Oecologia (2009) 161:759–769
DOI 10.1007/s00442-009-1410-1

COMMUNITY ECOLOGY - ORIGINAL PAPER

Determinants and consequences of interspecific body size variation in tetraphyllidean tapeworms

Haseeb Sajjad Randhawa · Robert Poulin

Received: 3 December 2008 / Accepted: 20 June 2009 / Published online: 10 July 2009

Abstract Tetraphyllidean cestodes are cosmopolitan, remarkably host specific, and form the most speciose and diverse group of helminths infecting elasmobranchs (sharks, skates and rays). They show substantial interspecific variation in a variety of morphological traits, including body size. Tetraphyllideans represent therefore, an ideal group in which to examine the relationship between parasite body size and abundance. The individual and combined effects of host size, environmental temperature, host habitat, host environment, host physiology, and host type (all likely correlates of parasite body size) on parasite length were assessed using general linear model analyses using data from 515 tetraphyllidean cestode species (182 species were included in analyses). The relationships between tetraphyllidean cestode length and intensity and abundance of infection were assessed using simple linear regression analyses. Due to the contrasting morphologies between shark and batoid hosts, and contrasting physiologies between sharks of the Lamnidae family and other sharks, analyses were repeated in different subsets based on host morphology and physiologies ("sharks" vs. batoids) to determine the influence of these variables on adult tetraphyllidean tapeworm body size. Results presented herein indicate that host body size, environmental temperature and host habitat are relatively important variables in models explaining interspecific variations in tetraphyllidean tapeworm length. In addition, a negative relationship between tetraphyllidean body size and intensity of infection was apparent. These results suggest that space constraints and ambient temperature, via their effects on metabolism and growth, determine adult tetraphyllidean cestode size. Consequently, a trade-off between size and numbers is possibly imposed by external forces influencing host size, hence limiting physical space or other resources available to the parasites.

Keywords Tetraphyllidea · Abundance · Body size · Depth · Latitude

Introduction

Body size is a fundamental property and characteristic of all living organisms that affects their mean density or abundance, in addition to all key life history parameters (Damuth 1981; Peters 1983). One particularly notable relationship that has emerged from a variety of studies is the relationship between body size and abundance: larger organisms are generally less abundant than smaller ones (Damuth 1981). This negative interspecific relationship between body size and abundance (or density) reveals a pattern that is remarkably consistent across a wide variety of plant (Enquist et al. 1998) and animal taxa (Damuth 1981, 1987; Blackburn and Gaston 1997; Carbone et al. 2007; Hausdorf 2007). Conversely, within many taxa, body size is positively associated with fecundity, i.e. larger organisms are generally more fecund than smaller ones. For example, fecundity is positively correlated with female body size in intestinal nematodes of mammals (Skorping et al. 1991). The pressures acting on the evolution of body

Communicated by Carla Caceres.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-009-1410-1) contains supplementary material, which is available to authorized users.

H. S. Randhawa (✉) · R. Poulin
Department of Zoology, University of Otago,
P.O. Box 56, Dunedin 9054, New Zealand
e-mail: haseeb.randhawa@otago.ac.nz

size and the consequences of achieving a given size are likely to be particularly severe for parasites. The nature and size of the host not only determine the resources available for parasite growth, but they also set the physical space constraints that restrict the maximum size attained by parasites, and consequently the maximum numbers that can be supported by one host.

Even though parasites outnumber free-living species (May 1992; Windsor 1998), the body of literature investigating the determinants and consequences of interspecific body size variation in parasites pales in comparison with that for free-living eukaryotes. In the few studies that have investigated the relationship between host body size (or mass) and size of parasites, the usual trend reported, although not universal, is that larger hosts harbour larger parasites (Morand et al. 1996; Poulin 1996a). From an evolutionary perspective, larger hosts may not impose the same selective constraints on parasite size as they provide larger habitats and a greater supply of resources than smaller hosts. Consequently, larger hosts can harbour a greater parasite biomass than smaller hosts (George-Nascimento et al. 2004). However, biomass depends on both parasite numbers and parasite size or mass; therefore, a plausible prediction would be that parasite intensity (mean number of worms per infected host) and abundance of infection (mean number of worms per host; sensu Bush et al. 1997) will be negatively correlated with parasite body size, i.e. large hosts provide sufficient space and resources to support many small parasites or a few large ones (see Poulin 2007). Furthermore, consistent with Bergmann's rule (as defined in Blackburn et al. 1999), in aquatic ectoparasitic taxa, such as copepods (Poulin 1995a), isopods (Poulin 1995b) and monogeneans (Poulin 1996b), latitude has been positively correlated with body size. Although not universal (see Poulin 1997), this latitudinal gradient in size is assumed to result from the effects of lower temperatures on metabolism, growth and lifespan. Consequently, one would predict that hosts at higher latitude should tend to be larger and harbour lower intensities of large-bodied parasites than hosts found in the tropics; in ectothermic hosts, both host body size and environmental temperature (roughly correlated with depth and latitude) could have separate effects on parasite body sizes.

Although it is well established that the size of tapeworms is inversely proportional to intensity of infection, i.e. "crowding effects" (Read 1951; Bush and Lotz 2000; Roberts 2000; Heins et al. 2002), studies relating to the effects of host size on the interspecific variation in parasite body size are lacking. To our knowledge, the effects of host size and environmental temperature on tapeworm body size have not been investigated. Tetraphyllidean tapeworms, in their definitive hosts, are an ideal group with which to investigate the effects of host body size and environmental temperature on parasite body size. Tetraphyllidean lengths vary by 3 orders of magnitude, from 1 mm to approximately 1 m (Caira and Reyda 2005). Moreover, nearly all elasmobranch species (sharks, skates and rays) examined to date for parasites harbour at least one species of these tapeworms (Caira et al. 2001); therefore, among the large and diverse set of hosts, size also varies significantly. Tetraphyllideans exhibit a high degree of host specificity (Caira and Jensen 2001; Caira and Reyda 2005); therefore, the size of a parasite species generally reflects its evolution in a single host species. Also, tetraphyllidean tapeworms include approximately 600 described species, parasitising almost exclusively the spiral intestine of elasmobranch fishes as adults (Caira and Reyda 2005); there is thus very little interspecific differences in microhabitat preferences within the host. Since the adults infect almost exclusively poikilotherms, they are likely to be affected by ambient temperature, which varies latitudinally and with depth. Little is known about the biology of tetraphyllideans and no complete tetraphyllidean life cycle has been described to date, although it is believed to include typically three hosts (Williams and Jones 1994), with elasmobranch hosts acquiring the worms by ingestion of infected intermediate hosts. Larval stages have been reported from both cetaceans (whales, dolphins and porpoises) and pinnipeds (seals and walruses) (Agusti et al. 2005a, b), teleost fishes (e.g. Wojciechowska 1990, 1993a, b; Williams and Jones 1994; Caira and Reyda 2005), chaetognaths (arrow worms) (Williams and Jones 1994), molluscs (Williams and Jones 1994; Pascual et al. 1995; Brickle et al. 2001; Caira and Reyda 2005), and a variety of arthropods, ctenophores, echinoderms, echiurans, and nemerteans (Caira and Reyda 2005).

The objectives of this study were to examine: (1) the influence of host body size (using length and weight as surrogates), environmental temperature (using depth and latitude as surrogates) and host habitat, environment and physiology on tetraphyllidean body size using general linear models (GLM); and (2) the relationship between tetraphyllidean body size and intensity or abundance of infection. The possible effect of number of proglottids (segment-like units making up the body of a tapeworm) per worm, on tetraphyllidean body size was also assessed. Furthermore, since sharks and batoids differ substantially in body form (Compagno 1999), analyses included this distinction and were repeated at both these host taxonomic levels in an attempt to control for host phylogenetic effects. Additionally, lamnid sharks (mackerel sharks, e.g. mako, porbeagle, salmon and great white sharks) differ physiologically from other elasmobranchs in that they are homeotherms (Carey and Teal 1969); therefore, analyses of the "shark" subset included physiology as an additional variable.

Materials and methods

Comprehensive dataset

Tetraphyllidean measurement data were compiled from original descriptions, or redescriptions, of adult worms available from the senior author's reprint collection (529 species) and completed using data available from the Global Cestode Database (42 species; Caira and Healy 2008; http://www.cestodedatabase.org) (see Electronic Supplementary Material S1). This extensive dataset therefore includes most tetraphyllidean species described up until November 2008. Except in cases where synonymies were well established or the validity of species was dealt with adequately in a taxonomic paper, no effort was made to deal with the issue of validity of species and therefore, several *species inquirenda* were included in the database. For each species, maximum length and surface area were used as estimates of body size. The latter was estimated by applying the formula for a rectangle ($L \times W$); where L and W represent maximum length and width of the parasite, respectively. Although tetraphyllidean width increases posteriorly (immature proglottids are narrower than mature or gravid ones), maximum width of the strobila is the value generally reported in species descriptions for width. Parasite volume would have been a more representative measure of an individual's biomass, but parasite thickness data were rarely available (<5% of species included herein). In addition to these parameters for body size, the maximum number of proglottids per worm was also recorded when available. The relationship between number of proglottids and worm length has not been investigated previously for this order of tapeworms. Since none of these measurement data (maxima for length, width, surface area, and number of proglottids) were normally distributed, they were log-transformed for analyses.

Several factors are likely to influence tetraphyllidean body size in elasmobranchs. A priori, we identified seven predictors: (1) host length, (2) host depth, (3) latitude, (4) host weight, (5) host habitat, (6) host environment, and (7) type of elasmobranchs ("shark" or batoid). In our analyses, depth and latitude are used as surrogates for environmental temperature, and host length and weight are used as surrogates for host size. Although host identity is generally reported in species descriptions, host size rarely is. Host identifications were compiled from the same sources as described above for tetraphyllideans. One of the aims of this paper is to determine whether tetraphyllidean size is positively correlated with habitat size, in this case, with size of the spiral intestine. There are no studies on the relationship between elasmobranch length or weight and size of the spiral intestine, though it is very likely to be strongly positive. For this reason, both length and weight data for each host species were obtained from FishBase (Froese and Pauly 2008; www.fishbase.org). The size of the spiral valve may be more accurately estimated using the size of the body cavity. This estimate was obtained by measuring the length of the host from the tip of its snout to the mid-point of the pelvic fins, from pictures available in FishBase or in Compagno et al. (2005); hereafter, "host length" refers to this measure. The rostrum was excluded from these measurements for representatives of the saw sharks (Pristiophoriformes) and sawfishes (Pristiformes). To be consistent with parasite data, only maxima for host lengths and weights were used. Both variables were log transformed in order to meet assumptions of normality. Secondly, latitude data corresponded to that of the type locality for each parasite, as compiled from sources described above. If coordinates did not accompany the type locality in the original description, they were obtained from Google Earth. Latitude data were transformed into decimal format and rounded to the nearest tenth of a degree. Since depth data are rarely reported in species descriptions, the typical depth ranges at which hosts live were obtained for each host species from FishBase and expressed as the mid-point of the depth range. The habitat and environment exploited by each host species, both categorical variables, were obtained from FishBase. Five types of habitats are exploited by elasmobranchs: bathydemersal, benthopelagic, demersal, pelagic, and reef associated. Elasmobranchs are adapted to: (1) freshwater, (2) brackish water, (3) marine; or a combination of the three types of environments.

Average intensity and abundance of infection for each parasite species were recorded, if available, to determine how they covary with parasite body size. Intensity and abundance data were taken from original descriptions, as mentioned above, or from published data on surveys available in the senior author's reprint collection (see Electronic Supplementary Material S1, S2). The precision of estimates of intensity and abundance of infection increases asymptotically with the number of hosts examined, generally reaching acceptable levels for sample sizes of 20 hosts or more (see Fig. 6.3 in Poulin 2007). Here, although surveys examining at least 20 host individuals would have been preferred, it is extremely unusual for several specimens of large species of sharks or rays to be captured and examined for cestodes. Thus, only those collated data obtained from fewer than six host individuals were excluded from this study. This provided an acceptable trade-off between representative samples of the host populations examined and the inclusion of sufficient observations for comparative purposes, at least for a preliminary analysis.

Relationships between parasite body size and predictor variables were assessed using GLM (normal distribution; identity link function). Of the six predictor variables included in analyses, four consisted of continuous (body length, host depth, type latitude of parasite, and host weight) and three of categorical (host habitat, environment and type of elasmobranch) variables for a total of 11 parameters. All possible main effects linear regression models were computed. Models were ranked according to their corrected Akaike information criterion (AIC_c) values. This value was obtained from the residual sum of squares for each model using the method outlined in Anderson (2008). The AIC_c differences (ΔAIC_c) and model weights (w_i) were computed to determine the relative importance and rank of each variable (see Anderson 2008). The latter approach provides insights into the importance of each variable, taking into account the possible multicollinearity between predictor variables and requires running all possible models so that each variable is of equal footing (Anderson 2008). When more than one model was supported, the multi-model inference approach was used (Burnham and Anderson 2002). Model-averaged parameter estimates were obtained by weighting parameters estimates according to model probabilities (see Anderson 2008). By averaging all models from our a priori set, "bad" models received a weight that tends towards zero, thus keeping model inclusion objective. The unconditional variances were obtained in order to calculate a 95% confidence interval for each variable, taking into account the sampling variance and the variance component for model selection uncertainty (Burnham and Anderson 2002; Anderson 2008). This approach provides an estimate of the "slope" for each parameter, independent from others present in the model (Anderson 2008). A priori, sets of potentially biologically significant second-degree interactions between predictor variables were selected and compared to models incorporating main effects included in the interaction. For instance, the relative importance of the interaction between predictor variables *A* and *B* was compared to the following models: (1) *A*, (2) *B*, (3) $A + B$, and (4) $A + B + (A \times B)$. The evidence ratios between the model including the interaction term and the "best" model from each set (based on AIC_c) was used to determine whether the inclusion of the interaction term improved the model significantly. Relationships between parasite body size and intensity and abundance were assessed using linear regression analyses.

Table 1 Summary of the top ten models for tetraphyllidean tapeworm body size based on corrected Akaike information criterion (AIC_c) values. Models are shown including the number of parameters (*K*), AIC_c differences (ΔAIC_c), and Akaike weights (w_i) of each model given the data

Model[a]	*K*	AIC_c	ΔAIC_c	w_i
Comprehensive dataset				
{2456}	6	−207.2905	0.0000	0.1079
{345}	5	−207.2445	0.0461	0.1055
{456}	5	−207.2235	0.0670	0.1044
{3456}	6	−206.8079	0.4826	0.0848
{245}	5	−206.2238	1.0667	0.0633
{2345}	6	−205.6154	1.6751	0.0467
{23456}	7	−205.3275	1.9630	0.0405
{1456}	6	−205.1501	2.1404	0.0370
{1345}	6	−205.0327	2.2578	0.0349
{12456}	7	−205.0226	2.2649	0.0348
"Sharks"				
{3}	3	−107.8760	0.0000	0.1489
{34}	4	−106.2387	1.6374	0.0657
{37}	4	−106.1875	1.6886	0.0640
{13}	4	−105.9796	1.8964	0.0577
{23}	4	−105.9512	1.9284	0.0569
{36}	4	−105.8451	2.0309	0.0539
{234}	5	−104.4581	3.4179	0.0270
{237}	5	−104.4509	3.4251	0.0269
{347}	5	−104.2349	3.6411	0.0241
{123}	5	−104.1597	3.7163	0.0232
Batoids				
{2456}	6	−104.1724	0.0000	0.0902
{345}	5	−103.2000	0.9724	0.0554
{456}	5	−103.0671	1.1054	0.0519
{3456}	6	−102.8903	1.2821	0.0475
{245}	5	−102.8009	1.3715	0.0454
{2345}	6	−102.5480	1.6244	0.0400
{23456}	7	−102.4860	1.6864	0.0388
{1456}	6	−102.0831	2.0893	0.0317
{1345}	6	−101.9884	2.1840	0.0303
{12456}	7	−101.9635	2.2089	0.0299

[a] Predictor variables: host length (*1*), host depth (*2*), latitude (type) (*3*), host weight (*4*), host habitat (*5*), host environment (*6*), host physiology (*7*)

Subsets

The comprehensive dataset was divided along host taxonomic boundaries ("sharks" vs. batoids) (Table 1) following the elasmobranch taxonomy proposed by Compagno (1999). Analyses of the "sharks" subset also included a "physiology" parameter to take into account the physiological differences between sharks of the family Lamnidae and other sharks. The analyses excluded one tetraphyllidean species infecting a member of the non-elasmobranch subclass Holocephalii (chimaeras). Unpaired *t*-tests were performed on tetraphyllidean length, and on each continuous predictor variable, to determine whether their means differed between "sharks" and batoids. Analyses were repeated for "sharks" and batoid subsets as described above.

Results

Complete dataset

Determinants of parasite body size

Data were obtained for 515 of 571 described tetraphyllidean species included in this study (see Electronic Supplementary Material S1). Data were unavailable from the other 56 species because either the descriptions did not include measurement information or the original sources could not be translated into English. Total body length varied from 1.4 mm to 1 m (mean = 57.6 mm), with the majority of species being smaller than 25 mm (Fig. 1). Tetraphyllidean length was strongly correlated with both width and surface area of parasites ($r = 0.837$; $P < 0.0001$; $n = 428$ and $r = 0.973$; $P < 0.0001$; $n = 427$, respectively); therefore, from this point onward, only relationships involving parasite length will be considered.

The maximum number of proglottids per worm ranged from three to 1,586 (mean = 143) with the majority possessing fewer than 60. Length of the parasite was strongly correlated with number of proglottids ($r = 0.881$; $P < 0.0001$; $n = 357$; Fig. 2); therefore, from this point onward, parasite length will be the only descriptor of parasite body size considered in analyses.

The GLM analyses included 182 species for which data were available for all predictor variables: (1) body length, (2) host depth, (3) type latitude of parasite, (4) host weight, (5) host habitat, (6) host environment, and (7) type of elasmobranch. The "best" model ($\text{AIC}_c = -207.29$) explaining interspecific variations in tetraphyllidean body size included host depth, host weight, host habitat, and host environment (Table 1). The ten "best" models all included host weight and habitat (Table 1). The relative importance of each variable identified both these factors as the most important (Table 2). Only model-averaged parameters of host weight and the pelagic and benthopelagic components of habitat had confidence intervals bounded away from zero (Table 2) indicating that host depth and host environment are pretending variables (noninformative variables that do not decrease the deviance when included in a model—see Anderson 2008). The only interaction to improve its sister model significantly was that between type latitude and type of elasmobranch (Table 3), indicating that type latitude is an important predictor variable of tetraphyllidean tapeworm body size in one group of elasmobranchs and not in the other.

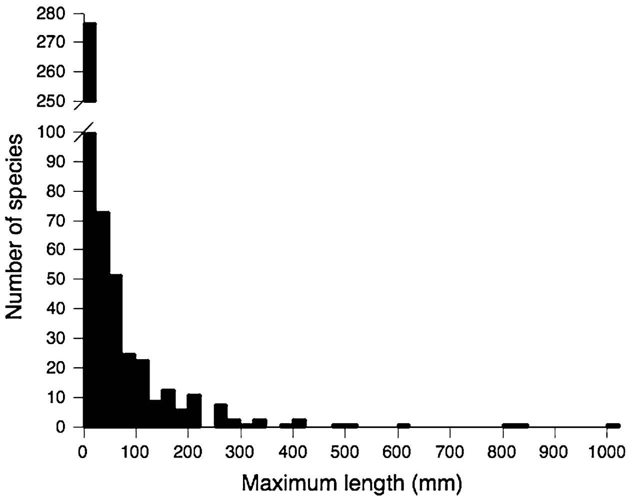

Fig. 1 Frequency distribution of maximum lengths for all species of tetraphyllidean cestodes included in this study ($n = 515$)

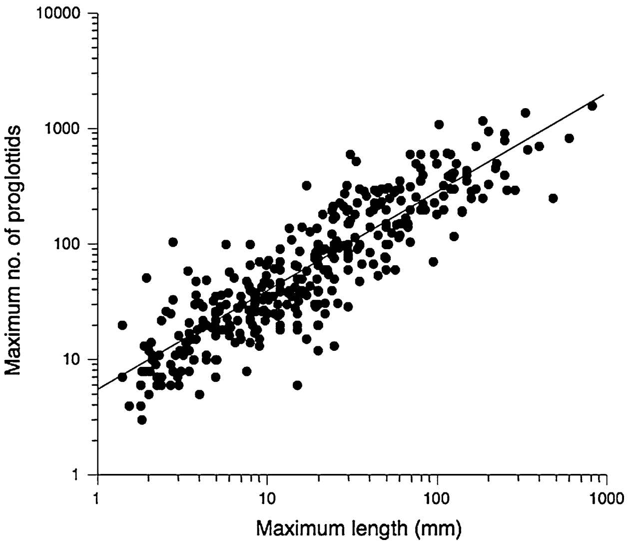

Fig. 2 Relationship between the maximum parasite length and the maximum number of proglottids per worm for species of tetraphyllidean cestodes included in this study for which these data were available ($n = 357$). The *line* represents the best-fit line from a simple linear regression. Log (max length) = [0.8899358 × log (max no. prog)] − 0.34245; $r = 0.88$; $P < 0.0001$. Note the logarithmic scale for both axes

Parasite size versus abundance/intensity

As expected, parasite intensity and abundance tended to decrease with increasing parasite length ($r = -0.276$; $P = 0.0433$; $n = 54$ and $r = -0.135$; $P = 0.3067$; $n = 59$, respectively) (Fig. 3), although only the former did so significantly.

Subset based on host taxonomy

Determinants of parasite body size

The dataset included species infecting chimaeras, unknown hosts, sharks, and batoids (1, 18, 182, and 371, respectively).

Table 2 Predictor variable relative importance weights [$w_+(i)$], ranks, weighted model average parameter estimates, and 95% confidence intervals. Parameter estimates in *bold* indicate those bounded away from zero. *BD* Bathydemersal; *BP* benthopelagic; *D* demersal; *P* pelagic; *B*, *M* brackish and marine; *F*, *B*, *M* freshwater + B + M

Comprehensive dataset				
Predictor variable	$w_+(i)$	Rank	Parameter estimate	Confidence interval
Host length	0.4153	6	0.1178	−0.1532 to 0.5091
Host depth	0.5011	4	0.0802	−0.0363 to 0.1968
Latitude (type)	0.4971	5	0.0019	−0.0009 to 0.0065
Host weight	0.8391	2	0.1716	**0.0408 to 0.3024**
Habitat (BD)	1.0000	1	0.3256	−0.0681 to 0.7193
Habitat (BP)	1.0000	1	0.3097	**0.0716 to 0.5477**
Habitat (D)	1.0000	1	−0.1467	−0.3245 to 0.0312
Habitat (P)	1.0000	1	−0.3531	**−0.6192 to −0.0870**
Environment (B, M)	0.5952	3	−0.0094	−0.1069 to 0.0881
Environment (F, B, M)	0.5952	3	−0.1003	−0.2652 to 0.0645
"Shark" or Batoid	0.2925	7	−0.0025	−0.0311 to 0.0262
"Sharks"				
Host length	0.3145	4	0.0540	−0.2498 to 0.3579
Host depth	0.2842	6	0.0282	−0.0771 to 0.1294
Latitude (type)	1.0000	1	0.0194	**0.0094 to 0.0295**
Host weight	0.3308	2	0.0055	−0.0836 to 0.0945
Habitat (BD)	0.2568	7	0.0394	−0.0702 to 0.1492
Habitat (BP)	0.2568	7	0.0631	−0.0250 to 0.1512
Habitat (D)	0.2568	7	0.0214	−0.0616 to 0.1043
Habitat (P)	0.2568	7	−0.0988	−0.2196 to 0.0220
Environment (B, M)	0.3275	3	−0.0290	−0.0881 to 0.0302
Environment (F, B, M)	0.3275	3	−0.0282	−0.1289 to 0.0726
Physiology	0.3008	5	0.0243	−0.0436 to 0.0921
Batoids				
Host length	0.6509	4	0.1427	−0.2051 to 0.4906
Host depth	1.0000	1	0.1966	−0.0226 to 0.4158
Latitude (type)	0.4538	5	−0.0008	−0.0041 to 0.0026
Host weight	0.8100	3	0.0847	−0.0288 to 0.1983
Habitat (BP)	0.8566	2	0.1790	**0.0799 to 0.2780**
Habitat (D)	0.8566	2	−0.1186	**−0.1790 to −0.0583**
Environment (B, M)	0.4068	6	−0.0678	−0.1718 to 0.0362
Environment (F, B, M)	0.4068	6	0.1121	−0.0999 to 0.3242

Only those infecting the latter two groups were included in analyses. Tetraphyllideans infecting sharks were significantly longer than those infecting batoids (70.3 and 51.4 mm, respectively; $t_{513} = 2.0013$; $P = 0.0459$). However, this difference disappears after correcting for the effects of host size, by incorporating the type of elasmobranch host as a predictor variable in our GLM analyses. As expected, shark hosts were significantly longer than batoid hosts (282.0 vs. 148.6 cm; respectively; $t_{377} = 8.0117$; $P < 0.0001$). Even though longer and infecting larger hosts, tetraphyllideans infecting sharks possessed fewer proglottids than those infecting batoids (121 vs. 152, respectively), albeit not significantly fewer ($t_{362} = 1.2930$; $P = 0.1968$). Shark hosts were found at significantly greater depths than batoid hosts (219.2 vs. 145.3 m; respectively; $t_{426} = 2.9403$; $P = 0.0035$). Type latitudes of tetraphyllidean tapeworms infecting shark hosts were not statistically different from those infecting batoid hosts (27.6 vs. 27.0, respectively; $t_{544} = 0.4727$; $P = 0.6366$).

The dataset included eight homeotherm (lamnid sharks) and 184 poikilotherm shark species, although only five and 75, respectively, were included in GLM analyses. Tetraphyllideans infecting lamnid sharks were not significantly smaller than those infecting other sharks (64.5 and 70.5 mm, respectively; $t_{168} = 0.1150$; $P = 0.9085$). Lamnid shark hosts were significantly longer and heavier than other shark hosts (571.6 vs. 268.7 cm; respectively; $t_{180} = 4.2097$; $P < 0.0001$ and 1842.6 vs. 339.3 kg; respectively,

Table 3 Summary of the interactions between predictor variables that significantly improved the main effects models. Models are shown including their AIC$_c$, w_i and evidence ratio (ER). *Lat* Latitude (type), *S/B* "shark" or batoid; for other abbreviations, see Table 1

Interaction	Model	AIC$_c$	w_i	ER
Complete dataset Lat × S/B	Lat	−194.0067	0.0147	66.3037
	S/B	−189.5570	0.0016	613.4360
	Lat + S/B	−193.2143	0.0099	98.5379
	Lat + S/B + (Lat × S/B)	−202.3952	0.9738	1.0000

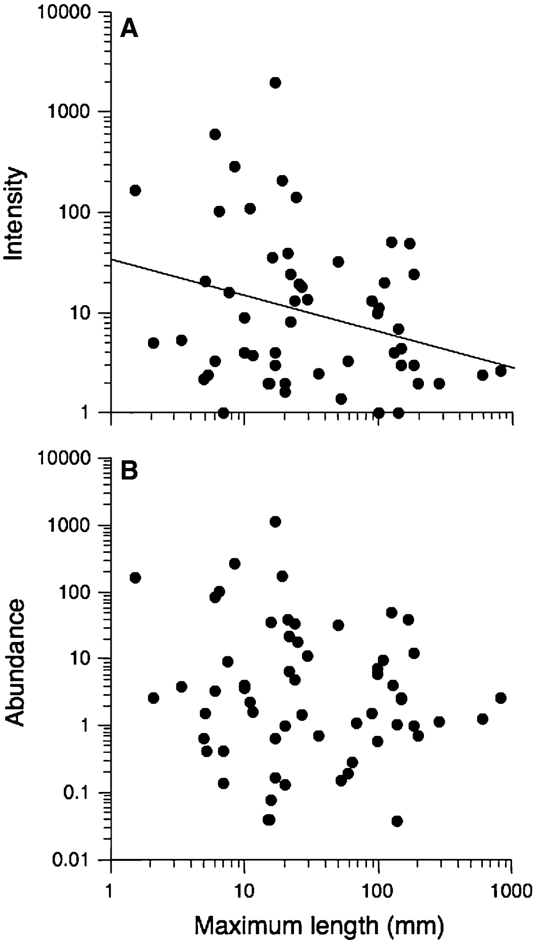

Fig. 3 Relationship between maximum parasite length and **a** intensity of infection ($n = 54$), and **b** parasite abundance ($n = 59$), for all tetraphyllidean species with a minimum of six hosts examined. The *line* represents the best-fit line for a simple linear regression. Note the logarithmic scale for both axes

$t_{91} = 4.7950$; $P < 0.0001$). Also, lamnid shark hosts were found at significantly greater depths and latitudes than other shark hosts (496.3 vs. 204.8 m; respectively; $t_{161} = 2.9062$; $P = 0.0042$ for depth and 42.1 vs. 27.1, respectively; $t_{180} = 2.8629$; $P = 0.0047$ for latitude).

The GLM analyses included 80 "shark" and 102 batoid species for which data were available for all predictor variables. The "best" "sharks" model (AIC$_c = -107.88$) included the single variable: latitude (Table 1). The same parameter was also included in all ten "best" models (Table 1). The relative importance of each variable identified latitude as the most important and the only one with a confidence interval bounded away from zero (Table 2). All other variables seem to act as pretending variables. The "best" batoid model (AIC$_c = -104.17$) included host depth, host weight, host habitat, and host environment (Table 1). No single variable was included in all ten "best" models, although host depth and habitat were considered the most important in relation to other variables. Only the benthopelagic and demersal parameters of the host habitat variable had a confidence interval bound away from zero (Table 2). Even though the isolated influence of this predictor variable on tetraphyllidean tapeworm body size is relatively small (2 mm or nearly 4%), it is nonetheless significant. Furthermore, consistent with results including models with interactions from the comprehensive dataset, latitude was identified as an important determinant for only one group of elasmobranchs, "sharks".

Parasite size versus abundance/intensity

Neither of the relationships between parasite abundance or intensity and parasite length for shark or batoid hosts ($n = 17$ and 15; $n = 41$ and 38, respectively) was statistically significant, most likely because of the few species that could be included in these analyses.

Discussion

Overall, our results highlight some of the forces that may have shaped the evolution of body sizes in tetraphyllidean cestodes. First, we found that host weight (proxy for size), and habitat are the key variables identified by our models; the former generally correlates positively with parasite body size, suggesting that space constraints and factors associated with host habitat have both acted to determine cestode adult sizes. Second, we found evidence that larger tetraphyllidean species tend to occur at lower intensities of infection, possibly because of the trade-off between size and numbers imposed by limited space or other resources.

Ultimately, an endoparasite's maximum size is limited by the physical size of the organ it exploits within a host individual. Therefore, larger elasmobranchs should provide larger habitats and greater availability of resources to tetraphyllidean cestodes than smaller ones. Results reported here indicate that parasite length is positively correlated with elasmobranch host weight. However, upon dividing the dataset along phylogenetic boundaries, host weight is a relatively important variable in batoid models, but not in "sharks".

Members of the shark family Lamnidae (mackerel sharks, e.g. mako, porbeagle, great white sharks) are capable of increasing body core temperatures by up to 20°C (Bernal et al. 2005), thus also increasing peristaltic movement and reducing digestion times (see Holmgren and Nilsson 1999). This leads to increases in food intake. Although larger than other sharks (571.6 cm and 1,842.6 kg vs. 268.7 cm and vs. 339.3 kg, respectively), they harbour smaller adult tetraphyllideans (64.5 vs. 70.5 mm, respectively). Increases in peristaltic movement and food intake may favour the establishment of smaller parasites, as larger ones are more likely to become detached as a result of the increased rate of passage of food through the digestive tract. Moreover, increases in food intake by members of this shark order could result in an increased acquisition of tetraphyllideans by their final hosts, hence resulting in the regulation of parasite biomass by density-dependent factors, thus enhancing intra- and inter-specific competition for resources and space, i.e. "crowding" (Read 1951; Roberts 2000).

Body size can follow a latitudinal gradient in both free-living and parasitic organisms, regardless of physiology, i.e. poikilotherm or homeotherm (Blackburn et al. 1999, and references therein). Studies investigating the effects of latitude on parasite body size have found a positive correlation in ectoparasites (Poulin 1995a, b, 1996b) and no effects of latitude on parasite body size in endoparasites (Poulin 1997). Our data show a strong correlation between tetraphyllidean cestode length and factors associated with environmental temperature in both shark and batoid hosts. Overall, tetraphyllidean body size is correlated with latitude in sharks and with depth in batoids, although their effect sizes vary. For instance, when the effects of latitude and depth are isolated for "sharks" and batoids, respectively, a shark at the equator will harbour tetraphyllidean tapeworms that are 6.5 mm (nearly 10%) shorter than those infecting sharks at a latitude of 45 degree, whereas tetraphyllideans infecting batoids at depths of 40 m (average depth of batoid hosts associated with reef habitats) will be 1.6 mm (approximately 3%) shorter than those infecting batoid hosts at a depth of 750 m (average depth of batoid hosts associated with bathydemersal habitats). It is possible that both these variables influence tetraphyllidean body size in both types of hosts. Unfortunately, the median latitude of individual tetraphyllidean species is not known. Furthermore, in the absence of specific information on tetraphyllidean transmission and preferred position in the water column, host depth is used herein as a proxy for environmental temperature to which the parasite is likely to be exposed. Shark body size is correlated with depth whereas body size of tetraphyllidean tapeworms infecting these sharks is correlated with latitude. Although certain groups of sharks occupy benthic habitats (e.g. angel sharks, carpet sharks and horn sharks), the majority of sharks feed in the water column. Assuming that intermediate host size varies along a temperature gradient and that size is a limiting factor to larval tapeworm growth, it may be that intermediate hosts preyed upon by sharks are found closer to the surface and therefore, vary in size according to a latitudinal gradient, not a depth gradient. Batoid body size is correlated with both depth and latitude, whereas body size of tetraphyllidean tapeworms infecting these batoids is influenced by depth only (relative importance of depth and latitude = 1 and 0.45, respectively; see Table 2). Batoids have evolved a dorso-ventrally flattened morphology adapted for living on, or near, the substrate and they specialise in feeding on prey biota associated with benthic habitats (Wilga et al. 2007). Most batoids have a relatively varied diet, feeding on a relatively greater diversity of prey associated with this habitat than others, whereas benthopelagic batoids seem to specialise on molluscs, especially cephalopods, and teleost fishes (FishBase). Unfortunately, the lack of data on feeding habit of specific elasmobranch species prevented us from adding a diet parameter to our GLM analyses. Although diet is likely to be correlated with habitat, it may be an influential variable on tetraphyllidean body size.

Except those infecting lamnid sharks, tetraphyllideans infect poikilotherms, thus are exposed to ambient temperatures. The number of homeotherm shark species ($n = 5$) was low and contributed to increasing the variance in our GLM analyses, which revealed no important influence of shark physiology on tetraphyllidean body size, However, the relationship between parasite length and depth in the shark family Lamnidae is opposite to that observed for other sharks ($r = -0.712$; $P = 0.0729$; $n = 7$ and $r = 0.351$; $P < 0.0001$; $n = 136$, respectively), whereas parasite length and latitude are positively correlated for both these groups, although only significantly so in non-lamnid sharks. Lamnid sharks have the capability to increase their body temperature in the gut region by as much as 20°C above ambient water temperature (Bernal et al. 2005). Therefore, they provide conditions for parasites more akin to those found in shallower waters or at lower latitudes, which may explain why these large sharks harbour relatively small tetraphyllidean tapeworms. Thus, even if lamnid sharks are found generally at greater depths and latitudes than other sharks, they are not infected with larger tetraphyllidean tapeworms.

Although depth and/or latitude does have an effect on parasite size, differences in vagility between different species of elasmobranch fishes (see Kohler et al. 1998) could mean that the type latitudes or depths used in this study do not adequately reflect the median range for the hosts. Shark vagility is positively correlated with body size and is affected by habitat (Musick et al. 2004). Type of habitat, particularly benthopelagic and pelagic, did influence parasite body size parameters overall and in batoids. To our knowledge, there are no large-scale data available on batoid vagility in the literature for comparison with that of sharks.

A given resource supply can only support a certain biomass, which is partitioned among many small or a few large individuals; this should result in a negative interspecific relationship between body size and abundance (Damuth 1981; Brown 1995). In parasite communities, patterns of abundance do not necessarily mirror those of free-living taxa. In nematodes parasitising mammals, the relationship between intensity of infection, a measure of parasite density within each infected host, and parasite body size is consistent with that observed in free-living taxa (Arneberg et al. 1998). However, those reported for other groups of parasites sometimes reveal a positive relationship between body size and abundance (Poulin 1999; Poulin and Justine 2008). The results of this study suggest that among tetraphyllidean cestodes parasitising elasmobranch fishes, parasite length is negatively correlated with intensity of infection (Fig. 3). These results are consistent with trends for other endoparasite groups (acanthocephalans and digeneans) of fish (Poulin 1999). Increases in fecundity are widely associated with larger body size in parasitic animals (Skorping et al. 1991; Poulin 1997, 2007). From an evolutionary perspective, if there are advantages to growing larger, i.e. increased fecundity, why is there a 3 orders of magnitude difference between the smallest and largest tetraphyllidean cestodes? Smaller parasites may be less affected by density-dependent factors; therefore, they may accumulate over time in their host and reach greater intensities of infection (Poulin 1999). As mentioned above, the maximum size attained by adult tetraphyllidean tapeworms may be evolutionarily constrained by the size of its intermediate host. The "crowding effect" in the intermediate host could limit larval growth (Heins et al. 2002), proportionally to the size of that host. It must also be pointed out that within elasmobranch species, larger host individuals generally harbour more individual cestodes than small ones (Friggens and Brown 2005), consistent with the "crowding effect" (Read 1951; Bush and Lotz 2000; Roberts 2000). If this pattern extends among host species, then larger host species harbouring larger worms could also accommodate more individual worms of any given size, another factor that could weaken the link between body size and abundance or intensity in tetraphyllidean cestodes.

Parasite abundance is generally obtained for a single parasite species. However, host individuals are often infected with more than one parasite species; therefore, the parasite biomass per host individual can be affected by both parasite abundance and richness (or diversity). Although larger hosts can support a greater biomass of parasites, biomass is not necessarily correlated with species richness (see Poulin 2007). However, for many groups of marine parasites, species richness is negatively correlated with latitude, i.e. species richness is greater in the tropics (Poulin and Rohde 1997; Rohde and Heap 1998; Rohde 2005). This trend is observed in both ectoparasites and endoparasites of fishes (Rohde 2002), although the relative species richness, defined as the number of parasite species per host species, is correlated with latitude only in ectoparasites (see Rohde 2005). The relative species richness of tetraphyllidean cestodes was not considered in this study, but based on the assumption that the relative species richness of parasites is unaffected by latitude (Rohde 2005), we would not expect to uncover a trend. However, since batoid hosts generally harbour more diverse tetraphyllidean assemblages than shark hosts (Caira and Reyda 2005), the effects of latitude on relative species richness for this cestode order need to be investigated further. Additionally, the effects of host depth range had no effect on parasite species richness in marine fish (Luque and Poulin 2004) and marine chondrichthyans (Luque and Poulin 2008). The effects of depth on relative species richness of this cestode order need to be investigated further.

In summary, host body weight, host depth, latitude, and host habitat are variables influencing the parasite body size in tetraphyllidean cestodes infecting elasmobranchs with latitude being the only important factor in sharks and host depth and habitat the most important in batoids. Consistent with trends observed in various plant and animal taxa, tetraphyllidean parasite body size is negatively correlated with intensity of infection, the equivalent of density for parasites. These results indicate that body size in these cestodes may be largely determined by ambient temperature, and that in turn body size constrains to some extent the number of conspecific parasites that can coexist within the same host individual. Ambient temperature shaping parasite body size may thus indirectly impact the population biology of parasites.

Acknowledgments The diligence of two anonymous reviewers is gratefully acknowledged and contributed to improving this manuscript. We thank David R. Anderson for advice regarding our analyses, Tommy Leung for translation of papers from Chinese to English and members of the Evolutionary and Ecological Parasitology Research Group at the University of Otago for useful comments on a previous version of this manuscript. Financial support from the New Brunswick Museum, through the Florence M. Christie Research Fellowship in Zoology to H. S. R., is gratefully acknowledged.

References

Agusti C, Aznar FJ, Raga JA (2005a) Tetraphyllidean plerocercoids from western Mediterranean cetaceans and other marine mammals around the world: a comprehensive morphological analysis. J Parasitol. doi:10.1645/GE-372R

Agusti C, Aznar FJ, Olson PD, Littlewood DTJ, Kostadinova A, Raga JA (2005b) Morphological and molecular characterization of tetraphyllidean merocercoids (Platyhelminthes: Cestoda) of striped dolphins (*Stenella coeruleoalba*) from the west Mediterranean. Parasitology. doi:10.1017/S0031182004006754

Anderson DR (2008) Model based inference in the life sciences: a primer on evidence. Springer, New York

Arneberg P, Skorping A, Read AF (1998) Parasite abundance, body size, life histories, and the energetic equivalence rule. Am Nat. doi: 10.1086/286136

Bernal D, Donley JM, Shadwick RE, Syme DA (2005) Mamma-like muscle powered swimming in a cold-water shark. Nature. doi: 10.1038/nature04007

Blackburn TM, Gaston KJ (1997) A critical assessment of the form of the interspecific relationship between abundance and body size in animals. J Anim Ecol 66:233–249

Blackburn TM, Gaston KJ, Loder N (1999) Geographic gradients in body size: a clarification of Bergmann's rule. Divers Distrib. doi:10.1046/j.1472-4642.1999.00046.x

Brickle P, Olson PD, Littlewood DTJ, Bishop A, Arkhipkin AI (2001) Parasites of *Loligo gahi*, with a phylogenetically based identification of their cestode larvae. Can J Zool. doi:10.1139/cjz-79-12-2289

Brown JH (2005) Macroecology. University of Chicago Press, Chicago

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York

Bush AO, Lotz JM (2000) The ecology of "crowding". J Parasitol. doi:10.1645/0022-3395(2000)086[0212:TEOC]2.0.CO;2

Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. J Parasitol 83:575–583

Caira JN, Jensen K (2001) An investigation of the co-evolutionary relationships between onchobothriid tapeworms and their elasmobranch hosts. Int J Parasitol. doi:10.1016/S0020-7519(01)00206-5

Caira JN, Reyda F (2005) Eucestoda (true tapeworms). In: Rohde K (ed) Marine parasitology. CSIRO, Collingwood, pp 92–104

Caira JN, Healy CJ (2008) Order Tetraphyllidea Carus, 1863. In: Caira JN, Jensen K, Healy CJ (eds) The global cestode database (online). www.cestodedatabase.org. Accessed April 2008

Caira JN, Jensen K, Healy CJ (2001) Interrelationships among tetraphyllidean and lecanicephalidean cestodes. In: Littlewood T, Bray RA (eds) Interrelationships of the Platyhelminthes. Taylor and Francis, London, pp 135–158

Carbone C, Rowcliffe JM, Cowlishaw G, Isaac NJB (2007) The scaling of abundance in consumers and their resources: implications for the energy equivalence rule. Am Nat. doi:10.1086/519858

Carey FG, Teal JM (1969) Mako and porbeagle: warm-bodied sharks. Comp Biochem Physiol 28:199–204

Compagno LJV (1999) Systematics and body forms. In: Hamlett WC (ed) Sharks, skates, and rays: the biology of elasmobranch fishes. John Hopkins University Press, Baltimore, pp 1–42

Compagno LJV, Dando M, Fowler S (2005) Sharks of the world. Princeton University Press, Princeton

Damuth J (1981) Population density and body size in mammals. Nature. doi:10.1038/290699a0

Damuth J (1987) Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy-use. Biol J Linn Soc. doi:10.1111/j.1095-8312.1987.tb01990.x

Enquist BJ, Brown JH, West GB (1998) Allometric scaling of plant energetics and population density. Nature. doi:10.1038/25977

Friggens MM, Brown JH (2005) Niche partitioning in the cestode communities of two elasmobranchs. Oikos. doi:10.1111/j.0030-1299.2005.13275.x

Froese R, Pauly D (eds) (2008) Fishbase. World Wide Web electronic publication. www.fishbase.org. version (04/2008)

George-Nascimento M, Munoz G, Marquet PA, Poulin R (2004) Testing the energetic equivalence rule with helminth endoparasites of vertebrates. Ecol Lett. doi:10.1111/j.1461-0248.2004.00609.x

Hausdorf B (2007) The interspecific relationship between abundance and body size in central European land snail assemblages. Basic Appl Ecol. doi:10.1016/j.baae.2006.03.005

Heins DC, Baker JA, Martin HC (2002) The "crowding effect" in the cestode *Schistocephalus solidus*: density-dependent effects on plerocercoid size and infectivity. J Parasitol. doi:10.1645/0022-3395(2002)088[0302:TCEITC]2.0.CO;2

Holmgren S, Nilsson S (1999) Digestive system. In: Hamlett WC (ed) Sharks, skates, and rays: the biology of elasmobranch fishes. John Hopkins University Press, Baltimore, pp 144–173

Kohler NE, Casey JG, Turner PA (1998) NMFS cooperative shark tagging program, 1962–93: an atlas of shark tag and recapture data. Mar Fish Rev 60(2):1–87

Luque JL, Poulin R (2004) Use of fish as intermediate hosts by metazoan parasites: a comparative analysis. Acta Parasitol 49:353–361

Luque JL, Poulin R (2008) Linking ecology with parasite diversity in Neotropical fishes. J Fish Biol. doi:10.1111/j.1095-8649.2007.01695.x

May RM (1992) How many species inhabit the Earth? Sci Am 267:42–48

Morand S, Legendre P, Gardner SL, Hugot J-P (1996) Body size evolution of oxyurid (Nematoda) parasites: the role of hosts. Oecologia 107:274–282

Musick JA, Harbin MM, Compagno LJV (2004) Historical zoogeography of the Selachii. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC, Boca Raton, pp 33–78

Pascual S, Resero M, Adrias C, Guerra A (1995) Helminth fauna of the short finned squid *Ilex coindetti* (Cephalopoda: Ommastrephidae) off NW Spain. Dis Aquat Organ. doi:10.3354/dao023071

Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge

Poulin R (1995a) Clutch size and egg size in free-living and parasitic copepods: a comparative analysis. Evolution 49:325–336

Poulin R (1995b) Evolutionary influences on body size in free-living and parasitic isopods. Biol J Linn Soc. doi:10.1111/j.1095-8312.1995.tb01035.x

Poulin R (1996a) The evolution of life history strategies in parasitic animals. Adv Parasitol 37:107–134

Poulin R (1996b) The evolution of body size in the Monogenea: the role of host size and latitude. Can J Zool 74:726–732

Poulin R (1997) Egg production in adult rematodes: adaptation or constraint? Parasitology. doi:10.1017/S0031182096008372

Poulin R (1999) Body size vs abundance among parasite species: positive relationships? Ecography. doi:10.1111/j.1600-0587.1999.tb00499.x

Poulin R (2007) Evolutionary ecology of parasites. Princeton University Press, Princeton

Poulin R, Justine J-L (2008) Linking species abundance distribution and body size in monogenean communities. Parasitol Res. doi:10.1007/s00436-008-0953-0

Poulin R, Rohde K (1997) Comparing the richness of metazoan ectoparasite communities of marine fishes: controlling for host phylogeny. Oecologia. doi:10.1007/s004420050160

Read CP (1951) The "crowding effect" in tapeworm infections. J Parasitol. doi:10.1645/0022-3395(2000)086[0206:TCEITI]2.0.CO;2

Roberts LS (2000) The crowding effect revisited. J Parasitol. doi:10.1645/0022-3395(2000)086[0209:TCER]2.0.CO;2

Rohde K (2002) Ecology and biogeography of marine parasites. Adv Mar Biol. doi:10.1016/S0065-2881(02)43002-7

Rohde K (2005) Latitudinal, longitudinal and depth gradients. In: Rohde K (ed) Marine parasitology. CSIRO, Collingwood, pp 348–351

Rohde K, Heap M (1998) Latitudinal differences in species and community richness and in community structure of metazoan ecto- and endoparasites of marine teleost fish. Int J Parasitol. doi:10.1016/S0020-7519(97)00209-9

Skorping A, Read AF, Keymer AE (1991) Life history covariation in intestinal nematodes in mammals. Oikos 60:365–372

Wilga CD, Motta PJ, Sanford CP (2007) Evolution and ecology of feeding in elasmobranchs. Integr Comp Biol. doi:10.1093/icb/icm029

Williams HH, Jones A (1994) Parasitic worms of fish. Taylor and Francis, London

Windsor DA (1998) Most of the species on Earth are parasites. Int J Parasitol. doi:10.1016/S0020-7519(98)00153-2

Wojciechowska A (1990) *Onchobothrium antarcticum* sp. n. (Tetraphyllidea) from *Bathyraja eatonii* (Günther, 1876) and a plerocercoid from *Notothenioidea* (South Shetlands, Antarctic). Acta Parasitol 35:113–117

Wojciechowska A (1993a) The tetraphyllidean and tetrabothiid cercoids from Antarctic bony fishes. I. Morphology. Identification with adult forms. Acta Parasitol 38:15–22

Wojciechowska A (1993b) The tetraphyllidean and tetrabothiid cercoids from Antarctic bony fishes. II. Occurrence of cercoids in various fish species. Acta Parasitol 38:113–118