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Distribution patterns and interactions of cestodes in the spiral intestine of the narrownose smooth-hound shark, *Mustelus schmitti* Springer, 1939 (Chondrichthyes, Carcharhiniformes)

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Abstract

The distribution patterns and the cestode species interactions within the spiral intestine of 20 specimens of *Mustelus schmitti* from coastal waters off Mar del Plata, Argentina were studied. Six cestode species were found: Tetraphyllideans *Calliobothrium barbarae*, *C. australis*, *C. lunae* and *Orygmatobothrium schmittii*, diphyllidean *Echinobothrium notoguidoi* and trypanorhynch *Eutetrarhynchus vooremi*. The most common number of parasite species per host was 3. Brillouin's diversity index ranged from 0.1 to 1.2. Berger-Parker dominance index indicated that *C. barbarae* was the dominant species, followed by *O. schmittii* and *C. australis*. *Calliobothrium barbarae*, *C. australis* and *O. schmittii* presented a broad distribution along the spiral intestine, whereas *C. lunae*, *E. notoguidoi* and *E. vooremi* showed a more restricted niche breadth. In general, the Renkonen's index showed no evidence of niche overlap in the range of distribution of the different species. In most of the infracommunities, intraspecific aggregation was stronger than interspecific aggregation, indicating that competition may play a little role. The distribution patterns of the *Calliobothrium* specimens concurs with the predictions of attachment sites for *Calliobothrium* species made by previous authors.

Key words

Cestodes, *Mustelus schmitti*, spiral intestine, interactions, distribution patterns

Introduction

Previous studies on cestode assemblages within the spiral intestine of sharks have been done by Cislo and Caira (1993) and Curran and Caira (1995). Cislo and Caira (1993) focused on the cestode communities of *Mustelus canis* (Mitchill, 1815), and found that the species showed site specificity, no evidence of interactions, and that the most posterior regions of the intestine were devoid of parasites. A similar pattern was observed in *Prionace glauca* (L., 1758), although 3 of the 4 tapeworms species showed site specificity (Curran and Caira 1995).

Three major selective forces for niche restriction in intestinal helminths have been proposed: Specialization (morphological or physiological) (Price 1984), efficiency in the reproduction (Rohde 1979) and competition (Holmes 1990). These major selection pressures are not mutually exclusive and reinforce each other in their effects on the distribution of intestinal helminths. Additionally, Brooks (1980) suggested that the parasite species that compose an assemblage within any host species are often phylogenetically determined. In fact, Cislo and Caira (1993) proposed that site specificity exhibited by the cestode species in *M. canis* may have a phylogenetic component. Moreover, Curran and Caira (1995) suggested that the anatomy of the spiral intestine may play an important role in the establishment of parasite species.

The distribution patterns of cestodes and their putative interactions within the spiral intestine of another narrownose smooth-hound shark, *Mustelus schmitti* Springer, 1939, is herein studied.

Materials and methods

Twenty specimens of *M. schmitti*, ranging from 51 to 76 cm in total length, were obtained from commercial fish trawlers in

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coastal waters off Mar del Plata (38°00´S, 57°33´W), Argentina, in 2001 (September and November), 2002 (May, August, September, October and November), and 2003 (February). The sharks were transported to the laboratory for examination. Each host was opened with a midventral incision and the spiral intestine was removed and cut away from the pyloric stomach anteriorly, and from the rectum posteriorly. Sampling procedures followed Cislo and Caira (1993), however, fixation was done with 10% formaldehyde solution instead of AFA (alcohol-formalin-acetic acid) for better results. Each intestine was dissected with a midventral incision along the ventral blood vessel and the spirals of the intestinal mucosa were cut to expose the surface of each chamber. Chambers were numbered from 1 to 8, first being adjacent to the stomach. Each tapeworm was removed from the mucosal surface of each chamber and its location recorded. The outline of the chambers was transferred to transparent sheets, digitalized, and the chamber's area were obtained using the computer program Skaletti 2.5. Differences among the area of the different chambers were tested using an analysis of variance (ANOVA) and posteriorly least significant difference (LSD) was calculated (Zar 1984). Spearman's coefficient correlation was used to investigate the relationship between shark size (total length) and the number of parasites in each infracommunity. Statistical significance was judged at $p = 0.05$.

Temporary mounts of each tapeworm were prepared for accurate identification. Whole mounts of representatives of all cestode species were also prepared to corroborate their identification with the species previously described from this host. Specimens for whole mounts were transferred to 70% ethanol, hydrated in a graded descending ethanol series, stained with Harris' haematoxylin, dehydrated, cleared with creosote and mounted in Canada balsam.

The following indices were calculated: Parasite prevalence and total abundance, according to Bush *et al*. (1997). At the infracommunity level, the species richness, diversity, dominance, niche breadth, niche overlap, and intraspecific and interspecific aggregation coefficients were considered as follows: Brillouin's diversity index (HB) because each infracommunity was fully censured (Magurran 1988), Berger-Parker dominance index (D), Levin's niche breadth (B), and Renkonen's niche overlap (R) according to Simková *et al.* (2000). In order to compare intraspecific aggregation vs interspecific aggregation, the coefficients of intraspecific (J) and interspecific (C) aggregation, and the reduction in competition caused by intraspecific aggregation in a pair of species (A) according to the coexistence aggregation model, were adapted considering each chamber of the spiral intestine as a different 'patch' (see Morand *et al*. 1999). Whenever it was possible, the infracommunities were classified as "light" and "heavy" infections according to the intensity of infections for the different species of cestodes, where "n" is the number of specimens and "*n*" the number of infracommunities.

Results

All hosts were infected by cestodes. A total of 732 parasites was found in the 20 specimens of *M. schmitti* examined for parasites. Up to 6 species of cestodes were found, all of which have previously been reported from this host: Three onchobothriids, *Calliobothrium barbarae* Ivanov et Brooks, 2002 (prevalence: 90%); *C. australis* Ostrowski de Núñez, 1973 (prevalence: 60%) and *C. lunae* Ivanov et Brooks, 2002 (prevalence: 30%); one phyllobothriid, *Orygmatobothrium schmittii* Suriano et Labriola, 2001 (prevalence: 80%); one trypanorhynch, *Eutetrarhynchus vooremi* Sao Clemente et Gómes, 1989 (prevalence: 35%) and one diphyllidean, *Echinobothrium notoguidoi* Ivanov, 1997 (prevalence: 25%) (Table I).

Table I. Prevalence, intensity and abundance of cestodes in the spiral intestine of *M. schmitti*

Cestode species	Number of infected hosts	Prevalence (%)	Mean intensity ± SD	Intensity of infection (min-max)	Mean abundance ± SD
C. barbarae	18	90	24.3 ± 33.8	2–136	21.9 ± 32.9
C. australis	12	60	10.1 ± 5.84	1–19	6.1 ± 6.8
C. lunae	6	30	2.1 ± 1.1	1–4	0.65 ± 1.1
O. schmittii	16	80	8.3 ± 5.8	1–26	6.65 ± 6.1
E. vooremi	7	35	1.5 ± 0.7	1–3	0.55 ± 0.8
E. notoguidoi	5	25	2.6 ± 1.5	1–5	0.65 ± 1.3

Table II. Size of each chamber of the spiral intestine of *M. schmitti*

Number of chamber	Size (cm^2) (mean ± SD)
1	14.93 ± 3.56*
2	6.38 ± 1.33
3	5.62 ± 1.50
4	5.20 ± 1.32
5	5.10 ± 1.31
6	5.11 ± 1.33
7	5.42 ± 1.53
8	10.20 ± 3.96*

*Differences in size are statistically significant at $p = 0.05$.

Compagno (1988) recognized 3 types of spiral intestines among elasmobranchs: Conicospiral, ring and scroll-type. *Mustelus schmitti* have the conicospiral type, in which the internal mucosal folds create 8 contiguous chambers. The ANOVA revealed that most chambers have a similar area, with exception of chambers 1 and 8 (Table II). In fact, the areas of these chambers are approximately twice the size of the other chambers.

No significant correlation was found between the total number of worms and host size (Spearman's range = 0.02–0.34; $p > 0.05$).

Total number of cestode was 4–143 tapeworms per host. Infracommunity species richness ranged from 1 to 5; the most frequent being 3. None of the hosts was found parasitized by all 6 cestode species. Only one fish had a monospecific infection with *C. barbarae*.

Brillouin's diversity index ranged from 0.1 to 1.2. Most of the infracommunities showed Brillouin's diversity values from 0.6 to 1.2 (Fig. 1).

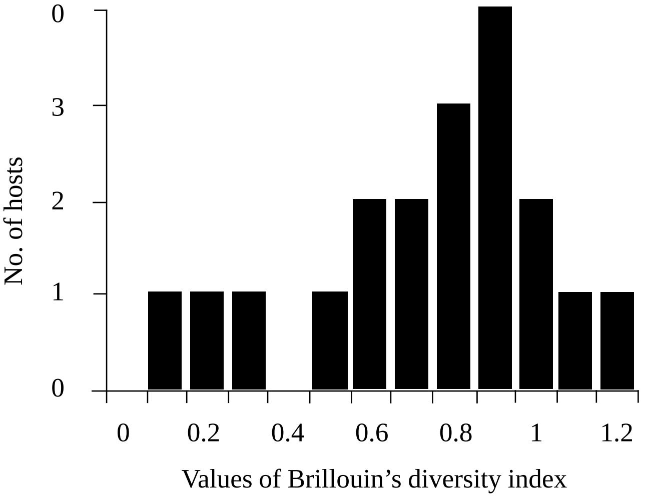

Fig. 1. Frequency distribution of Brillouin's diversity index in the infracommunities in the spiral intestine of *Mustelus schmitti*

According to Berger-Parker dominance index, *C. barbarae* was dominant in 50% of the infracommunities, followed by *O. schmittii* (35%) and *C. australis* (15%).

The distribution of cestodes along the spiral intestine presented variations in relation to the number of parasites. *C. barbarae* was found throughout the spiral intestine. Levin's niche breadth for this species ranged from 1 to 6; however, the values were 1–2 in most of the hosts, and 3–6 in 27% of the infracommunities (Fig. 2). In light infections (n < 20 worms, $n = 12$ infracommunities), the specimens of *C. barbarae* were restricted to chambers 1 and 2. In contrast, in heavy infections (n > 20 worms, $n = 6$ infracommunities), the specimens showed an extension of their distribution, occupying the chambers 1 to 7.

Orygmatobothrium schmittii and *C. australis* showed the greatest values of niche breadth, 3–6 for *O. schmittii* and 3–4 for *C. australis*, in more than 60% of the hosts (Fig. 2). *O. schmittii* was found from chambers 1 to 8. In light infections (n ≤ 10 worms, $n = 9$ infracommunities) the specimens of *O. schmittii* were distributed in chambers 4 to 6. The chambers occupied by this species in heavy infections varied greatly among hosts (n > 10 worms, $n = 4$ infracommunities); however, the general tendency for *O. schmittii* was the extension of its distribution anteriorly (chamber 1), and posteriorly (chambers 7 and 8).

Calliobothrium australis was distributed from chamber 1 to 8, but restricted to chambers 4 and 5 in hosts in which it was present in low numbers (n ≤ 10 worms, $n = 6$ infracommunities), and a wider distribution from chamber 3 to 8 in heavier infections (n >10 worms, $n = 6$ infracommunities).

Calliobothrium lunae, *E. vooremi* and *E. notoguidoi* showed a more restricted niche breadth. Niche breadth was less than 2 for *C. lunae* and *E. vooremi* in all the hosts; and 3 for *E. notoguidoi* in 20% of the hosts (Fig. 2). These species were found in small numbers (n ≤ 5 worms in all the hosts) and were only present in the four anteriormost chambers: *C. lunae* in chambers 1 and 2, *E. notoguidoi* in chambers 1 to 3 and *E. vooremi* in chambers 1 to 4.

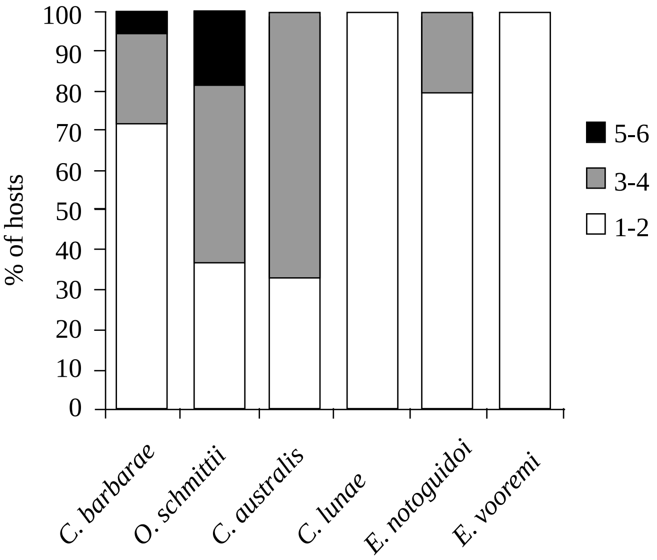

Fig. 2. Levin's niche breadth showed for each cestode species as percentages of the host sample

Even if most species were more likely to be distributed in the anterior chambers, the values of Renkonen's niche overlap between pairs of parasite species that co-occurred were low. The highest values of this index were registered in some infracommunities for the pairs *C. barbarae-C. lunae*, *C. lunae-E. vooremi*, *C. australis-O. schmittii* and *O. schmittii-E. notoguido* (Table III).

Table III. Niche overlap (Renkonen's index) between pairs of cestode species

	C. australis	*C. lunae*	*O. schmittii*	*E. vooremi*	*E. notoguidoi*
C. barbarae	0.14 ± 0.13 (0.37)*	0.40 ± 0.40 (0.86)	0.21 ± 0.40 (0.41)	0.10 ± 0.14 (0.36)	0.24 ± 0.25 (0.53)
C. australis		0.16 ± 0.13 (0.30)	0.27 ± 0.21 (0.61)	0.20 ± 0.24 (0.50)	0.19 ± 0.26 (0.55)
C. lunae			0.06 ± 0.09 (0.22)	0.47 ± 0.41 (0.75)	–
O. schmittii				0.10 ± 0.10 (0.25)	0.23 ± 0.23 (0.60)

*Mean Renkonen's index ± SD (max).

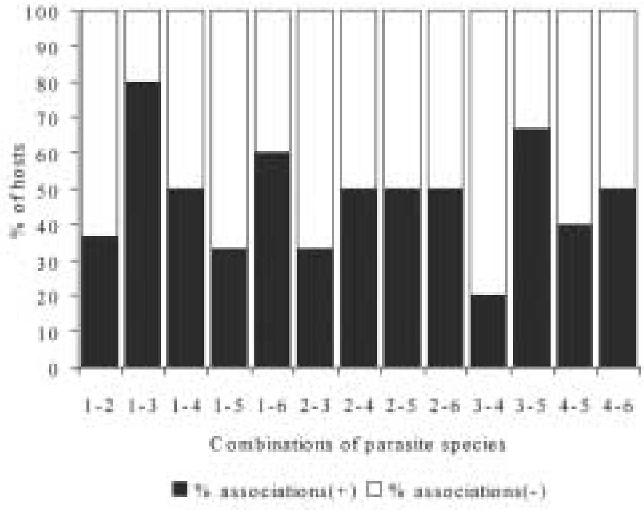

Fig. 3. Percentage of positive (C > 0) and negative (C < 0) associations by species pairs that co-occur in the infracommunities in the spiral intestine of *Mustelus schmitti*. **1.** *C. barbarae*, **2.** *C. australis*, **3.** *C. lunae*, **4.** *O. schmittii*, **5.** *E. vooremi*, **6.** *E. notoguidoi*

The values of Ives' intraspecific aggregation coefficient (J) are showed in Table IV. All cestode species showed J > 0 values, indicating that the individuals had an aggregated distribution within the spiral intestine of each shark. The highest values were registered in those infracommunities in which individuals of a species were found restricted to particular chambers.

Table IV. Intraspecific aggregation coefficient values for each cestode species in the spiral intestine of *M. schmitti*

Cestode species	J ± SD (min–max)*
C. barbarae	3.20 ± 2.08 (0.57–7.55)
C. australis	0.82 ± 0.77 (0.14–2.4)
C. lunae	2.65 ± 2.23 (2.57–5.33)
O. schmittii	0.60 ± 1.02 (0.06–2.81)
E. vooremi	0.67 ± 1.56 (1.26–4)
E. notoguidoi	1.70 ± 2.21 (1.28–4)

*J ± SD (min–max), intraspecific aggregation coefficient ± SD (min–max).

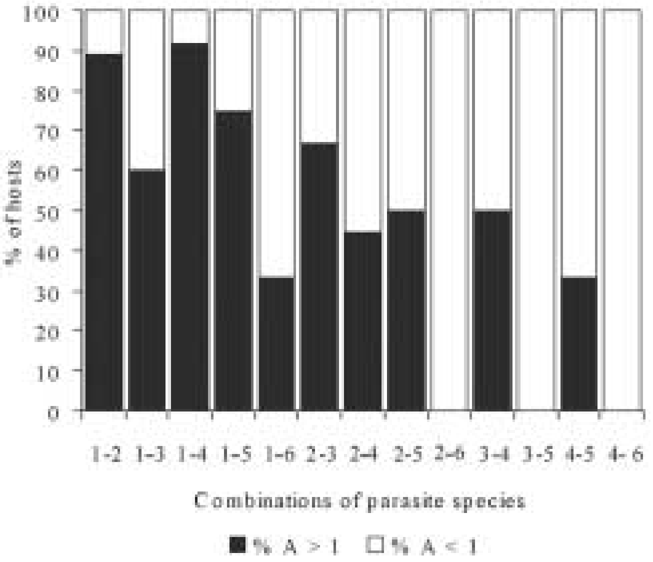

Fig. 4. Percentage of hosts with A > 1 values (intraspecific aggregation stronger than interspecific aggregation) and A < 1 values (interspecific aggregation stronger than intraspecific aggregation). **1.** *C. barbarae*, **2.** *C. australis*, **3.** *C. lunae*, **4.** *O. schmittii*, **5.** *E. vooremi*, **6.** *E. notoguidoi*. A – relative strength of intraspecific versus interspecific aggregation

The indices for parasite associations by species pairs do not reveal a pattern for high proportions of positive or negative associations in the infracommunities (Fig. 3).

The relative strength of intraspecific aggregation on interspecific aggregation was estimated using A (Fig. 4). The general tendency was a reduction of competition between pairs of parasite species due to intraspecific aggregation in the different infracommunities (A > 1). Values of A < 1 were observed in some infracommunities, however, in all the cases, one of the species in the pair was present in very low numbers. Therefore, the values of A < 1 do not account for the strength of interspecific interactions (pairs 1-6, 2-6, 3-5 and 4-6; Fig. 4).

Discussion

Species richness and total number of cestodes per host in the parasite assemblage within the spiral intestine of *M. schmitti* are consistent with the results found in other sharks. The species richness ranged from 1 to 5 in *M. schmitti*; 1–3 in *M. canis* (Cislo and Caira 1993); and 1–4 in *P. lauca* (Curran and Caira 1995). Even though the total number of cestodes per host in *M. chmitti* (4–143) was similar to *M. canis* (1–166) (Cislo and Caira 1993), the number of parasite individuals per host in *P. glauca* was quite larger (156–2,382), may be due to a larger size of the host, what implies the consumption of a greater volume of preys as intermediate hosts, as it has been suggested by Curran and Caira (1995). In *M. schmitti* the volume of some preys increase with fish size (Chiaramonte and Pettovello 2000). However, in this host species the number of worms per host was not related with the host size, even though this should be corroborated using a larger sample size.

It seems that there is no relation between the area available for attachment in the spiral intestine of *M. schmitti* and the number of cestodes, since the size of hosts was not significantly related with the number of parasites. The chambers with a smaller area (2, 3, 4 and 5) were occupied by the greatest number of cestodes. The largest chambers were 1 and 8, and even though chamber 1 harboured numerous parasites, chamber 8 was mostly free of parasites. Most species are distributed in the anterior chambers of the spiral intestine, and some of them show restricted sites of attachment and have never been found beyond the chamber 4 (*C. lunae*, *E. notoguidoi* and *E. vooremi*). The restricted sites of attachment for *C. lunae*, *E. vooremi* and *E. notoguidoi* in the anteriormost chambers and yet the absence of niche overlap among them, would be related to the fact that different species are not sufficiently abundant as to exert mutual pressures and where niche restriction has evolved independently of interspecific interactions (Price 1980). Probably, the aggregated distribution of the smaller species, like *C. lunae* and *E. notoguidoi*, enhances mating opportunities.

Even if it is more likely for *C. barbarae* to be located in the 2 anteriormost chambers, representatives of this species can expand their distribution in heavy infections. A similar pattern is showed by *C. australis* and *O. schmittii*. Both species presented broad distributions throughout the spiral intestine in light and heavy infections. However, these 2 species are more likely to be found infecting the middle rather than the anterior zone (e.g. chambers 4–5). It is worth noting that all the small body species (up to 22.0 mm long) (Ivanov 1997, Ivanov and Brooks 2002), with exception of *E. vooremi*, have site specificity for locations more anteriorly than the large body species (up to 99.0 mm long) (Ivanov 1996, Suriano and Labriola 2001, Ivanov and Brooks 2002). This might be related to a different use of the resources. Moreover, the large body size of *C. australis* and *O. schmittii*, could allow them to achieve a successful reproduction despite the spatial separation existing between individuals.

Niche overlap means that the species are in contact and able to interact. Therefore, the degree of niche overlap might help to detect putative competitive relationships among species (Schoener 1974). In general, no niche overlap between pairwise combinations of parasites that co-occur in the infracommunities was found. Even so, the higher values included pairs of species that belong to different orders or genera of cestodes, which might exhibit a different use of the resources. The only exception is the pair that includes the congeners *C. barbarae-C. lunae*; however, this could be an artifact since the presence of *C. lunae* was quite erratic. In any case, the lack of niche overlap found in this system must be considered with caution because among the many possible dimensions of a niche, only the distribution within the host has been taken into account. Anyhow, the lack of niche overlap in most of the infracommunities could indicate that there is no competition between the species of each pair, probably due to the low densities of the infrapopulations. In the infracommunities where positive or negative associations were registered, at least one of the species involved in the pair was present with a very low density and a consistent pattern of associations between those species was not observed. For example, *C. barbarae* and *C. lunae* registered a positive association in 80% of the infracommunities; however, *C. barbarae* was present in most of the infracommunities while the occurrence of *C. lunae* was variable. Consequently, when *C. lunae* was present it was very likely that *C. barbarae* was also present in the same infracommunity.

Calliobothrium barbarae was the only species found in a monospecific infection. This species displayed a similar distribution throughout the spiral intestine in monospecific and multiple infections. It seems that the presence of other cestode species might not affect the distribution of *C. barbarae*. However, additional information on monospecific infections is necessary to confirm this observation.

The coexistence aggregation model suggests that species coexistence can be favoured by reducing the intensity of competition by the aggregated utilization of fragmented resources. Thus, species are distributed in a way that interspecific interactions are reduced in order to facilitate coexistence (Morand *et al.* 1999, Simková *et al.* 2000). In this study, use of the A coefficient showed that there was a strong reduction of interspecific aggregation in relation to intraspecific aggregation, which might have facilitated the coexistence of cestodes in the spiral intestine.

Cestode assemblages in the spiral valve of *M. schmitti* fit the isolationist community model. According to this model, breadth and position of the realized niche of a parasite are independent of the presence of other species, even if overlapping of fundamental niche occurs (Rohde 1979, Price 1980, Holmes and Price 1986). In these communities, interspecific interactions are unlikely to be detected due to the low abundance of the species and the competition may play little role (Poulin 1998).

The distribution of cestodes within the spiral intestine of *M. schmitti* indicates that each species exhibits a preference for a particular zone of the intestine. In this system the posterior region of the intestine is commonly vacant, as is the case in other vertebrate hosts (Stock and Holmes 1987, Cislo and Caira 1993, Curran and Caira 1995). The intestinal tract may be considered like a complex linear gradient, since there are different conditions throughout its length, e.g. changes in the morphology of the mucosal surface, physicochemical properties, concentration of nutrients, etc. (Crompton 1973, Mettrick 1980). The configuration of the mucosal surface differs along the spiral intestine in elasmobranch species (Williams 1960, 1968; Williams *et al.* 1970; Carvajal and Dailey 1975; Borucinska and Caira 1993; McKenzie and Caira 1998). Unfortunately, no research exists on the topography of the intestinal surface in *M. schmitti* to allow the issue of whether mucosal structure is related to attachment site and distribution to be tested.

Brooks (1980) suggested that a cestode assemblage within a host species is often phylogenetically determined. It also seems to be the case that there is a phylogenetic component to site of attachment; thus, site specificity is an extension of host specificity (Brooks 1980). As parasite species differ in their degree of host specificity, they also differ in their degree of site specificity. In general, a parasite that is site specific is expected to occupy a similar site in a closely related host (Krasnov *et al.* 2004), and related parasites are expected to occupy similar sites in closely related hosts. So far, the cestode assemblages of 3 species of *Mustelus* Link, 1790 have been studied, all harbour at least 2 species of *Calliobothrium* van Beneden, 1850 (Euzet 1959, Cislo and Caira 1993, present study). Three groups of species can be distinguished in this tapeworm genus: (1) species with large bodies and laciniate segments [e.g. *C. australis*, *C. verticillatum* (Rudolphi, 1819)], (2) species with small bodies, non-laciniate segments and having an accessory piece between the bases of axial hook (e.g. *C. lintoni* Euzet, 1954, *C. violae* Nasin, Caira et Euzet, 1997, *C. lunae*), and (3) species with small bodies, non-laciniate, lacking the accessory piece (e.g. *C. barbarae*, *C. eschrichti* van Beneden, 1850). Within the spiral intestine of the 3 species of *Mustelus*, the specimens of *Calliobothrium* belonging to the group 1 were distributed in the middle region; whereas, the specimens belonging to groups 2 and 3 were attached in the anterior chambers. This pattern concurs with the predictions of attachment sites for species of *Calliobothrium* made by Nasin *et al.* (1997).

Even if the cestode assemblages in *M. schmitti* are more similar to *M. canis* rather than *P. glauca*, both species of *Mustelus* sharing a conicospiral type of intestine, the cestode fauna of *M. schmitti* is more diverse in species that also belong to a wider range of cestode orders. *M. schmitti* hosts 6 species in 3 orders [Tetraphyllidea (Onchobothriidae and Phyllobothriidae), Trypanorhyncha and Diphyllidea], whereas *M. canis* harbours only 4 species in 2 orders [Tetraphyllidea (Onchobothriidae) and Trypanorhyncha]. It might be expected that *M. schmitti* consumes a greater diversity of food items, and therefore has a greater chance of acquiring a wider range of infective stages. However, this is not supported by the literature. Although both sharks particularly feed on zoobenthos, the diet of *M. canis* is composed by a greater diversity of crustaceans and molluscs than *M. schmitti* (Capitoli *et al.* 1995, Vianna *et al.* 2000).

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