obtained for other *Stenella* spp. indicate that individuals can perform movements of > 100 km/day along the continental slope (Scott and Chivers, 2009). Mediterranean striped dolphins appear to be also highly mobile; there are reports of diel movements covering dozens of km (Gannier, 1999), and seasonal changes in abundance that would suggest migrations at the scale of hundreds of kilometres (Gómez de Segura et al., 2006; Laran and Drouot-Dulau, 2007; Panigada et al., 2011; Arcangeli et al., 2017).

Interestingly, a parasitological survey of 14 striped dolphins that were collected on the coasts of the Ligurian Sea during the 1990 epizootic reported a similar composition and comparable prevalence of helminth fauna as that of the present study (Manfredi et al., 1992). Whether or not this homogeneity was caused also by extensive dispersal of striped dolphins between these two regions is difficult to assess in this case. There is evidence of significant genetic differentiation between dolphins from the Spanish vs. Ligurian populations (Gaspari et al., 2007), thus the parasitological similarity could have resulted just from ecological convergence.

#### 4.5 Temporal trends

Infections of *Tri. globicephalae* in striped dolphins were sporadic and scattered throughout several decades. This cestode



species seems to be specific to members of the subfamily Globicephalinae and, in the western Mediterranean, it has been further detected in long-finned pilot whales *Globicephala melas* and Risso's dolphins *Grampus griseus* (Supplementary Tables S2, S3). Our findings suggest that the striped dolphin is a secondary host for this cestode, its unpredictable occurrence perhaps resulting from unusual host-parasite contacts.

On the contrary, *T. forsteri* and *S. triangularis* are typical cestode species of striped dolphins (Supplementary Tables S2, S3). In the study area, their long-term infection trends were contrasting, with infection levels decreasing slightly (*T. forsteri*) or strongly (*S. triangularis*) up to year 2000 and subsequently recovering. To understand why such decrease occurred, and why each species was affected differently, we would need detailed knowledge on the life-cycle of both parasites. Unfortunately, no such information exists, although the general life-cycle for tetrabothriid cestodes is suggested to be complex, involving zooplanktonic organisms as first intermediate hosts, and fish or cephalopods as second intermediate hosts (Hoberg, 1987; Hoberg, 1996; Hoberg and Soudachanh, 2021). Thus, a potentially vast number of both biotic and abiotic factors could influence transmission dynamics of *T. forsteri* and *S. triangularis*, as evidenced for other TTPs infecting marine mammals (Des Clers and Wootten, 1990; Des Clers and Andersen, 1995; Stobo and Fowler, 2001).

It is worth noting, however, that three aspects of the patterns found in this study are compatible with the potential effects of a sudden significant reduction of the striped dolphin population in 1990. First, the dolphin mortality decreased the number of adult worms that successfully released infective stages, which could result in lower infections in dolphins in the following years (see MacDonald and Brisson, 2022). Second, the effect should be expected to be more pronounced in *S. triangularis*, at least for one reason, i.e., there seems to be a smaller number of other cetacean hosts supporting this cestode population. Out of the odontocete species analysed for parasites in the study area, *S. triangularis* has only been further detected in bottlenose dolphins, with low prevalence, whereas *T. forsteri* infects three other cetacean species, some with moderate prevalence (Table S2). Finally, the increase in infection levels of *T. forsteri* and, particularly, *S. triangularis* after year 2000 would be not surprising if we consider that the striped dolphin population also experienced a fast population recovery in just a decade (Gómez de Segura et al., 2006). Note that some decoupling is expected between the recovery of the host and the parasite populations (Anderson and May, 1978). This is also congruent with the absence of a significant effect of the variable 'Group (epizootic vs. non-epizootic)' in our models, since the effect of the first morbillivirus outbreak seems to have extended over the next years, rather than being restricted to year 1990. In addition, this outbreak was far more severe and affected a much higher number of dolphins than the following ones in 2007 and 2011 (Raga et al., 2008; Rubio-Guerrero et al., 2013), which would explain the absence of an observable effect of the other epizootic events in the abundance/prevalence of TTPs.

Long-term trends of the acanthocephalan *B. capitatum* (= *B. vasculosum*) are striking. This parasite was detected just once in striped dolphins before and after 1990, respectively, but in nearly half of those analysed in 1990 (34 of 74 dolphins), when infections were widespread across the study area. Moreover, as noted above, the striped dolphin acts as an accidental host for this parasite and likely acquired infections via prey shared with their 'true' cetacean hosts (see Hoberg et al., 1993; Costa et al., 2000; Gregori et al., 2012). Acanthocephalans identified as *B. vasculosum* have never been reported in other cetacean species from the study area, and *B. capitatum* only in the long-finned pilot whale, *Globicephala melas*, as adult (Raga and Balbuena, 1993; see also references in Table S2). The sperm whale, *Physeter macrocephalus* could also be a host for *B. capitatum* (Amin and Margolis, 1998) but has not been analysed for parasites in the study area. Therefore, these two odontocetes could be considered as the putative source of the infections observed in striped dolphins.

The reason(s) for such puzzling temporal pattern of *B. capitatum* (= *B. vasculosum*) in striped dolphin is(are) difficult to ascertain. First, we could hypothesize that, for some reason, the production of infective stages was exceptional in 1990 but, if so, the effects should last longer than a year in the trophic web. Species of *Bolbosoma* are relatively long-lived in paratenic hosts (Costa et al., 2000), similarly to other TTPs, for which a lifespan of several years is not uncommon (Kuhn et al., 2016). Second, we could postulate that, in 1990, striped dolphin fed on infected prey that were seldom exploited in other years. However, there is no evidence for this; although striped dolphins shifted diet from more oceanic to more neritic prey during the period 1990-2012, the change was gradual and did not entail the disappearance of any of the common fish prey taxa (Aznar et al., 2017). Third, we could argue that, in 1990, the dolphins immunocompromised by the DMV provided more favourable conditions for a longer permanence of *B. capitatum* in the intestine, thus significantly increasing their likelihood of detection. Yet, we did not find *B. capitatum* in dolphins likewise affected by the DMV in the 2007 or 2011 epizootics. Finally, we could speculate that migratory prey brought infections from elsewhere but, again, why this did occur only in 1990? In summary, the singular infection pattern of *B. capitatum* is hard to explain and was likely multi-causal in nature. Further monitoring of the intestinal helminth fauna of striped dolphins in the western Mediterranean could shed more light on this enigmatic parasite.

## 5 Conclusions

To our knowledge, this study represents the first investigation of multi-decadal changes in the parasites of a marine top-predator. It was possible to document interesting patterns than open research avenues but, as it might be expected, interpretation was difficult due to broad gaps in the basic knowledge of the parasites' biology. Therefore, this study serves as (i) a baseline to monitor parasites of cetaceans in the western Mediterranean, (ii) a foundation for comparative studies in other geographic areas and, (iii) a plea for

more integrative studies in the oceanic realm, for which parasites should be considered an integral element.

## Data availability statement

Datasets are available on request: The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation. Sequence data are available in Genbank and accession numbers are provided in Table 1.

## Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because our study is based on dolphin carcasses that get ashore along the Spanish coast. The Spanish legal system does not require any permission from an ethics committee in order to analyze cetacean carcasses. Nonetheless, permission and funding to collect stranded dolphins was given by the wildlife services of the regional governments, which are the official institutions in charge of managing and protecting wildlife.

## Author contributions

AG: Conceptualization, Formal Analysis, Methodology, Writing – original draft, Data curation, Writing – review & editing. JR: Funding acquisition, Writing – review & editing. NF: Methodology, Writing – review & editing, Data curation. FA: Conceptualization, Formal Analysis, Funding acquisition, Methodology, Writing – original draft, Data curation, Supervision, Writing – review & editing.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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## Supplementary material

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