

Field and Laboratory Studies of Zebra Mussel (*Dreissena polymorpha*) Infection by the Ciliate *Conchophthirus acuminatus* in the Republic of Belarus

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This study quantifies the infection prevalence and intensity of the European, commensal, host-specific ciliate *Conchophthirus acuminatus* (Scuticociliatida: Conchophthiridae) in five zebra mussel populations within the Republic of Belarus. Laboratory and field experiments were also conducted to assess variables affecting infection. *C. acuminatus* was found in zebra mussels in all five waterbodies sampled: Naroch, Myastro, and Lukomskoe Lakes, Skema Stream, and in the Svisloch River. Prevalence was always 100%, with the exception of shallow areas (≤ 0.5 m depth) in the Svisloch River. This was possibly the result of the elimination of the majority of infected zebra mussels each winter by a combination of factors, including ice scour, mallard duck predation, and fluctuating water levels. As a result, zebra mussels are not permanently present at shallow depths, and the mussels that we randomly sampled there during the summer were thus smaller (i.e., younger) and less infected than those present in deeper sections of the river. This is the first study to quantify the intensity of *Conchophthirus* infection in zebra mussels. When infection prevalence was 100%, it was not uncommon for zebra mussels to have 500–2,000 *C. acuminatus* in their mantle cavities, particularly those mussels ca. 15–30 mm in length. Zebra mussels, while relatively small bivalves, have one of the highest intensities ever reported for ciliates in the order Scuticociliatida. Infection intensity correlated directly with mussel length (range in $r^2 = 0.83$ – 0.92). Transinfection of zebra mussels with *C. acuminatus* was achieved both in the laboratory and field, and represented the first successful trials to initiate protozoan infection in *Dreissena*. Laboratory experiments demonstrated that *C. acuminatus* rapidly leave their dying zebra mussel hosts, and this suggested that these mussels are likely a major source for the spread of *C. acuminatus* infection. Field trials indicated that the

presence of mussels with high intensity infections can cause an increase in the levels of infection (both prevalence and intensity) in other zebra mussels in their microhabitat. © 1998 Academic Press

Key Words: Conchophthiridae; infection prevalence; infection intensity; Dreissenidae.

INTRODUCTION

There are 34 known species of symbionts associated with zebra mussels (*Dreissena polymorpha*), including ciliates, trematodes, nematodes, oligochaetes, mites, chironomids, and leaches. The ciliate *Conchophthirus acuminatus* (Scuticociliatida: Conchophthiridae) (Fig. 1) is the most common of these organisms (Molloy *et al.*, 1997). Although North American sampling has been conducted (L. E. Burlakova, A. Y. Karatayev, and D. P. Molloy, unpublished data), this species has been found only in European populations of *D. polymorpha*, including Denmark (Fenchel, 1965), Poland (Dobrzanska, 1958), Hungary (Raabe, 1950), Macedonia (Raabe, 1966), Bulgaria (Raabe, 1934), and Switzerland (Claparède and Lachmann, 1858). Its symbiotic relationship with zebra mussels, although obligate, is far more likely to be commensal than parasitic. Food vacuoles in *Conchophthirus* spp. from other bivalve species have been reported to typically contain algae, bacteria, and sloughed-off epithelial cells (Kirby, 1941). Contents of the food vacuoles of *Conchophthirus* in *Dreissena* have never been investigated. In the absence of such information, we assume that they are essentially commensals and are not actively consuming live epithelial cells.

Conchophthirus spp. have an obligate association with bivalves and likely can tolerate only brief periods in open waters, as during their transfer to new hosts (Kidder, 1934). *C. acuminatus*, in particular, is extremely host specific since it has been found exclusively in *D. polymorpha* (Molloy *et al.*, 1997). For example, Raabe (1950) wrote that he never observed *C. acumina-*

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FIG. 1. View of right side of body of *C. acuminatus* containing oral groove (differential contrast, scale bar, 10 μm).

tus in Unionidae, even though their shells were sometimes completely covered by *C. acuminatus*-infected *D. polymorpha*.

C. acuminatus is most frequently observed on the surfaces of the visceral mass and gills of zebra mussels where they creep about using their short, dense cilia (Molloy *et al.*, 1997). The anterior portion of their left side is concave and possesses thigmotactic cilia, enabling them to adhere tightly to surfaces. These thigmotactic cilia can beat independently of other cilia and become stiff and motionless when touching a substratum (Fenchel, 1965).

Although there are several reports of the prevalence of *C. acuminatus* infection (i.e., percentage of mussels with ciliates) (Fenchel, 1965; Raabe, 1956, 1966, 1971), to our knowledge, the intensity of infection (i.e., number of ciliates per infected mussel) has never been investigated. This report addresses this information gap by quantifying the prevalence and intensity of *C. acuminatus* infection in zebra mussel populations within the Republic of Belarus and by conducting

laboratory and field experiments to assess variables affecting these parameters.

MATERIALS AND METHODS

1994 Field Sampling

We studied the zebra mussel populations in Naroch, Myastro, and Lukomskoe Lakes, in Skema Stream, and in the Svisloch River in Belarus. Naroch Lake (54°50'N, 26°45'E) and Myastro Lakes (54°51'N, 26°55'E) are 110 km northwest of Minsk and are connected to each other by Skema Stream. Lukomskoe Lake (54°40'N, 29°05'E) is located 120 km northeast of Minsk, and the Svisloch River (53°55'N, 27°30'E) flows directly through Minsk. Naroch is the largest lake in Belarus (surface area 79.6 km², average depth 8.9 m, maximum depth 24.8 m). Zebra mussels were first documented in Naroch in 1989 (Ostapenya *et al.*, 1993), and in 1994 their mean (\pm SE) density throughout the lake was 758 (\pm 240) $\cdot \text{m}^{-2}$ and biomass averaged 115 (\pm 30) g $\cdot \text{m}^{-2}$ (Burlakova, 1998). Myastro Lake (surface area 13.1 km², average depth 5.4 m, maximum depth 11.3 m) was invaded by zebra mussels in 1984 (Ostapenya *et al.*, 1994), and in 1995 mean (\pm SE) density throughout the lake was 645 (\pm 147) $\cdot \text{m}^{-2}$ and biomass averaged 288 (\pm 118) g $\cdot \text{m}^{-2}$ (Burlakova, 1998). Lukomskoe Lake (surface area 34.7 km², average depth 6.6 m, maximum depth 11.5 m) has been a cooling reservoir for a thermal power station since 1969. Zebra mussels were found in this lake for the first time in 1972 (Lyakhnovich *et al.*, 1982). In 1989 their mean density in the lake was 501 $\cdot \text{m}^{-2}$ and average biomass was 178 g $\cdot \text{m}^{-2}$ (Karatajev, 1992). In the section of the Svisloch River where we collected our samples, width was ca. 50 m, mean depth was ca. 1 m, and maximum depth was ca. 2 m. In 1995 mean (\pm SE) density in the Svisloch River within the city of Minsk was 2,500 (\pm 1,585) $\cdot \text{m}^{-2}$ and biomass averaged 1,183 (\pm 883) g $\cdot \text{m}^{-2}$ (Burlakova, 1998).

We collected several hundred zebra mussels from one or more sites in each waterbody (Table 1) and held them at 3°C in the laboratory prior to determining their infection prevalence and intensity. Mussels from both Naroch and Myastro Lakes were dissected within 24 h, from the Skema Stream within 48 h, and from Lukomskoe Lake within 72 h. Before dissection, we cleaned and dried shell surfaces and measured mussel length to the nearest millimeter with calipers. In Naroch Lake, Lukomskoe Lake, and Skema Stream, we tested whether the intensity of infection by *C. acuminatus* differed among zebra mussels of different lengths using the following protocol: mussels were cut open with a scalpel, their mantle cavities were repeatedly flushed with unchlorinated tap water from a pipette to remove all ciliates from epithelial surfaces, and the

TABLE 1
Prevalence of *C. acuminatus* Infection in Zebra Mussel Populations in Belarussian Waterbodies

Waterbody	Date	Depth (m)	Temperature (°C)	Mussels dissected	Prevalence (%)
Naroch Lake	August 1994	1.5–2.0	20	100	100
Myastro Lake	August 1994	1.5–2.0	20	100	100
Lukomskoe Lake	September 1994	1.5–2.0	22	50	100
		1.5–2.0	18	50	100
Skema Stream	August 1994	1.5	22	100	100
Svisloch River	August 1994	0.3	22	50	0
	June–September 1995	0.5	13–23	47	58 (50–86)
	July 1995	1.5	22	50	100

number of *C. acuminatus* were counted in a plankton counting chamber using a stereomicroscope (20–70×).

1994 Laboratory Transinfection Experiments

To determine how quickly *C. acuminatus* invade new hosts, two experiments were set up in August 1994 in which zebra mussels from Naroch Lake [i.e., 100% prevalence (Table 1)] were placed at one end of a tray (L × W × H = 30 × 20 × 5 cm) containing 2.4 L of unchlorinated tap water (18–20°C) and an equal number of Svisloch River mussels from a 0.3-m depth [i.e., 0% prevalence (Table 1)] placed at the opposite end. Four such trays were set up in this fashion, with one tray of mussels dissected after 1, 2, 3, and 4 days. In Experiment 1, live Naroch mussels were used, but in Experiment 2, we delivered a lethal injury to the Naroch mussels by cutting their posterior adductor muscle immediately before placing them in each of the four trays. This allowed us to assess whether the death of an infected mussel might affect transinfection.

1995 Field Experiments

To test whether depth was an important variable affecting prevalence, 47 zebra mussels from a shallow (0.5 m) and 50 from a deeper area (1.5 m) within the Svisloch River were collected and dissected in 1995 (Table 1). The distance between the sites was ca. 10 m. In addition, we determined the size-frequency distribution at each site by measuring the length of ca. 300 randomly collected mussels to the nearest millimeter with calipers.

To determine how quickly under natural conditions *C. acuminatus* can invade a new host and increase infection intensity, we conducted a 4-month experiment in the Svisloch River in 1995 using mussels 20–23 mm in length. We held mussels of a very high infection intensity and others of a very low infection intensity in a single cylindrical cage (diameter = 25 cm; height = 40 cm) on the river bottom at a 0.5-m depth. Its iron frame was covered by 5-mm mesh net. All mussels used in the experiment were measured and marked with 3-mm-diameter bee tags. We collected mussels from Naroch

Lake (12°C) on May 24 (*C. acuminatus* prevalence ca. 100%). Mussels were refrigerated in water for 6 days at 3°C, after which 100 mussels were placed in the benthic cage in the Svisloch River. After 12 days (on June 12), 100 mussels which were naturally present on rocks in the Svisloch River at 0.5 m depth (*C. acuminatus* prevalence ca. 86%) were tagged, measured, and mixed in with the Naroch mussels within the cage. Water temperature in the Svisloch River was 20–23°C during the first 90 days of the experiment and thereafter declined to 13°C by the end of September. During the experiment, we periodically removed 7–10 Naroch and 7–10 Svisloch mussels from the cage and dissected them to determine infection prevalence and intensity (Fig. 2). Mean (±SE) mussel length in these Naroch and Svisloch mussel samples ranged, respectively, from 20.9 (±1.5) to 23.0 (±0.9) mm and from 20.4 (±0.7) to 21.9 (±0.9) mm. In addition, at each sampling time we collected 8 Svisloch “control” mussels from the river

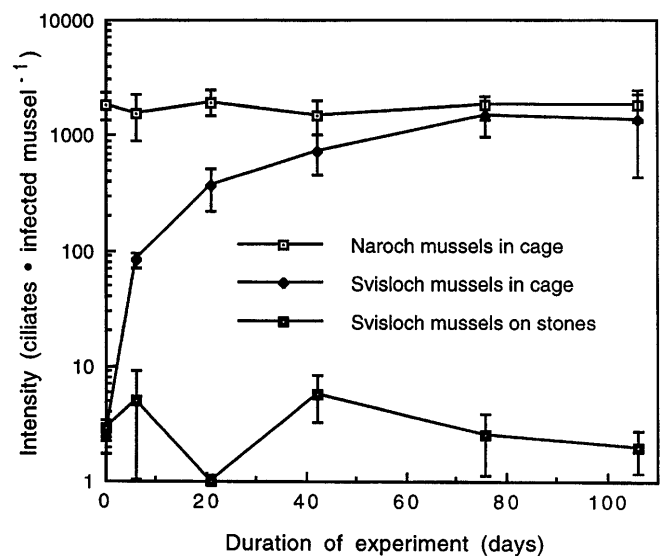


FIG. 2. Dynamics of the intensity of zebra mussel infection by *C. acuminatus* in an experimental cage in the Svisloch River (mean ± SE indicated).

bottom near the cage; their mean (\pm SE) length ranged from 20.8 (\pm 0.7) to 22.7 (\pm 1.6) mm.

RESULTS AND DISCUSSION

Field Sampling: Distribution, Prevalence, and Intensity of Infection

C. acuminatus was found in zebra mussels in all five waterbodies sampled. Prevalence was always 100%, the only exceptions being the shallow samples (\leq 0.5 m depth) taken in the Svisloch River both in 1994 (0%) and 1995 (58%) (Table 1). 100% prevalence of *C. acuminatus* infection in zebra mussels has been previously reported in two Danish lakes (Fenchel, 1965) and in nonsaline waters in Poland (Raabe, 1956). According to Anderson and May (1981), prevalence of infection within a host population is generally inversely related to its pathogenicity. Thus, the high prevalence of *C. acuminatus* that we and others (see above) have observed further indicates that these ciliates are commensals. In addition, no signs or symptoms of disease were evident in any of the infected mussels examined during this study.

Why were the lowest prevalences recorded in the shallow water samples in the Svisloch River? In shallow regions of this river, the majority of zebra mussels are eliminated each winter by a combination of factors, including ice scour, mallard duck predation (Kozulin, 1995), and fluctuating water levels. As a result, zebra mussels are not permanently present at shallow depths, and the mussels that we randomly sampled there were thus smaller (i.e., younger) than those present at the 1.5-m deep sampling site. At this deeper site, the mussel population was composed of mussels up to 3 years old (i.e., \geq 26 mm long) as indicated by size frequency distributions (Fig. 3). We suggest that the significant difference ($P < 0.001$, t test) observed in 1995 in infection prevalence at the 0.5 m vs 1.5 m depth (58 vs 100%, Table 1) was a reflection of the annual reduction in infected hosts in the shallower area. In his study of *C. acuminatus* in Macedonian zebra mussels, Raabe (1966) 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, 50% prevalence). Fenchel (1965) suggested that since ciliates infect new hosts by being passively sucked in, it is to be expected that prevalence would correlate positively with host density. Our field data support his hypothesis since zebra mussels at the 1.5- and 0.5-m-deep sampling sites were, respectively, 1.6 times more dense (8,454 vs 5,440 mussels \cdot m $^{-2}$) and 3.3 times greater in biomass (4,438 vs 1,356 g \cdot m $^{-2}$).

This is the first study to quantify the intensity of *Conchophthirus* infection in zebra mussels. In our samples when infection prevalence was 100%, it was not uncommon for zebra mussels to have 500–2,000 *C.*

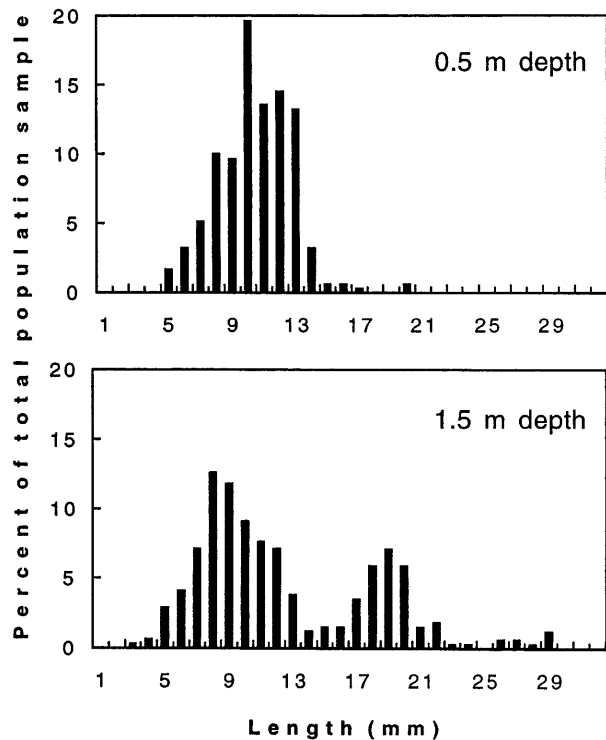


FIG. 3. Size-frequency distribution of zebra mussels at differing depths in the Svisloch River.

acuminatus in their mantle cavities, particularly those mussels ca. 15–30 mm in length (Fig. 4). The smallest infected mussel was 2 mm long and contained only a single ciliate, whereas the maximum number of ciliates (5,100) was observed in a 28-mm-long zebra mussel from Naroch Lake. In their study of unionids in Illinois, Antipa and Small (1971) observed that intensity of *Conchophthirus curtus* infection ranged from a few per host to over a thousand. In contrast, Kidder (1933) reported that infection intensity of *Peniculistoma mytili* (Scuticociliatida: Peniculistomatidae) in North American *Mytilus edulis* was rarely more than 50–75 ciliates \cdot mussel $^{-1}$, with an average of 5–10 ciliates \cdot mussel $^{-1}$. In his Danish fieldwork with *M. edulis*, Fenchel (1965) reported maximum, mean ciliate intensities in any 10-mm-length class as 21 *P. mytili* in 21- to 30-mm mussels and 501 *Ancistrum mytili* (Scuticociliatida: Ancistridae) in 41- to 50-mm mussels. In his studies in the northeastern United States, Kidder (1934) noted that the maximum intensity of *Conchophthirus anodontae* infection was in the “hundreds” in his unionid samples. Our field data, therefore, were surprising since zebra mussels, while relatively small bivalves, have one of the highest intensities ever reported for ciliates in the order Scuticociliatida. Ciliate size, however, may partially explain the low intensity of *P. mytili* since this species is approximately three times the length of *C. acuminatus* and thus may require

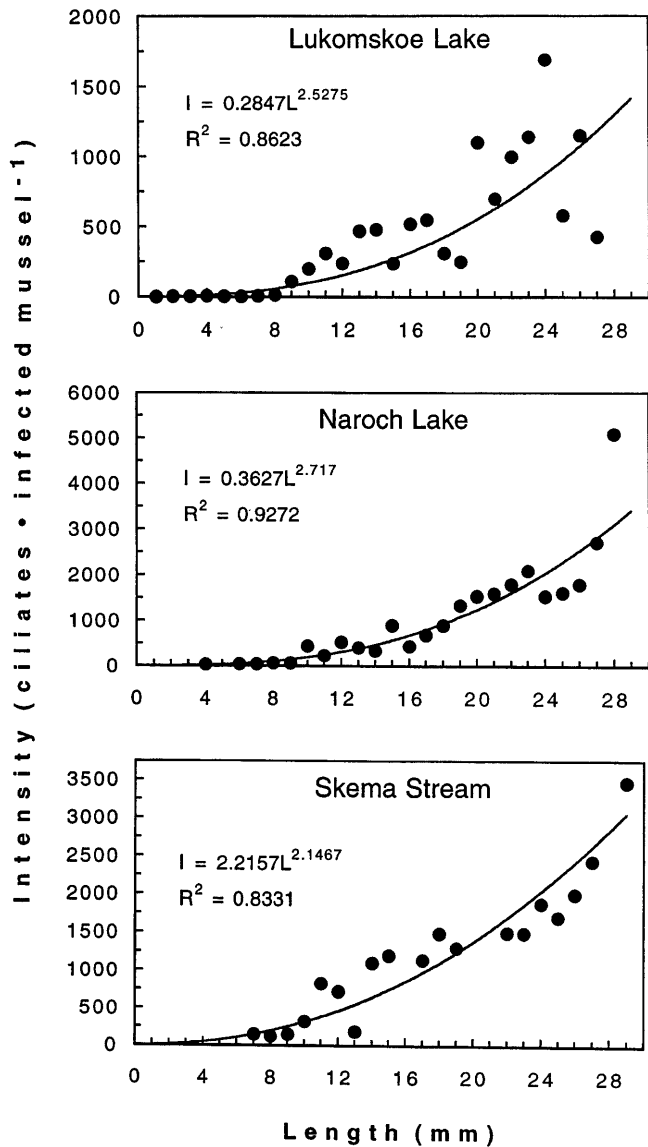


FIG. 4. Power equations expressing the relationship between zebra mussels length (L) and intensity of infection (I) by *C. acuminatus* in different waterbodies.

greater resources (e.g., space, food) within the mantle cavity.

Infection intensity correlated directly with mussel length in the three waterbodies sampled, and a power equation was calculated to estimate infection intensity based on mussel length in each waterbody (Fig. 4). Intensity increased only slightly with increasing size in mussels 2–10 mm long, but increased rapidly with length in larger mussels (Fig. 4). A similar pattern of very low ciliate intensity in mussels ≤10 mm long was observed by Fenchel (1965) in *P. mytili* and *A. mytili* infection of *M. edulis*.

Laboratory Transinfection Trials

Experiment 1: Use of Live Naroch Mussels. Infection of Svisloch mussels by *C. acuminatus* from Naroch mussels was achieved in the laboratory (Table 2). This represented the first successful trial ever conducted to initiate protozoan infection in *Dreissena*. From an initial complete lack of infection among the Svisloch mussels, prevalence and intensity rose to 100% and 3.9 ciliates · mussel⁻¹ by day 1 (Table 2). Intensity in these newly infected Svisloch mussels, however, remained low throughout the remaining 3 days of the experiment (maximum, 8.1 ciliates · mussel⁻¹). In contrast, infection intensity in the Naroch mussels constantly increased during the 4-day experiment. We suggest that a sudden increase in water temperature may have stimulated ciliate reproduction in these naturally infected Naroch mussels; prior to the beginning of this 18–20°C experiment, these Naroch mussels were held at 3°C for 4 days. We have observed similar sudden increases in *C. acuminatus* intensity when zebra mussels are refrigerated and then warmed (L. E. Burlakova, A. Y. Karatayev, and D. P. Molloy, unpublished data).

Experiment 2: Dying Naroch Mussels. In the trials in which Naroch mussels were fatally injured, infection prevalence in the Svisloch mussels within the tray also rose to 100% within 24 h (Table 3). Intensity in these newly infected Svisloch mussels, however, was significantly ($P < 0.001$, *t* test) greater than in Experiment 1

TABLE 2

The Intensity^a and Prevalence of Zebra Mussels Infected with *C. acuminatus* from Naroch Lake (infected population) and Svisloch River (uninfected) during Laboratory Experiment

	Mean intensity (±SE) (% Prevalence in parentheses)				
	Day 0	Day 1	Day 2	Day 3	Day 4
Infected	291 ± 65 (100)	349 ± 83 (100)	782 ± 180 (100)	857 ± 231 (100)	1294 ± 272 (100)
Uninfected	0.0 (0)	3.90 ± 1.17 (100)	8.10 ± 1.79 (100)	5.60 ± 2.09 (100)	6.43 ± 3.24 ^b (77)

Note. Cell values are number of ciliates per mussel ± SE in 10 mussels.

^a Ciliates · infected mussel⁻¹.

^b N = 9.

TABLE 3

The Intensity^a and Prevalence of Zebra Mussels Infected with *C. acuminatus* from Naroch Lake (killed mussels) and Svisloch River (live mussels) in Laboratory Experiments

	Mean intensity (\pm SE) (% Prevalence in parentheses)				
	Day 0	Day 1	Day 2	Day 3	Day 4
Infected	291.0 \pm 65.0 (100)	287.0 \pm 82.0 (100)	2.9 \pm 0.9 (70)	0.0 (0)	0.0 (0)
Uninfected	0.0 (0)	257.9 \pm 101.0 (100)	100.0 \pm 14.5 (100)	23.7 \pm 6.0 (100)	6.9 \pm 2.7 (80)

Note. Cell values are numbers of ciliates per mussel \pm SE in 10 mussels.

^a Ciliates \cdot infected mussel⁻¹.

(257.9 vs 3.9 ciliates \cdot mussel⁻¹). The number of ciliates in the dead and dying Naroch mussels decreased over time, reaching zero within 3 days. Intensity also decreased from day 1 through day 4 in the Svisloch mussels, and this was almost certainly due to the poor water quality resulting from the decaying Naroch mussels. These data support Fenchel (1965) who suggested that ciliates in nondreissenid bivalves are likely to occasionally leave their hosts, but certainly if the host is "damaged mechanically" or dying. He found that dead bivalves did not contain any of their *Conchophthirus* spp. Exactly the same pattern occurred in our laboratory transinfection experiments. We suggest, therefore, that zebra mussels that are dying naturally in the field are a major source of *Conchophthirus* for infection of other members of the population.

Field Transinfection Trials

Placement of individuals of high infection intensity (i.e., Naroch mussels) into the benthic cage containing mussels of low intensity (i.e., Svisloch mussels) had a dramatic affect on infection in the latter group. Within only 6 days of exposure (June 12–18), mean prevalence in the caged Svisloch mussels increased from 86 to 100% and mean intensity from 2.8 to 82.0 ciliates \cdot mussel⁻¹ (Fig. 2). Intensity in these caged Svisloch mussels constantly continued to increase within the first 60 days and then began to level off. After 77 days (by August 28) the mean infection intensity (1,490 ciliates \cdot mussel⁻¹) in the caged Svisloch mussels was actually not significantly different ($P = 0.32$, t test) from that in the Naroch mussels (1,800 ciliates \cdot mussel⁻¹). In contrast, throughout the experiment the mean intensity of infection in the Svisloch control mussels (i.e., those which were naturally present at the same depth on rocks 0.5–4.0 m distant from the cage) did not significantly change during the experiment and ranged from 1.0 to 5.8 ciliates \cdot mussel⁻¹ (Fig. 2). We also observed that the infection intensity in the caged Naroch mussels did not significantly change throughout the 4-month experiment (Fig. 2). These data support two hypotheses: (1)

that the presence of mussels with high intensity infections can serve as a source for increasing the levels of infection (both prevalence and intensity) in other mussels in their microhabitat (i.e., our cage); and (2) that intensities in the order of $1.5\text{--}2.0 \times 10^3$ ciliates \cdot mussel⁻¹ may be the carrying capacity for the 20- to 23-mm-long zebra mussels used in this experiment.

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