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Seasonal Dynamics of *Conchophthirus acuminatus* (Ciliophora, Conchophthiridae) Infection in *Dreissena polymorpha* and *D. bugensis* (Bivalvia, Dreissenidae)

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Summary

Although considerable research has been carried out on *Dreissena* spp., relatively little is known about the symbiotic organisms living within them. We report a two-year study of the dynamics of infection by the commensal ciliate *Conchophthirus acuminatus* in *D. polymorpha* and *D. bugensis* populations in the Dnieper River in the Ukraine and in four *D. polymorpha* populations in Belarus. *C. acuminatus* was present in all samples. The moderate to high infection prevalence and moderate infection intensity that we recorded in *D. polymorpha* populations were in contrast to the low prevalence and very low intensity of infection observed in *D. bugensis*. Recording *C. acuminatus* in *D. bugensis* represents the first record of any ciliate species from this mussel and the first report of *C. acuminatus* in a host other than *D. polymorpha*. Since infection prevalence and intensity strongly correlated with the size of *D. polymorpha*, the presence of large, infected mussels is likely important to serve as a reservoir for maintaining infection in the overall population. To infect new host mussels, *C. acuminatus* must disperse into surrounding waters, and we suggest that a period of mass dispersal may be synchronized to occur when new potential hosts, i.e., juvenile mussels, become abundant.

Key words: Endosymbiont; Zebra mussel; Commensal; Belarus; Ukraine

Introduction

Zebra mussels, *Dreissena* spp., are well known macrofouling bivalves in European freshwaters [16, 23]. The introduction of *Dreissena polymorpha* and *D. bugensis* into North America during the 1980s further expanded scientific investigations on the biology and control of these bivalves due to their adverse economic [17] and ecological [24] impacts. Although considerable ecological research has been carried out both in Europe and North America [5, 6], relatively little effort has been made to study their interrelationships with symbiotic organisms living within these mussels. This information gap is currently being addressed by a network of over a dozen scientists from Europe, North America, and the former Soviet Union as a research project of the International Research Consortium on Molluscan Symbionts (IRCOMS; http//www.nysm. nysed.gov/biology/ircoms/bio_ircoms.html). IRCOMS efforts are initially focusing on the development of a fundamental database characterizing the systematics, biology, ecology, and distribution of *Dreissena*'s endosymbionts.

This present IRCOMS contribution represents the first study of the seasonal dynamics of the obligate, mantle-cavity ciliate *Conchophthirus acuminatus* (Scuticociliatida: Conchophthiridae) and builds on the following four previous IRCOMS investigations of *Dreissena*'s mantle-cavity ciliates. Burlakova et al. [2] reported the first transinfection trials of *C. acuminatus* in *D. polymorpha* and outlined factors affecting infection intensity (i.e., number of ciliates per infected mussel). Laruelle et al. [11] demonstrated the value of histological analysis as a technique capable of precisely determining the location of mantle cavity ciliates, including *C. acuminatus*, within *D. polymorpha* and characterizing their symbiotic relationships at the cellular level. Karatayev et al. [7, 8] provided further details of the distribution of *C. acuminatus* in Belarussian waterbodies.

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D. polymorpha is widely distributed in temperate European waterbodies, and *C. acuminatus* is its most common, obligate endosymbiont [15]. European populations of *D. bugensis* are almost exclusively found in the Ukraine, and prior to the present study, this dreissenid species had never been investigated for the presence of endosymbiotic ciliates. Although its feeding on the sperm cells of *D. polymorpha* has been documented [11], *C. acuminatus* is likely a commensal organism which ingests a variety of organic particles present on *Dreissena*'s mantle epithelial surfaces. Since *C. acuminatus* has only been reported from *D. polymorpha*, it has been considered to be extremely host specific [15]. Our study expands its host range with the first record of *C. acuminatus* in *D. bugensis*. In addition, we report the seasonal dynamics of *C. acuminatus* infection in *D. polymorpha* and *D. bugensis* populations in the Dnieper River in the Ukraine and also in two *D. polymorpha* populations in Belarus.

Material and Methods

The five waterbodies included in this study were the Svisloch River, Dnieper-Bug Canal, Lukomskoe Lake, and Lepelskoe Lake in Belarus and the Dnieper River in the Ukraine. Specific sampling locations were: Svisloch River (53°55'N, 27°32'E) within Minsk; Dnieper-Bug Canal (52°06'N, 26°00'E) at 250 km southwest of Minsk; Lukomskoe Lake (54°40'N, 29°05'E) and Lepelskoe Lake (54°54'N, 28°44'E) at 120 km northeast of Minsk; Dnieper River (52°20'N, 30°15'E) within Kiev.

D. polymorpha had colonized the Svisloch River in the mid-1980s, and the sampling location we chose in this river had a width of ca. 50 m, mean depth of ca. 1 m, and maximum depth of ca. 2 m. In Lukomskoe Lake (surface area 36.7 km^2, mean depth 6.6 m, maximum depth 11.5 m), *D. polymorpha* was found for the first time in 1972 [13]. From 1805 until the end of the 19th century, Lepelskoe Lake (surface area 9.2 km^2, mean depth 4.5 m, maximum depth 26.8 m) was a part of the Dnieper-Zapadnaya Dvina Canal. *D. polymorpha* was first reported from Lepelskoe Lake in 1929 [18], but probably colonized this lake much earlier, shortly after construction of the Dnieper-Zapadnaya Dvina Canal. Dnieper-Bug Canal (width ca. 30 m, mean depth ca. 1.6 m, and maximum depth ca. 4 m) was built in 1775 to connect the Dnieper River (Black Sea Basin) to the Zapadnyi Bug River (Baltic Sea Basin), and *D. polymorpha* probably colonized this canal shortly thereafter.

In 1996, samples were taken monthly in the Svisloch and Dnieper Rivers from May through October and also in December. In 1997, samples were taken as follows: in the Svisloch River in January and from March through December, in the Dnieper River from May through December, and in the Dnieper-Bug Canal from June through November; in Lukomskoe Lake and Lepelskoe Lake only in June.

All mussels sampled in this study were collected at ca. 1.5–2.5 m depth, refrigerated at 5–10 °C, and dissected within 72 hr. Benthic temperature was measured at the time of collection. To determine the size-frequency distribution of the *Dreissena* population, 200–600 mussels were randomly chosen from a sample and measured to the nearest millimeter with a caliper. In 1996, we collected one sample at each sampling time in each waterbody. To determine infection prevalence (i.e., number of infected mussels among total number examined) in each sample, ca. 250–350 live mussels were dissected after sorting them into seven 5-mm size classes based on shell length (1 mm ≤ L < 5 mm; 5 ≤ L < 10 mm; 10 mm ≤ L< 15 mm; 15 ≤ L < 20 mm; 20 mm ≤ L < 25 mm; 25 ≤ L < 30 mm; and 30 mm ≤ L < 35 mm). In each size class, 50 mussels were examined for prevalence whenever possible. In 1997, to determine sample variance we collected three replicate samples each time from each waterbody. In each replicate, 17 mussels from each size class were randomly selected and dissected to determine prevalence and 7 for intensity. Thus, wherever possible, at each sampling time and for each size class, we examined ca. 50 mussels for prevalence and ca. 20 mussels for intensity. Both prevalence and intensity of infection in each mussel species were calculated considering the percentage of each 5-mm size class in the population.

Before dissection, we cleaned and dried shell surfaces and measured mussel length to the nearest millimeter with calipers. Mussels were then cut open with a scalpel, and their mantle cavities were repeatedly flushed with unchlorinated tap water from a pipette to remove all ciliates from exposed epithelial surfaces. Because *C. acuminatus* are also present within gill water tubes and suprabranchial cavities [11], gills were lacerated with forceps and then flushed by pipette. The number of *C. acuminatus* in all rinse water was determined in a plankton counting chamber using a stereomicroscope (20-70X). To compare the infection intensity and prevalence of *C. acuminatus* in each mussel species in each waterbody, we analyzed data by one- and two-way ANOVA, I model (fixed effects) using Statistica software (Windows Release 5.0 B, StatSoft, Inc.).

Results

Infection in *D. polymorpha*: *C. acuminatus* was present in all *D. polymorpha* samples in all five waterbodies studied, and mean infection prevalence was moderate to high, ranging from 74.9% to 99.6% (Table 1). Mean infection prevalence in *D. polymorpha* in the Svisloch and Dnieper Rivers during May–December 1996 and 1997 did not differ significantly either between years or between these two rivers (respectively, $P = 0.35$ and $P = 0.49$; two-way ANOVA). In contrast, during May-December 1997 mean infection intensity in *D. polymorpha* in the Svisloch River was significantly higher than in the Dnieper River ($P < 0.001$, two-way ANOVA), indicating that intensity was not strictly predictable from prevalence. Mean infection intensity (± SE) in *D. polymorpha* was moderate and ranged from 118.1 ± 19.9 to 525.2 ± 68.5 ciliates/mussel (Table 1).

Infection in *D. bugensis:* Infection was present in all *D. bugensis* samples, but prevalence was relatively low, averaging only 39.2 % and 16.0%, respectively, in 1996 and 1997 (Table 1). Infection intensity was very low with a mean (± SE) of 4.6 ± 0.8 ciliates/mussel.

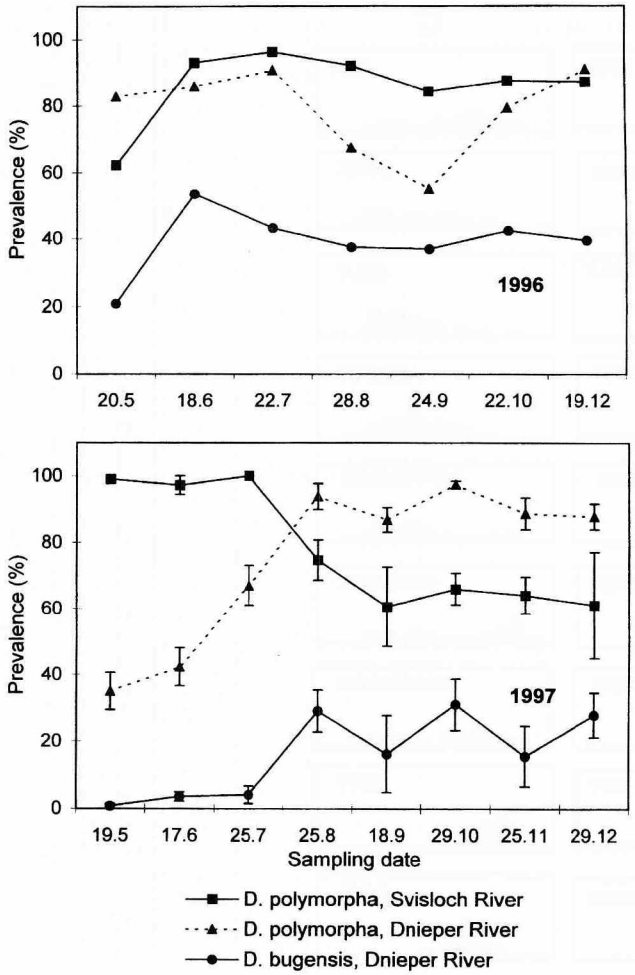

Fig. 1. Dynamics of the prevalence of *C. acuminatus* in *Dreissena* spp. from the Svisloch and Dnieper rivers in 1996 and 1997 (mean ± SE indicated).

Comparison of infection in *Dreissena* spp.: Mean infection prevalence in *D. bugensis* in the Dnieper River was significantly lower than that in *D. polymorpha* in both 1996 and 1997 and did differ significantly between years ($P < 0.001$; $P = 0.033$, two-way ANOVA; Fig. 1). The mean prevalence in *D. polymorpha* in 1996 and in 1997 was, respectively, ca. two and five times higher than in *D. bugensis* (Table 1). Mean infection intensity in *D. bugensis* was also significantly lower than in *D. polymorpha* in the Dnieper River ($P < 0.001$, one-way ANOVA) and lower than that in all others waterbodies studied ($P < 0.001$, one-way ANOVA; Table 1).

Mussel size and infection prevalence: The prevalence of infection in *D. polymorpha* strongly increased with mussels size, reaching 100% in the largest mussels in almost all waterbodies studied (Table 2). Prevalence in *D. polymorpha* both in the Svisloch and the Dnieper Rivers varied considerably throughout each sampling period (Fig. 1) and strongly related to mussel size-frequency distribution (Fig. 2). Mussels <10 mm long invariably had the lowest prevalence in each population at each sample time. Consequently, prevalence rates in *Dreissena* spp. (Fig. 1) were almost always lowest in each river at the time of the year when these small mussels were most abundant: 62% and 61% prevalence in the Svisloch River in *D. polymorpha*, respectively, in May 1996 and September 1997 (Fig. 1, Fig. 2 – Column A); 55–68% and 35% infection in Dnieper *D. polymorpha*, respectively, in August–September 1996 and May 1997 (Fig. 1, Fig. 2 – Column B); 21% and 1% infection in Dnieper *D. bugensis*, respectively, in May 1996 and May 1997 (Fig. 1, Fig. 2 – Column C). Conversely, prevalence in both *Dreissena* spp. was almost always highest when mussels <10 mm were relatively absent.

Season and infection intensity: Infection intensity in *D. polymorpha* in the Svisloch River had a pro-

Table 1. Mean prevalence and intensity (± SE) of *Dreissena* infection with *C. acuminatus* in waterbodies sampled.

Waterbody	Date	Temperature (°C)	Mussels dissected	Prevalence (%)	Intensity (ciliates/mussel)
Dreissena polymorpha					
Svisloch River	May–December 1996	3–18	1201	86.1 ± 4.3	–[a]
	May–December 1997	2.5–23	2200	79.5 ± 3.8	118.1 ± 19.9
Dnieper-Bug Canal	June–November 1997	6–23	1527	96.7 ± 1.1	525.2 ± 68.5
Lukomskoe Lake	June 1997	20.5	256	91.6 ± 7.0	357.9 ± 128.3
Lepelskoe Lake	June 1997	19.0	304	99.6 ± 0.2	154.0 ± 39.5
Dnieper River	May–December 1996	6–23	1028	78.9 ± 5.0	–[a]
	May–December 1997	1–21	1499	74.9 ± 4.9	26.2 ± 3.5
Dreissena bugensis					
Dnieper River	May–December 1996	6–23	1295	39.2 ± 3.7	–[a]
	May–December 1997	1–21	1544	16.0 ± 3.1	4.6 ± 0.8

[a] Not recorded

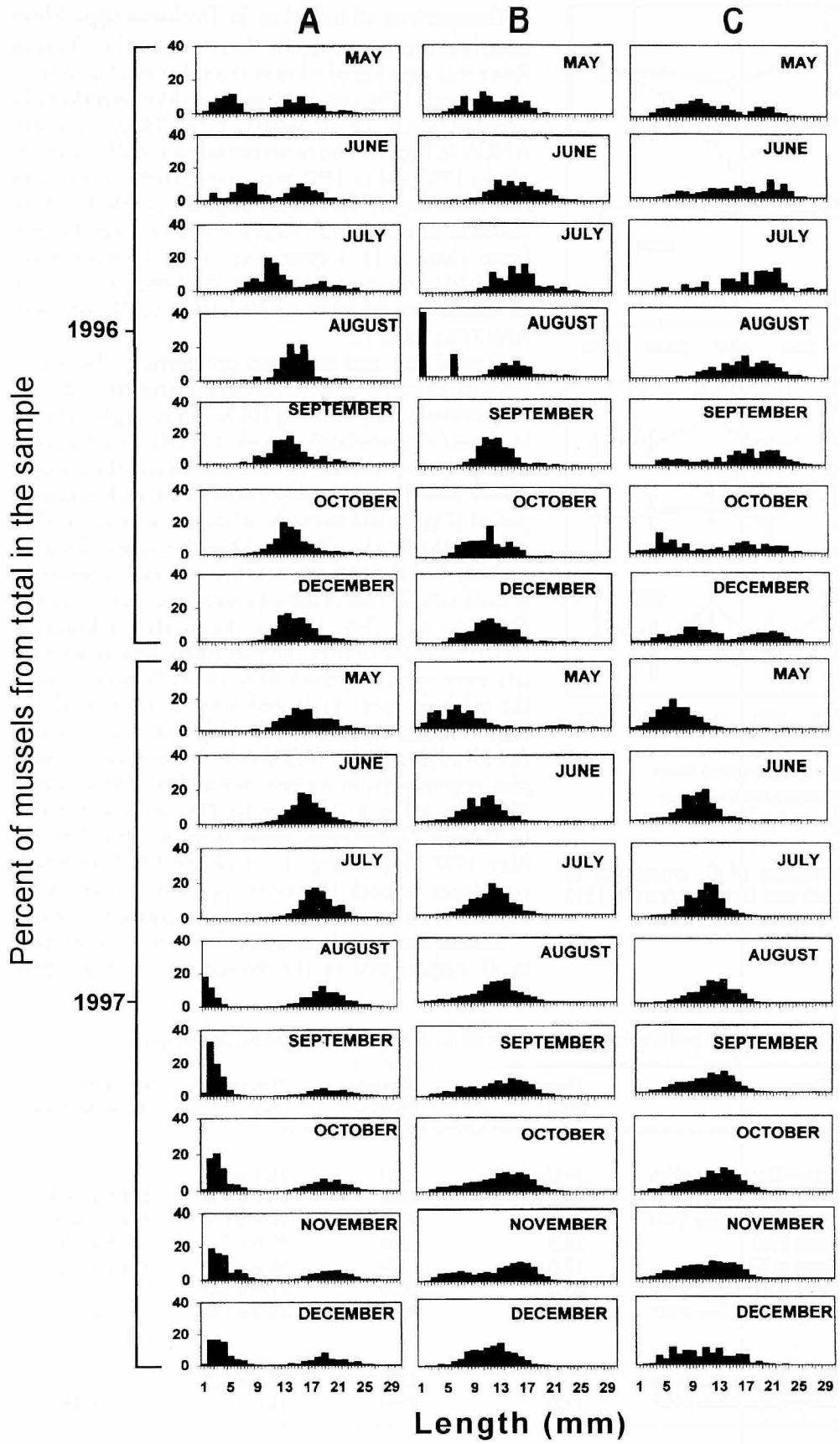

Fig. 2. Size-frequency distribution of *D. polymorpha* in Svisloch River (column A), in Dnieper River (column B), and *D. bugensis* in Dnieper River (column C) from May 1996 to December 1997.

Table 2. Prevalence (% ± SE) of *C. acuminatus* infection in *Dreissena* of different size classes.

Waterbody	Date	Size classes, mm					
		1.0–4.9	5.0–9.9	10.0–14.9	15.0–19.9	20.0–24.9	25.0–29.9
Dreissena polymorpha							
Svisloch River	avg. 1996	60.0 ± 32.0	82.0 ± 10.5	88.9 ± 1.8	91.4 ± 3.0	86.4 ± 4.1	100
	avg. 1997	36.9 ± 4.6	80.3 ± 4.7	98.8 ± 0.6	98.4 ± 0.7	99.5 ± 0.3	99.1 ± 0.9
Dnieper-Bug Canal	avg. 1997	79.4 ± 5.5	96.4 ± 1.8	99.7 ± 0.3	100	99.3 ± 0.4	100
Lukomskoe Lake	June 1997	68.6 ± 22.6	74.0 ± 27.1	100	100	100	–[a]
Lepelskoe Lake	June 1997	83.3 ± 15.2	100	100	100	100	100
Dnieper River	avg. 1996	29.2	74.2 ± 7.5	86.8 ± 7.4	96.1 ± 1.0	57.4 ± 15.6	100
	avg. 1997	50.9 ± 7.2	73.7 ± 5.8	79.4 ± 4.7	89.0 ± 3.1	90.7 ± 7.4	–[a]
Dreissena bugensis							
Dnieper River	avg. 1996	7.1 ± 2.0	29.5 ± 11.3	37.9 ± 5.8	40.0 ± 6.7	49.3 ± 9.9	53.4 ± 9.0
	avg. 1997	8.8 ± 2.6	19.1 ± 4.1	15.9 ± 3.5	13.3 ± 3.3	39.5 ± 13.0	–[a]

[a] Not recorded

nounced peak in August (Fig. 3) and was considerably lower in the spring, early summer, and autumn. The seasonal dynamics of *D. polymorpha* infection with *C. acuminatus* in the Dnieper River were also characterized by a single peak in August. In contrast, we did not find this same pattern in *D. bugensis*.

Mussel size and infection intensity: Infection intensity increased with mussels size in all *D. polymorpha* populations sampled, and all correlations were always statistically significant (Fig. 4). In contrast, little evidence of correlation was found between length and infection intensity in *D. bugensis* (Fig. 4).

Discussion

Ciliate distribution: It was not surprising that *C. acuminatus* was present in all five waterbodies included in this study, as almost all European populations of *D. polymorpha* sampled to date are infected by *C. acuminatus*. In contrast, *C. acuminatus* has never been recorded from North American *Dreissena* populations [3, 25, authors, unpublished data], and this supports the hypothesis that *Dreissena* spp. were transported to North America as planktonic larvae – a stage physically too small for harboring *C. acuminatus* infection.

Host range: This study is the first to record a ciliate species from *D. bugensis* and the first report of *C. acuminatus* in a host other than *D. polymorpha*. *Conchophthirus* spp. tend to be host specific [1, 9, 19], and thus we predict that *C. acuminatus* will only be found in *Dreissena* spp. In commenting on its host specificity, Raabe [19] noted that he never observed *C. acuminatus* in Unionidae, even though their shells were sometimes completely covered by *C. acuminatus*-infected *D. polymorpha*. In the same light, it is not surprising that *Conchophthirus* spp. which are present in North American

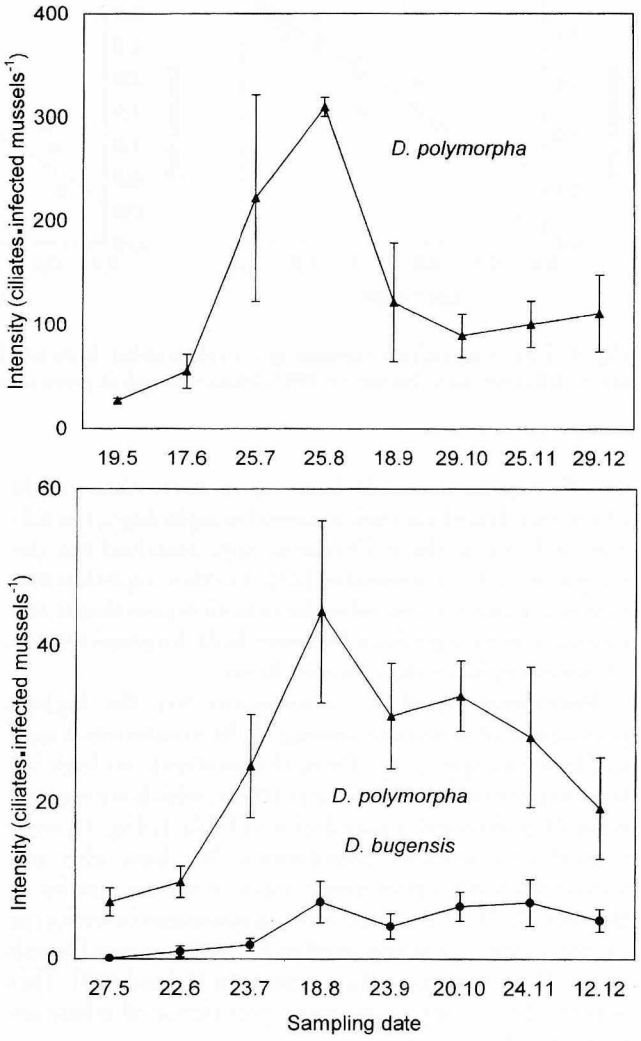

Fig. 3. Dynamics of the intensity of *C. acuminatus* in *Dreissena* spp. from the Svisloch (top) and Dnieper (bottom) rivers in 1997 (mean ± SE indicated).

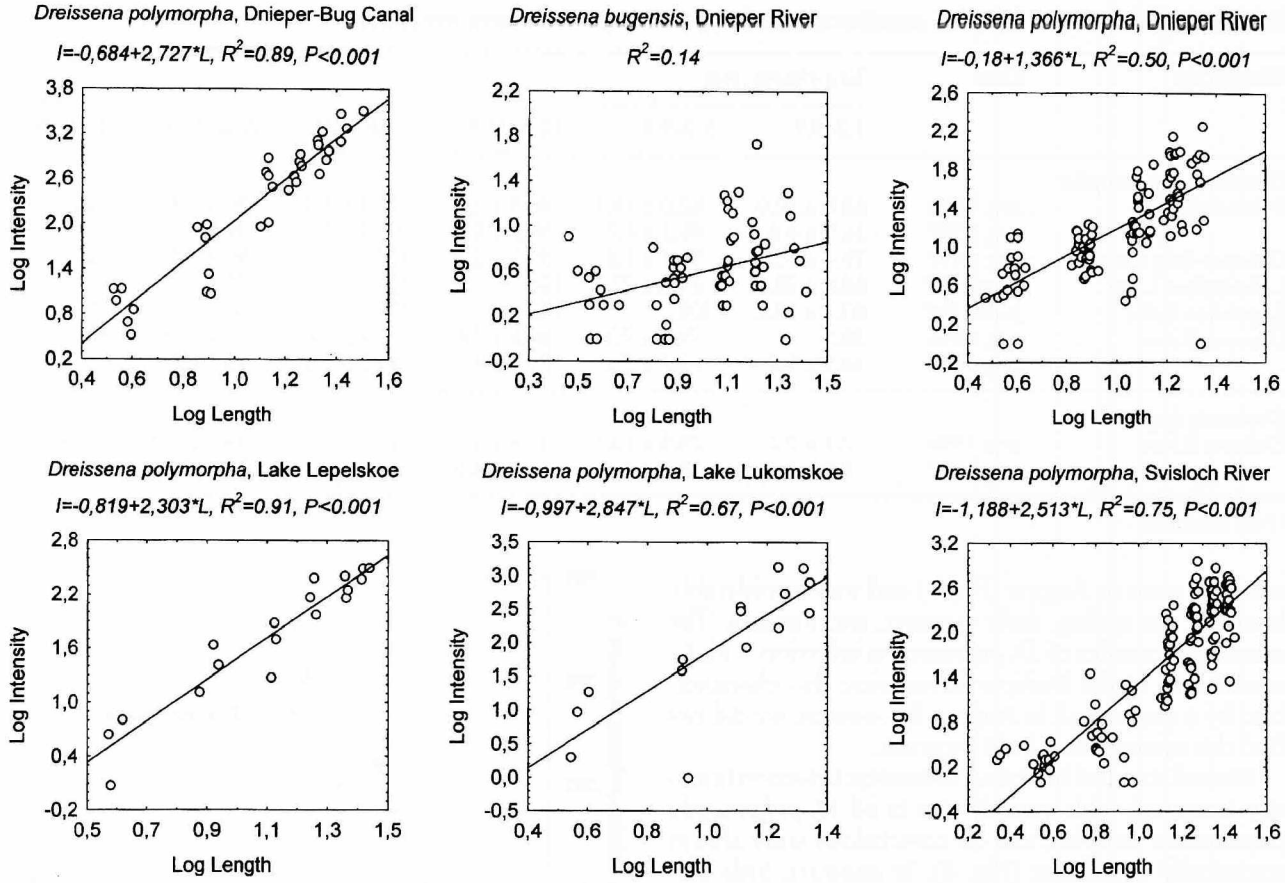

Fig. 4. Linear equations expressing the relationship between *Dreissena* length (L) and intensity of infection (I) by *C. acuminatus* in different waterbodies in 1997. Mussel length is given in mm, intensity in ciliates per infected mussel.

and European unionids have never been observed in *Dreissena*. Based on their external morphology, the ciliates in both of these *Dreissena* spp. matched the description of *C. acuminatus* [22]. Further experimentation is required to test why the infection prevalence and intensity were significantly lower in *D. bugensis* than in *D. polymorpha* in the Dnieper River.

Prevalence level: *C. acuminatus* has the highest prevalence of infection among all 34 symbionts found in *Dreissena* spp. [15]. Thus, the moderate to high infection prevalences, some near 100%, which we recorded in *D. polymorpha* populations (Table 1, Fig. 1), were typical of European populations. We have also observed such high prevalence rates in recent studies in Belarus [2, 7]. Prevalence of *C. acuminatus* infection in *D. polymorpha* was reported to be 100% in two Danish lakes [4] and in non-saline waters in Poland [20]. This was the first study to monitor prevalence of ciliate infection in *Dreissena*.

Intensity level: *Dreissena*, while relatively small bivalves, have one of the highest intensities of infection with any *Conchophthirus* sp. ever reported for ciliates in the order Scuticociliatida [2]. In our study, infection intensities in *D. polymorpha* were relatively moderate and varied from 1 to 6,276 ciliates/mussels. This latter maximum intensity was found in a 27-mm mussel from Dnieper-Bug Canal. Based on mussel length, these data were very similar to those reported from our previous study in Naroch Lake, Belarus [2] in which intensity in *D. polymorpha* varied from 1 ciliate in a 2-mm mussel to 5,100 ciliates in a 28-mm mussel. The highest *C. acuminatus* intensity we have ever recorded was 14,035 ciliates in a 27-mm *D. polymorpha* from Lake Lotviny, Belarus [8]. Our data indicated that infection intensity in the overall *D. polymorpha* population peaked in August in both rivers studied, but further research is needed to confirm that this may be a common pattern in *C. acuminatus* populations.

Mussel length and infection intensity: It was not surprising that mussel size correlated directly with infection intensity. In our previous study of *C. acuminatus* infection in *D. polymorpha* [2], we also observed such high correlations (range in R^2 = 0.83–0.92). The lowest correlation between size and infection intensity

in *D. polymorpha* in the current study was found in the Dnieper River ($R^2 = 0.50$, Fig. 4) and occurred at the same time that the lowest infection intensity was recorded (i.e., 26 ciliates/mussel, Table 1). It appears that this correlation is lowest at low infection intensities regardless of host dreissenid since intensity in *D. bugensis* was always low (Fig. 4) and little correlation between size and infection intensity was ever noted for this species.

Maintenance of infection in a *D. polymorpha* population: Since infection prevalence and intensity strongly correlated with the size of *D. polymorpha*, the presence of large, infected mussels is likely important to serve as a reservoir for maintaining infection in the overall population. In our previous study [2], we indicated that in shallow regions of the Svisloch River the majority of *D. polymorpha* were eliminated each winter by a combination of factors, including ice scour, mallard duck predation, and fluctuating water levels. As a result, *D. polymorpha* were not permanently present at shallow depths (≤ 0.5 m), and the mussels that we randomly sampled in such locations were thus smaller (i.e., younger) and their density was lower than those present at the 1.5-m deep sampling site. Therefore, a significantly lower prevalence ($P < 0.001$, *t* test) was observed at the 0.5-m deep site (58%) than at the 1.5-m deep site (100%). In his study of *C. acuminatus* in Macedonian *D. polymorpha*, Raabe [21] also observed that the prevalence of infection was highest at depths of ca. 0.5–20 m compared to the rocky shoreline (< 0.5 m), but it is unknown whether this was the result of the mussels on the rocky shoreline being smaller in size (i.e., younger) and thus less likely to be infected. In our previous study [2], we found that 20–23 mm *D. polymorpha* from two separate waterbodies in Belarus, when held together in a cage under field conditions, reached the same *C. acuminatus* carrying capacity (i.e., infection intensities rose to and remained at $1.5–2.0 \times 10^3$ ciliates). Thus, we believe that the differences in infection intensity recorded in *D. polymorpha* from the Svisloch and the Dnieper rivers in the present study (Fig. 3) were likely determined in part by a combination of habitat characteristics (e.g., water chemistry, food availability) and host characteristics (e.g., mussel density and size-structure). We hypothesize, therefore, that *D. polymorpha* of a given length in each population may have its own carrying capacity of infection intensity. Upon reaching this population density, a *C. acuminatus* population may have density-dependent feedback mechanisms which slow its rate of reproduction within a host and/or increase its emigration from its host mussel in order to maintain a rather constant population size within the mussel.

Life cycle synchrony: In order to infect new host mussels, *C. acuminatus* must disperse into surrounding waters, and Kidder [9] has indicated that *Conchophthirus* spp. likely can tolerate only brief periods in open waters. To minimize the time required for such host transfer, we suggest that a period of mass ciliate dispersal may be synchronized to occur when new potential hosts, i.e., juvenile *Dreissena*, become abundant. We have previously experimentally demonstrated that *C. acuminatus* rapidly leave dying *D. polymorpha* [2]. This latter study supported Fenchel [4] who indicates that ciliates in bivalves occasionally leave their hosts, but are more likely to do so when the host is "damaged mechanically" or dying. Therefore, *D. polymorpha* that are naturally dying could be a major source of *C. acuminatus* to initiate infection in other members of the population, especially young-of-the-year mussels. According to Lvova [12], many of the older *D. polymorpha* in a population die within a brief period of time after spawning. In infected populations, this would theoretically result in mass emigration of *C. acuminatus* from dead mussels in order to search for new hosts.

Other factors affecting infection levels: Although not specifically examined by this study, two other factors likely impact *C. acuminatus* infection: host density and salinity level. Fenchel [4] suggested that since ciliates infect new hosts by being passively sucked in through their inhalant siphon, it is to be expected that prevalence would correlate positively with host density. Burlakova et al. [2] experimentally demonstrated that the presence of mussels with high intensity infections can serve as a source for increasing the levels of infection (both infection prevalence and intensity) in other mussels in their microhabitat. *C. acuminatus* is less tolerant to salinity than *D. polymorpha* and thus infection prevalence was observed to decline from 100 to 0% with increasing salinity in a Polish bay [20]. Since there are some *Conchophthirus* spp. that are symbionts in marine bivalves [10], it would be interesting to examine *Dreissena* populations in areas of varying salinity in the Caspian Sea and Dnieper-Bug Liman for the presence of species other than *C. acuminatus*. *Dreissena* are native to both of these waterbodies and are locally abundant.

Endosymbiont Research Model: Since *C. acuminatus* is the most common *Dreissena* endosymbiont with the highest prevalence and intensity of infection in Europe [15], it is easily field collected. Thus, further studies of the interactions between *C. acuminatus* and *Dreissena* could represent a very convenient means of addressing numerous fundamental questions relating to symbiosis, including: symbiont dispersal, life cycle features improving infection probability, synchronization of host and symbiont life cycles, strains of symbiont and host, factors responsible for specificity, intraspecific symbiotic competition; underlying mechanisms of host specificity, and infection strategies. Moreover,

since there is considerable interest in the parasitic endosymbionts of *Dreissena* spp. [14, 15], the information derived from a *Conchophthirus* (i.e., commensal) model could be directly compared with parallel data from species that either debilitate or kill *Dreissena.*

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