

Gastrointestinal helminth community of loggerhead sea turtle *Caretta caretta* in the Adriatic Sea

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ABSTRACT: We analysed the intestinal helminth community of 70 loggerhead sea turtles *Caretta caretta* with a curved carapace length ranging from 25 to 85.4 cm, recovered dead in neritic foraging habitats in the Adriatic Sea in 1995 to 2004. The overall prevalence of infection was high (70.0%), with a mean abundance of 36.8 helminth parasites per turtle. Helminth fauna comprised 5 trematodes (*Calycodes anthos*, *Enodiotrema megachondrus*, *Orchidasma amphiorchis*, *Pachypsolus irroratus*, *Rhytidodes gelatinosus*) and 3 nematodes (*Sulcascaris sulcata*, *Anisakis* spp., *Hysterothylacium* sp.), with 6 taxa specific for marine turtles. In terms of infection intensity and parasite abundance, *O. amphiorchis* was the dominant species (mean intensity: 49.8; mean abundance: 12.8), followed by *R. gelatinosus* (30.5 and 8.3, respectively) and *P. irroratus* (23.5 and 7.0, respectively), while larval *Anisakis* spp. exhibited the highest prevalence (34.3%). The intensity of helminth infection ranged from 1 to 302 (mean: 52.6 ± 69.1) and was not correlated with the size of turtles; this relationship held for all species, except *R. gelatinosus* ($r_s = 0.556$, $p < 0.05$). In comparison to other marine habitats, the helminth community of Adriatic loggerheads is characterised by higher species diversity (Shannon-Wiener $H' = 1.58$) and evenness ($E = 0.76$), and lower dominance values (Berger-Parker $d = 0.35$), which can be attributed to the life history and feeding ecology of sea turtles in recruited neritic grounds and the diversity of their benthic prey.

KEY WORDS: Helminth parasites · Sea turtles · Trematodes · Nematodes · Diversity · Population health · Mediterranean

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INTRODUCTION

The loggerhead sea turtle *Caretta caretta* (Linnaeus, 1758) is an endangered, large, long-lived marine vertebrate with a worldwide distribution (IUCN 2009). This migratory species has a complex and plastic life history (Hawkes et al. 2006, McClellan &

Read 2007, Casale et al. 2008) characterised by 2 major ecological stages. During early development, loggerheads undergo an obligate epipelagic oceanic stage, when they feed on gelatinous pelagic animals. As they grow, they gradually shift to shallow neritic habitats and concentrate their diet on a variety of benthic prey (Bjorndal 1997, Bolten 2003, Casale et

al. 2008, Lazar et al. 2011a). Due to this highly opportunistic feeding strategy (Bjørndal 1997), coupled with a site fidelity for neritic foraging habitats (Lazar et al. 2004, Broderick et al. 2007, Casale et al. 2007) and long lifespan (Heppell et al. 2003), loggerheads are susceptible to infection with numerous trematodes and nematodes (Dodd 1988, George 1997) transmitted via intermediate hosts such as invertebrates and fish (Esch et al. 2002).

Interactions between the population biology of host and helminth parasites are of fundamental importance to the population dynamics of both the parasite and the infected host population (Anderson & May 1978). Generally, parasites that kill their hosts are less likely to be transmitted to other hosts and will remain at low prevalence, while parasites that have little effect on host mortality and demography will usually be more prevalent. Gastrointestinal helminths often exploit the food resources in the host's digestive tract, usually producing a limited immune response and little pathological impact. However, large numbers of parasites may reduce food intake and nutrient absorption, and induce nutritional stress of the host (Petkevičius 2007), thus affecting an individual's health, growth and reproductive output (Anderson & May 1978).

The shallow neritic zone of the Adriatic Sea, characterised by high macrofaunal density dominated by sedentary invertebrates (Vatova 1949, Zavodnik & Vidaković 1987, McKinney 2007), represents one of the largest and most important neritic feeding grounds for loggerhead sea turtles in the Mediterranean (Margaritoulis et al. 2003, Lazar et al. 2004, 2011a, Zbinden et al. 2008). The composition of helminth fauna in loggerheads from the western Adriatic shows a wide range of helminth prevalence (27.7 to 78.6%), likely attributable to small sample sizes ($n = 14$ to 18) in the studies done so far (Manfredi et al. 1998, Piccolo & Manfredi 2001, Scaravelli et al. 2005).

Due to the key role of Adriatic foraging habitats in the life history of Mediterranean loggerhead turtles and the possible effects of parasites on the demography of this endangered species, we quantitatively analysed the helminth community structure in the resident loggerhead population. We reviewed the preliminary data of Kučinić et al. (2008) for the eastern Adriatic and included them in the present study. We compared the component community structure of helminths in Adriatic loggerheads with those in other regions in the Mediterranean and in the adjacent area of the north-eastern Atlantic and analysed ecological factors which may determine community composition of gastrointestinal helminths in this sea turtle species.

MATERIALS AND METHODS

Sampling and species identification

Between 1995 and 2004, we collected 70 loggerhead sea turtles, with a mean notch–tip curved carapace length (CCL) of 45.0 ± 13.6 cm (CCL range: 25.0 to 85.4 cm). Since *Caretta caretta* is an endangered species, sampling of endoparasites was only conducted on turtles found dead following incidental capture by fisheries ($n = 55$, 78.6%) or dead stranded ($n = 12$, 17.1%) in the eastern Adriatic Sea (Croatia and Slovenia; Fig. 1). In the case of 3 turtles, the recovery method was unknown. Most of the loggerheads were recovered in the northern Adriatic ($n = 64$, 91.4%), while 6 carcasses (8.6%) were found in its central waters.

We performed general necropsies and isolated the digestive tracts (oesophagus, stomach and intestines). The contents were rinsed in clear water through a 1 mm mesh sieve and fixed in 4% buffered formaldehyde. We determined the sex of turtles by visual examination of gonads and accessory ducts during necropsies (Wynneken 2001). Out of 70 loggerheads, we identified 37 females and 25 males, while sex determination was impossible for 8 turtles due to tissue decomposition.

Parasites were isolated from the gut contents under a stereomicroscope and fixed in 70% ethanol. Trematodes were prepared for detailed morphological examination by staining in Semichon's acetocarmine, dehydration through an alcohol series,

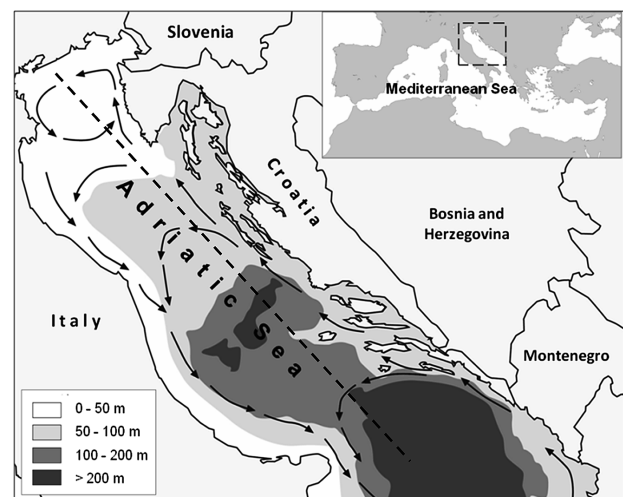


Fig. 1. Study area of the Adriatic Sea showing sea floor depth, direction of main surface currents (arrows) and division into the eastern and the western Adriatic basin (dotted line)

clearing in toluene and mounting in Canada balsam (Lasee & True 2004). Nematodes were examined under light microscopy at 20× and 100× magnifications, after preparation in glycerine jelly (Lasee & True 2004). Identification of parasites was carried out following Euzet et al. (1972), Blair & Limpus (1982), Manfredi et al. (1998), Bray (2005) and Blair (2005a,b).

Quantitative descriptors of parasite infection and statistical analysis

Parasite population structure was quantified through prevalence, mean intensity and mean abundance of each species (Margolis et al. 1982, Bush et al. 1997), calculated in the Quantitative Parasitology Program (QP 3.0; Reiczigel & Rózsa 2005). The 95% confidence intervals of prevalence were calculated by Sterne's exact method, while for the mean intensity and mean abundance, we applied bootstrapping with 2000 bootstrap replications (Reiczigel & Rózsa 2005). The degree of aggregation of parasites was expressed as the ratio of the variance to the mean.

We classified identified helminths either as specialists with a limited range of hosts, or as generalists exploiting more host species (Santoro et al. 2010a and references therein). In order to investigate the extent of infections in examined turtles, we arbitrarily divided animals into 2 categories based on the number of isolated parasites: turtles with light infection (<100 parasite specimens per turtle) and those with heavy infection (≥100 parasite specimens per turtle).

Differences in infection levels between sexes, seasons (warm season: May to October; cold season: November to April) and life stages of turtles were tested by permutational multivariate analysis of variance (PERMANOVA; Anderson 2005). For this, loggerheads were split into 2 ontogenetic groups: small juveniles (CCL < 40 cm; n = 30) undergoing the transitional oceanic-neritic life stage (Žiža et al. 2003, Lazar et al. 2008, Lazar & Žiža 2010), and neritic individuals (CCL > 40 cm; n = 40) which predominantly feed on the sea floor (Lazar 2009, Lazar et al. 2011a). However, because some factors did not bear a sufficient number of variables (e.g. particular season or life stages, where only 5 adults were sampled versus 65 juveniles), a 1-way design was applied to square root-transformed data and Euclidian distance to assess the combined effects of tested variables on parasite abundances. Influence of body size (CCL) on the abundance and the prevalence of parasites was

analysed by Spearman's rank correlation (Zar 1999). Statistical analyses were carried out with SPSS 17.0 (SPSS Inc.) and significance was assumed for values of $p < 0.05$.

Descriptors of parasite communities

We described the parasite infracommunity within a single host, and the component community within the host population (Bush et al. 1997, Poulin 1997) by:

(1) species richness (S), defined as the total number of helminth species;

(2) the Berger-Parker dominance index ($d = N_{\max} / N$, where N_{\max} is the number of individuals of the most abundant species, and N is the total number of individuals);

(3) the Shannon-Wiener index ($H' = -\sum p_i \ln p_i$, where p_i is the proportion of individuals in the i th species); and

(4) Pielou's evenness index (E), using species richness (S) ($E = H' / \log(S)$).

Formulas were calculated as described by Magurran (1988) using Primer Version 5 (Primer-E, Plymouth).

Furthermore, we compared the patterns of component community structure of helminths in loggerhead turtles from our study to those in other marine habitats in the Mediterranean and adjunct area of the Atlantic Ocean using the diversity indices described above (Shannon-Wiener index, Pielou's evenness index and Berger-Parker dominance index). As the calculation of indices requires comparable sample sizes (Wolda 1981), this was only done for 2 regions, western Mediterranean (Balearic Islands; n = 54; Aznar et al. 1998) and north-eastern Atlantic (Madeira Archipelago; n = 57; Valente et al. 2009), for which all the metadata for indices calculation were available.

RESULTS

The overall prevalence of helminth infection was 70.0% with 49 infected turtles. Parasitic communities comprised 8 helminth taxa: 5 digenetic trematodes and 3 nematodes (Table 1). We collected 2577 helminth specimens in total, with digenetic trematodes being dominant (71.4% of total helminth abundance). The mean intensity of infection was 52.6 helminths per host, while the observed mean abundance was 36.8 parasites per turtle. As to the host specificity, helminth fauna was composed of 6 taxa exclusive to marine turtles and 2 nematodes that

Table 1. *Caretta caretta*. Infection parameters of gastrointestinal helminth parasites in loggerhead sea turtles (n = 70) from the Adriatic Sea (CI: confidence interval; s: specialist for sea turtles; g: generalist)

Taxon/Species	No. of infected turtles	Prevalence (95% CI) (%)	Mean intensity (95% CI)	Mean abundance (95% CI)	Variance-to-mean ratio	Specificity to host	No. of parasites detected
Trematoda							
<i>Calycodes anthos</i> (Braun, 1899)	2	2.9 (0.8–8.6)	8.5 (2.0–8.5)	0.2 (0.0–1.0)	13.42	s	17
<i>Enodiotrema megachondrus</i> (Looss, 1901)	3	4.3 (1.2–11.9)	11.3 (11.0–11.7)	0.5 (0.0–1.1)	11.02	s	34
<i>Orchidasma amphiorchis</i> (Braun, 1899)	18	25.7 (16.3–37.1)	49.8 (27.6–84.3)	12.8 (6.4–25.4)	108.87	s	897
<i>Pachypsolus irroratus</i> (Rudolphi, 1819)	21	30.0 (20.0–42.1)	23.5 (12.4–49.4)	7.0 (3.4–15.7)	77.55	s	493
<i>Rhytidodes gelatinosus</i> (Rudolphi, 1819)	19	27.1 (17.7–38.6)	30.5 (13.8–79.1)	8.3 (3.2–23.4)	163.57	s	579
Trematoda sp.	1						2
Nematoda							
<i>Anisakis</i> spp.	24	34.3 (24.0–46.4)	15.3 (3.9–55.5)	5.2 (1.4–20.6)	174.75	g	366
<i>Hysterothylacium</i> sp.	2	2.9 (0.5–9.8)	1.5 (1.0–1.5)	0.04 (0.0–0.1)	1.65	g	3
<i>Sulcascaris sulcata</i> (Rudolphi, 1918)	14	20.0 (11.9–31.3)	13.3 (5.8–34.6)	2.7 (1.0–8.0)	58.54	s	186

occur in various hosts (Table 1). With the exception of larval-stage *Anisakis* spp., the parasites were only recorded in adult forms. The trematode *Orchidasma amphiorchis* was the most abundant species, with 897 individuals recorded in 18 turtles. If prevalence is considered, the dominant parasite was *Anisakis* spp., present in 24 infected turtles (prevalence: 34.3%), followed by *Pachypsolus irroratus* (prevalence: 30.0%). Our finding of genus *Hysterothylacium* is the first record of this parasite in loggerhead sea turtles. Two adult trematode specimens were damaged during isolation and could be identified only as Trematoda sp.

Since the variance-to-mean ratio of parasites per host was greater than 1 for all taxa, the endoparasitic community presented a distinctive overdispersed pattern of distribution, with *Anisakis* spp. and *Rhytidodes gelatinosus* displaying highly aggregated distributions (Table 1). Most of the infected turtles exhibited light infections (81.6%), with a mean of 15.9 ± 18.2 parasites per individual turtle, while 9 loggerheads (18.4%) were heavily infected (mean: 178.4 ± 73.1). The highest number of parasites was found in a loggerhead turtle of 63.0 cm CCL, which contained 302 specimens of *R. gelatinosus*. Turtles exhibiting heavy infections were infected with either 1 (n = 5) or 2 parasite species (n = 4). In the cases of heavy infection with 2 parasite species, 1 species was dominant with 75 to 90% abundance. The dominant species involved in multiple heavy infections were *Pachypsolus irroratus*, *Orchidasma amphiorchis* and *Anisakis* spp.

Helminth infections were present throughout all size classes of turtles analysed in our study, ranging from 25.0% in adults (>70 cm CCL) to 84.0% in small juveniles with 30 to 40 cm CCL (Fig. 2). The prevalences of the 3 most abundant species (*Orchidasma amphiorchis*, *Rhytidodes gelatinosus* and *Pachypsolus irroratus*) were not evenly distributed among host size classes, with *O. amphiorchis* showing a negative correlation with increasing host size ($r_s = -0.943$, $p < 0.01$; Fig. 3). Body size (CCL) and abundance of parasites was only significantly correlated for *R. gelatinosus* ($r_s = 0.556$, $p < 0.05$). There was a combined effect of life stage and sex ($p = 0.044$) on helminth abundance in individual turtles, with small juvenile males harbour-

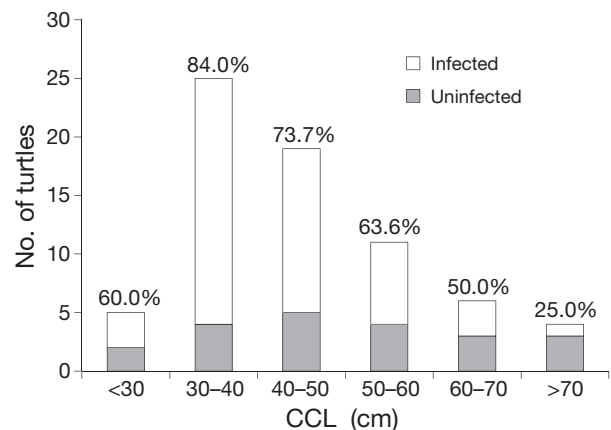


Fig. 2. *Caretta caretta*. Distribution of infected and uninfected loggerhead sea turtles against curved carapace length (CCL), with infection prevalences (%)

ing higher parasite abundances than small juvenile females (CCL < 40 cm). No such discrepancy between sexes was observed in neritic-stage loggerheads.

The community structure of helminth parasites revealed a high species diversity (Shannon-Wiener $H' = 1.58$) and low dominance values (Berger-Parker $d = 0.35$; Table 2). While species richness ranged from 1 to 5 in individual hosts, loggerheads were most frequently infected with only 1 (36.7%) or 2 species (30.6%). Parasite diversity was highest in 2 turtles (CCL = 36.6 and 58.6 cm) where we detected multiple infections with 5 helminth species, represented by a relatively small number of specimens (mean number of specimens per parasite species: 5.8 ± 4.4 and 8.2 ± 9.7 , respectively).

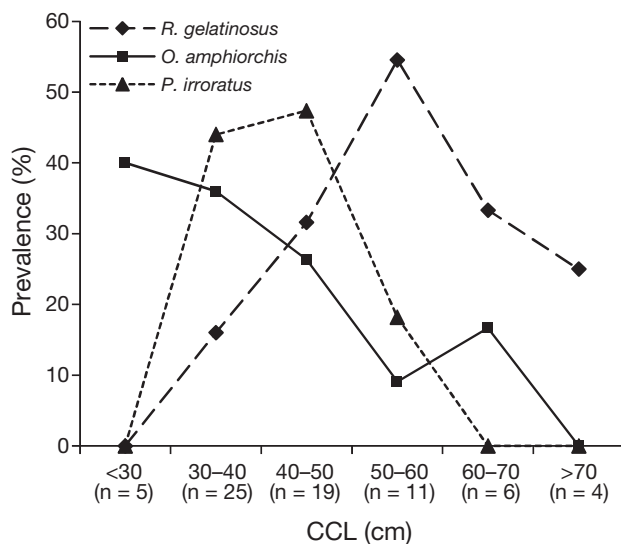


Fig. 3. *Caretta caretta*. Infection prevalence (%) of the 3 most dominant helminth parasites (*Rhytidodes gelatinosus*, *Orchidasma amphiorchis*, *Pachypsolus irroratus*) against loggerhead sea turtle curved carapace length (CCL)

The helminth communities reported from loggerhead turtles in different regions are summarised in Table 2. In comparison to examined loggerhead turtles from the western Mediterranean (Aznar et al. 1998), or the north-eastern Atlantic (Valente et al. 2009), the helminth community in the Adriatic Sea loggerhead turtles exhibited higher diversity ($H' = 1.58$), with *Orchidasma amphiorchis* as the dominant species. Diversity and evenness of parasite infracommunities were evidently lower in the western Mediterranean ($H' = 0.29$) and northeast Atlantic ($H' = 0.78$), with faunal composition characterised by a strong dominance of *Enodiotrema megachondrus*.

DISCUSSION

Composition and aggregation of helminth communities

The patterns of gastrointestinal helminth communities in wildlife populations are mostly influenced by host ranging patterns, host population density, intraspecific and interspecific contact rates, and diet (Hudson et al. 2002). Loggerhead sea turtles are large ectotherms which travel great distances and consume a wide range of prey species. As a consequence of phylogenetic barriers between sea turtles and other marine hosts, and since the loggerhead is the only abundant sea turtle species in the Mediterranean (Margaritoulis et al. 2003), helminth infracommunities exhibit a predictable composition mainly dominated by digenetic trematodes and nematodes (Aznar et al. 1998).

Although all recorded trematodes had already been identified as parasites of loggerhead sea turtles (Santoro et al. 2010a), details of the distribution of

Table 2. *Caretta caretta*. Comparison of helminth community structure of loggerhead sea turtles from 3 geographic regions. Data are given as available from the literature, or calculated from the source data. CCL = curved carapace length (cm); P: prevalence; S: species richness; H' : Shannon-Wiener diversity index; E : Pielou's evenness index; d : Berger-Parker dominance index

Locality	Turtles		Helminths							
	n	CCL range	P (%)	n	S	H'	E	d	Dominant	Most prevalent
Adriatic Sea ^a (Slovenia and Croatia)	70	25–85	70	2577	8	1.58	0.76	0.35	<i>Orchidasma amphiorchis</i>	<i>Anisakis</i> spp.
W Mediterranean ^b (Balearic Islands, Spain)	54	34–69	100	7098	5	0.29	0.18	0.93	<i>Enodiotrema megachondrus</i>	<i>Enodiotrema megachondrus</i>
NE Atlantic ^c (Madeira, Portugal)	57	15–61	45.6	143	8	0.78	0.38	0.76	<i>Enodiotrema megachondrus</i>	<i>Anisakis</i> spp.

^aPresent study; ^bAznar et al. (1998); ^cValente et al. (2009)

Table 3. *Caretta caretta*. Prevalence (%) of gastrointestinal helminth parasites of loggerhead sea turtles in the Mediterranean and north-east (NE) Atlantic. Only those species recorded with > 10% prevalence in at least 1 study are shown

Taxon/species	NE Atlantic		W Mediterranean			Central Mediterranean			E Mediterranean		
	Madeira, Portugal ^a (n = 57)	Balearic Is., Spain ^b (n = 54)	Valencia, Spain ^c (n = 44)	Calabria, Italy ^c (n = 12)	Sicily, Italy ^c (n = 22)	Sicily, Italy ^c (n = 18)	Campania, Italy ^c (n = 32)	Egypt ^d (n = 33)	Adriatic, Italy ^e (n = 18)	Adriatic, Italy ^f (n = 14)	Adriatic, Italy ^g (n = 14)
Trematoda/Digenea											
<i>Calycodes anthos</i>	1.8	46.3	45.5	58.3	50.0	44.4	28.1	12.1	14.3		2.9
<i>Diaschistorchis pandus</i>								12.1			
<i>Enodiotrema megachondrus</i>	24.6	96.3	79.5	75.0	90.9	66.7	25.0	3.0	21.4		4.3
<i>Enodiotrema</i> sp.										21.4	
<i>Hemiuroidea</i> sp.		27.8	15.9								
<i>Orchidasma amphiorchis</i>							25.0		21.4		25.7
<i>Pachypsolus irroratus</i>		5.6			4.5	5.6			14.3		30.0
<i>Plesiochorus cymbiformis</i>									14.3		
<i>Pleurogonius trigonocephalus</i>			4.5				9.4	30.0	28.6	14.3	
<i>Rhytidodes gelatinosus</i>	3.5	5.6	2.3		4.5	5.6	9.4	51.5	28.6	7.2	27.1
Nematoda											
<i>Anisakis</i> spp.	35.7										34.3
<i>Kathania leptura</i>			2.3				15.6	18.3		7.2	
<i>Sulcascaris sulcata</i>							25.0	24.2	71.4	21.4	20.0
Total number of helminth taxa	8	5	7	2	6	4	11	9	8	6	8

^aValente et al. (2009); ^bAznar et al. (1998); ^cSantoro et al. (2010a); ^dSey (1977); ^eScaravelli et al. (2005); ^fManfredi et al. (1998); ^gPiccolo & Manfredi (2001); ^hpresent study

developmental stages and life cycles in intermediate/paratenic and definitive hosts are largely unknown. Life cycles with pelagic intermediate hosts have only been proposed for *Enodiotrema megachondrus* and *Calycodes anthos* (Santoro et al. 2010a). In contrast to trematodes specific to marine turtles, 2 of the 3 identified nematodes are generalists (*Anisakis* spp. and *Hysterothylacium* sp.), infecting a variety of hosts. *Anisakis* spp. was the most prevalent parasite in the present study. It was only recorded in larval forms, which made species identification based upon morphological characteristics impossible. This genus contains a complex of sibling species which may be differentiated only by genetic analysis. Mitochondrial DNA sequencing of *Anisakis* spp. in loggerheads from the central and western Mediterranean (Santoro et al. 2010a) and the distribution of dominant species within this complex in the Mediterranean (Mattiucci & Nascetti 2006, Santoro et al. 2010b) and the Adriatic Sea (Petri et al. 2011) suggest that larvae from the present study most likely belong to *A. pegreffii*.

Larval-stage *Anisakis* are found in crustaceans, squid and fish, while adults parasitize the gastrointestinal tracts of marine mammals (Mattiucci & Nascetti 2006, 2008). Sea turtles are considered as accidental paratenic hosts harbouring larvae with no possibility for further development, and therefore represent ecological dead end hosts (Santoro et al. 2010a,b). With the exception of our study and that of Valente et al. (2009) in the north-eastern Atlantic, only low prevalences of *Anisakis* spp. have been recorded in loggerhead turtles (<10%; Table 3 and references therein). According to Valente et al. (2009), a high prevalence of *Anisakis* spp. larvae in loggerheads may be explained by a high abundance of their definitive hosts—marine mammals—in the area. Recent studies have shown high diversity and abundance of cetaceans in the Adriatic Sea, especially of bottlenose dolphins (Bearzi et al. 2009, Fortuna et al. 2010), which may explain the generally high abundance of *Anisakis* spp. in the region (Mladineo 2004, Mladineo et al. 2011) and, consequently, the high infection rates in loggerheads.

The low prevalence and low abundance of *Hysterothylacium* sp. found in our study (2.9% and 0.04%, respectively), and the complete absence of this genus in loggerheads from other localities, might indicate accidental infection. Infection with this parasite could occur through the inges-

tion of fish discarded from fishing vessels, since the adult stages of the species live in teleosts (Bruce et al. 1994, Torres et al. 1998).

The nematode *Sulcascaris sulcata* is a frequently recorded parasite of loggerhead sea turtles (Baylis 1923, Sey 1977, Sprent 1977, Manfredi et al. 1998, Piccolo & Manfredi 2001, Scaravelli et al. 2005, Santoro et al. 2010a). It has a life cycle modulated between benthic gastropods and bivalves as intermediate hosts and marine turtles as definitive hosts (Lichtenfels et al. 1978, Berry & Cannon 1981). As slow moving and sessile intermediate hosts cannot contribute to the large-scale dispersal of parasites (Thieltges et al. 2009), the distribution of *S. sulcata* is restricted to shallow coastal regions where these benthic molluscs are abundant. In the Mediterranean, the occurrence of *S. sulcata* in loggerheads seems to be limited to its eastern basin, while the species is absent in the western Mediterranean and north-eastern Atlantic populations, as well as in those from the larger part of the central Mediterranean (Table 3 and references therein).

A similar distribution pattern seems to be shared by *Rhytidodes gelatinosus*, which exhibits a low prevalence in loggerheads throughout the Mediterranean and north-eastern Atlantic, but has been frequently found in shallow regions along the northern African shelf (Egypt) and in the Adriatic Sea (Table 3).

Host ontogeny and helminth infections

The ontogeny and life history of a host have major influence on the species richness and abundance of its parasite communities (Santoro et al. 2010a). In loggerhead turtles, the duration of the developmental stages and the size at recruitment to the neritic zone differ between populations (Bjornedal et al. 2000, Limpus & Limpus 2003). Loggerheads in the Adriatic Sea, for example, exhibit an early ontogenetic habitat shift (CCL \geq 30 cm), when they start to feed primarily upon benthic invertebrates, such as benthic molluscs, cnidarians and crustaceans (Žiža et al. 2003, Lazar et al. 2008, 2011a). These small juveniles that occupy neritic habitats in the northern Adriatic still carry parasite loads from their oceanic habitats, but at the same time they start to be exposed to parasites from the benthic food webs. Our finding of *Enodiotrema megachondrus*, a species with pelagic intermediate hosts, only in small juvenile loggerheads (CCL ranging from 25.0 to 36.6 cm; $n = 3$) supports this

assumption. Moreover, the highest prevalence of helminth parasites was recorded in turtles with a CCL ranging from 30 to 40 cm (84.0%; Fig. 2), which were undergoing the transitional period from oceanic to neritic habitats. This suggests that the transitional oceanic–neritic period in the loggerhead's life history is associated with an elevated risk of helminth acquisition.

The helminth community structure of loggerhead turtles from the western Mediterranean and the north-eastern Atlantic are characterised by high Berger-Parker dominance indices for *Enodiotrema megachondrus* (0.93 and 0.76 respectively; Table 2). In Balearic waters, *E. megachondrus* was present in 96.3% of hosts (Aznar et al. 1998), while loggerheads from the Madeira Archipelago exhibited low prevalence (24.6%) of infections due to oligotrophic conditions in the vast oceanic zone, where intermediate hosts are dispersed and in low population densities (Valente et al. 2009). Although this sea turtle species may temporarily switch to bottom feeding in the vicinity of seamounts or around oceanic islands (Bolten 2003), both marine regions primarily constitute oceanic developmental habitats. For example, dietary analyses have emphasised pelagic tunicates and discarded fish from bycatch as the major prey of loggerheads in the western Mediterranean (Balearic Islands; Tomás et al. 2001). Similarly, studies in the north-eastern Atlantic (Azores) have shown an epipelagic behavioural pattern of juveniles, with 75% of the time spent in the top 5 m of the water column and 80% of dives to depths of only 2 to 5 m (Bolten 2003). This feeding strategy is reflected in the helminth parasite community, which is dominated by species with pelagic life cycles. In the Adriatic, parasites such as *E. megachondrus* and *Calycodes anthos* were present in loggerheads at low prevalence and were only found in small juvenile turtles. Our study area, however, included neritic feeding habitats (Lazar et al. 2004, 2011a), resulting in a markedly different composition of the helminth parasite community, which was characterised by a lower dominance value (Berger-Parker $d = 0.35$), a higher diversity (Shannon-Wiener $H' = 1.58$) and *Orchidasma amphiorchis* as the dominant species. Established differences between helminth communities of loggerheads in the oceanic and neritic zones confirm the importance of host ontogeny and diet in the structuring of gastrointestinal parasitic communities (Santoro et al. 2010a).

Most of the turtles analysed in the present study (>90%) were recovered from the shallow waters of

the northern Adriatic (<100 m depth; Fig. 1). In these waters, all turtles, regardless of size and sex, access the same food resources throughout the year. This should result in an even susceptibility to parasite infections and a lack of differences in infracommunity structure between sexes and seasons, as observed in other marine habitats of loggerheads in the Mediterranean (Santoro et al. 2010a). The sex-related differences which we found in parasite abundances in small juveniles ($p < 0.05$) can plausibly be attributed to the statistically small sample size of animals in this life stage, but might also be the result of a difference in movement patterns between oceanic males and females (Casale et al. 2002).

In conclusion, loggerhead turtles using the feeding habitats of the Adriatic Sea exhibited relatively high infection rates (70%) with intestinal helminths. The available helminth species, combined with the specific life history and broad diet of the host, are likely the main factors shaping parasite community composition and richness. Helminth populations in the Adriatic exhibited aggregated distribution, mostly causing light infections. However, anthropogenic drivers such as fisheries interactions and pollution may alter the dynamics of parasites and host (Kennedy & Watt 1994, Des Clers & Wootten 1990). High fishing effort and pollution have already been identified as major threats to resident loggerhead populations (Lazar & Tvrtković 1995, Casale et al. 2004, 2010, Storelli et al. 2007, Lazar & Gračan 2011, Lazar et al. 2011b). The potential influence of intestinal parasites on the demographics of host populations is therefore a factor of concern, particularly for small juvenile loggerheads in the Adriatic Sea.

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