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Observations on the Life Cycle of *Proteocephalus tumidocollus* (Cestoda: Proteocephalidae) in Steelhead Trout, *Oncorhynchus mykiss*

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ABSTRACT: The life cycle of *Proteocephalus tumidocollus* in a brackish water, aquacultural pond involves steelhead trout (*Oncorhynchus mykiss*) as definitive hosts, and freshwater (*Diaptomus* sp., *Paracyclops fimbriatus poppei*) or benthic marine (*Halicyclops* sp.) copepods as intermediate hosts. Steelhead trout do not feed on copepods directly. Instead, they consume the macroalga *Enteromorpha* sp. with epiphytic copepods attached. Between May 1981 and July 1982, there were no statistically significant monthly variations in prevalence, mean intensity, or relative density of *P. tumidocollus* in steelhead trout. However, there were marked decreases in mean intensity and relative density and a marked increase in the percentage of cestodes that were gravid in January to March 1982 when *Enteromorpha* sp. was absent from the pond.

KEY WORDS: *Proteocephalus tumidocollus,* Proteocephalidae, Cestoda, life cycle, seasonality, steelhead trout, *Oncorhynchus mykiss,* California.

Wagner (1953) described *Proteocephalus tumidocollus* from rainbow and brook trout from the California Trout Company, Mentone, California. Five reports of *P. tumidocollus* have since been published (Hicks and Threlfall, 1973; Hanek and Molnar, 1974; Arthur et al., 1976; Mamer, 1978; Arai and Mudry, 1983).

Wagner (1954) studied the life cycle of *P. tumidocollus* in freshwater. He fed its eggs to the copepods *Cyclops vernalis, Eucyclops agilis, Eucyclops speratus,* and *Tropocyclops prasinus,* which became infected. He was unable to infect the copepods *Macrocyclops albidus* and *Paracylops fimbriatus poppei* nor several other invertebrates. Procercoids developed rapidly at 20°C and became infective to trout at 9 to 19 days postinfection (PI). Trout definitive hosts became infected by eating copepod intermediate hosts. Second intermediate hosts were not required, although large trout could become infected by eating small infected trout.

Proteocephalus tumidocollus is common in steelhead trout, *Oncorhynchus mykiss* (Walbaum), in the brackish water ponds of the Arcata Wastewater Aquaculture Project, Arcata, California. While freshwater species of *Proteocephalus* are common and well studied, brackish water species are rare and poorly known (Wardle and McLeod, 1952; Yamaguti, 1959; Freze, 1965; Schmidt, 1986). The Arcata system offered an unusual opportunity to examine the seasonality and life cycle of a *Proteocephalus* sp. in brackish water.

Materials and Methods

Infected steelhead trout were obtained from South Pond (0.6 ha, avg. depth 2 m, avg. salinity 14.5 ppt), Arcata Wastewater Aquaculture Project, Arcata, California. Uninfected steelhead trout fry were obtained from the Humboldt State University Fish Hatchery. Fish were held in 19–38-liter aquaria supplied with 11°–17°C aerated, filtered water. Potential invertebrate hosts were sieved from South Pond (brackish water), the adjacent oxidation pond of the Arcata sewage treatment plant (freshwater), or from the adjacent Butcher's Slough on Humboldt Bay (seawater). Invertebrates were cultured in 2–19-liter aquaria (11°–17°C) and fed yeast and flaked fish food.

Seasonal occurrence of *P. tumidocollus* in steelhead trout from South Pond was determined from fish collected by angling at weekly intervals from 12 May 1981 to 31 July 1982. Seven to 20 fish were obtained at each sampling. Fish total length and weight were recorded prior to necropsy. Necropsy procedures were standard (Hoffman, 1967). Food items in stomachs of fish hosts were analyzed quantitatively using percent composition by weight (Bowen, 1983).

Adult cestodes were placed in 0.7% saline and allowed to shed eggs for use in life history studies. Eggs were used to expose cultured invertebrates, which were examined for developing procercoids from 30 min to 86 days after initial exposure. In addition, 150 wild *Anisogammarus confervicolus* (Stimpson) (Amphipoda) from South Pond were examined for natural procercoid infections.

To infect experimental fish definitive hosts, invertebrates from cultures were fed to hatchery-reared (cestode-free) steelhead trout fry. Twenty-five fish were fed *Anisogammarus confervicolus* (Amphipoda), and 25 fish were fed a combination of *Corophium spinicorne*

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Table 1. Levels of infection of *Proteocephalus tumidocollus* and percentage of cestodes gravid in steelhead trout, *Oncorhynchus mykiss*, from South Pond, Arcata Wastewater Aquaculture Project, California, May 1981 to July 1982.

Month	No. of fish examined	No. of fish infected (%)	Mean intensity*	Relative density†	Range in nos. per infection	Percentage of cestodes gravid
1981						
May	14	6 (42.8)	8.5	3.6	2–28	74.5
June	12	3 (25.0)	7.7	1.9	6–7	13.0
July	8	4 (50.0)	5.8	2.9	2–4	13.0
August	16	2 (12.5)	1.5	0.2	1–2	0
September	18	8 (44.4)	7.5	3.3	1–37	25.0
October	18	8 (44.4)	4.8	2.1	1–10	92.1
November	20	6 (30.0)	17.7	5.3	2–84	19.8
December	7	2 (28.6)	5.0	1.4	4–6	70.0
1982						
January‡	13	4 (30.8)	6.0	1.8	1–11	100
February‡	12	6 (50.0)	2.5	1.2	1–5	93.3
March‡	8	1 (12.5)	2.0	0.3	2	100
April	16	7 (43.8)	30.0	13.1	1–66	96.2
May	20	10 (50.0)	19.7	9.8	1–125	29.4
June	18	7 (38.9)	10.7	4.2	1–48	57.3
July	16	4 (25.0)	8.2	2.1	1–25	0

* Total number of cestodes in sample ÷ number of infected hosts in sample.
† Total number of cestodes in sample ÷ total number of hosts in sample.
‡ No *Enteromorpha* sp. in South Pond.

Stimpson (Amphipoda) and *Gnorimosphaeroma oregonensis* (Dana) (Isopoda). Twenty-five fish were fed a mixture of small Copepoda, including *Diaptomus* sp., 1 planktonic and 1 benthic species of *Halicyclops, Paracyclops fimbriatus poppei* (Rehberg), and *Tigriopus californicus* (Baker). Seventy-two fish were held as controls and were fed a commercial trout pellet. After 8 wk, all fish were killed and examined for cestodes. In addition, 26 three-spined sticklebacks (*Gasterosteus aculeatus* L.) from South Pond were examined for cestodes to see if they might be capable of passing juvenile cestodes on to steelhead trout via predation.

Results

Proteocephalus tumidocollus was recovered from the pyloric ceca of 78 of 216 (36.1%) steelhead trout examined from South Pond during the seasonal survey. It was present in all months of the year. There was no marked seasonal variation in prevalence (Table 1). Relative density and mean intensity seemed to vary seasonally with peaks in November 1981 and May 1982; however, these variations were not statistically significant by analysis of variance ($P < 0.05$). There was a marked decrease in mean intensity and relative density in January to March 1982 when *Enteromorpha* sp. was absent from South Pond. Prevalence, mean intensity, and relative density all increased as fish total length increased. Gravid cestodes occurred in all but 2 mo and were most prevalent in winter, particularly in those months when *Enteromorpha* sp. was absent from South Pond (Table 1).

Analysis of stomach contents from 68 steelhead trout from South Pond showed that on a percent composition by weight basis, they ate: *Corophium spinicorne* (Amphipoda) 36.70%, *A. confervicolus* (Amphipoda) 29.90%, detritus 11.90%, *Enteromorpha* sp. (macroalga) 4.80%, mysids (Crustacea) 3.60%, *G. aculeatus* (fish) 2.50%, *G. oregonensis* (Isopoda) 2.12%, filamentous algae 1.90%, earwigs (terrestrial insects) 1.70%, Diptera 1.41%, unidentifiable fish larvae 1.20%, annelids 1.60%, unidentifiable invertebrates 0.36%, crabs 0.30%, and copepods 0.01%. *Enteromorpha* sp. was eaten whenever it was available in South Pond (May to December 1981, April to July 1982).

Experimental infections were established in the copepods *Diaptomus* sp., *P. fimbriatus poppei,* and a benthic species of *Halicyclops.* The freshwater copepod *Acanthocyclops* (*A.*) *vernalis* (Fischer) was also experimentally infected. This species enters South Pond when the pond is filled using a mixture of treated sewage effluent and seawater. However, it cannot tolerate the salinity in South Pond for very long. *Anisogammarus confervicolus* (Amphipoda), *C. spinicorne* (Am-

phipoda), *G. oregonensis* (Isopoda), *T. californicus* (Copepoda), and a planktonic species of *Halicyclops* (Copepoda) were refractory to experimental infection. None of 150 wild *A. confervicolus* examined from South Pond was infected.

Three of 25 hatchery-reared steelhead trout fed copepods (*Diaptomus* sp., 1 planktonic and 1 benthic species of *Halicyclops, P. fimbriatus poppei, T. californicus*) from exposed cultures had immature *P. tumidocollus* at 56 days PI. One fish had 3 cestodes and 3 fish had 1 immature cestode each. All cestodes were attached to the pyloric ceca. None of the 25 fish fed exposed *A. confervicolus,* none of the 25 fish fed exposed *C. spinicorne* and *G. oregonensis,* and none of the 72 control fish was infected. None of 26 three-spined sticklebacks examined from South Pond harbored cestodes even though smaller sticklebacks fed almost exclusively on copepods.

Discussion

Both marine (benthic *Halicyclops* sp.) and freshwater (*Diaptomus* sp., *P. fimbriatus poppei*) copepods are suitable intermediate hosts for *Proteocephalus tumidocollus* in South Pond. In addition, the entire life cycle takes place in brackish water. This utilization of a marine host and brackish water is unusual among species of *Proteocephalus* (Wardle and McLeod, 1952; Yamaguti, 1959; Freze, 1965; Schmidt, 1986).

Copepod intermediate hosts of *P. tumidocollus* are not an important item in the diet of steelhead trout definitive hosts in South Pond (0.01% by weight). However, the benthic *Halicyclops* sp. and *P. fimbriatus poppei* are epiphytic on the macroalga *Enteromorpha* sp. *Enteromorpha* sp. accounted for up to 30.1% by weight of the diet of steelhead trout in some months (4.8% over the entire study). Thus, steelhead trout in South Pond most likely become infected by incidentally ingesting copepods as they feed on *Enteromorpha* sp. This incidental mode of infection has not to our knowledge been reported previously.

There were no statistically significant monthly variations in prevalence, mean intensity, or relative density of *P. tumidocollus* in steelhead trout in South Pond. However, there was a marked decrease in both mean intensity and relative density, and a marked increase in the percentage of cestodes recovered from steelhead trout that were gravid in January to March 1982 when *Enteromorpha* sp. was absent from South Pond. In the absence of *Enteromorpha* sp., steelhead trout do not eat significant numbers of copepods. Hence, new infections do not occur. Measures of infection intensity are reduced and cestodes from older infections tend to become gravid. Thus, seasonal cycles in abundance or maturity of *P. tumidocollus* in steelhead trout in South Pond depend largely on the seasonal occurrence of *Enteromorpha* sp. *Enteromorpha* sp. is normally present in South Pond as long as South Pond remains sufficiently brackish. When there is sufficient rain to dilute South Pond (most likely in the winter rainy season), *Enteromorpha* sp. dies back and in some years disappears altogether.

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Literature Cited

Arai, H. P., and D. R. Mudry. 1983. Protozoan and metazoan parasites of fishes from the headwaters of the Parsnip and McGregor rivers, British Columbia: a study of possible parasite transfaunations. Canadian Journal of Fisheries and Aquatic Sciences 40:1676–1684.

Arthur, J. R., L. Margolis, and H. P. Arai. 1976. Parasites of fishes of Aishihik and Stevens lakes, Yukon Territory, and potential consequences of their interlake transfer through a proposed water diversion for hydroelectrical purposes. Journal of the Fisheries Research Board of Canada 33:2489–2499.

Bowen, S. H. 1983. Quantitative description of the diet. Pages 325–336 *in* L. A. Nielsen and D. L. Johnson, eds. Fisheries Techniques. American Fisheries Society, Bethesda, Maryland.

Freze, V. I. 1965. Proteocephalata in Fish, Amphibians, and Reptiles. Essentials of Cestodology, Vol. 5. Akademiya Nauk S.S.S.R. Gel'mintologicheskaya Laboratoriya. (Israel Program for Scientific Translations, Jerusalem. 1969. 597 pp.)

Hanek, G., and K. Molnar. 1974. Parasites of freshwater and anadromous fishes from Matamek River System, Quebec. Journal of the Fisheries Research Board of Canada 31:1135–1139.

Hicks, F. J., and W. Threlfall. 1973. Metazoan parasites of salmonids and coregonids from coastal Labrador. Journal of Fish Biology 5:399–415.

Hoffman, G. L. 1967. Parasites of North American Freshwater Fishes. University of California Press, Berkeley. 486 pp.

Mamer, B. E. 1978. The parasites of trout in northwest Washington. Journal of Parasitology 64:314.

Schmidt, G. D. 1986. CRC Handbook of Tapeworm Identification. CRC Press, Inc., Boca Raton, Florida. 675 pp.

Wagner, E. D. 1953. A new species of *Proteocephalus* Weinland, 1858, (Cestoda), with notes on its life history. Transactions of the American Microscopical Society 72:364–369.

———. 1954. The life history of *Proteocephalus tumidocollus* Wagner, 1953, (Cestoda), in rainbow trout. Journal of Parasitology 40:489–498.

Wardle, R. A., and J. A. McLeod. 1952. The Zoology of Tapeworms. University of Minnesota Press, Minneapolis. 780 pp.

Yamaguti, S. 1959. Systema Helminthum. Vol. 2. The Cestodes of Vertebrates. Interscience Publishers, Inc., New York. 860 pp.