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HELMINTH POSITION WITHIN THE INTESTINE OF NATURALLY INFECTED PIKE (*ESOX LUCIUS*) RELATIVE TO HOST STOMACH CONTENTS

Allen W. Shostak* and Terry A. Dick†
Department of Zoology, University of Manitoba, Winnipeg, Manitoba, Canada R3T 2N2

ABSTRACT: The positions of 3 cestode species, *Triaenophorus crassus* Forel, *Triaenophorus nodulosus* (Pallas), and *Proteocephalus pinguis* LaRue, and a nematode, *Raphidascaris acus* (Bloch), within the intestine of naturally infected pike (*Esox lucius* L.) were evaluated with respect to the presence or absence and state of digestion of host stomach contents. The positions of scolices and strobilae of the cestodes did not vary with respect to host stomach contents. By contrast, *R. acus* was anterior (near the stomach) when the stomach contained partially digested items, posterior when the stomach was empty, and in an intermediate position when the stomach contained only intact items. These results are interpreted as migration of *R. acus*, but not *T. crassus*, *T. nodulosus*, or *P. pinguis*, in response to feeding activity of the host. Adult and larval *R. acus* migrated, but the extent of migration was reduced in hosts harboring *T. crassus*, more so for larval than adult *R. acus*.

Spatial relationships among intestinal helminths are used frequently to address questions of interspecific interactions and community structure (e.g., Kennedy, 1985; Lotz and Font, 1985; Stock and Holmes, 1988). Because helminths are capable of undergoing various types of migrations within the intestine (Croll, 1976; Crompton, 1976; Gray, 1977; Hobbs, 1980), ecological interpretations may be rendered more difficult if extensive migrations exist and are not recognized. Migrations may be ontogenetic, occurring during growth and maturation of a parasite, or daily, cued by a stimulus such as ingestion of a meal by the host (Read and Kilejian, 1969; Hopkins, 1970; MacKenzie and Gibson, 1970; Bailey, 1971; Croll, 1976; Gray, 1977).

Few studies have addressed helminth migrations in naturally infected hosts, yet these are the hosts most frequently used to provide species-rich and abundantly populated helminth communities for ecological analysis. MacKenzie and Gibson (1970) reported that a trematode, *Podocotyle* sp., and the nematodes *Cucullanus heterochronus*, *Cucullanus minutus*, and *Contracaecum aduncum* migrated within the intestine of flounders when food was withheld from the host. Williams et al. (1970) found similar evidence of migration in cod infected with *Contracaecum aduncum* and rays infected with the trematode *Otodistomum* sp. and the cestode *Grillotia* sp. Hobbs (1980) found that the position of *Cephaluris* spp. nematodes in the intestine of pikas varies according to gut lumen contents. Bush and Holmes (1986) found no evidence for migration by helminths of lesser scaup according to time of day.

We conducted a seasonal study of the ecology of intestinal helminths in pike (*Esox lucius* L.) from several lakes in Manitoba, Canada. The possibility of helminth migrations in response to host feeding was of concern because we planned to compare helminth communities across seasons and host populations, where qualitative and quantitative aspects of the feeding by the host may vary. We hypothesized that, if daily migrations related to feeding activity of the host were absent, the positions of intestinal helminths should be random with respect to the stomach contents of wild-caught hosts. Alternatively, nonrandom positions would be consistent with the presence of a migration.

MATERIALS AND METHODS

Hosts

Pike (n = 339) were collected from 3 lakes in Manitoba: Falcon L. (49°42′N, 95°54′W) during April 1981–1984; Heming L. (54°53′N, 101°07′W) during June and July 1981; and 2 sites on Southern Indian L. (SIL) (56°47′N, 98°54′W) during June, July, and August 1981 and March, June, July, and August 1982. SIL-A was a channel connecting 2 main lake basins, and SIL-B, 15 km distant, was a large bay narrowly connected to the main lake body.

Gill nets were used to collect all fish during March and April, and about 50% of fish in June. We assumed that data from fish obtained using gill nets were not biased by host stress because net sets were short (usually 1–4 hr), water temperatures at that time were cold

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* Present address: Department of Zoology, University of Alberta, Edmonton, Alberta, Canada T6G 2E9.

† Reprint requests to T.A.D.

(4–10 C), and direct observation of net-captured fish at Falcon L. revealed that, following a brief period of thrashing at first capture, fish appeared calm until removal from the net. Fish that were dead or moribund when removed from the nets were not used in this study. The remainder of fish in June, and all in July and August, were collected by angling, using an artificial lure. Fish collected by angling were landed within 30 sec of first being hooked.

Upon removal from the net or landing, fish were killed by a blow to the head. Within 2 min, the stomach and intestine were removed and quick-frozen in an ethanol–dry ice mixture (Bush and Holmes, 1986), and kept frozen until examination. Time of death was recorded for each fish.

All pike were 3 yr of age or older, as indicated by annuli on the cleithrum. Pike were 244–853 mm fork length, but at SIL (from which 70% of samples were obtained) the size range was narrower (500 ± 50 mm). Mean length of intestine was 63 ± 5% of fork length.

Helminth removal

Intestines were thawed partially and laid onto a waxed board. Pins were inserted to demarcate the intestine into 20 equal intervals between the junction of stomach and intestine and the junction of intestine and rectum. Then, 1 of 2 procedures was used to collect worms.

One procedure, done on 119/202 hosts from SIL-A, provided information on attachment site (scolex or mouth) distribution for all species, and, for cestodes, the linear distribution of strobilae. Transverse cuts were made through the intestine adjacent to each pin. Numbers of individuals of each species attached in that section were determined by counts of anterior extremities. Then, helminth pieces in each intestinal section were sorted by genus (or species, if possible) and dried at 70 C for 48 hr prior to dry weight determination to the nearest 0.01 mg.

Another procedure, done on 83/202 hosts from SIL-A and all other hosts, provided data on attachment site distributions comparable to the first procedure and additional data on intact worms. Intestines were slit longitudinally, and then transverse cuts were made through the intestinal wall at the location of each pin such that worm bodies were not cut. Each section, with all worms having their anterior extremity in that section, was placed in a petri dish. Then, individual helminths were identified and counted.

Stomach contents

Stomach contents were identified and total length was taken for intact items. Empty stomachs were termed category 1. Stomachs that contained food items, with all items identifiable and intact, were assumed to contain a recent meal and were termed category 2. Stomachs that contained food items, where at least 1 item was digested to the point of being unidentifiable or incomplete, were assumed to contain older meals and were termed category 3. A pooled category 2+3 was used simply to indicate the presence of food items.

Data analysis

Positions along the intestine are reported in units of percent intestinal length, where the junction with the stomach is anterior (0% position), and the junction with the rectum is posterior (100% position). The attachment site of the median worm of each species in each host was calculated according to the method of Bush and Holmes (1986); the same protocol was used on dry weight data to calculate the median position of cestode strobilae (the point at which 50% of the mass of each species was anterior). Statistical analyses were performed using these medians, with medians from different hosts serving as replicates.

For statistical analyses, hosts were stratified according to stomach contents (categories 1–3) and origin (lake, month). Insufficient data were obtained to permit additional stratification by time of day, and we pooled data across all times. Although precise times of collection varied among locales, sampling was concentrated between 0900 and 1700 hr CST.

Statistical procedures followed Sokal and Rohlf (1981). Two-group comparisons (food absent vs. present) used the Mann–Whitney test, and 3-group comparisons (food absent, recent meal, old meal) used the Kruskal–Wallis test. All data are reported as $\bar{x} \pm 1$ SD (n). Results were considered significant at $P < 0.05$.

RESULTS

Analyses were done for the 4 most common species of helminths found: the cestodes *Proteocephalus pinguis* LaRue (in all lakes, prevalence = 99%), *Triaenophorus crassus* Forel (in Falcon L. and SIL, prevalence = 94%), and *Triaenophorus nodulosus* (Pallas) (in all lakes, prevalence = 37%), and the nematode *Raphidascaris acus* (Bloch) (in all lakes, prevalence = 88%). For dry weight determinations on samples from SIL-A, strobilae of *T. nodulosus* could not be distinguished reliably from those of *T. crassus.* However, those dry weights were most indicative of the position of *T. crassus* because *T. nodulosus* was in <25% of those pike, was smaller than *T. crassus,* and comprised only 3–10% of the *Triaenophorus* individuals in those pike.

Predominant food items were small fish (<100 mm fork length) at Falcon L. and Heming L., large fish (>100 mm fork length) at SIL-A, and crustaceans and insects at SIL-B. Only 1 case of cannibalism was noted. Detailed data are presented elsewhere (Shostak, 1986).

Cestodes

Data pooled across host samples showed that positions of scolices of *T. crassus* and *T. nodulosus* and strobilae of *Triaenophorus* spp. did not vary significantly with stomach contents (Table I). Comparisons of category 1 vs. 2+3 for data stratified by lake and month supported these results: only 1 of 7 comparisons involving scolices of *T. crassus* (SIL-A, June, more anterior in category 1), 1 of 9 involving scolices of *T. nodulosus* (SIL-A, June, more anterior in category 1), and

TABLE I. Positions of *Triaenophorus crassus, Triaenophorus nodulosus, Proteocephalus pinguis,* and *Raphidascaris acus* in the intestine of *Esox lucius,* for 3 categories of host stomach contents.

				Probability†	
	Category 1*	Category 2*	Category 3*	Kruskal–Wallis	Mann–Whitney
T. crassus					
Scolices	26 ± 7 (155)‡	25 ± 8 (74)	26 ± 7 (59)	0.727	0.557
T. nodulosus					
Scolices	30 ± 14 (63)	30 ± 13 (31)	25 ± 10 (31)	0.146	0.266
Triaenophorus					
Strobilae	27 ± 7 (51)	30 ± 8 (29)	29 ± 8 (39)	0.230	0.088
P. pinguis					
Scolices	16 ± 8 (184)	17 ± 9 (81)	17 ± 5 (73)	0.484	0.229
Strobilae	20 ± 10 (50)	27 ± 11 (29)	23 ± 8 (39)	0.012	0.025
R. acus					
Mouths	29 ± 12 (153)	22 ± 14 (74)	16 ± 12 (71)	<0.001	<0.001

* 1, Stomach empty; 2, stomach containing only undigested items; 3, stomach containing at least 1 partially digested item.

† Kruskal–Wallis test compared categories 1, 2, and 3; Mann–Whitney test compared category 1 (stomach empty) with categories 2+3 (stomach contents present).

‡ Percent position; $\bar{x}$ ± 1 SD (n).

0 of 4 involving strobilae of *Triaenophorus* spp. were significant (Mann–Whitney test).

Positions of scolices of *P. pinguis* in pooled data did not vary significantly with stomach contents (Table I), and only 1 of 10 comparisons (category 1 vs. 2+3) for data stratified by lake and month (SIL-B, June, more anterior in category 1) were significant (Mann–Whitney test). Pooled data showed differences in position of strobilae of *P. pinguis* relative to stomach contents (Table I), but examination of stratified data did not support this interpretation because all 4 comparisons were insignificant (Mann–Whitney tests). The significant difference in the pooled sample was probably an artifact of pooling: mean positions in the March and June samples were <10%, with sample size biased toward category 1, whereas mean positions in July and August samples were >20%, with sample sizes biased toward category 2+3.

Nematodes

Positions of the mouths of *R. acus* in pooled data varied significantly with stomach contents (Table I). A trend in the pooled data for positions to be posterior in category 1, intermediate in category 2, and anterior in category 3 (Table I) was evident in 8 of 9 host samples stratified by lake and month (Table II). Comparisons of category 1 with 2+3 by the Mann–Whitney test were significant in 7 of 9 cases, and comparisons of categories 1, 2, and 3 (Kruskal–Wallis test) were significant or marginally significant ($P <$ 0.10) in 6 of 8 cases (Table II).

A previous study (Shostak and Dick, 1986) suggested a possible interaction between *T. crassus* and larval *R. acus.* We selected data from hosts for which separate counts of larval and adult *R. acus* had been made and examined positions of *R. acus* relative to the presence or absence of *T. crassus* and to host stomach contents. Positions of adults and larvae varied significantly with host stomach contents, whether *T. crassus* was present or absent (Table III), but the magnitude of this difference (in percent of intestinal length) varied. The maximum difference in mean position among categories was: for adults, 30% with *T. crassus* absent and 22% with *T. crassus* present; for juveniles, 25% with *T. crassus* absent and 7% with *T. crassus* present.

DISCUSSION

The time of feeding by each pike was unknown, but their stomach contents enabled relative ranking by time since their previous meal: least for stomachs containing only intact items, intermediate for stomachs with partially digested items, and greatest for empty stomachs. It is known from studies on mammals (Mettrick and Podesta, 1974) that following a meal a steep nutrient gradient, declining posteriorly, is formed. As time passes the gradient becomes less steep and eventually nutrient levels are low throughout the intestine. Applying that principle to the present study, the observation that pike ate large food items, but infrequently (based on the many empty stomachs), suggests that large but infrequent pulses of digestion products pass down their in-

TABLE II. Geographic and seasonal variation in positions of *Raphidascaris acus* in the intestine of *Esox lucius*, for 3 categories of host stomach contents.

	Category 1*	Category 2*	Category 3*	Probability†	
				Kruskal–Wallis	Mann–Whitney
Heming L.					
June	45 ± 2 (2)‡	19 ± 16 (2)	6 ± 5 (4)	0.075	0.044
July	48 ± 13 (5)	25 ± 31 (5)	10 ± 13 (7)	0.043	0.027
Falcon L.					
April	24 ± 13 (40)	16 ± 6 (2)	14 ± 12 (8)	0.082	0.026
SIL-A§					
March	28 ± 8 (8)	28 ± 16 (3)	20 (1)	0.572	0.865
June	30 ± 7 (17)	9 ± 9 (7)	8 ± 7 (6)	<0.001	<0.001
July	28 ± 9 (33)	24 ± 13 (34)	14 ± 10 (22)	<0.001	<0.001
August	29 ± 12 (34)	26 ± 11 (12)	23 ± 10 (21)	0.360	0.163
SIL-B§					
June	35 ± 9 (5)	17 ± 9 (6)	30 ± 8 (2)	0.045	0.033
July	40 ± 20 (6)	24 (1)	– (0)	–	0.313
August	40 ± 12 (3)	23 ± 2 (2)	4 (1)	0.117	0.050

* 1, Stomach empty; 2, stomach containing only undigested items; 3, stomach containing at least 1 partially digested item.

† Kruskal–Wallis test compared categories 1, 2, and 3; Mann–Whitney test compared category 1 (stomach empty) with categories 2+3 (stomach contents present).

‡ Percent position; $\bar{x}$ ± 1 SD (n).

§ Southern Indian Lake: Site A is a channel connecting 2 main lake basins; site B, 15 km away, is a bay with a narrow connection to the main lake.

testine. The data presented 2 patterns of helminth position with respect to stomach contents of the host, one for cestodes and another for nematodes.

Cestodes

Positions of scolices and strobilae of *T. crassus, T. nodulosus,* and *P. pinguis* generally did not differ significantly with respect to stomach contents of the host. The only exceptions were some comparisons of June samples from SIL, suggesting a seasonal variation in the relationship between worm position and stomach contents, but we rejected this possibility due to the following inconsistencies: (1) significant differences were noted for scolex position of *Triaenophorus* spp. at SIL-A but not SIL-B, and for strobila position of *P. pinguis* at SIL-B but not SIL-A; (2) attachment of *T. nodulosus* and *T. crassus* is associated with fibroblastic infiltration (Pronina and Pronin, 1982; Shostak and Dick, 1986), consistent with long-term attachment in 1 location. Therefore it is unlikely that the significant differences in scolex positions reflect movement each time the host feeds.

Our data were most suitable for detecting migrations cued directly by the presence of host stomach contents. It is possible that migration commenced in advance of the ingestion of a meal, cued by an indirect stimulus such as intestional nervous activity (Mettrick and Cho, 1981). If this occurred in pike, positions of their cestodes should have changed already by the time a meal arrived in the host's stomach, yet we observed no difference in cestode positions between the categories of "stomach empty" and "stomach with recent meal." We conclude that the 3 species of

TABLE III. Positions of adult and larval *Raphidascaris acus* in the intestine of *Esox lucius* relative to the presence of *Triaenophorus crassus,* for 3 categories of host stomach contents.

R. acus	*T. crassus*	Category 1*	Category 2*	Category 3*	Probability†
Adult	Absent	40 ± 20 (18)‡	28 ± 30 (4)	10 ± 11 (11)	0.001
	Present	34 ± 16 (62)	15 ± 11 (32)	12 ± 10 (17)	<0.001
Larval	Absent	30 ± 16 (17)	18 ± 20 (5)	5 ± 4 (12)	<0.001
	Present	26 ± 11 (71)	19 ± 12 (38)	19 ± 15 (20)	0.013
Total	Absent	35 ± 16 (21)	23 ± 27 (7)	8 ± 10 (13)	<0.001
	Present	27 ± 12 (80)	17 ± 11 (39)	18 ± 12 (20)	<0.001

* 1, Stomach empty; 2, stomach containing only undigested items; 3, stomach containing at least 1 partially digested item.

† Kruskal–Wallis test comparing categories 1, 2, and 3.

‡ Percent position; $\bar{x}$ ± 1 SD (n).

cestode in pike did not migrate in response to feeding activity of the host.

Nematodes

Our data showed that *R. acus* migrates. Worm position varied relative to host stomach contents, and the phenomenon was detected in collections of pike from different lakes and at several times of year. The more anterior position of *R. acus* when food was present in the stomach of pike was consistent with results of studies on other nematodes (*C. heterochronus, C. minutus,* and *C. aduncum* by MacKenzie and Gibson [1970]; *C. aduncum* by Williams et al. [1970]; *Nippostrongylus brasiliensis* by Croll [1976]; *Anisakis* sp. and *Phocanema decipiens* by McClelland [1980]). Ascarid nematodes, of which *Raphidascaris, Anisakis, Contracaecum,* and *Phocanema* are members, are known to feed on intestinal contents (Chitwood and Chitwood, 1974). Our interpretation that the data revealed a feeding migration for *R. acus* is strengthened by observations that they were furthest from empty stomachs, closer when a recently ingested meal was present, and nearest the stomach when digestion of the meal was well under way. Moreover, the position of *R. acus* in the intestine of pike often corresponds to the location of partially digested food items, and, in vitro, the worms concentrate around pieces of decomposing fish (A. J. Szalai, pers. comm.).

Adult *R. acus* had a more extensive migration than did larvae, suggesting a shift in behavior of *R. acus* during the course of its development within the definitive host. The position of larval *R. acus* is associated strongly with lesions in the intestinal wall of pike caused by attachment of *T. crassus,* and larvae may acquire their food from those lesions or inhabit them as an aid in maintaining position within the intestine (Shostak and Dick, 1986). These lesions may alter normal migratory movements of larvae, as our observations suggest that larvae migrated similarly to adults when *T. crassus* was absent, but less than adults when *T. crassus* was present.

Migrations and helminth community structure

Positions of intestinal helminths are used to interpret the role of interspecific interaction in structuring helminth communities (Holmes 1961; Kennedy, 1985; Lotz and Font, 1985; Bush and Holmes, 1986; Holmes and Price, 1986; Stock and Holmes, 1988). Migrations may confound these interpretations, as little is known regarding factors that promote or inhibit migration in the setting of a natural helminth community. It is likely that parasite factors (e.g., ability to reposition within intestine and feeding guild), host factors (e.g., frequency and quantity of meals and poikilothermy vs. homeothermy), and interactions between host and parasite or among parasites are involved.

It was interesting that the species that migrated was a nematode, whereas the 3 species that did not migrate were cestodes. These 2 groups feed in dramatically different ways. Nematodes belong to the "engulfer" guild (ingest host tissues or intestinal contents), and cestodes to the "absorber" guild (absorb nutrients across the body surface) (Bush and Holmes, 1986; Stock and Holmes, 1988). Engulfers would be expected to respond to the presence of a food bolus, in order to feed on particulate matter. It might be expected a priori that engulfers would migrate, and many appear to do so (MacKenzie and Gibson, 1970; Williams et al., 1970; Croll, 1976; Hobbs, 1980; McClelland, 1980). Predictions regarding migration by absorbers are more difficult because the tendency for a species to migrate probably is influenced by its ability to move, its specific nutrient requirements, the intestinal gradients of those nutrients, and their rates of supply (which may in turn be influenced by the host's feeding behavior and the presence of other species of parasite). A number of these factors can account for an absence of migration by cestodes of pike. As noted earlier, the 2 species of *Triaenophorus* probably have limited ability to relocate their scolices. The intestine of pike is short and has a uniform structure throughout the anterior half (Bucke, 1971) where all cestodes were found. Thus, although nutrients may be supplied in pulses following meals, peristaltic activity may disperse them throughout the anterior intestine and rapidly diminish gradients that might cue migrations. The cooccurrence of 3 absorbers also raises the possibility that interspecific interactions inhibited migration. Although some cestodes can migrate in multispecies infections (Williams et al., 1970), reports of cestode migration generally involve single-species infections (e.g., Read and Kilejian, 1969; Hopkins, 1970; Gray, 1977), whereas reduced or absent migrations are reported from multispecies infections (Silver et al. 1980; Bush and Holmes, 1986). Data from single-species infections of pike that would enable resolution of the role of interactions are lacking.

It is clear that the phenomenon of migration will complicate the study of community structure of intestinal helminths of pike. This study identified a nematode (*R. acus*) that migrates in response to food in the host's stomach, presumably increasing access to particulate material. However, migratory activity of the nematode was modified in the presence of a cestode (*T. crassus*) that did not migrate. Moreover, migration patterns of adult and larval *R. acus* varied according to the presence of absence of *T. crassus*.

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