John Janovy Publications   Papers in the Biological Sciences

12-2009

Community Structure and Seasonal Dynamics of *Dactylogyrus* spp. (Monogenea) on the Fathead Minnow (*Pimephales promelas*) from the Salt Valley Watershed, Lancaster County, Nebraska

Alaine Knipes
University of Nebraska - Lincoln, lainey244@yahoo.com

John J. Janovy Jr.
University of Nebraska - Lincoln, jjanovy1@unl.edu

COMMUNITY STRUCTURE AND SEASONAL DYNAMICS OF *DACTYLOGYRUS* SPP. (MONOGENEA) ON THE FATHEAD MINNOW (*PIMEPHALES PROMELAS*) FROM THE SALT VALLEY WATERSHED, LANCASTER COUNTY, NEBRASKA

Alaine K. Knipes and John Janovy, Jr.
School of Biological Sciences, University of Nebraska–Lincoln, Lincoln, Nebraska 68588. *e-mail: alaineknipes@huskers.unl.edu*

ABSTRACT: The gill monogene communities of *Pimephales promelas* (fathead minnow) in 3 distinct sites on converging streams were investigated from 2004 to 2006 in 3 different seasons. Thirty collections of *P. promelas* were made in southeastern Nebraska along 3 converging tributaries: Elk Creek (40.88534°N, 96.83366°W), West Oak Creek (40.9082°N, 96.81432°W), and Oak Creek (40.91402°N, 96.770583°W), Lancaster County, Nebraska. In all, 103 *P. promelas* were collected from Elk Creek, 115 from West Oak Creek, and 78 from Oak Creek and examined for gill monogenes. Among the *P. promelas* collected, 93.5% were infected with up to 3 species of *Dactylogyrus,* including *Dactylogyrus simplex* Mizelle, 1937, *Dactylogyrus bychowskyi* Mizelle, 1937, and *Dactylogyrus pectenatus* Mayes, 1977. Mean intensities at Elk Creek, West Oak Creek, and Oak Creek were 17.6, 22.8, and 25.1, and prevalences 88, 95, and 97%, respectively. At these 3 sites: (1) *P. promelas* does not share *Dactylogyrus* species with *Semotilus atromaculatus* (Creek chub) or *Notropis stramineus* (Sand shiner); (2) fish size and sex are not predictive of *Dactylogyrus* infection; (3) *Dactylogyrus* spp. vary (not always predictably) in their seasonal occurrence; (4) populations of *Dactylogyrus* spp. respond to environmental differences among sites; and (5) the community structure of *Dactylogyrus* spp. (order of abundance) is independent of environment.

Dactylogyrus Diesing, 1850 (Platyhelminthes: Monogenoidea), is a highly diverse genus with more than 900 described species that are parasitic primarily on gills of cyprinid fishes, the largest and widest continuously distributed fish family in the world's fresh waters (Gibson et al., 1996; Nelson, 2006). More than 131 *Dactylogyrus* species have been reported from North America (Gibson et al., 1996). The fathead minnow, *Pimephales promelas* Rafinesque, 1820, is a North American cyprinid commonly reared for fishing bait and has a parasite fauna that is well documented (Hoffman, 1999; Weichman and Janovy, 2000). This minnow occurs in streams with diverse characteristics and thus is a good candidate for use in studies aimed at discovering the roles environment and fish distribution play in structuring monogene populations and communities.

Weichman and Janovy (2000) described the gill monogene community of *P. promelas* in 2 diverging first-order streams in Lancaster County, Nebraska, from April to October 1998. They found 3 species of *Dactylogyrus* occurring on fathead minnows, including *Dactylogyrus simplex,* Mizelle, 1937, *Dactylogyrus bychowskyi,* Mizelle, 1937, and *Dactylogyrus pectenatus* Mayes, 1977. The distribution of larval trematodes (''blackspot'') on these same hosts indicated that fish were more or less restricted to certain tributaries of the drainage (Weichman and Janovy, 2000), suggesting that their monogene communities might also reveal differences attributable to isolation and habitat effects. Unpublished blackspot data from the present study are consistent with those of Weichman and Janovy (2000).

Dactylogyrus spp. are ectoparasites with direct life cycles. Each individual monogene on the gills is the result of a separate encounter with an infective stage, and, when that individual monogene dies, it will fall off. It is generally accepted that the life spans of *Dactylogyrus* spp. are shorter than those of their fish hosts. Therefore, individual fish will continually lose and gain gill monogenes so that seasonal occurrence data may be indicative of the abundance of the infective stage in the environment.

A high degree of host specificity, characteristic of *Dactylogyrus* spp., reveals opportunities for, and suggests mechanisms of, parasite dispersal through the environment because those

parasites are bound by their particular host's movements through that habitat. When a host's movement is restricted, the movements of its *Dactylogyrus* species should be similarly restricted. Although stable environmental and host conditions might be expected to yield stable parasite populations, variations in environmental conditions, namely, site or seasonal differences in water temperature and flow rate, might be expected to have important impacts on the behavior of fish and the distribution of their parasites in lotic systems. Thus, a study of the ways in which 3 congeneric species of parasites distribute themselves among fish of a single species at 3 abiotically different, but geographically proximate, streams will provide insight into the ways in which populations of parasite species respond to environmental conditions and distribute themselves in nature.

The purpose of the present study was to explore communities of *Dactylogyrus* spp. in an effort to understand how, despite variations in transmission conditions, the parasites are maintained in the environment. We describe seasonal population dynamics and community structure of 3 *Dactylogyrus* spp. in 3 distinct sites on converging streams in southeastern Nebraska over a period of 3 yr. The study sought to determine (1) host specificity of *Dactylogyrus* spp. infecting *P. promelas* within the 3-stream system, (2) the role of host demographics (size, sex) in providing structure to populations of *Dactylogyrus* species, (3) seasonal and yearly dynamics of *Dactylogyrus* spp. populations within sites, (4) population structure differences of *Dactylogyrus* spp. within sites, and (5) population and community structure (order of abundance) of *Dactylogyrus* spp. among sites. In particular, this study tested the following null hypotheses: (1) no difference in abundance, intensity, and prevalence among 3 congeners coexisting within sites and (2) no difference in community structure (order of abundance) of 3 congeners among 3 distinct sites. Rejection of the null hypotheses would reveal innate parasite species differences in fecundity and transmission mechanisms, thus providing insight into factors contributing to species diversification within a genus of monogenes. This study of seasonal dynamics constitutes the first multisite, multiyear study of a complex community of *Dactylogyrus* spp. on a native North American cyprinid species.

This study, therefore, tests the biological hypothesis that closely related species, with direct aquatic life cycles, respond differently

to shared environmental conditions. Substantial fluctuations in stream flow and stable differences between streams provide the abiotic conditions necessary for testing such a hypothesis (Janovy et al., 1997).

MATERIALS AND METHODS

A total of 296 *P. promelas* was examined. Minnows were collected by seine from Elk Creek (Elk) (40.88534°N, 96.83366°W), West Oak Creek (West Oak) (40.9082°N, 96.81432°W), and Oak Creek (Oak) (40.91402°N, 96.770583°W), Lancaster County, Nebraska, between July 2004 and October 2006. Sample sizes were dictated by the number of fish captured and by the number that could be examined within 48 hr of capture. Fish were brought to the laboratory at the University of Nebraska–Lincoln in buckets with aerators and dissected within 48 hr of collection. All fish were identified according to Plieger (1997). Fish were measured for standard length (STL) and total length (TTL), and sexed, and the gills removed and placed in 1:4,000 formalin (Kritsky et al., 1986).

Monogenes were brushed from the host gills and preserved in alcohol-formalin-acetic acid according to Pritchard and Kruse (1982). They were then washed in 70% ethyl alcohol (ETOH), stained with Semichon's acetocarmine, dehydrated through an ETOH series, cleared in xylene, and permanently mounted on slides with Damar's balsam (Spectrum Chemical, Gardena, California). Living worms also were studied and recorded using video and digital photography. Monogene identification was based on comparison of copulatory structures and on measurements of scelerotized hamuli, hooks, and connective bars of the haptor (Murith and Beverley-Burton, 1985), as found in original species descriptions (Mizelle, 1937; Mayes, 1976, 1977).

Population structure was described as prevalence (PR), mean abundance (MA), and mean intensity (MI), using terminology of Bush et al. (1997). Community structure was described as order of abundance and species richness. Richness is the number of *Dactylogyrus* species occurring on an individual fish. Host STL and TTL were measured for each fish, and STL alone was statistically deemed to be the best measure of host size. All values are reported as mean ± 1 standard deviation (SD).

The chi-square test was used to compare PR within and among *Dactylogyrus* spp., among seasons, and among sites. The chi-square test was also used to compare PR of *Dactylogyrus* spp. between male and female hosts. Student's *t*-test was used to compare differences in mean abundance among *Dactylogyrus* spp., among seasons, and among sites. Total MA and MI of the 3 *Dactylogyrus* spp. were compared among sites using ANOVA. Approximate *t*-tests were calculated when variances were heteroscedastic (Sokal and Rohlf, 1995). Bonferroni corrections based on number of comparisons were used, i.e., testing at significance level of $0.05/3 = 0.017$, to safeguard against false significances due to multiple tests on the same data. Pearson's correlation was used to determine relationships among host STL and *Dactylogyrus* abundance, as well as to determine relationships among host STL and species richness per individual host.

Environmental data were recorded 4 times in 2005 and twice in 2006, at all 3 collection sites. Air and water temperatures were measured using a Fisherbrand® glass thermometer (Fisher, Pittsburgh, Pennsylvania). Depth and width at collection sites were measured using a tape measure. Flow rate was measured using a standard USGS Top Setting Wading Rod with a Pygmy Current Meter. The pH of water was measured using a pocket-sized pHep® meter. The electrical conductivity (EC) of water was measured using a DiST WP conductivity/TDS meter. Water samples were brought back to the University of Nebraska–Lincoln in sterile 32-oz Nalgene® containers. In the lab, heterotrophic plate count (HPC) was measured using the IDEXX SimPlate for HPC method. Following the 48-hr incubation period, SimPlates were examined for fluorescing wells, each of which corresponded to most probable number of total waterborne bacteria in the water sample.

RESULTS

General observations

A total of 5,976 monogenes of *Dactylogyrus* was removed from the gills of 276 infected *P. promelas* examined between July 2004 and October 2006. In total, 3,525 worms from 210 *P. promelas* were identified to species; 40 of those worms were immature and identifiable only to the generic level. At all 3 collection sites, the gill parasite community comprised 3 species, including *D. simplex, D. bychowskyi,* and *D. pectenatus.* The 3 *Dactylogyrus* species found on *P. promelas* were never found on either of the 2 other fish species examined (*Notropis stramineus,* n = 129; *Semotilus atromaculatus,* n = 109) in 3 yr of collections. One species (*D. rubellus*) was found on *Notropis stramineus,* and 3 species (*D. tenax, D. microphallus,* and *D. attenuatus*) were found on *Semotilus atromaculatus.* In 3 yr, none of the 6 species from *N. stramineus* and *S. atromaculatus* was ever found on *P. promelas.*

Dactylogyrus species richness on *P. promelas* was 2.10 ± 1.08 species per fish. Overall PR (based on n = 210 *P. promelas*) was 92.1%, MA was 20.40 ± 22.82, and MI was 22.20 ± 22.95. In total, *P. promelas* were infected with zero (9.1%), 1 (19.1%), 2 (28.6%), or 3 (43.3%) species of *Dactylogyrus.* The order of abundance of *Dactylogyrus* spp. was stable in all collections at all sites, with the exception of the summer of 2004 at Elk and fall 2004 at West Oak.

Site data

The 3 collection sites differ in their average air and water temperature, pH, width and depth, flow rate, HPC, turbidity, and EC (Table I). All 3 sites are located in an agricultural area approximately 16 km outside the Lincoln, Nebraska, city limits, though they differ in their surrounding land use. Elk is narrow, tree lined, and well shaded; West Oak is narrow, among farmed fields, and exposed; and Oak is wide, among farm fields and depressed with steep banks. Although the 3 sites are within the same watershed, they differ in their ability to tolerate storm-related water level changes. Overall, Elk has the least variable flow rate, whereas both West Oak and Oak are subject to highly variable flow rates.

Host sex and size

Overall, male fish (mean STL 4.99 cm ± 1.06) were larger than females (4.90 cm ± 0.77). In some collections, males were significantly larger than females; however, the differences were not consistent, and, in 1 collection, females were significantly larger than males (Table II). In some collections, fish at Elk were significantly smaller than fish at Oak and West Oak, though the differences were not consistent and sometimes even reversed (Table III).

There were no significant differences in PR or MA of *D. simplex, D. bychowskyi,* or *D. pectenatus* between male and female fish in any collection at any site, except at Elk in summer 2005, when females had a significantly higher MA of *D. pectenatus* than males ($t = 1.83, P < 0.05$) (Table IV).

At all 3 sites, larger fish had greater total *Dactylogyrus* abundance than smaller fish. There were significant positive correlations between STL and abundance of *D. bychowskyi* and *D. pectenatus* at Elk and West Oak, and between STL and abundance of *D. simplex* at West Oak (Figs. 1, 2). There were no significant correlations between STL and abundance of any of the 3 *Dactylogyrus* spp. at Oak (Fig. 3). Although the null hypothesis of no relationship was rejected in the cases mentioned, the r^2 values were all less than 0.10.

There were no significant correlations for STL and *Dactylogyrus* spp. richness at Elk or Oak ($r = 0.002, P > 0.05$; and $r =$

TABLE I. Site data: air temperature, water temperature, pH, depth, width, flow rate, heterotrophic plate count (HPC), turbidity, and electrical conductivity (EC).*

Collection site	Air (°C)	Water (°C)	pH	Depth (ft)	Width (ft)	Flow rate (ft/sec)	HPC (MPN/ml)	Turbidity (NTU)	EC (μS/cm)
Elk Creek									
2005									
May	—	16.0	7.7	0.8	4.5	0.7	1.1×10^4	21.7	0.7
June	18.5	18.0	8.2	1.5	6.5	0.5	—	76.0	0.7
July	22.5	21.0	7.8	1.3	6.8	0.2	5.1×10^4	47.7	0.9
August	25.0	23.0	8.4	1.2	6.3	0.7	1.4×10^4	23.4	0.9
2006									
May	23.0	20.0	8.4	1.7	7.3	0.3	2.1×10^4	16.7	0.7
July	25.0	21.0	8.7	2.5	—	0.1	1.8×10^4	11.8	0.9
Total	22.8	19.8	8.2	1.5	6.3	0.3	2.3×10^4	32.9	0.8
West Oak Creek									
2005									
May	24.0	19.0	7.8	0.6	4.0	0.6	1.1×10^4	29.8	0.6
June	18.5	17.5	8.0	0.3	4.0	1.6	—	901.0	0.4
July	20.0	19.5	8.2	0.8	8.4	0.2	1.4×10^4	30.8	0.6
August	27.0	21.0	8.1	0.7	8.3	0.1	1.2×10^4	23.3	0.6
2006									
May	22.5	18.0	8.2	0.8	5.0	0.1	2.9×10^4	21.1	0.6
July	23.0	20.0	8.2	0.8	2.7	0.1	1.7×10^4	39.5	0.6
Total	22.5	19.1	8.1	0.7	5.4	0.5	1.7×10^4	174.3	0.6
Oak Creek									
2005									
May	27.0	17.5	7.9	1.8	30.0	0.7	7.6×10^3	74.9	1.1
June	18.5	18.5	8.0	1.5	30.0	2.1	—	679.0	0.8
July	29.0	23.0	8.2	1.0	29.5	0.8	7.4×10^4	20.9	1.2
August	32.0	25.5	8.2	1.4	30.8	0.3	2.6×10^4	29.9	2.1
2006									
May	25.5	20.0	8.5	1.2	10.7	0.7	2.4×10^4	25.8	1.4
July	25.0	22.0	8.7	1.3	—	0.6	2.2×10^4	48.8	1.1
Total	26.2	21.1	8.3	1.4	26.2	0.9	3.1×10^4	146.6	1.3

* MPN/ml = most probable number of microorganisms per milliliter; NTU = nephelometric turbidity units; μS/cm = micro-Siemens per centimeter.

0.196, $P > 0.05$, respectively), but there was a significant positive correlation at West Oak ($r = 0.203$, $P < 0.05$), although again the r^2 value was less than 0.10.

Within site comparisons

Elk Creek: Seventy-five (85.23%) of 88 *P. promelas* collected at Elk were infected with *Dactylogyrus* spp. A total of 709 *D. simplex,* 261 *D. bychowskyi,* and 132 *D. pectenatus* was collected from the gills of 67, 56, and 53 *P. promelas,* respectively. Overall, *Dactylogyrus* spp. MA and MI at Elk were 16.36 ± 17.45 (range 0–122) and 19.20 ± 17.41, respectively.

In all years, *D. simplex* occurred on *P. promelas* in all seasons at Elk (Table V). There were no significant seasonal differences in PR, MA, or MI of *D. simplex,* except for MA and MI in 2005. At Elk there were no significant between-year differences in PR, MA, or MI of *D. simplex,* except for PR in fall, and for MA and MI in spring and summer. In all years, *D. bychowskyi* occurred on *P. promelas* in all seasons at Elk, except in fall 2004. There were no significant seasonal differences in PR, MA, or MI of *D. bychowskyi,* except for PR and MA in 2005. At Elk, there were no significant between-year differences in PR, MA, or MI of *D. bychowskyi,* except for PR and MA in spring and summer. In all

years, *D. pectenatus* occurred on *P. promelas* in all seasons at Elk, except in fall 2004. There were no significant seasonal differences in PR, MA, or MI of *D. pectenatus,* except for PR and MA in 2005. At Elk, there were no significant between-year differences in PR, MA, or MI of *D. pectenatus,* except for PR in spring and summer.

At Elk, there were no significant differences in PR, MA, or MI among *Dactylogyrus* spp. except in spring 2005, summers 2004, 2005, and 2006, and spring 2006 (Table VI).

The MA and MI of *D. simplex* peaked in summer in all years at Elk. The PR of *D. simplex* peaked in summer in 2004, in fall in 2005, and in spring in 2006. The PR of *D. bychowskyi* peaked in summer in all years. The MA of *D. bychowskyi* peaked in summer in 2004 and 2005 and in spring in 2006. The MI of *D. bychowskyi* peaked in summer in 2004, in fall in 2005, and in spring in 2006. The PR of *D. pectenatus* peaked in summer in all years. The MA of *D. pectenatus* peaked in summer in 2004 and 2005, and again in the spring in 2006.

West Oak Creek: Seventy-four (96.10%) of 77 *P. promelas* collected at West Oak were infected with *Dactylogyrus* spp. A total of 1,020 *D. simplex,* 282 *D. bychowskyi,* and 142 *D. pectenatus* was collected from the gills of 69, 59, and 48 *P.*

TABLE II. Collections of *Pimephales promelas:* sites, dates, STL (cm), and significance tests.*

Collection date	Male		Female		Tests of significance: male STL vs. female STL
	n	STL ± 1 SD (range)	n	STL ± 1 SD (range)	
Elk Creek					
2004					
Summer	2	4.5 ± 0.2 (4.3–4.6)	13	4.9 ± 0.6 (4.2–6.0)	$t = 1.13, P > 0.05$
Fall	2	6.0 ± 0.4 (5.7–6.2)	7	5.1 ± 0.5 (4.5–5.7)	$t = 2.30, P < 0.05$
2005					
Spring	1	4.0	6	4.9 ± 0.6 (4.0–5.6)	—
Summer	6	4.2 ± 0.7 (3.5–5.3)	14	4.3 ± 0.7 (3.1–5.6)	$t = 0.22, P > 0.05$
Fall	3	3.2 ± 0.4 (2.9–3.7)	4	3.7 ± 0.9 (2.8–5.0)	$t = 0.84, P > 0.05$
2006					
Spring	6	5.8 ± 0.5 (5.2–6.4)	8	5.3 ± 0.4 (4.7–6.0)	$t = 2.59, P < 0.05$
Summer	12	4.3 ± 0.6 (3.1–5.5)	9	4.4 ± 1.0 (3.6–6.8)	$t = 0.32, P > 0.05$
West Oak Creek					
2004					
Summer	2	5.7 ± 1.5 (4.6–6.7)	14	5.3 ± 0.7 (4.2–6.2)	$t = 0.64, P > 0.05$
Fall	1	6.7	7	5.9 ± 0.7 (5.2–6.8)	—
2005					
Spring	2	6.5 ± 0.8 (5.9–7.0)	6	5.7 ± 0.3 (5.3–6.3)	$t^1 = 1.38, P > 0.05$
Summer	16	4.3 ± 1.3 (2.8–6.8)	6	5.4 ± 1.0 (4.5–7.2)	$t = 1.96, P < 0.05$
Fall	5	4.5 ± 0.9 (3.2–5.7)	11	4.0 ± 0.4 (3.3–4.5)	$t = 1.33, P > 0.05$
2006					
Spring	7	5.7 ± 0.7 (4.7–6.5)	1	4.5	—
Summer	15	5.0 ± 0.9 (3.2–6.4)	4	4.7 ± 0.5 (4.0–5.2)	$t = 0.82, P > 0.05$
Oak Creek					
2004					
Summer	5	5.7 ± 0.1 (5.6–5.9)	5	5.2 ± 0.4 (4.6–5.6)	$t = 2.85, P < 0.05$
Fall	1	3.3	3	4.4 ± 0.6 (3.9–5.0)	—
2005					
Spring	6	6.4 ± 0.3 (6.1–7.0)	12	5.2 ± 0.3 (4.6–5.6)	$t = 7.26, P < 0.05$
Summer	9	5.0 ± 1.0 (3.0–6.2)	1	5.1	—
Fall	8	4.9 ± 0.8 (3.8–6.1)	6	5.0 ± 0.8 (3.9–6.0)	$t = 0.18, P > 0.05$
2006					
Spring	5	5.9 ± 0.4 (5.3–6.2)	3	4.5 ± 0.2 (4.3–4.7)	$t = 6.03, P < 0.05$
Summer	8	5.2 ± 0.5 (4.1–5.6)	5	4.8 ± 0.3 (4.5–5.2)	$t = 1.58, P > 0.05$

* SD = standard deviation; STL = standard length.

TABLE III. Standard length (cm) of *P. promelas:* comparisons among collection sites.*

Collection date	Elk		West Oak		Oak	
	n	STL ± 1 SD (range)	n	STL ± 1 SD (range)	n	STL ± 1 SD (range)
Summer 2004	15	4.85 ± 0.54 (4.2–6.0)	17	5.30 ± 0.72 (4.2–6.7)	10	5.45 ± 0.40 (4.6–5.9)†
Fall 2004	9	5.26 ± 0.60 (4.5–6.2)‡	8	6.0 ± 0.67 (5.2–6.8)§	5	3.86 ± 0.81 (2.9–5.0)
Spring 2005	12	4.36 ± 0.89 (2.9–5.6)	9	5.88 ± 0.51 (5.3–7.0)‖	18	5.59 ± 0.63 (4.6–7.0)#
Summer 2005	25	4.0 ± 0.86 (2.3–5.6)	23	4.49 ± 1.38 (2.3–7.2)	10	4.98 ± 0.92 (3.0–6.2)¶
Fall 2005	7	3.51 ± 0.75 (2.8–5.0)	16	4.17 ± 0.61 (3.2–5.7)	14	4.97 ± 0.78 (3.8–6.1)**
Spring 2006	14	5.5 ± 0.50 (4.7–6.4)	8	5.58 ± 0.75 (4.5–6.5)	8	5.35 ± 0.76 (4.3–6.2)
Summer 2006	21	4.38 ± 0.77 (3.1–6.8)	20	4.93 ± 0.79 (3.2–6.4)	13	5.05 ± 0.45 (4.1–5.6)††

* SD = standard deviation; STL = standard length. Significance level $P < 0.017$.
† OC STL significantly greater than EC, $t = 3.02$.
‡ EC STL significantly greater than OC, $t = 3.68$.
§ WC STL significantly greater than OC, $t = 5.16$.
‖ WC STL significantly greater than OC, $t = 4.55$.
OC STL significantly greater than EC, $t = 4.43$.
¶ OC STL significantly greater than EC, $t = 2.99$.
** OC STL significantly greater than EC, $t = 4.07$. OC STL significantly greater than WC, $t = 3.15$.
†† OC STL significantly greater than EC, $t = 3.23$.

TABLE IV. Comparisons of male and female *P. promelas* infected with *Dactylogyrus* spp.: dates, sample sizes, and infection indices at 3 sites.*

Collection date	n	Male MA ± 1 SD (range) D. simplex	D. bychowskyi	D. pectenatus	n	Female MA ± 1 SD (range) D. simplex	D. bychowskyi	D. pectenatus	Tests of significance: male vs. female Ds	Db	Dp
Elk Creek											
2004											
Summer	2	4.0 ± 5.7 (0–8)	2.0 ± 2.8 (0–4)	0.50 ± 0.7 (0–1)	10	3.5 ± 4.1 (0–9)	0.8 ± 1.2 (0–3)	2.0 ± 3.7 (0–10)	No	No	No
Fall	1	0	0	0	6	2.0 ± 3.5 (0–9)	0	0	—	—	—
2005											
Spring	1	1.0	4.0	0	6	3.7 ± 3.5 (0–8)	1.7 ± 0.5 (0–1)	0.8 ± 1.6 (0–4)	—	—	—
Summer	6	6.8 ± 6.9 (0–15)	2.3 ± 2.6 (0–6)	1.2 ± 1.0 (0–2)	14	18.4 ± 23.5 (4–97)	5.0 ± 6.3 (0–20)	2.5 ± 1.65 (0–5)	No	No	F > M
Fall	3	3.3 ± 2.1 (1–5)	3.0 ± 5.2 (0–9)	0.8 ± 1.0 (0–2)	4	6.8 ± 6.6 (2–16)	3.0 ± 4.1 (0–9)	0.8 ± 1.0 (0–2)	No	No	No
2006											
Spring	6	11.5 ± 8.9 (0–21)	6.0 ± 7.1 (0–19)	1.8 ± 2.2 (2–11)	6	6.5 ± 6.8 (0–18)	6.0 ± 4.0 (2–11)	2.7 ± 4.2 (0–11)	No	No	No
Summer	9	9.1 ± 8.1 (0–20)	3.6 ± 3.1 (1–11)	1.6 ± 1.1 (0–3)	7	10.7 ± 6.6 (0–22)	3.0 ± 4.1 (0–12)	1.6 ± 1.5 (0–4)	No	No	No
West Oak Creek											
2004											
Summer	2	4.0 ± 5.7 (0–8)	6.0 ± 8.5 (0–12)	3.0 ± 4.2 (0–6)	12	7.5 ± 8.6 (0–29)	2.8 ± 2.3 (0–9)	1.1 ± 1.1 (0–4)	No	No	No
Fall	1	5.0	0	2.0	7	4.6 ± 5.6 (1–17)	0.9 ± 0.9 (0–2)	1.0 ± 1.4 (0–3)	—	—	—
2005											
Spring	2	2.0 ± 2.8 (0–4)	1.5 ± 2.1 (0–3)	1.0 ± 1.4 (0–2)	6	14.2 ± 12.3 (1–37)	2.2 ± 1.2 (0–3)	0.8 ± 0.8 (0–2)	No	No	No
Summer	6	16.8 ± 9.5 (5–27)	5.5 ± 4.5 (2–13)	2.8 ± 2.2 (0–6)	5	28.4 ± 24.9 (2–62)	9.6 ± 12.1 (1–30)	5.4 ± 5.6 (1–12)	No	No	No
Fall	4	13.0 ± 14.7 (0–34)	1.0 ± 1.4 (0–3)	0.5 ± 0.6 (0–1)	9	7.9 ± 7.2 (0–24)	0.7 ± 1.1 (0–3)	0.7 ± 1.1 (0–3)	No	No	No
2006											
Spring	7	24.0 ± 13.7 (0)	3.1 ± 2.4 (1–7)	1.1 ± 1.1 (0–2)	1	3.0	2.0	1.0	—	—	—
Summer	9	16.0 ± 12.7 (0–35)	7.1 ± 10.1 (0–33)	4.4 ± 7.3 (0–23)	4	25.0 ± 28.9 (3–67)	8.8 ± 6.2 (5–18)	1.5 ± 1.7 (0–4)	No	No	No
Oak Creek											
2004											
Summer	4	10.0 ± 16.0 (1–34)	6.8 ± 4.6 (1–12)	0.5 ± 0.6 (0–1)	5	5.8 ± 2.7 (3–9)	3.8 ± 4.1 (0–9)	0	No	No	—
Fall	1	4.0	0	1.0	3	3.3 ± 2.1 (1–5)	1.0 ± 1.7 (0–3)	0.7 ± 1.2 (0–2)	—	—	—
2005											
Spring	4	5.5 ± 0.6 (5–6)	3.0 ± 1.8 (1–5)	0.5 ± 0.6 (0–1)	12	4.7 ± 4.2 (0–14)	1.9 ± 2.1 (0–7)	0.5 ± 0.5 (0–1)	No	No	No
Summer	6	7.8 ± 6.9 (1–18)	2.7 ± 2.1 (0–5)	0.2 ± 0.4 (0–1)	1	12	2	0	—	—	—
Fall	5	2.8 ± 3.0 (0–7)	0.4 ± 0.9 (0–2)	0	5	3.0 ± 4.2 (0–10)	1.0 ± 1.7 (0–4)	0	No	No	No
2006											
Spring	5	14.4 ± 8.5 (6–24)	1.6 ± 1.5 (0–4)	0.8 ± 0.8 (0–2)	3	9.7 ± 8.2 (4–19)	0.3 ± 0.6 (0–1)	0	No	No	—
Summer	5	28.0 ± 18.8 (10–57)	9.0 ± 8.9 (1–21)	3.2 ± 1.6 (2–6)	3	66.0 ± 54.1 (10–118)	13.3 ± 9.9 (2–20)	3.3 ± 2.1 (1–5)	No	No	No

* Db = *D. bychowskyi*; Dp = *D. pectenatus*; Ds = *D. simplex*; MA = mean abundance; SD = standard deviation. Significance level $P < 0.05$.
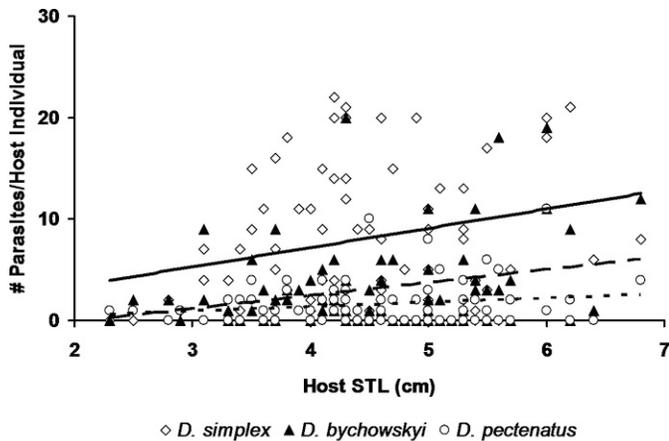
FIGURE 1. Scatter plots of parasites per host versus host standard length (cm) at Elk Creek. *Dactylogyrus simplex,* $y = 1.90x - 0.41$, $r^2 = 0.02$, $P > 0.05$; *D. bychowskyi,* $y = 1.28x - 2.68$, $r^2 = 0.07$, $P < 0.05$; *D. pectenatus,* $y = 0.43x - 0.40$, $r^2 = 0.03$, $P < 0.05$.

FIGURE 3. Scatter plots of parasites per host versus host standard length (cm) at Oak Creek. *Dactylogyrus simplex,* $y = -0.33x - 12.54$, $r^2 = 0.0002$, $P > 0.05$; *D. bychowskyi,* $y = 0.51x - 0.43$, $r^2 = 0.01$, $P > 0.05$; *D. pectenatus,* $y = 0.52x - 0.49$, $r^2 = 0.001$, $P > 0.05$.

promelas, respectively. Overall, *Dactylogyrus* spp. MA and MI at West Oak were 24.19 ± 23.05 (range 0–107) and 25.18 ± 22.98, respectively.

In all years, *D. simplex* occurred on *P. promelas* in all seasons at West Oak (Table VII). There were no significant seasonal differences in PR, MA, or MI of *D. simplex* in any year. At West Oak, there were no significant between-year differences in PR, MA, or MI of *D. simplex,* except for PR and MA in summer, and MI in fall. In all years, *D. bychowskyi* occurred on *P. promelas* in all seasons at West Oak. There were no significant seasonal differences in PR of *D. bychowskyi,* except in 2005 and 2004. At West Oak, there were no significant between-year differences in PR, MA, or MI of *D. bychowskyi* in any season. In all years *D. pectenatus* occurred on *P. promelas* in all seasons at West Oak. There were no significant seasonal differences in PR, MA, or MI of *D. pectenatus,* except in 2004 and 2005. At West Oak, there were no significant between-year differences in PR, MA, or MI of *D. pectenatus* in any season.
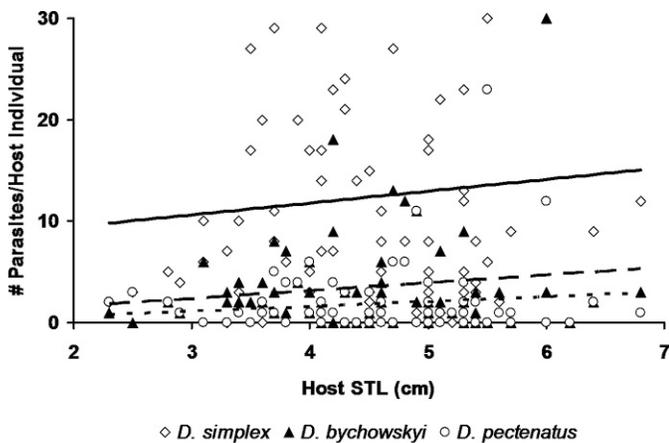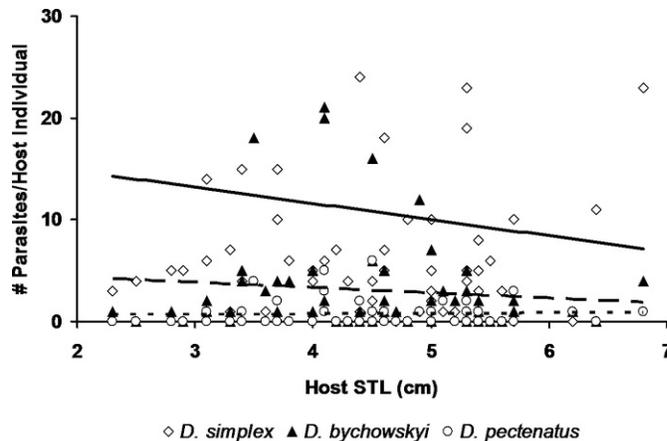
At West Oak, there were no significant differences in PR, MA, or MI among *Dactylogyrus* spp., except in fall 2005, summers 2004, 2005, and 2006, and springs 2005 and 2006 (Table VIII).

The PR of *D. simplex* peaked in fall in 2004, in summer in 2005, and in spring in 2006 at West Oak. The MA and MI of *D. simplex* peaked in summer in 2004 and 2005, and in spring of 2006. The PR of *D. bychowskyi* peaked in summer in 2004 and 2005, and in spring of 2006. The MA and MI of *D. bychowskyi* peaked in summer in all years. The PR and MA of *D. pectenatus* peaked in summer in all years. The MI of *D. pectenatus* peaked in fall 2004, and in summer 2005 and 2006.

Oak Creek: Sixty-one (96.83%) of 63 fathead minnows collected at Oak were infected with *Dactylogyrus* spp. A total of 692 *D. simplex,* 203 *D. bychowskyi,* and 44 *D. pectenatus* was collected from the gills of 58, 44, and 24 *P. promelas,* respectively. Overall, *Dactylogyrus* spp. MA and MI at Oak were 21.51 ± 28.52 (range 0–145) and 22.29 ± 28.73, respectively.

In all years, *D. simplex* occurred on *P. promelas* in all seasons at Oak (Table IX). There were no significant seasonal differences in PR, MA, or MI of *D. simplex,* in any year. At Oak, there were no significant between-year differences in PR, MA, or MI of *D. simplex,* except for MA and MI in spring. In all years *D. bychowskyi* occurred on *P. promelas* in all seasons at Oak. There were no significant seasonal differences in PR, MA, or MI of *D. bychowskyi* except PR and MA in 2004, PR in 2005, and MA in 2006. At Oak, there were no significant between-year differences in PR, MA, or MI of *D. bychowskyi* in any season. In all years, *D. pectenatus* occurred on *P. promelas* in all seasons at Oak, except in fall 2005. There were no significant seasonal differences in PR, MA, or MI of *D. pectenatus,* except for PR in 2005, and for PR and MA in 2006. At Oak, there were no significant between-year differences in PR, MA, or MI of *D. pectenatus,* except for PR and MA in summer, and PR in fall. There were no significant between-year differences in MI of *D. pectenatus* in any season. At Oak, there were significant differences in PR, MA, or MI among *Dactylogyrus* spp. in all collections (Table X).

The PR of *D. simplex* was 100% in all seasons in 2004 and 2006 and peaked in summer 2005. The MA and MI of *D. simplex* peaked in summer in all years. The PR of *D. simplex* peaked in

FIGURE 2. Scatter plots of parasites per host versus host standard length (cm) at West Oak Creek. *Dactylogyrus simplex,* $y = 3.43x - 5.41$, $r^2 = 0.06$, $P < 0.05$; *D. bychowskyi,* $y = 1.74x - 5.55$, $r^2 = 0.09$, $P < 0.05$; *D. pectenatus,* $y = 0.85x - 2.62$, $r^2 = 0.07$, $P < 0.05$.

TABLE V. Seasonal and between-year comparisons: dates, sample sizes, and infection indices of *Dactylogyrus* spp. on *P. promelas* at Elk Creek.*

Collection date	No. of fish	*D. simplex*			*D. bychowskyi*			*D. pectenatus*		
		PR	MA ± 1 SD	MI ± 1 SD	PR	MA ± 1 SD	MI ± 1 SD	PR	MA ± 1 SD	MI ± 1 SD
Summer 2004	12	50.0	3.6 ± 4.1	7.2 ± 2.6	41.7	1.0 ± 1.5	2.4 ± 1.3	41.7	1.8 ± 3.4	4.2 ± 4.4
Fall 2004	7	42.9	1.7 ± 3.3	4.0 ± 4.4	0.0	0.0	0.0	0.0	0.0	0.0
Spring 2005	9	88.9	2.8 ± 3.1	3.1 ± 3.1	22.2	0.6 ± 1.3	2.5 ± 2.1	22.2	0.6 ± 1.3‡	2.5 ± 2.1
Summer 2005	24	83.3	13.6 ± 19.2§	16.4 ± 19.9‖	79.2#	4.1 ± 5.1¶	5.2 ± 5.3	87.5**	2.1 ± 1.5††	2.4 ± 1.4
Fall 2005	7	100.0‡‡	5.3 ± 5.2	5.3 ± 5.2	57.1	3.0 ± 4.2	5.3 ± 4.4	42.9	0.6 ± 0.8	1.3 ± 0.6
Spring 2006	12	83.3	9.0 ± 8.0§§	10.8 ± 7.5‖‖	91.7##	6.0 ± 5.5¶¶	6.6 ± 5.4	66.7***	2.3 ± 3.2	3.4 ± 3.5
Summer 2006	16	81.3	9.8 ± 7.3†††	12.1 ± 6.1‡‡‡	93.8§§§	3.3 ± 3.4‖‖‖	3.5 ± 3.4	75.0	1.6 ± 1.3	2.1 ± 1.0
Total	88	76.1	8.1 ± 11.1	10.6 ± 12.5	63.6	3.0 ± 3.5	4.7 ± 3.6	60.0	1.5 ± 2.1	2.6 ± 2.2

* MA = mean abundance; MI = mean intensity; PR = prevalence; SD = standard deviation. Significance level $P < 0.017$.
† In 2005, PR of *Dp* significantly greater in summer than spring, $\chi^2 = 13.21$.
‡ In spring, PR of *Dp* significantly greater in 2005 than 2004, $\chi^2 = 8.38$.
§ In 2005, MA of *Ds* significantly greater in summer than spring, $t^1 = 2.68$. In summer, MA of *Ds* significantly greater in 2005 than 2004, $t^1 = 2.46$.
‖ In 2005, MI of *Ds* significantly greater in summer than spring, $t^1 = 2.88$. In 2005, MI of *Ds* significantly greater in summer than fall, $t^1 = 2.28$.
In 2005, PR of *Db* significantly greater in summer than spring, $\chi^2 = 9.17$.
¶ In 2005, MA of *Db* significantly greater in summer than spring, $t^1 = 3.10$. In summer, MA of *Db* significantly greater in 2005 than 2004, $t^1 = 2.73$.
** In 2005, PR of *Dp* significantly greater in summer than fall, $\chi^2 = 6.18$. In summer, PR of *Dp* significantly greater in 2005 than 2004, $\chi^2 = 8.38$.
†† In 2005, MA of *Dp* significantly greater in summer than spring, $t = 2.64$. In 2005, MA of *Dp* significantly greater in summer than fall, $t = 2.50$.
‡‡ In fall, PR of *Ds* significantly greater in 2005 than 2004, $\chi^2 = 5.6$ ($P < 0.05$).
§§ In spring, MA of *Ds* significantly greater in 2006 than 2005, $t^1 = 2.46$.
‖‖ In spring, MI of *Ds* significantly greater in 2006 than 2005, $t^1 = 2.93$.
In spring, PR significantly greater in 2006 than 2005, $\chi^2 = 10.51$.
¶¶ In spring, MA of *Db* significantly greater in 2006 than 2005, $t^1 = 2.31$.
*** In spring, PR of *Dp* significantly greater in 2006 than 2005, $\chi^2 = 4.07$ ($P < 0.05$).
††† In summer, MA of *Ds* significantly greater in 2006 than 2004, $t^1 = 2.87$.
‡‡‡ In summer, MI of *Ds* significantly greater in 2006 than 2004, $t^1 = 2.48$.
§§§ In summer, PR of *Db* significantly greater in 2006 than 2004, $\chi^2 = 9.11$.
‖‖‖ In summer, MA of *Db* significantly greater in 2006 than 2004, $t^1 = 2.41$.

summer in 2004 and 2006 and in spring in 2005. The MA and MI of *D. bychowskyi* peaked in summer in all years. The PR of *D. pectenatus* peaked in fall in 2004, spring in 2005, and summer in 2006. The MA and MI of *D. pectenatus* peaked in fall in 2004, spring 2005, and summer 2006.

Among site comparisons

In all years the PR, MA, and MI of *D. simplex* did not differ significantly among sites in any season except in summer 2004

when PR was significantly higher at Oak than at Elk ($\chi^2 = 6.30$, $P < 0.017$), in fall 2004 when PR was significantly higher at West Oak than at Elk ($\chi^2 = 6.23$, $P < 0.017$), and in spring of 2006 when MA was significantly higher at West Oak than at Elk ($t^1_s = 2.44$, $P < 0.017$). Total MA and MI of *D. simplex* did not differ significantly among Elk, West Oak, and Oak ($F_{2,226} = 2.57$, $P = 0.08$; $F_{2,191} = 1.34$, $P = 0.26$, respectively).

The PR, MA, and MI of *D. bychowskyi* did not differ significantly among sites in any season except in spring 2005 when PR was significantly higher at Oak than at Elk ($\chi^2 = 10.65$,

TABLE VI. Community structure: dates, sample sizes, and infection indices of 3 *Dactylogyrus* spp. on *P. promelas* at Elk Creek.*

Collection date	No. of fish	*D. simplex*			*D. bychowskyi*			*D. pectenatus*		
		PR	MA ± 1 SD	MI ± 1 SD	PR	MA ± 1 SD	MI ± 1 SD	PR	MA ± 1 SD	MI ± 1 SD
Summer 2004	12	50.0	3.6 ± 4.1	7.2 ± 2.6†	41.7	1.00 ± 1.5	2.4 ± 1.3	41.7	1.8 ± 3.4	4.2 ± 4.4
Fall 2004	7	42.9	1.7 ± 3.3	4.0 ± 4.4	0.0	0.0	0.0	0.0	0.0	0.0
Spring 2005	9	88.9‡	2.8 ± 3.1§	3.1 ± 3.1	22.2	0.6 ± 1.3	2.5 ± 2.1	22.2	0.6 ± 1.3	2.5 ± 2.1
Summer 2005	24	83.3	13.6 ± 19.2‖	16.4 ± 19.9#	79.2	4.1 ± 5.1	5.2 ± 5.3	87.5	2.1 ± 1.5	2.4 ± 1.4
Fall 2005	7	100.0	5.3 ± 5.2	5.3 ± 5.2	57.1	3.0 ± 4.2	5.3 ± 4.4	42.9	0.6 ± 0.8	1.3 ± 0.6
Spring 2006	12	83.3	9.0 ± 8.0¶	10.8 ± 7.5**	91.7	6.0 ± 5.5	6.6 ± 5.4	66.7	2.3 ± 3.2	3.4 ± 3.5
Summer 2006	16	81.3	9.8 ± 7.3††	12.1 ± 6.1‡‡	93.8	3.3 ± 3.4	3.5 ± 3.4	75.0	1.6 ± 1.3	2.1 ± 1.0
Total	88	76.1	8.1 ± 11.1	10.6 ± 12.5	63.6	3.0 ± 3.5	4.7 ± 3.6	60.0	1.5 ± 2.1	2.6 ± 2.2

* MA = mean abundance; MI = mean intensity; PR = prevalence; SD = standard deviation. Significance level $P < 0.017$.
† MI of *Ds* significantly greater than *Db*, $t = 3.73$.
‡ PR of *Ds* significantly greater than *Db*, $\chi^2 = 8.1$. PR of *Ds* significantly greater than *Dp*, $\chi^2 = 8.1$.
§ MA of *Ds* significantly greater than *Db*, $t = 1.93$. MA of *Ds* significantly greater than *Dp*, $t = 1.93$.
‖ MA of *Ds* significantly greater than *Db*, $t = 2.36$. MA of *Ds* significantly greater than *Dp*, $t = 2.94$.
MI of *Ds* significantly greater than *Db*, $t = 2.42$. MI of *Ds* significantly greater than *Dp*, $t = 3.13$.
¶ MA of *Ds* significantly greater than *Dp*, $t = 2.71$.
** MI of *Ds* significantly greater than *Dp*, $t = 2.57$.
†† MA of *Ds* significantly greater than *Db*, $t = 3.23$. MA of *Ds* significantly greater than *Dp*, $t = 4.47$.
‡‡ MI of *Ds* significantly greater than *Db*, $t = 4.68$. MI of *Ds* significantly greater than *Dp*, $t = 5.87$.

TABLE VII. Seasonal and between-year comparisons: dates, sample sizes, and infection indices of *Dactylogyrus* spp. on *P. promelas* at West Oak Creek.*

Collection date	No. of fish	*D. simplex*			*D. bychowskyi*			*D. pectenatus*		
		PR	MA ± 1 SD	MI ± 1 SD	PR	MA ± 1 SD	MI ± 1 SD	PR	MA ± 1 SD	MI ± 1 SD
Summer 2004	14	71.4	7.2 ± 8.2	10.1 ± 8.0	85.7	3.2 ± 3.4†	3.8 ± 3.3‡	71.4§	1.4 ± 1.7	1.9 ± 1.7
Fall 2004	8	100.0	4.6 ± 5.2	4.6 ± 5.2	50.0	0.8 ± 0.9	1.5 ± 0.6	50.0	1.1 ± 1.4	2.3 ± 1.0
Spring 2005	9	88.9	10.6 ± 11.2	11.9 ± 11.2	66.7	1.8 ± 1.4	2.7 ± 0.5	55.6	0.8 ± 0.8	1.4 ± 0.6
Summer 2005	12	100.0‖	20.8 ± 17.9#	20.8 ± 17.9	100.0¶	6.8 ± 8.3**	6.8 ± 8.3	83.3	3.7 ± 4.1††	4.4 ± 4.1
Fall 2005	13	84.6	9.5 ± 9.7	11.2 ± 9.6‡‡	38.5	0.8 ± 1.2	2.0 ± 1.0	38.5	0.6 ± 1.0	1.6 ± 0.9
Spring 2006	8	100.0	21.4 ± 14.7	21.4 ± 14.7	100.0	3.0 ± 2.2	3.0 ± 2.2	62.5	1.1 ± 1.0	1.8 ± 0.5
Summer 2006	13	92.3	18.8 ± 18.3	20.3 ± 18.2	92.3	7.6 ± 8.8	8.3 ± 8.9	69.2	3.5 ± 6.2	5.1 ± 7.0
Total	77	89.6	13.3 ± 14.1	14.8 ± 14.2	76.6	3.7 ± 5.7	4.8 ± 6.1	62.3	1.8 ± 3.3	3.0 ± 3.8

* MA = mean abundance; MI = mean intensity; PR = prevalence; SD = standard deviation. Significance level $P < 0.017$.
† In 2004, MA of *Db* significantly greater in summer than fall, $t^1_s = 2.59$ ($P < 0.05$).
‡ In 2004, MI of *Db* significantly greater in summer than fall, $t^1_s = 2.24$ ($P < 0.05$).
§ In 2004, PR of *Dp* significantly greater in summer than fall, $\chi^2 = 5.14$ ($P < 0.05$).
‖ In summer, PR of *Ds* significantly greater in 2005 than 2004, $\chi^2 = 4.05$ ($P < 0.05$).
In summer, MA of *Ds* significantly greater in 2005 than 2004, $t^1_s = 2.41$.
¶ In 2005, PR of *Db* significantly greater in summer than fall, $\chi^2 = 10.86$.
** In 2005, MA of *Db* significantly greater in summer than fall, $t^1_s = 2.50$.
†† In 2005, MA of *Dp* significantly greater in summer than fall, $t^1_s = 2.53$.
‡‡ In fall, MA of *Ds* significantly greater in 2005 than 2004, $t^1_s = 1.75$ ($P < 0.05$).

$P < 0.017$), in summer of 2004 when MA was significantly higher at Oak than at Elk ($t^1_s = 2.74$, $P < 0.017$), and in spring 2006 when MA and MI were significantly higher at Elk than at Oak ($t^1_s = 2.94$, $P < 0.017$; $t^1_s = 2.74$, $P < 0.017$, respectively). Total MA and MI of *D. bychowskyi* did not differ significantly among Elk, West Oak, and Oak ($F_{2,226} = 0.42$, $P = 0.66$; $F_{2,156} = 0.01$, $P = 0.99$, respectively).

The PR, MA, and MI of *D. pectenatus* did not differ significantly among sites in any season except in summer 2005 when PR and MA were significantly higher at West Oak than Oak ($\chi^2 = 8.65$, $P < 0.017$; $t^1_s = 2.97$, $P < 0.017$, respectively), significantly higher at Elk than Oak ($\chi^2 = 8.65$, $P < 0.017$; $t^1_s =$ 5.65, $P < 0.017$, respectively), and in summer 2004 when MA was significantly higher at West Oak than at Oak ($t^1_s = 2.39$, $P < 0.017$). Total MI of *D. pectenatus* did not differ significantly among Elk, West Oak, and Oak ($F_{2,120} = 1.25$, $P = 0.29$); however, MA did differ significantly ($F_{2,226} = 4.15$, $P = 0.017$).

Community structure

At Elk, abundance of *D. simplex* was significantly positively correlated with abundance of *D. bychowskyi* and with abundance of *D. pectenatus*. Abundance of *D. bychowskyi* was significantly positively correlated with abundance of *D. pectenatus* (Table XI).

TABLE VIII. Community structure: dates, sample sizes, and infection indices of 3 *Dactylogyrus* spp. on *P. promelas* at West Oak Creek.*

Collection date	No. of fish	*D. simplex*			*D. bychowskyi*			*D. pectenatus*		
		PR	MA ± 1 SD	MI ± 1 SD	PR	MA ± 1 SD	MI ± 1 SD	PR	MA ± 1 SD	MI ± 1 SD
Summer 2004	14	71.4	7.2 ± 8.2†	10.1 ± 8.0‡	85.7	3.2 ± 3.4	3.8 ± 3.3	71.4	1.4 ± 1.7	1.9 ± 1.7
Fall 2004	8	100.0	4.6 ± 5.2	4.6 ± 5.2	50.0	0.8 ± 0.9	1.5 ± 0.6	50.0	1.1 ± 1.4	2.3 ± 1.0
Spring 2005	9	88.9	10.6 ± 11.2§	11.9 ± 11.2‖	66.7	1.8 ± 1.4	2.7 ± 0.5#	55.6	0.8 ± 0.8	1.4 ± 0.6
Summer 2005	12	100.0	20.8 ± 17.9¶	20.8 ± 17.9**	100.0	6.8 ± 8.3	6.8 ± 8.3	83.3	3.7 ± 4.1	4.4 ± 4.1
Fall 2005	13	84.6††	9.5 ± 9.7‡‡	11.2 ± 9.6§§	38.5	0.8 ± 1.2	2.0 ± 1.0	38.5	0.6 ± 1.0	1.6 ± 0.9
Spring 2006	8	100.0	21.4 ± 14.7‖‖	21.4 ± 14.7##	100.0	3.0 ± 2.2	3.0 ± 2.2	62.5	1.1 ± 1.0	1.8 ± 0.5
Summer 2006	13	92.3	18.8 ± 18.3¶¶	20.3 ± 18.2***	92.3	7.6 ± 8.8	8.3 ± 8.9	69.2	3.5 ± 6.2	5.1 ± 7.0
Total	77	89.6	13.3 ± 14.1	14.8 ± 14.2	76.6	3.7 ± 5.7	4.8 ± 6.1	62.3	1.8 ± 3.3	3.0 ± 3.8

* MA = mean abundance; MI = mean intensity; PR = prevalence; SD = standard deviation. Significance level $P < 0.017$.
† MA of *Ds* significantly greater than *Dp*, $t = 2.63$.
‡ MI of *Ds* significantly greater than *Dp*, $t = 3.18$.
§ MA of *Ds* significantly greater than *Dp*, $t = 2.61$.
‖ MI of *Ds* significantly greater than *Dp*, $t = 2.64$.
MI of *Db* significantly greater than *Dp*, $t = 3.94$.
¶ MA of *Ds* significantly greater than *Db*, $t = 2.44$. MA of *Ds* significantly greater than *Dp*, $t = 3.23$.
** MI of *Ds* significantly greater than *Db*, $t = 2.44$. MI of *Ds* significantly greater than *Dp*, $t = 3.07$.
†† PR of *Ds* significantly greater than *Db*, $\chi^2 = 5.85$. PR of *Ds* significantly greater than *Dp*, $\chi^2 = 5.85$.
‡‡ MA of *Ds* significantly greater than *Db*, $t = 3.20$. MA of *Ds* significantly greater than *Dp*, $t = 3.26$.
§§ MI of *Ds* significantly greater than *Db*, $t = 3.13$. MI of *Ds* significantly greater than *Dp*, $t = 3.28$.
‖‖ MA of *Ds* significantly greater than *Db*, $t = 3.50$. MA of *Ds* significantly greater than *Dp*, $t = 3.89$.
MI of *Ds* significantly greater than *Db*, $t = 3.50$. MI of *Ds* significantly greater than *Dp*, $t = 3.77$.
¶¶ MA of *Ds* significantly greater than *Dp*, $t = 2.85$.
*** MI of *Ds* significantly greater than *Dp*, $t = 2.65$.

TABLE IX. Seasonal and between-year comparisons: dates, sample sizes, and infection indices of *Dactylogyrus* spp. on *P. promelas* at Oak Creek.*

Collection date	No. of fish	D. simplex			D. bychowskyi			D. pectenatus		
		PR	MA ± 1 SD	MI ± 1 SD	PR	MA ± 1 SD	MI ± 1 SD	PR	MA ± 1 SD	MI ± 1 SD
Summer 2004	9	100.0	7.7 ± 10.2	7.7 ± 10.2	77.8†	5.1 ± 4.3‡	6.6 ± 3.7	22.2	0.2 ± 0.4	1.0 ± 0
Fall 2004	5	100.0	3.6 ± 1.5	3.6 ± 1.5	20.0	0.6 ± 1.3	3.0 ± 0	40.0‖‖	0.6 ± 0.9	1.5 ± 0.7
Spring 2005	16	87.5	4.9 ± 3.7	5.6 ± 3.3	87.5§	2.2 ± 2.0	2.5 ± 2.0	50.0‖	0.5 ± 0.5	1.0 ± 0
Summer 2005	7	100.0	8.4 ± 6.5	8.4 ± 6.5	85.7	2.6 ± 1.9#	3.0 ± 1.7	14.3	0.1 ± 0.4	1.0 ± 0
Fall 2005	10	70.0	2.9 ± 3.5	4.1 ± 3.5	30.0	0.7 ± 1.3	2.3 ± 1.5	0	0	0
Spring 2006	8	100.0	12.6 ± 8.1	12.6 ± 8.1	62.5	1.1 ± 1.1	1.8 ± 1.3	37.5	0.5 ± 0.8	1.3 ± 0.6
Summer 2006	8	100.0	42.3 ± 37.7¶	42.3 ± 37.7**	100.0	10.6 ± 8.9††	10.6 ± 8.9	100.0‡‡	3.3 ± 1.7§§	3.3 ± 1.7
Total	63	92.1	11.0 ± 18.6	11.9 ± 19.1	69.8	3.2 ± 4.8	4.6 ± 5.2	38.1	0.7 ± 1.2	1.8 ± 1.4

* MA = mean abundance; MI = mean intensity; PR = prevalence; SD = standard deviation. Significance level $P < 0.017$.
† In 2004, PR of *Db* was significantly greater in summer than fall, $\chi^2 = 4.38$ ($P < 0.05$).
‡ In 2004, MA of *Db* was significantly greater in summer than fall, $t^1 = 2.90$.
§ In 2005, PR of *Db* was significantly greater in summer than fall, $\chi^2 = 8.99$ ($P < 0.05$).
‖ In 2005, PR of *Dp* was significantly greater in spring than fall, $\chi^2 = 7.22$.
In 2005, MA of *Db* was significantly greater in summer than fall, $t^1 = 2.39$.
¶ In spring, MA of *Ds* was significantly greater in 2006 than 2005, $t^1 = 2.57$.
** In spring, MI of *Ds* was significantly greater in 2006 than 2005, $t^1 = 2.34$ ($P < 0.05$).
†† In 2006, MA of *Db* was significantly greater in summer than spring, $t^1 = 3.00$.
‡‡ In 2006, PR of *Dp* was significantly greater in summer than spring, $\chi^2 = 7.27$; In 2006, MA of *Dp* was significantly greater in summer than spring, $t^1 = 2.83$; In summer, PR of *Dp* was significantly greater in 2006 than 2005, $\chi^2 = 10.37$; In summer, PR of *Dp* was significantly greater in 2006 than 2004, $\chi^2 = 6.53$.
§§ In summer, MA of *Dp* was significantly greater in 2006 than 2004, $t^1 = 4.98$; In summer, MA of *Dp* was significantly greater in 2006 than 2005, $t^1 = 5.12$.
‖‖ In fall, PR of *Dp* was significantly greater in 2004 than in 2005, $\chi^2 = 4.61$.

At West Oak, abundance of *D. simplex* was significantly positively correlated with abundance of *D. bychowskyi* and *D. pectenatus*. Abundance of *D. bychowskyi* was significantly positively correlated with abundance of *D. pectenatus*. At Oak, abundance of *D. simplex* was significantly positively correlated with abundance of *D. bychowskyi* and *D. pectenatus*. Abundance of *D. bychowskyi* was significantly positively correlated with abundance of *D. pectenatus*.

DISCUSSION

The major contribution of this paper is the demonstration that host sex, size, and collection site are secondary to that of innate parasite species differences in fecundity and transmission in the structuring of *Dactylogyrus* populations and communities. This study is the first to demonstrate that among a community of *Dactylogyrus* spp., on a single host species, order of abundance

TABLE X. Community structure: collection dates, sample sizes, and infection indices of 3 *Dactylogyrus* spp. on *P. promelas* at Oak Creek.*

Collection date	No. of fish	D. simplex			D. bychowskyi			D. pectenatus		
		PR	MA ± 1 SD	MI ± 1 SD	PR	MA ± 1 SD	MI ± 1 SD	PR	MA ± 1 SD	MI ± 1 SD
Summer 2004	9	100.0†	7.7 ± 10.2	7.7 ± 10.2	77.8‡	5.1 ± 4.3§	6.6 ± 3.7	22.2	0.2 ± 0.4	1.0 ± 0
Fall 2004	5	100.0‖	3.6 ± 1.5#	3.6 ± 1.5	20.0	0.6 ± 1.3	3.0 ± 0	40.0	0.6 ± 0.9	1.5 ± 0.7
Spring 2005	16	87.5	4.9 ± 3.7¶	5.6 ± 3.3**	87.5	2.2 ± 2.0††	2.5 ± 2.0	50.0	0.5 ± 0.5	1.0 ± 0
Summer 2005	7	100.0‡‡	8.4 ± 6.5§§	8.4 ± 6.5	85.7	2.6 ± 1.9‖‖	3.0 ± 1.7	14.3	0.1 ± 0.4	1.0 ± 0
Fall 2005	10	70.0##	2.9 ± 3.5	4.1 ± 3.5	30.0	0.7 ± 1.3	2.3 ± 1.5	0	0	0
Spring 2006	8	100.0	12.6 ± 8.1¶¶	12.6 ± 8.1***	62.5	1.1 ± 1.1	1.8 ± 1.3	100.0§§§	0.5 ± 0.8	1.3 ± 0.6
Summer 2006	8	100.0	42.3 ± 37.7†††	42.3 ± 37.7‡‡‡	100.0	10.6 ± 8.9	10.6 ± 8.9	100.0	3.3 ± 1.7	3.3 ± 1.7
Total	63	92.1	11.0 ± 18.6	11.9 ± 19.1	69.8	3.2 ± 4.8	4.6 ± 5.2	38.1	0.7 ± 1.2	1.8 ± 1.4

* MA = mean abundance; MI = mean intensity; PR = prevalence; SD = standard deviation. Significance level $P < 0.017$.
† PR of *Ds* significantly greater than *Dp*, $\chi^2 = 11.46$.
‡ PR of *Db* significantly greater than *Dp*, $\chi^2 = 7.14$.
§ MA of *Db* significantly greater than *Dp*, $t = 3.38$.
‖ PR of *Ds* significantly greater than *Db*, $\chi^2 = 6.67$.
MA of *Ds* significantly greater than *Db*, $t = 3.31$. MA of *Ds* significantly greater than *Dp*, $t = 3.81$.
¶ MA of *Ds* significantly greater than *Db*, $t = 2.58$. MA of *Ds* significantly greater than *Dp*, $t = 4.75$.
** MI of *Ds* significantly greater than *Db*, $t = 4.19$.
†† MA of *Db* significantly greater than *Dp*, $t = 3.26$.
‡‡ PR of *Ds* significantly greater than *Dp*, $\chi^2 = 10.5$.
§§ MA of *Ds* significantly greater than *Dp*, $t = 3.35$.
‖‖ MA of *Db* significantly greater than *Dp*, $t = 3.31$.
PR of *Ds* significantly greater than *Dp*, $\chi^2 = 10.77$.
¶¶ MA of *Ds* significantly greater than *Db*, $t = 3.94$. MA of *Ds* significantly greater than *Dp*, $t = 4.20$.
*** MI of *Ds* significantly greater than *Db*, $t = 3.69$. MI of *Ds* significantly greater than *Dp*, $t = 3.90$.
††† MA of *Ds* significantly greater than *Db*, $t = 2.31$. MA of *Ds* significantly greater than *Dp*, $t = 2.92$.
‡‡‡ MI of *Ds* significantly greater than *Db*, $t = 2.31$. MI of *Ds* significantly greater than *Dp*, $t = 2.92$.
§§§ PR of *Ds* significantly greater than *Dp*, $\chi^2 = 7.27$.

TABLE XI. *r*-Values of abundance correlations for 3 *Dactylogyrus* spp. at 3 sites in southeastern Nebraska.

	D. simplex	*D. bychowskyi*	*D. pectenatus*
Elk Creek			
D. simplex	1.00	0.57*	0.37*
D. bychowskyi		1.00	0.39*
D. pectenatus			1.00
West Oak			
D. simplex	1.00	0.63*	0.83*
D. pectenatus		1.00	0.45*
D. pectenatus			1.00
Oak Creek			
D. simplex	1.00	0.74*	0.72*
D. bychowskyi		1.00	0.79*
D. pectenatus			1.00

* Significance level at $P < 0.017$.

(community structure) remained unchanged over time and space in a watershed.

The results lead to a failure to reject the null hypothesis of no difference in community structure (order of abundance) of 3 congeners coexisting within sites. In the present study, *D. simplex* was the most commonly occurring species of gill parasite on *P. promelas,* followed by *D. bychowskyi* and *D. pectenatus.* Koskivaara et al. (1991) found 2 *Dactylogyrus* spp. dominated a complex community in 3 Finnish lakes, though the order of PR of the less common species varied. The low MI of *D. pectenatus* in the present study is consistent with a low MI found by King and Cone (2009). The results thus reveal inherent differences between congeners infecting the same host species, differences that must be related to reproduction, development, and parasite contributions to transmission.

The community of gill parasites found on *P. promelas* in the present study also was consistent with previously published reports from Elk and West Oak (Weichman and Janovy, 2000) and with a parasite fauna in its native range (Hoffman, 1999). These results add to the Weichman and Janovy (2000) work, by the addition of a third study site and 2 additional years, thus strengthening the contention that in this system order of abundance of *Dactylogyrus* spp. remained stable over time and space. Thus, some facet of the biology of *D. simplex* contributes to its high abundance and prevalence when compared to other *Dactylogyrus* spp. on the same hosts in the same environments.

In the first-order streams, Elk and West Oak, larger *P. promelas* had somewhat higher abundances of *Dactylogyrus* spp. than smaller individuals. At West Oak, larger *P. promelas* had somewhat higher species richness than smaller hosts. At Oak, there were no correlations between STL and *Dactylogyrus* spp. abundance or richness. These results suggest that host size plays a somewhat greater role in determining *Dactylogyrus* abundance at first-order streams than in second-order streams. Relationships between host size and *Dactylogyrus* spp., abundance (Öztürk, 2002; Aydogdu, 2003; Öztürk and Altunel, 2006), and richness (Guégan et. al., 1992) have been demonstrated in some systems. In other systems, however, no relationship between host size and *Dactylogyrus* spp. abundance was demonstrated (King and Cone, 2009). However, the generally inconsistent and weak nature of

these correlations indicate that *Dactylogyrus* spp. infections in this system are independent of host STL. There are also no consistent, significant differences between male and female fish in PR or MA of *D. simplex, D. bychowskyi,* or *D. pectenatus,* indicating infection of *P. promelas* with *Dactylogyrus* spp. is independent of host sex. Barse (1998) also found no relationship between host sex and *Salsuginus* sp. prevalence or density. Indeed, there is virtually no previous work with dactylogyrids demonstrating significant abundance or prevalence differences according to host sex. For the present, the general rule probably should be that *Dactylogyrus* spp. do not discriminate between host sexes, regardless of potential secondary sexual characters in those hosts.

Previous population studies examined seasonal occurrence of a *Dactylogyrus* sp. (Aydogdu et al., 2003; Lamková et al., 2007), but few examined seasonal changes over more than 1 yr (Öztürk and Altunel, 2006). Dzika (1987) studied a community of 4 *Dactylogyrus* spp. for a 2-yr period and found that prevalence and abundance was lowest between October and November and increased in early spring, with the particular dynamics being species specific. Pojmańska (1995) confirmed Dzika's work and observed relationships between occurrence and reproductive dynamics of *Dactylogyrus* spp. and the long-term climate conditions of the species' region of origin. The current study, to our knowledge, is the first to examine seasonal dynamics of a complex *Dactylogyrus* community on a Native North American host species at multiple sites, over multiple years.

The results lead to the rejection the null hypothesis of no difference in abundance, intensity, and prevalence among 3 congeners coexisting within 3 sites. They show no consistent patterns of seasonal fluctuations in either abundance or prevalence in any of the sites or for any of the 3 *Dactylogyrus* spp. studied, although abundances and prevalences tend to be highest in summer collections. The elevated parasite infections in summer agree with other studies, which note the favorable influence of the warmer season on reproduction and survival of *Dactylogyrus* spp. (Pojmańska, 1995). In the current study, the 3 streams are subject to periodic flooding with major changes in flow rates and water levels, although snail populations suggest that Elk, with both *Helisoma trivolvis* and *Physa* sp. populations, is in some way abiotically different from the West Oak and Oak, both of which have only *Physa* sp. populations. Annual precipitation evidently influences transmission dynamics, however, because between-year differences, within a particular site, are generally greater than within-year differences at those same sites. *Dactylogyrus* species populations at West Oak were the most stable between years, followed by Oak and Elk.

In every collection at West Oak, PR of all 3 *Dactylogyrus* spp. was greater than zero. For all 3 *Dactylogyrus* spp., total PR, MA, and MI were highest at West Oak. The observed differences in *Dactylogyrus* spp. populations among sites were not consistent over 3 yr; however, there was an important, though not statistically significant, trend in which total MA and MI of all 3 species was highest at West Oak. Total PR of *D. bychowskyi* and *D. pectenatus* was also highest at West Oak, though total PR of *D. simplex* was highest at Oak, the fastest flowing and most variable of the 3 sites. The trend, in which species are more abundant and in higher PR at West Oak, indicates that some aspect of the environment at West Oak is more conducive to infection with *Dactylogyrus* spp. than it is at the other sites. *Dactylogyrus simplex* differs in some fundamental way from its congeners,

highlighting the importance of studying multiple population parameters in order to understand congeneric species' biology. Further investigation of abiotic site differences will be necessary to determine the particular role of site in forming the *Dactylogyrus* spp. populations.

Rohde (1989) asserted that host-parasite systems are good models for investigating evolutionary and ecological mechanisms that contribute to biological diversity. *Dactylogyrus* spp. and their cyprinid hosts are particularly good systems for this work because both are exceedingly diverse and widely distributed, and multispecies infections are common. For example, Šimková et al. (2004), using molecular techniques, determined that much of the diversification within the *Dactylogyrus* sp.–cyprinid fishes model was a result of intrahost speciation, a phenomenon they noted had rarely been recognized in host–parasite associations, thereby highlighting the power of this system in the study of evolution and biological diversity. The current small-scale, ecological study provides evidence of population and community dynamics in nature reveals congeners differ in their ability to infect, thereby supporting the conclusions of intrahost speciation based on molecular phylogenetic data by Šimková et al. (2004).

ACKNOWLEDGMENTS

LITERATURE CITED

AYDOGDU, A., A. KOSTADINOVA, AND M. FERNANDEZ. 2003. Variations in the distribution of parasites in the common carp, *Cyprinus carpio,* from Lake Iznik, Turkey: Population dynamics related to season and host size. Helminthologia **40:** 33–40.

BARSE, A. M. 1998. Gill parasites of mummichogs, *Fundulus heteroclitus* (Teleostei: Cyprinodontidae): Effects of season, locality, and host sex and size. Journal of Parasitology **84:** 236–244.

BUSH, A. O., K. D. LAFFERTY, J. M. LOTZ, AND A. W. SHOSTAK. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. Journal of Parasitology **83:** 575–583.

DZIKA, E. 1987. Annual occurrence dynamics of common monogeneans on the gills of bream from Lake Goslawskie (Poland). Acta Parasitologica Polonica **32:** 121–137.

GIBSON, D. I., T. A. TIMOFEEVA, AND P. I. GERASEV. 1996. A catalogue of the nominal species of the genus *Dactylogyrus* Diesing, 1850 and their host genera. Systematic Parasitology **25:** 3–48.

GUÉGAN, J.-F., A. LAMBERT, C. LÉVÊQUE, C. COMBES, AND L. EUZET. 1992. Can host body size explain the parasite species richness in tropical freshwater fishes? Oecologia **90:** 197–204.

HOFFMAN, G. L. 1999. Parasites of North American freshwater fishes, 2nd ed. Comstock Publishing Associates, Ithaca, New York, 539 p.

JANOVY, J., JR., S. D. SNYDER, AND R. E. CLOPTON. 1997. Evolutionary constraints on population structure: The parasites of *Fundulus zebrinus* (Pisces: Cyprinodontidae) in the South Platte River of Nebraska. Journal of Parasitology **83:** 584–592.

KING, S. D., AND D. K. CONE. 2009. Infections of *Dactylogyrus pectenatus* (Monogenea: Dactylogyridae) on Larvae of *Pimephales promelas* (Teleostei: Cyprinidae) in Scott Lake, Ontario, Canada. Comparative Parasitology **76:** 110–112.

KOSKIVAARA, M., E. T. VALTONEN, AND M. PROST. 1991. Dactylogyrids on the gills of roach in central Finland: Features of infection and species composition. International Journal for Parasitology **21:** 565–572.

KRITSKY, D. C., V. E. THATCHER, AND W. A. BOEGER. 1986. Neotropical Monogenea. 8. Revision of *Urocleidoides* (Dactylogyridae, Ancyrocephalinae). Proceedings of the Helminthological Society of Washington **53:** 1–37.

LAMKOVÁ, K., A. ŠIMKOVÁ, M. PALÍKOVÁ, P. JURAJDA, AND A. LOJEK. 2007. Seasonal changes of immunocompetence and parasitism in chub (*Leuciscus cephalus*), a freshwater cyprinid fish. Parasitology Research **101:** 775–789.

MAYES, M. 1976. The adult platyhelminth parasites of Nebraska fishes. Ph.D. Dissertation. University of Nebraska–Lincoln, Lincoln, Nebraska, 207 p.

———. 1977. New species of *Gyrodactylus* and *Dactylogyrus* Trematoda Monogenea from fishes of Nebraska, USA. Journal of Parasitology **63:** 805–809.

MIZELLE, J. D. 1937. Ectoparasites of the blunt-nosed minnow (*Hyborhynchus notatus*). American Midland Naturalist **18:** 612–621.

MURITH, D., AND M. BEVERLEY-BURTON. 1985. *Salsuginus* Beverley-Burton, 1984 (Monogenea: Ancyrocephalidae) from Cyprinodontoidei (Atheriniformes) in North America with descriptions of *Salsuginus angularis* (Mueller, 1934) Beverley-Burton, 1984 from *Fundulus diaphanous* and *Salsuginus heterocliti* n. sp. from *F. heteroclitus.* Canadian Journal of Zoology **63:** 703–714.

NELSON, J. S. 2006. Fishes of the world, 4th ed. John Wiley & Sons, Hoboken, New Jersey, 601 p.

ÖZTÜRK, M. O. 2002. Metazoan parasites of the tench (*Tinca tinca* L.) from Lake Uluabat, Turkey. Israel Journal of Zoology **48:** 285–293.

———, AND F. N. ALTUNEL. 2006. Occurrence of *Dactylogyrus* infection linked to seasonal changes and host fish size on four cyprinid fishes in Lake Manyas, Turkey. Acta Zoologica Academiae Scientiarum Hungaricae **52:** 407–415.

PFLIEGER, W. L. 1997. The fishes of Missouri. Missouri Department of Conservation, Jefferson City, Missouri, 372 p.

POJMAŃSKA, T. 1995. Seasonal dynamics of occurrence and reproduction of some parasites in four cyprinid fish cultured in ponds. II. Monogenea. Acta Parsitologica **40:** 79–84.

PRITCHARD, M. H., AND G. O. W. KRUSE. 1982. The collection and preservation of animal parasites. University of Nebraska Press, Lincoln, Nebraska, 141 p.

ROHDE, K. 1989. Simple ecological systems, simple solutions to complex problems. Evolutionary Theory **8:** 305–350.

ŠIMKOVÁ, A., S. MORAND, E. JOBET, M. GELNAR, AND O. VERNEAU. 2004. Molecular phylogeny of congeneric monogenean parasites (*Dactylogyrus*): A case of intrahost speciation. Evolution **58:** 1001–1018.

SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry: The principles and practice of statistics in biological research, 3rd ed. W. H. Freeman and Company, New York, New York, 887 p.

WEICHMAN, M. A., AND J. JANOVY, JR. 2000. Parasite community structure in *Pimephales promelas* (Pisces: Cyprinidae) from two converging streams. Journal of Parasitology **85:** 654–656.