Intestinal helminth fauna of the shortfin mako *Isurus oxyrinchus* (Elasmobranchii: Lamnidae) in the northeast Atlantic Ocean

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ABSTRACT: Large oceanic sharks represent a suitable model to investigate the influence of a host's oceanic conditions on the structure of its helminth communities. In this study, we describe the intestinal helminth fauna, and investigate determinants of infracommunity structure, in 39 specimens of shortfin mako *Isurus oxyrinchus* collected in the NE Atlantic. Six cestode species were found in the spiral valve of makos: 3 are typical from lamnid sharks, namely, gravid specimens of *Clistobothrium montaukensis*, *Gymnorhynchus isuri* and *Ceratobothrium xanthoceph-alum*, and 3 are immature specimens of cestode species common to several elasmobranchs, namely, *Dinobothrium septaria*, *Nybelinia lingualis*, and *Phyllobothrium* cf. *lactuca*. In addition, L3 larvae of *Anisakis* sp. type I were detected. Infracommunities were species poor and had low total helminth abundance. The result of Schluter's variance ratio test was compatible with the hypothesis of independent colonization of helminth taxa. These results conform to previous studies on oceanic predators that have hypothesized that these hosts should have depauperate and unpredictable helminth infracommunities because oceanic conditions hamper parasite transmission. However, mean species richness and mean total abundance of cestodes of shortfin mako and other oceanic sharks did not significantly differ from those of elasmobranchs from other habitats. This suggests that the large body size and prey consumption rates of oceanic sharks offset the negative 'dilution' effect of oceanic habitat on transmission rates. Additionally, or alternatively, parasites of oceanic sharks may have expanded the use of intermediate hosts through the trophic web to spread out the risk of failure to complete their life cycles.

KEY WORDS: *Isurus oxyrinchus* · Helminth fauna · Parasites · Infracommunity · Species richness · Pelagic · Oceanic

INTRODUCTION

The shortfin mako *Isurus oxyrinchus* (Rafinesque, 1810) is a highly migratory shark of the family Lamnidae that is widespread in temperate and tropical waters of all oceans from about 50°N to 50°S; it is rarely found in waters below 16°C (Compagno 2001). As is typical of lamnids, the shortfin mako is a fast epipelagic species that acts as an apex predator in oceanic trophic webs (López et al. 2009). The diet of shortfin makos is generalist and mostly includes teleosts, cephalopods and crustaceans, although cetaceans, chelonians and other elasmobranchs may also be consumed (Maia et al. 2006, Preti et al. 2012, Porsmoguer et al. 2014). The shortfin mako is currently included in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species within the 'Vulnerable' category (Cailliet et al.

2012), because this species suffers heavy mortality as bycatch or as a target species of commercial longline fisheries around the world (Mejuto et al. 2009).

Large pelagic oceanic sharks such as the shortfin mako represent an interesting model to investigate the role of the host's habitat in providing structure to its helminth communities. Previous studies on sea turtles (Valente et al. 2009, Santoro et al. 2010), marine birds (Hoberg 1996, 2005), cetaceans (Balbuena & Raga 1993, Mateu et al. 2014) and teleosts (Costa et al. 2012, Santoro et al. 2014) have suggested that the pelagic oceanic realm may exert a strong influence on the helminth infracommunities of large marine predators. First, infective stages of trophically transmitted helminths are assumed to be physically more 'diluted' in the vast, isotropic pelagic environment than in demersal or benthic habitats. As noted by several authors (Collard 1970, Campbell et al. 1980, Randhawa & Poulin 2010), helminth transmission in the pelagic habitat is defined in a 3-dimensional space, whereas in benthic demersal habitats it occurs in a roughly 2-dimensional layer. Second, oceanic organisms, including both intermediate and definitive hosts of helminth parasites, exhibit lower population density, and are usually more vagile, than neritic organisms. Thus, pelagic oceanic helminths arguably face the challenge of finding hosts (Fraija-Fernández et al. 2015) and their transmission rates are expected to be low. Consequently, helminth infracommunities of large oceanic predators are predicted to be species poor, with low diversity and abundance of helminths. Also, infracommunities should harbour random subsets of the locally available helminths that are able to contact these hosts (Mateu et al. 2014).

The helminth fauna of the shortfin mako has been surveyed in numerous studies (e.g. Linton 1922, Euzet 1956, Robinson 1959, Cabrera 1991, Ruhnke 1993, Caira & Bardos 1996, Knoff et al. 2002, 2007, Lyons et al. 2015). Most of these studies, which are based on small host sample sizes (<5 hosts), have been carried out in the eastern Atlantic or Pacific oceans, and provide mainly taxonomic data. There is, however, a shortage of quantitative information from a helminth community perspective. This problem is common to parasitological studies of other large sharks because opportunistic sampling usually precludes obtaining large, homogenous host samples to analyse.

Shortfin makos are regularly caught in longline fisheries operating in the northeastern Atlantic. This situation provided a unique opportunity to describe the intestinal helminth fauna of the shortfin mako in a poorly surveyed region, and to obtain parameters at both infracommunity and component community levels. In particular, we investigated the extent to which oceanic conditions influence the structure of helminth infracommunities in this large oceanic shark by comparing our results with those obtained in other parasitological studies on elasmobranchs.

MATERIALS AND METHODS

Sample collection

The shortfin mako is not protected under Spanish Law and catches have an economical interest. A total of 39 shortfin makos obtained in the port of Vigo (Galicia, Spain) were analysed for intestinal helminths. Sharks were caught by longline fisheries operating in the northeast Atlantic Ocean, between 40° N, 20° W and 35° N, 10° W (Fig. 1). Thirty-five sharks were caught in October 2012 and 4 in March 2013. Sharks were measured and sexed, collecting the stomach and the intestine (spiral valve), before the fish auction. The sample was composed of 19 males and 20 females, with total lengths ranging from 99 to 254 cm (mean ± SD: 143.9 ± 37.7 cm).

The intestine was stored at −20°C for later analysis in the laboratory. After thawing, each intestine was rinsed with tap water over a 0.02 mm mesh and the solid contents were collected. The intestine wall was also thoroughly examined for attached helminths. Parasites were collected under a stereomicroscope, washed in 0.9% saline, counted, and fixed and preserved in 70% ethanol. Cestodes were stained
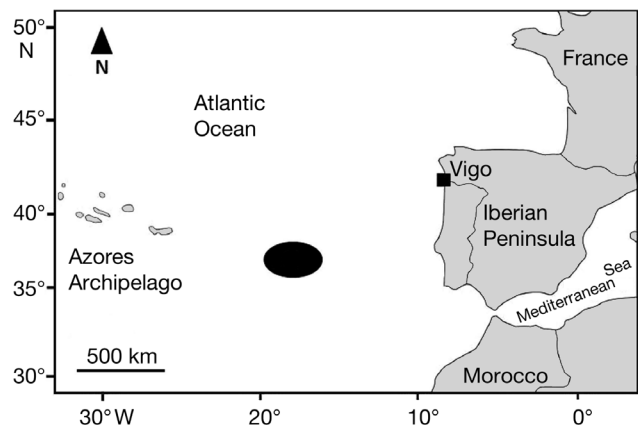

Fig. 1. Area where shortfin makos *Isurus oxyrinchus* were captured by longline fisheries. The oval dot indicates the area where the fishing boats were operating during the captures. The square dot indicates the port of Vigo, where the sharks were eviscerated. Modified from Porsmoguer et al. (2014)

with iron acetocarmine (Georgiev et al. 1986) and mounted on Canada balsam. Specimens were identified based on Khalil et al. (1994) and specific references (Ruhnke 1993, 2011, Palm 1999, Knoff et al. 2007). Larval nematodes were cleared in glycerine and examined as temporary mounts. Voucher specimens are deposited at the Natural History Museum of London with the following accession numbers: *Clistobothrium montaukensis*, NHMUK 2016.9.29.1-3; *Gymnorhynchus isuri*, NHMUK 2016.9.29.4-5; *Ceratobothrium xanthocephalum*, NHMUK 2016.9.29.6-8; *Dinobothrium septaria*, NHMUK 2016.9.29.9-11; *Nybelinia lingualis*, NHMUK 2016.9.29.12-14; *Phyllobothrium* cf. *lactuca*, NHMUK 2016.9.29.15-17; and L3 larvae of *Anisakis* sp. type I, NHMUK 2016.9.29.18-20. Additional material can be found at the Collection of the Marine Zoology Unit, Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Spain.

Statistical analyses

We recorded prevalence (percentage of hosts in the sample infected by a helminth species), mean intensity (average number of individuals of a helminth species per host in the sample of hosts infected with this species) and mean abundance (average number of individuals of a helminth species per host in the total sample of hosts) for each helminth taxon following Bush et al. (1997). Total helminth abundance, species richness and Brillouin's index of diversity were used as descriptors of infracommunities (i.e. helminth communities of individual hosts). Total helminth abundance is here considered as the number of individuals of all helminth species, and species richness as the number of helminth species per individual shark. The 95% CI for prevalence was calculated with Sterne's exact method (Reiczigel 2003). The 95% CI for mean abundance and mean intensity of each helminth taxon, as well as for mean total helminth abundance, mean species richness and mean Brillouin's index, were obtained with the bias-corrected and accelerated bootstrap method using 20 000 replications (Rózsa et al. 2000).

A Spearman's correlation test was performed to investigate whether the abundance of each helminth species and infracommunity parameters varied significantly with host length, and Mann-Whitney U tests were performed to explore significant differences in parasitological parameters between male and female sharks. The overall association between helminth species was investigated using a variance ratio test (Schluter 1984). The aim of this test is to compare the observed variance in helminth species richness per shark with the variance expected assuming that the occurrence of each species is independent from that of the others (see Schluter 1984 for details). To create the null distribution under an independent colonization hypothesis, we fixed the observed value of species' occurrences per shark but randomized the occurrence of each species among sharks, assuming that the likelihood of infection of all individual hosts was equiprobable. This process was repeated 20 000 times.

General linear mixed models (GLMMs) were used to explore whether mean species richness and mean total abundance of intestinal cestodes were significantly smaller in shortfin makos and other oceanic elasmobranchs than in other elasmobranchs. We focused on cestodes because they are, by far, the most diverse helminth group infecting elasmobranchs (Caira & Jensen 2014), and many surveys only provide infection data on cestodes. Data from other host species were obtained from parasitological surveys with host sample sizes ≥10 (see the Supplement at www.int-res.com/articles/suppl/d123p045_supp.xlsx). Most studies do not provide data on mean species richness or mean total abundance. In these cases, we calculated species richness by summing up prevalences (expressed as decimals) of all intestinal helminth taxa, and mean total abundance based on mean abundances of individual taxa.

In the comparison of species richness, we used the ratio between infracommunity richness and component community richness as the dependent variable. In this way, we controlled for differences of local cestode availability (for brevity we will refer to this variable as 'corrected infracommunity richness'). Host sample size (as a measure of sampling effort) and habitat (oceanic pelagic elasmobranchs vs. other elasmobranchs) were used as predictors. In some species, there was more than one survey available (see the Supplement), thus 'individual survey' was included as a random variable in the model. Type I sum of squares was used to control for sampling effort before making the contrast for habitat. In the comparison of mean total abundance, data were log_{10}-transformed to achieve linearity, and the same set of predictors was used. In all models, we treated species as independent observations, i.e. we did not apply independent contrasts (see e.g. Poulin 1997) because quantitative data of helminth communities from elasmobranchs are still limited. Thus, the comparisons should be considered as preliminary, awaiting more complete analyses with data from further surveys when available.

The free software Quantitative Parasitology v.3 (www.zoologia.hu/qp/qp.html) was used to calculate infracommunity parameters and to set the 95% CIs of parameters. The free software EcoSim (www.uvm. edu/~ngotelli/EcoSim/EcoSim.html) was used to perform Schluter's test and the statistical package SPSS v.22 was used for the remaining analyses (SPSS). Statistical significance was set at p < 0.05.

RESULTS

A total of 2117 helminth specimens were collected, and all sharks except 4 were infected with at least 1 helminth taxa. Nematodes identified as L3 larvae of *Anisakis* sp. type I were found throughout the intestine of 17 sharks (Table 1), some specimens being partially digested. Six species of cestode from the orders Tetraphyllidea, Trypanorhyncha and Phyllobothriidea were also found in the intestine (Table 1). At least some individuals with gravid proglottids were detected in 3 species, including *Clistobothrium montaukensis* Ruhnke, 1993, *Gymnorhynchus isuri* Robinson, 1959 and *Ceratobothrium xanthocephalum* Monticelli, 1892. *C. montaukensis* was the most prevalent taxon, infecting 32 sharks; it also numerically dominated infracommunities since in 27 sharks it made up over 50% of the total helminth abundance. A total of 21 individuals of *G. isuri* were found in 3 hosts, whereas individuals of *C. xanthocephalum* specimens were found in 8 sharks. One infection in a female shark reached 942 individuals of this cestode species (Table 1). In some sharks, the scolex was embedded in the intestinal wall and was typically surrounded by a fibrotic capsule.

In 3 cestode species, no individuals with gravid proglottids were found: *Nybelinia lingualis* (Cuvier, 1817), *Dinobothrium septaria* (Van Beneden, 1889) and *Phyllobothrium* cf. *lactuca* (Van Beneden, 1850) (Table 1). Thirty-nine *N. lingualis* were found in the intestine of 7 sharks, whereas only 14 specimens of *D. septaria* were found in a single shark. *P. lactuca* was found in 4 sharks. In this species, the poor state of preservation of specimens made it difficult to find the anterior accessory sucker of bothridia and, in some cases, only 2 out of the 4 suckers could be observed.

No significant relationship between host body length and the abundance of any helminth species or infracommunity parameters was found (range of Spearman r = −0.139–0.345, p > 0.05). In addition, no significant differences were detected in the abundance of any helminth species or infracommunity descriptors between sexes (range of Mann-Whitney U = 90–102, p > 0.25). Schluter's variance test indicated no significant departure from the null hypothesis of random colonization of helminth taxa. The observed value was not significantly lower (p = 0.958) or higher (p = 0.058) than those obtained in the null distribution.
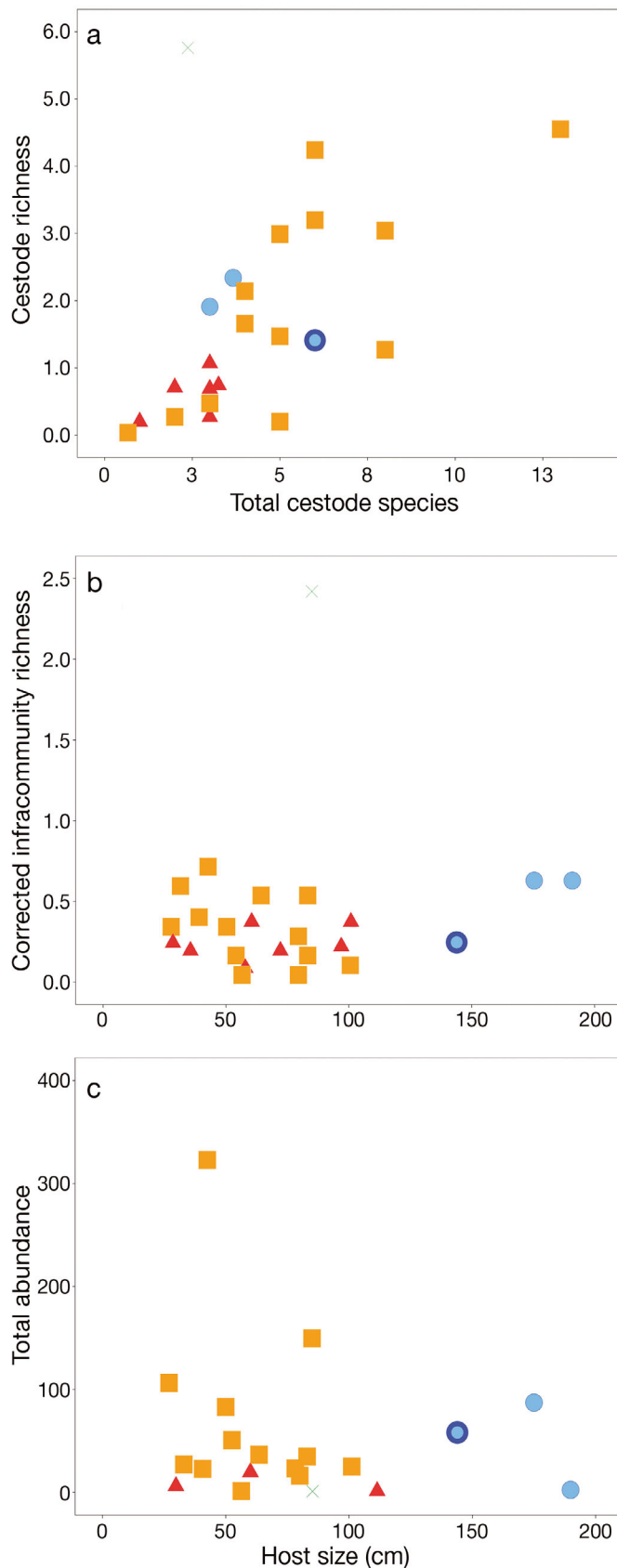
Species richness at the infracommunity level ranged from 0 to 4 (mean [95% CI]: 1.85 [1.49–2.18]), and was low compared with species number at the component community level (7 spp.). However, the difference was not higher than that observed in other elasmobranchs, regardless of their habitat (Fig. 2a,b). In fact, other pelagic oceanic sharks, i.e. the blue shark *Prionace glauca* and the porbeagle *Lamna nasus*, do not depart from the common pattern of difference observed in non-oceanic elasmobranchs (Fig. 2a,b;

Table 1. Infection parameters of intestinal helminths found in 39 shortfin makos *Isurus oxyrinchus* from the Northeast Atlantic Ocean

Species	Prevalence (%) Overall (95% CI)	Intensity Mean (95% CI) [range]	Abundance Mean (95% CI)
Order Tetraphyllidea			
Ceratobothrium xanthocephalum	20.5 (9.7–35.7)	180.8 (47.9–536.3) [1–942]	37.1 (8.6–141)
Dinobothrium septaria	2.6 (0.2–13.6)	14 ([a]) [[b]]	0.4 (0–1.1)
Order Trypanorhyncha			
Gymnorhynchus isuri	7.7 (2.1–20.3)	7 (1–12) [1–16]	0.5 (0–2.3)
Nybelinia lingualis	17.9 (8.6–33.2)	5.6 (1.6–16.6) [1–27]	1 (0.2–3.9)
Order Phyllobothriidea			
Clistobothrium montaukensis	82.1 (66.8–91.4)	17.6 (13.8–24.5) [1–78]	14.4 (10.8–20.4)
Phyllobothrium cf. *lactuca*	10.3 (3.6–24.1)	8.5 (2.5–18.3) [2–22]	0.9 (0.2–3.2)
Order Rhabditida			
Anisakis sp. L3 larvae type I	43.6 (27.8–60.3)	8.76 (2.1–33.9) [1–110]	3.8 (0.9–15.3)

[a]Sample is too small to calculate the value
[b]Cannot be calculated with only one infection

see also the Supplement). This conclusion was supported by the GLMM results. Contrary to what was expected, the corrected infracommunity richness in pelagic oceanic sharks was higher than that from other elasmobranchs; the associated probability was close to significance (Table 2). Brillouin's index (0.264 [0.176–0.370], range: 0–0.972) and mean total helminth abundance (58.1 [28.0–161.7], range: 0–964) were low in shortfin makos of our sample. However, values of mean total abundance tended to be higher than those observed in most elasmobranchs (Fig. 2c). Furthermore, the GLMM results indicated that mean total abundance of helminths in pelagic oceanic sharks was higher than that from other elasmobranchs and close to significance (Table 2). No significant effect of host sample size was detected in any model (Table 2).

DISCUSSION

The parasite fauna of shortfin mako in our sample was composed of 7 species, all of which except *Dinobothrium septaria* had already been reported in this host (see below). However, up to 9 additional species, all belonging to the order Trypanorhyncha, have been found in the intestine of makos globally (Palm 2004, Randhawa & Poulin 2010, and references therein). Three species, i.e. *Nybelinia schmidti*, *N. pintneri* and *Myxonybelinia californica*, occur in South Africa and Tasmania (Palm 1999, Palm & Beveridge 2002), the Pacific Ocean (Yamaguti 1934, Heinz & Dailey 1974) and off the coast of California (Palm, 2004), respectively. Also, *Hepatoxylon megacephalum* appear to be restricted to large sharks in the Southern Hemisphere (Bates 1990, Waterman & Sin 1991, Beveridge & Campbell 1996), although there is an additional record in the nursehound *Scyliorhinus stellaris* from the Mediterranean (Hartwich & Kilias 1992).

Fig. 2. Comparison of richness and mean abundance of parasite infections in elasmobranch species from different habitats. For clarity, in species with more than one survey, an average of helminth species richness and total abundance are used. Complete data can be found in the Supplement at www.int-res.com/articles/suppl/d123p045_suppl.xlsx. Habitat of each species: bathydemersal (red triangles); benthopelagic (green cross); demersal (orange squares); pelagic oceanic (blue circles). Values related to our survey (shortfin mako) are circled. (a) Relationship between infracommunity cestode richness and the total number of cestode species infecting the host. (b) Relationship between corrected infracommunity richness and mean host size. (c) Relationship between total abundance of parasites with mean host size

Table 2. Results of the general linear mixed models to account for corrected infracommunity richness and total abundance of cestode fauna of pelagic oceanic sharks vs. elasmobranchs from other habitats. The parameter for pelagic oceanic sharks was set to zero and, therefore, the parameter for 'habitat' represents the value for other elasmobranchs

Predictor	Parameter	SE	t	df	p
Infracommunity richness					
Host sample size	−0.000290	0.000562	−0.516	34.3	0.609
Habitat	−0.222	0.122	−1.823	18.7	0.084
Total abundance					
Host sample size	−0.002657	0.001564	−1.699	31.4	0.099
Habitat	−0.820	0.449877	−1.822	22.6	0.082

However, 5 species have previously been reported in the North Atlantic but were not detected in our survey. Two species of the Sphyriocephalidae, i.e. *Sphyriocephalus viridis* and *Heterosphyriocephalus tergestinus*, are parasites typical from pelagic and deep-sea sharks (Dallarés et al. 2016). Although plerocercoid larvae have been detected in our study area, there is only a single record of each species in shortfin makos (Dallarés et al. 2017), suggesting that infections in makos could be infrequent. In contrast, of the other 3 non-detected species, *Gymnorhynchus gigas* and *Molicola horridus* are typical from shortfin makos (Bates 1990, Palm 2004), and *Hepatoxylon trichiuri* also occurs in other pelagic sharks (Bates 1990, Waterman & Sin 1991, Beveridge & Campbell 1996). Furthermore, there are records of these 3 species in intermediate hosts in the NE Atlantic (Heinz & Dailey 1974, Casado et al. 1999, Vázquez-López et al. 2000, Gibson et al. 2005); thus, their absence from our survey could be due to low sample numbers, particularly if prevalences are low (see also below).

The L3 larvae of *Anisakis* sp. type I are ubiquitous in the oceanic realm and may correspond to any of the 6 species of *Anisakis* that have odontocete cetaceans as main definitive hosts (Mattiucci & Nascetti 2008). Two of these species, *A. simplex* (*sensu stricto*) and *A. pegreffii*, have been reported in the study area (Beverley-Burton et al. 1977, Paggi et al. 1998, Kuhn et al. 2011). The diet of the shark individuals analysed in our sample was described by Porsmoguer (2015) and includes fish and squid prey, i.e. *Histioteuthis* sp., *Xiphias gladius*, *Euthynnus alletteratus*, *Scomberesox saurus*, and *Scomber scombrus*, that are susceptible to infection with these anisakid species (Bussiéras & Baudin-Laurencin 1973, Abaunza et al. 1995, McDonald & Margolis 1995, Mattiucci et al. 1997, Culurgioni et al. 2010). It is interesting that larvae were found free in the intestine lumen of makos and not encysted in the stomach wall as commonly occurs in typical in-termediate or paratenic fish hosts (Mattiucci & Nascetti 2008). This could suggest that shortfin makos likely are accidental hosts for these larvae.

Species of *Clistobothrium* seem to be specific to lamnid sharks (Dailey & Vogelbein 1990, Ruhnke 1993, Randhawa & Brickle 2011). *C. montaukensis* had only been reported in the shortfin mako in the northwestern Atlantic (Ruhnke 1993), although a closely related, unidentified species of *Clistobothrium* was reported from porbeagle sharks *Lamna nasus* in the Falkland Islands (Randhawa & Brickle 2011). Molecular evidence indicates that porbeagle sharks are infected with *C.* cf. *montaukensis* through the squid *Doryteuthis gahi* (Randhawa & Brickle 2011). However, there is also morphological, molecular and ecological evidence that cetaceans act as intermediate hosts for species of *Clistobothrium* (Aznar et al. 2007). In fact, adults of *C. carcharodoni*, collected from great white sharks *Carcharodon carcharias* in New Zealand, were closely related to plerocercoid larvae collected in squid-feeding cetaceans from the western Mediterranean (Randhawa 2011). The diet of the shortfin makos analysed in this study included at least 7 species of oceanic squid (Porsmoguer et al. 2014), but remains of cetaceans were also found in the stomach of several individuals (Porsmoguer et al. 2015). Thus, there is the possibility that *C. montaukensis* use squids and/or cetaceans as intermediate hosts to infect shortfin makos.

Gymnorhynchus isuri has only been reported in shortfin makos, and seems to be a widespread species, with records in the north- and southwestern Atlantic (Caira & Bardos 1996, Knoff et al. 2002) and New Zealand waters (Robinson 1959). *Ceratobothrium xanthocephalum* apparently infects only species of *Lamna* and *Isurus* (Euzet 1956, 1994, Schmidt 1986). Shortfin makos accumulate the largest number of records for this cestode species, including Japan (Yamaguti 1934), New Zealand (Robinson 1959), the northeastern (Euzet 1956) and northwestern Atlantic (Olson & Caira 1999), and the Pacific coast of North America (Lyons et al. 2015). Plerocercoid larvae of *Gymnorhynchus* spp. and *C. xanthocephalum* have been reported in pelagic oceanic teleosts (Gibson et al. 2005), including some species (e.g. the swordfish *X. gladius*) that were found in the stomach contents of our mako sample (Porsmoguer 2015). Therefore, an oceanic life cycle could be inferred, with teleosts serving as second intermediate hosts.

We did not find gravid worms in 3 tapeworm species. *D. septaria* is typical of lamnid sharks, and have been found in porbeagle sharks in North Atlantic (Woodland 1927, Euzet 1956) and South Atlantic (Randhawa & Brickle 2011), and great white sharks from the North Atlantic (Woodland 1927). In our survey, only 14 individuals of this cestode were recovered from a single shark, and none had gravid proglottids, suggesting a recent or an accidental infection.

Nybelinia lingualis has been reported widely in the Atlantic and South Australia (Palm & Walter 2000) and seems to be an ecologically ubiquitous species. Plerocercoid larvae occur in a number of benthic, demersal and pelagic teleosts and cephalopods (Palm 1999, Palm & Walter 2000, Gibson et al. 2005). Adults also exhibit low host specificity and have been reported in pelagic and demersal sharks, as well as in pelagic rays (Palm & Overstreet 2000, Palm & Walter 2000, Knoff et al. 2002). There are records of adult *N. lingualis* in shortfin makos from the southwestern Atlantic (Knoff et al. 2002) and the western Mediterranean (Cabrera 1991, Palm & Walter 2000). However, none of the 39 specimens of *N. lingualis* collected from 7 sharks in this study were gravid, thus raising the question of whether or not shortfin makos are suitable hosts for this species.

Finally, the specimens of *Phyllobothrium* collected as immature specimens in 4 sharks from this study resembled *P. lactuca* but their poor state of preservation precluded an unequivocal identification at species level. *P. lactuca* typically infects elasmobranchs dwelling in shelf and upper slope waters, rarely oceanic sharks (e.g. Euzet 1956, Ruhnke 1996, Sène et al. 1999). There is an old record of this cestode in *Oxyrhina spallanzanii* (= *I. oxyrhinchus*) (see Williams 1968). Records of *P. lactuca* in shortfin makos probably represent accidental infections.

In summary, all helminth species reported in this study are almost exclusively found in sharks, mainly members of the family Lamnidae inhabiting oceanic waters. This pattern of specificity is common to other elasmobranchs, the intestinal helminth fauna of which is peculiar and very specific as a whole (Caira & Pickering 2013). The helminths found in shortfin makos, with the exception of *C. montaukensis*, had low infection levels, and the variance ratio test indicated independent colonization of each helminth species. In addition, no significant correlation was found between the length of the host and species richness or total abundance of intestinal helminths. In infracommunities of intestinal helminths, an absence of structure has been related to the lack of competitive interactions between species (see e.g. Curran & Caira 1995 for a large shark species). However, a low recruitment rate of parasites has been invoked as a more likely factor accounting for independent colonization of helminths in intestinal infracommunities of oceanic vertebrates such as sea turtles (Santoro et al. 2010) or cetaceans (Mateu et al. 2014). Low recruitment would be dependent on the 'dilution' of infective stages in the oceanic habitat (Randhawa & Poulin 2010, Mateu et al. 2014), but also on a low number of infective stages transmitted with each prey. In this respect, the size of larvae could be an issue because there seems to be an inverse relationship between the size of parasites and their intensity of infection (see e.g. Randhawa & Poulin 2009 for parasites of elasmobranchs). Interestingly, the larval size for 3 of the tapeworm species infecting shortfin makos is presumably large (i.e. over 1 cm long) (see measurements for allied species in Pascual et al. 1994, Williams & Bunkley-Williams 1996).

Contrary to what we expected, the cestode infracommunities of shortfin makos and other pelagic oceanic sharks were not particularly depauperate compared with those from other elasmobranchs, e.g. *Prionace glauca*, *Squalus acanthias*, *Etmopterus spinax* and *Leucoraja naevus* (see Fig. 2); in fact they tended to be more diverse. This observation could be related to 3 potential factors. First, we cannot rule out that parameters at the infracommunity level are blurred by phylogenetic effects (i.e. the degree of diversification and specificity of cestode taxa in each host group) and/or differences in the local availability of cestodes. Nevertheless, we attempted to minimize these effects by dividing mean infracommunity richness by component community richness. For instance, bathydemersal sharks are typically infected with very few cestode species (Caira & Pickering 2013; see Fig. 2a), but corrected infracommunity richness was similar to that from other elasmobranchs (Fig. 2b).

Second, shortfin makos and other pelagic sharks are apex predators with the largest body size of all elasmobranch species in the sample (Fig. 2b,c). In addition, makos and other lamnid sharks are capable of increasing their temperature by up to 20°C (Bernal et al. 2005). Accordingly, they should have higher metabolic demands and higher rates of prey consumption, thus increasing the likelihood of contact with infective stages of many parasites (Aznar et al. 2004), particularly if they are generalist predators (Joyce et al. 2002, McCord & Campana 2003, López et al. 2009). In other words, a large body size could

help offset the negative 'dilution' effect of oceanic habitat on transmission rates. Finally, it could be that the 'dilution effect' associated with oceanic conditions is inconsequential if parasites are adapted to expand the use of intermediate hosts through the trophic web. In fact, it has been suggested that many marine parasites have reduced host specificity as a strategy to spread out the risk of failure to complete their life cycles (Marcogliese 1995, 2002).

Consequently, it would seem premature to extract solid conclusions about the influence of the oceanic habitat on the helminth assemblage of shortfin makos based on the available data. However, we think that interspecific comparative approaches are necessary to advance hypotheses about such influences. This approach would also require that proper infracommunity parameters are published in surveys of elasmobranchs and other oceanic vertebrates.

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