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Host specificity of adult versus larval cestodes of the elasmobranch tapeworm order Trypanorhyncha

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Abstract

Host specificity between the adult and final larval stages (plerocercus, plerocercoid, or merocercoid) of a diversity of trypanorhynch species was compared using the host specificity index (HS_s). Index values were generated for a total of 63 species representing all five trypanorhynch superfamilies and 11 families. Host specificity of both adults and final larvae was found to be widely variable among species, ranging from very high (oioxenous) to very low (euryxenous) for both stages. However, in general, host specificity was highest for the adult stage in the definitive host (mean $HS_s = 3.86$) and lowest for the final larval stage in the second intermediate host (mean $HS_s = 6.29$). This difference was found to be significant using the Wilcoxon signed-rank test. Limited data available for procercoids in the first intermediate host suggest that this stage exhibits a degree of specificity intermediate between that of the former two stages (mean $HS_s = 4.23$). No taxonomic trend was seen. Species with a plerocercoid final larval stage (mean $HS_s = 8.62$) were significantly less host-specific than those with plerocerci or merocercoids (mean $HS_s = 5.56$). This result may reflect the use of paratenic hosts by species possessing the relatively more resilient plerocercoid as their final larval stage. These results provide an example of how HS_s can be used to compare levels of host specificity, in this instance, among stages of polyxenous life cycles. They also emphasise the importance of articulating the life cycle stage under consideration when general statements are made about host specificity.

Keywords: Cestoda; Host specificity; Host specificity index HS_s; Polyxenous life cycle; Procercoid; Plerocercoid; Plerocercus; Merocercoid; Trypanorhyncha

1. Introduction

Many groups of parasites are polyxenous, utilising two or more hosts over the course of their development. A question of interest in such organisms is the relative degree of host specificity exhibited by the different life cycle stages of a species. The issue of whether general trends exist in the relative degrees of host specificity of different life cycle stages is one of the more intriguing aspects of the biology of polyxenous organisms. For example, Poulin (2007) noted that it has been predicted that parasites with complex life cycles should display a higher specificity for their intermediate host than for their definitive host. Specific examples of this trend are known. For example, the sporocysts and redia of *Schistosoma japonicum* exhibit a greater degree of host specificity for their molluscan first intermediate host, than the adult does for its definitive host (e.g. Kennedy, 1975). In contrast, in other taxa it is the adult stage that has been shown to be more host-specific. For example, whereas the adult of the bothriocephalidean cestode *Triaenophorus nodulosus* parasitises only fish of the genus *Esox*, the procercoid of this species has the ability to parasitise a wide variety of copepods (Kuperman, 1981). Similarly, Esch and Fernández (1993) found that metacercariae of the digenean *Clinostomum campanulatum* exhibit much less specificity for the intermediate and/or paratenic fish host than the adult does for the bird definitive host. It could also

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be argued that transmission mode may play a role in determining the degree of host specificity of a particular life cycle stage.

However, the issue of relative specificity among the life cycle stages of polyxenous species remains largely untested (see Poulin, 2007). This is due, in part, to a lack of data. In many instances comprehensive host data are not available for one or more of the life cycle stages under consideration either as a result of lack of sampling effort, inaccessibility of existing data or, more commonly, because larval stages cannot be reliably identified to species. Another contributing factor has been the lack of an objective method for the rigorous quantitative assessment of the degree of host specificity from a phylogenetic perspective. The latter circumstance has recently substantially improved with the development of several indices (Caira et al., 2003; Poulin and Mouillot, 2003, 2005) of host specificity designed to allow host taxonomy to be incorporated into specificity assessments. As a consequence, it is now possible to quantitatively address questions of relative host specificity.

Trypanorhynch cestodes are a group of polyxenous parasites that are particularly appropriate for such investigation. Their life cycle stages typically consist of a procercoid, followed by a plerocercus (or in some species a plerocercoid or merocercoid) and ultimately the adult. An individual trypanorhynch passes through at least three different hosts over the course of its life (Dollfus, 1942; Mattis, 1986. Development of two tetrarhynchidean cestodes from the northern Gulf of Mexico. Ph.D. Thesis, University Southern Mississippi). The taxonomy of trypanorhynchs relies heavily on tentacle armature (Campbell and Beveridge, 1994), a feature present in both the adult and the final larval stage of these tapeworms, and thus the final larval stage can be identified reliably to species. Perhaps most importantly, however, comprehensive host data for trypanorhynchs have recently been made available by Palm (2004) who compiled approximately 4000 host/parasite records for larval and adult trypanorhynchs. Although trypanorhynchs are generally considered to exhibit relatively low host specificity at any particular life stage (e.g., Palm et al., 1997, 2007; Beveridge et al., 2000; Palm, 2004; Palm and Klimpel, 2007), detailed studies on particular species have suggested otherwise (e.g., Beveridge and Jones, 2000; Beveridge and Duffy, 2005). However, apart from a statement by Dollfus (1942) that it is rare for a trypanorhynch to parasitise only a single host species in each of its three life cycle stages (most have multiple hosts in all three life cycle stages), little attention has been paid to the relative host specificities of the adult versus larval stages in this order of parasites.

The primary goal of this paper is to evaluate the relative host specificities of the adult and final larval stage (i.e., plerocercus, plerocercoid or merocercoid) of a diversity of trypanorhynchs to determine if a general specificity trend exists within the polyxenous life cycle pattern exhibited by this group. As a secondary goal we hope to illustrate how host specificity indices, such as HS_s, can be used to add rigor to assessments of a wide spectrum of questions about relative host specificity, even beyond life cycle stages, as such qualitative indices allow statistical tests to be employed to address specific questions. For example, while this index has been applied to a diversity of species in some groups of cestodes that parasitise elasmobranchs (see Caira et al., 2003), it has never been applied to trypanorhychs. Similarly, although Palm (2004) predicted that certain trypanorhynch taxa, such as tentaculariids, are generally less host-specific than the eutetrarhynchids, this hypothesis remains untested. The final goal of this paper is to focus attention on the fact that in polyxenous species, different life cycle stages may exhibit widely divergent degrees of host specificity and thus general statements about the host specificity of groups should include articulation of the life cycle stage under consideration (e.g. Polyanskii, 1955; Holmes, 1990; Marcogliese, 1995). Our hope is that this will help to elucidate the potential of different life cycle stages to contribute to the exploration and exploitation of new hosts and habitats, and thus, ultimately, their contribution to the evolutionary trajectories of species.

2. Materials and methods

In general, host association data for the 63 trypanorhynch species included here were taken from Palm (2004). However, in the cases of three species, additional data beyond Palm (2004) were available and were included. These species are *Callitetrarhynchus speciosus* (Palm, personal observations), *Pintneriella musculicola* (Palm, personal observations), and *Mixonybelinia beveridgei* (see Knoff et al., 2004). Only those species for which comprehensive host data were available for both the adult and the final larval stage (i.e, plerocercus, plerocercoid or merocercoid) were considered.

Host specificity at the species level was assessed using the specificity index (HS_s) of Caira et al. (2003). This index was chosen over both that of Poulin and Mouillot (2003) and over the modified index of Poulin and Mouillot (2005) because it places more weight on hosts of higher taxonomic ranks in assessments of specificity, and also over the latter index because prevalence data were not available. Host specificity values ranging between 1 and ~10 were calculated independently for the final larval stage and adult of each species based on their occurrence in species, genera, families, orders and classes of hosts using the software available at http://darwin.eeb.uconn.edu/specificity/specificity.html. The standardised terminology for categories of host specificity proposed by Caira et al. (2003), based on terms in common use in the literature, was also followed. Thus, a species with an HS_s value of 0 was considered oioxenous (O in Table 1 and Fig. 1), between 0 and 3.004 mesostenoxenous (MS in Table 1 and Fig. 1), between 3.004 and 5.5743 metastenoxenous (MT in Table 1 and Fig. 1), and greater than 5.5743 euryxenous (E in Table 1 and Fig. 1). These values largely correspond to spe-

Table 1
Host specificity data for larval and adult trypanorhynchs, arranged by relative specificity of adults versus larvae (i.e., by HSsL − HSsA)

Trypanorhynch superfamily	Trypanorhynch family/subfamily	Trypanorhynch species	Larval hosts						Adult hosts						Larval HS_s	Larval spcfty cat[b]	Adult HS_s A	Adult spcfty cat[b]	HS_s L − HS_s A	Relative spcfty A versus L[c]	Final larval host[d]	Final larval type[e]
			No. Species	No. Genera	No. Families	No. Orders	No. Classes	Rank	No. Species	No. Genera	No. Families	No. Orders	No. Classses	Rank								
Gymnorhynchoidea	Gymnorhynchidae	*Gymnorhynchus gigas*	1	1	1	1	1	1	4	4	2	2	1	45665798	0.0000	O	7.6596	E	−7.66	cl	F	M
Eutetrarhynchoidea	Eutetrarhynchidae	*Eutetrarhynchus leucomelanus*	6	3	1	1	1	2003	4	4	2	1	1	377248	3.3017	MT	5.5766	E	−2.27	l	I	PS
Otobothrioidea	Otobothriidae	*Proemotobothrium southwelli*	2	2	2	1	1	375251	2	2	2	2	1	45663801	5.5743	E	7.6596	E	−2.09	l	F	PS
Lacistorhynchoidea	Grillotiinae	*Dasyrhynchus variouncinnatus*	4	3	2	1	1	376251	8	3	2	2	1	45664805	5.5755	E	7.6596	E	−2.08	l	F	PS
Gymnorhynchoidea	Gymnorhynchidae	*Molicola horridus*	5	4	2	1	1	377249	3	3	2	2	1	45664800	5.5766	E	7.6596	E	−2.08	l	F	M
Tentacularioidea	Tentaculariidae	*Mixonybelinia southwelli*	6	6	5	1	1	1496001	4	4	3	3	1	90953349	6.1749	E	7.9588	E	−1.78	l	F	PD
Lacistorhynchoidea	Pterobothriidae	*Pterobothrium kingstoni*	1	1	1	1	1	1	2	1	1	1	1	2	0.0000	O	0.3103	MT	−0.31	s	F	PS
Gymnorhynchoidea	Gilquiniidae	*Gilquinia squali*	2	2	2	2	1	45663801	6	5	5	3	1	91697856	7.6596	E	7.9600	E	−0.30	s	F	M
Otobothrioidea	Otobothriidae	*Otobothrium insigne*	2	1	1	1	1	2	3	1	1	1	1	3	0.3010	MS	0.4771	MS	−0.18	s	F	PS
Eutetrarhynchoidea	Eutetrarhynchidae	*Paroncomegas araya*	2	2	1	1	1	1001	5	2	1	1	1	1004	3.0004	MT	3.0017	MT	0.00	s	I	PS
Gymnorhynchoidea	Aporhynchidae	*Aporhynchus norvegicus*	1	1	1	1	1	1	1	1	1	1	1	1	0.0000	O	0.0000	O	0.00	s	I	?
Lacistorhynchoidea	Grillotiinae	*Grillotia amblyrhynchos*	1	1	1	1	1	1	1	1	1	1	1	1	0.0000	O	0.0000	O	0.00	s	F	PS
Lacistorhynchoidea	Grillotiinae	*Grillotiella exile*	1	1	1	1	1	1	1	1	1	1	1	1	0.0000	O	0.0000	O	0.00	s	F	PS
Otobothrioidea	Otobothriidae	*Otobothrium alexanderi*	1	1	1	1	1	1	1	1	1	1	1	1	0.0000	O	0.0000	O	0.00	s	F	PS
Lacistorhynchoidea	Grillotiinae	*Paragrillotia similis*	1	1	1	1	1	1	1	1	1	1	1	1	0.0000	O	0.0000	O	0.00	s	F	PS
Lacistorhynchoidea	Grillotiinae	*Pseudogrillotia basipunctata*	1	1	1	1	1	1	1	1	1	1	1	1	0.0000	O	0.0000	O	0.00	s	F	PS
Lacistorhynchoidea	Grillotiinae	*Dasyrhynchus pacificus*	12	6	5	2	1	46784557	7	4	4	2	1	46411305	7.6701	E	7.6666	E	0.00	s	F	PS
Tentacularioidea	Sphyriocephalidae	*Sphyriocephalus tergestinus*	7	7	4	2	1	46414290	3	3	3	2	1	46038051	7.6667	E	7.6631	E	0.00	s	F	PD
Tentacularioidea	Tentaculariidae	*Nybelinia thyrsites*	6	5	5	2	1	46783556	4	4	3	2	1	46039049	7.6701	E	7.6631	E	0.01	s	F	PD
Lacistorhynchoidea	Lacistorhynchinae	*Lacistorhynchus dollfusi*	21	17	12	7	1	270215370	10	7	4	4	1	135869642	8.4317	E	8.1331	E	0.30	s	F	PS
Lacistorhynchoidea	Grillotiinae	*Dasyrhynchus giganteus*	5	5	3	1	1	751496	6	2	1	1	1	377250	5.8759	E	5.5766	E	0.30	s	F	PS
Eutetrarhynchoidea	Eutetrarhynchidae	*Parachristianella trygonis*	4	4	3	1	1	750499	4	3	2	1	1	376251	5.8754	E	5.5755	E	0.30	s	I	PS
Eutetrarhynchoidea	Eutetrarhynchidae	*Oncomegas australiensis*	2	1	1	1	1	2	1	1	1	1	1	1	0.3010	MT	0.0000	O	0.30	s	I	PS
Lacistorhynchoidea	Lacistorhynchinae	*Floriceps saccatus*	16	14	12	3	1	94277745	6	4	2	2	1	45665800	7.9744	E	7.6596	E	0.31	s	F	PS
Tentacularioidea	Tentaculariidae	*Kotorella pronosoma*	5	4	4	4	1	135866652	13	7	3	2	1	46042043	8.1331	E	7.6631	E	0.47	s	F	PD
Tentacularioidea	Tentaculariidae	*Nybelinia anthicosum*	10	10	6	4	1	136614134	3	3	3	2	1	46038051	8.1355	E	7.6631	E	0.47	s	F	PD
Lacistorhynchoidea	Grillotiinae	*Grillotia heptanchi*	17	14	12	7	1	270212411	5	5	3	3	1	90954346	8.4317	E	7.9588	E	0.47	s	F	PS
Lacistorhynchoidea	Grillotiinae	*Grillotia cf smarisgora* (CA)	7	4	4	4	1	135866654	2	2	2	2	1	45663801	8.1331	E	7.6596	E	0.47	s	F	PS
Lacistorhynchoidea	Grillotiinae	*Grillotia erinaceus*	65	53	30	14	1	570346646	22	9	6	4	1	136613155	8.7561	E	8.1355	E	0.62	s	F	PS
Tentacularioidea	Tentaculariidae	*Heteronybelinia nipponica*	10	9	8	7	1	268744295	2	2	2	2	1	45663801	8.4293	E	7.6596	E	0.77	s	F	PD
Lacistorhynchoidea	Lacistorhynchinae	*Callitetrarhynchus gracilis*	140	90	37	10	1	407143645	16	8	4	2	1	46415292	8.6097	E	7.6667	E	0.94	s	F	PS
Lacistorhynchoidea	Lacistorhynchinae	*Lacistorhynchus tenuis*	51	44	31	16	2	3055436280	7	6	4	4	1	135868645	9.4851	E	8.1331	E	1.35	m	F& I	PS

(*continued on next page*)

Table 1 (*continued*)

Trypanorhynch superfamily	Trypanorhynch family/subfamily	Trypanorhynch species	Larval hosts						Adult hosts						Larval HS_s	Larval spcfty cat[b]	Adult HS_s A	Adult spcfty cat[b]	HS_s L – HS_s A	Relative spcfty A versus L[c]	Final larval host[d]	Final larval type[e]
			No. Species	No. Genera	No. Families	No. Orders	No. Classes	Rank	No. Species	No. Genera	No. Families	No. Orders	No. Classses	Rank								
Eutetrarhynchoidea	Eutetrarhynchidae	*Eutetrarhynchus ruficollis*	12	11	6	2	2	2451271777	3	2	2	2	1	45663801	9.3894	E	7.6595	E	1.73	m	I	PS
Tentacularioidea	Tentaculariidae	*Mixonybelinia lepturi*	6	6	5	3	2	2495810851	3	3	3	2	1	46038051	9.3972	E	7.6631	E	1.73	m	F& I	PD
Tentacularioidea	Sphyriocephalidae	*Hepatoxylon megacephalum*	26	23	17	11	2	2846166373	2	2	2	2	1	45663801	9.4543	E	7.6596	E	1.79	m	F	PD
Tentacularioidea	Tentaculariidae	*Nybelinia indica*	29	24	22	9	2	2763670817	5	4	2	2	1	45665799	9.4415	E	7.5951	E	1.85	m	F	PD
Tentacularioidea	Sphyriocephalidae	*Hepatoxylon trichiuri*	86	68	43	19	3	4853887801	5	5	3	2	1	46040046	9.6861	E	7.6631	E	2.02	m	I	PD
Lacistorhynchoidea	Pterobothriidae	*Pterobothrium lintoni*	7	7	6	3	1	92070106	8	3	3	1	1	749506	7.9641	E	5.8748	E	2.09	m	F	PS
Otobothrioidea	Otobothriidae	*Otobothrium penetrans*	4	3	2	1	1	376251	8	4	1	1	1	3002	5.5755	E	3.4774	MT	2.10	m	F	PS
Lacistorhynchoidea	Grillotiinae	*Grillotia dollfusi*	2	2	2	1	1	375251	3	2	1	1	1	1002	5.5743	E	3.0009	MS	2.57	m	F	PS
Lacistorhynchoidea	Grillotiinae	*Pseudogrillotia perelica*	9	5	2	1	1	378249	2	2	1	1	1	1001	5.5778	E	3.0004	MS	2.58	m	F	PS
Lacistorhynchoidea	Lacistorhynchinae	*Callitetrarhynchus speciosus*[a]	46	33	20	5	1	185885103	4	3	2	1	1	4321	8.2692	E	5.5740	MT	2.70	m	F	PS
Gymnorhynchoidea	Rhopalothylacidae	*Pintneriella musculicola*[a]	5	3	3	1	1	749503	2	2	1	1	1	1001	5.8748	E	3.0004	MS	2.87	m	F	PS
Lacistorhynchoidea	Grillotiinae	*Grillotia rowei*	6	3	1	1	1	2003	1	1	1	1	1	1	3.3017	MT	0.0000	O	3.30	cm	F	PS
Tentacularioidea	Tentaculariidae	*Tentacularia coryphaenae*	82	60	44	22	3	4853887801	11	5	2	1	1	378251	9.6861	E	5.5778	E	4.11	cm	F& I	PD
Otobothrioidea	Otobothriidae	*Poecilancistrum caryophyllum*	28	21	6	2	1	47169638	8	4	1	1	1	3002	7.6737	E	3.4774	MT	4.20	cm	F	PS
Lacistorhynchoidea	Grillotiinae	*Grillotia borealis*	2	2	2	1	1	375251	5	1	1	1	1	5	5.5743	E	0.6990	MS	4.88	cm	F	PS
Lacistorhynchoidea	Lacistorhynchinae	*Bombycirhynchus sphyraenaicum*	3	3	3	1	1	749501	1	1	1	1	1	1	5.8748	E	0.0000	O	5.87	cm	F	PS
Lacistorhynchoidea	Grillotiinae	*Pseudogilquinia microbothria*	7	5	5	1	1	1495007	1	1	1	1	1	1	6.1746	E	0.0000	O	6.17	cm	F	PS
Lacistorhynchoidea	Lacistorhynchinae	*Floriceps minacanthus*	13	9	7	2	1	47527062	4	1	1	1	1	4	7.6769	E	0.6021	MS	7.07	cm	F	PS
Eutetrarhynchoidea	Progrillotiidae	*Progrillotia dasyatidis*	7	6	3	2	1	46041043	2	1	1	1	1	2	7.6631	E	0.3103	MS	7.35	cm	F	PS
Tentacularioidea	Tentaculariidae	*Nybelinia gopalai*	6	5	4	3	1	91326600	2	1	1	1	1	2	7.9606	E	0.3010	MS	7.66	cm	F	PD
Lacistorhynchoidea	Lacistorhynchinae	*Pseudolacistorhynchus shipleyi*	3	2	2	2	1	45663802	1	1	1	1	1	1	7.6596	E	0.0000	O	7.66	cm	F	PS
Lacistorhynchoidea	Grillotiinae	*Pseudogrillotia epinepheli*	4	2	2	2	1	45663803	1	1	1	1	1	1	7.6596	E	0.0000	O	7.66	cm	F	PS
Lacistorhynchoidea	Pterobothriidae	*Pterobothrium australiense*	3	3	3	2	1	4638051	1	1	1	1	1	1	7.6631	E	0.0000	O	7.66	cm	F	PS
Gymnorhynchoidea	Gymnorhynchidae	*Molicola uncinatus*	6	6	5	2	1	46784551	1	1	1	1	1	1	7.6701	E	0.0000	O	7.67	cm	F	M
Eutetrarhynchoidea	Eutetrarhynchidae	*Oncomegas javensis*	12	11	9	5	1	181888736	2	1	1	1	1	2	8.2598	E	0.3010	MS	7.96	cm	F	PS
Lacistorhynchoidea	Lacistorhynchinae	*Pseudolacistorhynchus noodi*	4	4	4	3	1	91325602	1	1	1	1	1	1	7.9606	E	0.0000	O	7.96	cm	F	PS
Lacistorhynchoidea	Grillotiinae	*Grillotia smaris-gora*	6	5	5	3	1	91697856	1	1	1	1	1	1	7.9624	E	0.0000	O	7.96	cm	F	PS
Tentacularioidea	Tentaculariidae	*Mixonybelinia beveridgei*[a]	9	7	5	4	1	13624087	1	1	1	1	1	0	8.1343	E	0.0000	O	8.13	cm	F	PD
Eutetrarhynchoidea	Eutetrarhynchidae	*Prochristianella hispida*	7	4	3	2	2	2450151052	4	1	1	1	1	4	9.3892	E	0.6021	MS	8.79	cm	I	PS
Tentacularioidea	Tentaculariidae	*Heteronybelinia yamagutii*	21	20	17	11	2	2846163431	1	1	1	1	1	1	9.4543	E	0.0000	O	9.45	cm	F& I	PD
Tentacularioidea	Tentaculariidae	*Nybelinia surmenicola*	74	39	22	14	5	9526620401	1	1	1	1	1	1	9.9789	E	0.0000	O	9.98	cm	F& I	PD

[a] Data from source other than Palm (2004).

[b] O, oioxenous; MS, mesoxenous; MT, metastenoxenous; E, euryxenous.

[c] Relative specificities of larvae and adults; cl, adult conspicuosuly less specific; l, adult less specific; similar specificities; m, adult more specific; cm, adult conspicuously more specific.

[d] F, fish final intermediate host; I, invertebrate final intermediate host.

cies that infect only a single host species (oioxenous), greater than one species in a single host genus (mesostenoxenous), greater than one genus in a single family (metastenoxenous), and hosts belonging to more than one family (euryxenous).

The relative specificity of larval and adult stages was determined as follows. For each species, the HS_s value of the adult was subtracted from the HS_s value of the final larval stage. Species in which the result was a positive or negative number less than 1 in magnitude were considered to have the same specificity at these two life cycle stages (s in Table 1). Species in which the result was a negative number greater than 1 in magnitude were considered to be less specific as adults than as larvae (l in Table 1); those in which the result was a negative number greater than 3 in magnitude were considered to be conspicuously less specific as adults than as larvae (cl in Table 1). Species in which the result was a positive number greater than 1 were considered to be more host-specific as adults than as larvae (m in Table 1); those in which the result was a positive number greater than 3 in magnitude were considered to be conspicuously more host-specific as adults than as larvae (cm in Table 1). A difference between index values of a magnitude of 3 or greater was selected as the criterion of choice as an indicator of conspicuous differences because the approximate point of the boundaries between the categorisations of mesostenoxeny and metastenoxeny, and between metastenoxeny and euryxeny, are ~3 and ~2.5 index points, respectively, and thus 3 was considered to be sufficiently conservative to be meaningful.

Wilcoxon signed-rank tests (Wilcoxon, 1945) were used to test for significant differences in comparisons of host specificity index values (i) between larvae and adults of all 63 species, (ii) between the seven species of eutetrarhynchids and 13 tentaculariids for both larvae and adults, and (iii) between the 15 species exhibiting plerocercoids and the 48 species with plerocerci or merocercoids. This non-parametric approach was chosen not only because of its conservative nature, but also because of the skewed nature of index values calculated across parasite taxa.

3. Results

Adult and final larval stage host data were obtained for 63 species exemplifying all five superfamilies of trypanorhynchs (sensu Palm, 2004). These consisted of eight species of Eutetrarhynchoidea representing two of the four known families, six species of Gymnorhynchoidea representing all four families, 29 species of Lacistorhynchoidea representing both families in the superfamily and both subfamilies of Lacistorhynchidae (Grillotiinae and Lacistorhynchinae), five species of Otobothrioidea representing one of the four families, and 15 species of Tentacularioidea representing both families. The HS_s values calculated for larval and adult stages and the results of the determinations of relative host specificity for these species are provided in Table 1.

The average HS_s value for the final larval stages of the 63 species was 6.29; the average HS_s value for the corresponding adult stages was 3.86. Based on the more relaxed specificity criterion described above, six (9%) of the 63 species were found to be less host-specific as adults than as larvae (cl and l in Table 1), 25 species (39.7%) exhibited essentially the same degree of host specificity as larvae and adults (s in Table 1), and 32 species (50.7%) were more host-specific as adults than as larvae (m and cm in Table 1). When the more conservative criterion of differences exceeding a total of three index values was used to determine conspicuous difference in specificity, the result is slightly different; one species (1.6%) is conspicuously less host-specific as an adult than as a larva (cl in Table 1) and 20 species (31.7%) are conspicuously more host-specific as adults than as larvae (cm in Table 1). The comparative specificity categorisations of larvae versus adults were as follows: oioxenous – 8 (12.7%) versus 19 (30.2%), mesostenoxenous – 1 (1.6%) versus 10 (15.9%), metastenoxenous – 4 (6.3%) versus 5 (7.9%), euryxenous – 50 (79.3%) versus 29 (46%). The Wilcoxon signed-rank test comparing HS_s values of larvae with adults was significant ($P = 1.091\text{e}{-05}$). The Wilcoxon signed-rank test for differences in HS_s values between species with plerocercoids versus those with plerocerci or merocercoids was significant ($P = 5.5\text{e}{-5}$). The mean HS_s value for species with plerocercoids was 8.62, for those with plerocerci or merocercoids was 5.56. The results of the Wilcoxon signed-rank tests were not significant for comparisons made between the HS_s values of the eutetrarhynchid species and the tentaculariid species for either larval ($P = 0.0812$) or adult stages ($P = 0.1503$). The mean larval HS_s value for eutetrarhynchids was 5.64, for tentaculariids 8.36; the mean adult HS_s value for eutetrarhynchids was 3.24, for tentaculariids 5.21.

4. Discussion

Our results suggest that, in general, the final larval stage (plerocercoid, plerocercus or merocercoid) of trypanorhynchs is significantly less host-specific than the adult stage. In only a very few cases were adults found to be less host-specific than their final larval counterparts, and in only a single case (*Gymnorhynchus gigas*) was the adult stage found to be conspicuously less host-specific than its corresponding larval stage. In most cases, the degree of host specificity exhibited by the adult of a species was similar to, or greater than, that of its corresponding final larval stage. This trend was seen across the spectrum of host specificity values. Thus, among the species found to exhibit the same level of host specificity as larvae and adults, are species that are oioxenous at both life cycle stages and also species that are euryxenous at both stages. Similarly, among those species found to exhibit a greater degree of specificity as adults than as larvae, some are oioxenous, some mesostenoxenous and, in one case, metastenoxenous as adults. Further, in general the final larval stages parasit-

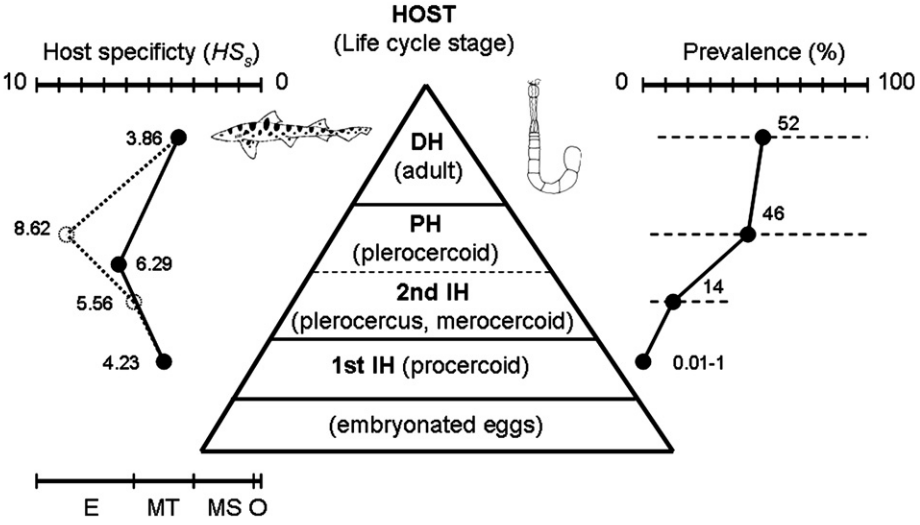

Fig. 1. Schematic relationship between host specificity (HS_x) and prevalence among trypanorhynch life cycle stages in their respective hosts. Specificity is highest for the adults in the definitive host, lowest for the plerocercoid, plerocercus, or merocercoid in the second intermediate or paratenic host, and intermediate for the procercoid in the first intermediate host. Solid line at left illustrates mean HS_x value when second intermediate and paratenic hosts are combined; dotted line when HS_x values are presented separately. Horizontal dashed lines at right indicate ranges of observed prevalence values from literature sources. DH, definitive host; PH, paratenic host; 1st IH, first intermediate host; 2nd IH, second intermediate host; O, oioxenous; MS, mesostenoxenous; MT, metastenoxenous; E, euryxenous.

ise hosts representing a greater number of taxonomic categories than do the adults.

There does not appear to be a taxonomic trend to these results. All five trypanorhynch superfamilies are represented among the few taxa exhibiting less host specificity as adults than as larvae, and also among those exhibiting the relatively same level of specificity and greater specificity, regardless of whether the more relaxed or more conservative index value criterion was used. Thus our results fail to support the notion of Palm (2004) that the host specificity of trypanorhynchs depends on the taxonomic group under consideration. For example, his suggestion that tentaculariids are generally less host-specific than eutetrarhynchids was refuted by the results of the Wilcoxon signed-rank tests, which were not significant for comparisons made either between larvae or adults of these families. This conclusion is interesting because it implies that, although different life cycles have been explored by different trypanorhynch taxa, all of these taxa have maintained a set of less and more host-specific species. However, it is important to note that taxa such as gilquiniids, aporhynchids, and eutetrarhynchids, which appear to use invertebrates rather than teleosts as their final intermediate hosts, are relatively under-represented within this dataset. Such taxa, in particular, warrant further investigation; not only do they pass through invertebrates rather than vertebrates as their final intermediate hosts, but they also generally develop as plerocercoids and employ fewer total hosts in their life cycles. Thus it is possible that additional sampling may reveal other differences possibly linked to host specificity. It will be interesting to determine if the generalisations made here are found to be robust when host data become available for a broader sampling of trypanorhynch taxa in general. As it stands, there is a phylogenetic bias to the dataset employed here because comprehensive host data were available for more species in some families (e.g., Tentaculariidae and Lacistorhynchidae) than in others (e.g., Gilquiniidae and Pterobothriidae).

It is interesting to place these results into context relative to the remaining developmental stage in the life cycle of trypanorhynch cestodes. As noted above, most trypanorhynchs pass through three distinct life cycle stages over the course of their development: (i) procercoid, (ii) plerocercus plerocercoid or merocercoid, and (iii) adult. Up to this point, we have said little about specificity of procercoids. Although available host data are insufficient to allow robust characterisation of host specificity of procercoids in the first intermediate host, the data that are available (most of them experimental) provide some insight into this issue. Procercoids of the seven species for which information is available parasitise taxa in one or more orders of copepod crustaceans (e.g. Ruszkowski, 1934; Marshall et al., 1934; Dollfus, 1942; Marshall and Orr, 1955; Euzet, 1959. Recherches sur les cestodes tétraphyllides des sélaciens des côtes de France. Thèse de Ph.D. Faculté des Sciences, Université de Montpellier, Montpellier, France; Mudry and Dailey, 1971; Mattis, 1986. Development of two tetrarhynchidean cestodes from the northern Gulf of Mexico. Ph.D. Thesis, University Southern Mississippi; Palm, 2004). Their HS_s values range from 0 (e.g., *Lacistorhynchus tenuis*, *Aporhynchus norvegicus*, and *Parachristianella monomegacantha*) to 7.96 (*Prochristianella hispida*), with an average HS_s value of 4.23. Thus, the trend that emerges is one in which host specificity is generally highest for the adult stage in the definitive host (mean $HS_s = 3.86$), lowest for the final larval stage in the second intermediate host (mean $HS_s = 6.29$), and somewhat intermediate between these two values (mean $HS_s = 4.23$) for the procercoid in the first intermediate host (see Fig. 1). This pattern is consistent with that proposed by such early workers as Dollfus (1942) for species such as *Grillotia erinaceus*. However, it is important to note that, among all of the life cycle stages of trypanorhynchs, procercoids have been particularly poorly sampled and this poor sampling effort may have resulted in an overestimate of the host specificity of procercoids for their first intermediate hosts at this time.

It is important to consider one final aspect of the biology of trypanorhynchs when interpreting the results presented here. It is generally thought that the developmental pathways of at least some trypanorhynchs involve one, or possibly more, paratenic hosts (Mattis, 1986. Development of two tetrarhynchidean cestodes from the northern Gulf of Mexico. Ph.D. Thesis, University Southern Mississippi; Palm, 2004). As a consequence, the host data presented here for the final larval stage (plerocercoid, plerocercus or merocercoid) may, in some cases, actually represent a combination of data for both final intermediate and paratenic hosts. Unfortunately, the extent to which paratenic hosts are used by trypanorhynchs, while possible to determine with the appropriate amount of data (Palm, 1999), is unknown for most species. Nonetheless, some inferences can be made. For example, the final larval stage type (i.e., plerocercoid, plerocercus or merocercoid) may provide some insight as to whether a species exploits one or more paratenic hosts. This is because, whereas the plerocercoid is a solid-bodied, robust stage that is likely to withstand the rigors of passage among several hosts, the plerocercus and merocercoid are more delicate and thus may not survive such passage; rather than a solid body, both the plerocercus and merocercoid possess a fluid-filled blastocyst into which the scolex may be retracted and, in the latter case, also invaginated. If this is the case, species whose larval data may consist of a combination of data from both final intermediate and paratenic hosts are those that possess a plerocercoid stage (PD in Table 1). Indeed, the result of the Wilcoxon signed-rank test indicates that species with a plerocercoid stage are significantly less host-specific at this stage than are species with plerocerci or merocercoids. If this result actually reflects the difference between species that use paratenic hosts and those that do not, the mean HS_s value for the final intermediate host presented above (i.e., 6.29), might be more appropriately broken down into a value (5.56) for species with pleroceri or merocercoids (i.e., a value that truly represents specificity for the final intermediate host) and a value (8.63) for species with plerocercoids (i.e., a value that likely reflects specificity for both the final intermediate host and paratenic hosts combined). This modification is illustrated with the dashed line in Fig. 1.

The results of the analyses conducted here provide some support for the observation of Palm (2004) that host specificity in trypanorhynchs is generally comparatively low overall relative to that seen in other cestodes that parasitise elasmobranchs. Whereas nearly half (i.e., 46%) of adult HS_s values and over three-quarters (i.e.,79.6%) of larval HS_s values for the trypanorhynch species examined here were indicative of euryxeny, only one of the 44 litobothriidean and onchobothriid species examined by Caira et al. (2003) had adult HS_s values greater than 0 (ie., other than oioxeny). However, it is important to recognise that oioxenous trypanorhynch species are known; in fact 16 species of trypanorhynchs were oioxenous as adults. It is also important to note that 11 of these species, while oioxenous as adults, were euryxenous as larvae.

The patterns of host specificity discussed above have important implications for the ecology and dispersal mechanisms of trypanorhynch cestodes, particularly when other variables such as prevalence and intensity, and thus also abundance, are taken into consideration. Unfortunately, detailed prevalence and intensity data are limited for most trypanorhynch infections at any of the stages in the life cycle. Nonetheless, the following observations can be made based on available literature (see Fig. 1). Marcogliese (1995) suggested that the crustacean first intermediate host in the polyxenous life cycle of helminths is generally infected at a very low prevalence of 0.01–1.0% relative to other stages. This is likely to hold true for trypanorhynchs. Experimental infections of copepods with *Poecilancistrum caryophyllum* have shown that the size of the oncosphere larva relative to that of its copepod host provides an upper boundary on the intensity of infection at approximately one to two oncospheres and thus ultimately procercoids, as infections of greater intensity are generally lethal to the copepod (Mattis, 1986. Development of two tetrarhynchidean cestodes from the northern Gulf of Mexico. Ph.D. Thesis, University Southern Mississippi). As a consequence, intensities of infection of copepods with procercoids in natural situations are likely to be similarly low and so too, then, is the abundance. In contrast, Jakob and Palm (2006) found the prevalence of infection of plerocerci in predatory fish in Java to range from 2.9% to 40% with a mean of 13.5% ($n = 4$), and prevalence of infection with plerocercoids to range from 2.9% to 100% with a mean of 45.9% ($n = 17$). The prevalence of trypanorhynchs within the definitive host also appears to vary conspicuously among species, and to be considerably higher than that seen for procercoids. For example, whereas *Prochristianella tumidula* had a prevalence of 6% in the 49 individuals of *Mustelus canis* examined by Cislo and Caira (1993) and *Mecistobothrium myliobati* a prevalence of 7% in 28 specimens of *Urobatis halleri* examined by Friggens and Brown (2005), *Grillotia similis* occurred in 81.8% of the 22 specimens of *Ginglymostoma cirratum* examined by Caira and Gavarrino (1990) and Beveridge and Jones (2000) found the prevalence of *Prochristianella spinulifera* to be 100% in the 10 specimens of *Rhinobatos typos* examined. When these data are combined with data for additional species from Cislo and Caira (1993) and Friggens and Brown (2005) for seven additional species, the mean prevalence of these 10 trypanorhynch species is 52% in the definitive, elasmobranch host individual. It is interesting that all 10 of these trypanorhynch species develop from a plerocercus stage. The extent to which the prevalence of trypanorhynchs in the definitive host is a function of the host specificity of the preceding larval stage for its intermediate (or paratenic) host and of the procercoid for the first intermediate host remains to be determined.

The results presented here emphasise the importance of articulating the life cycle stage under consideration when generalisations about host specificity in polyxenous taxa are made. We have shown here that conspicuous differences in host specificity can exist among the life cycle stages of individual trypanorhynch species. It seems likely that differences likewise exist among life cycle stages in other polyxenous systems as noted, for example, by Baer (1951). The magnitude and direction of such differences may be explored using metrics such as HS_S. Similarly, predictions about specificity as it relates to other aspects of trypanorhynch biology would be interesting to pursue with these methods. For example, Palm (2004) predicted that cosmopolitan trypanorhynch species are likely to be less host-specific than species with more limited geographical distributions. This remains to be explored in the trypanorhynchs and other elasmobranch tapeworms. This study includes data for 63 of the ~270 known species of trypanorhynchs. As additional host–parasite records for trypanorhynchs are compiled, and as more hosts are studied, the potential of these cestodes to serve as a model system (Palm and Klimpel, 2007) to better understand the ecology and co-evolutionary history of parasitic life cycles in the marine ecosystem will be revealed.

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