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PATTERNS OF EMERGENCE AND SURVIVAL OF *CONCHOPHTHIRUS ACUMINATUS* (CILIOPHORA: CONCHOPHTHIRIDAE) FROM *DREISSENA POLYMORPHA* (BIVALVIA: DREISSENIDAE)

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ABSTRACT This is the first study to quantify the periodic emergence of a *Conchophthirus* sp. from its bivalve host. Emergence rates of *C. acuminatus* from *Dreissena polymorpha* over the entire 24-day experiment appeared to be directly correlated with infection intensity. The rate of ciliate emergence from individual mussels varied considerably throughout the experiment at both 14°C and 21°C. It was not uncommon to have a sampling period in which no emergence was observed immediately followed by a period of high emergence, e.g., at 14°C from 0 to 25 ciliates and at 21°C from 0 to 720 ciliates. The total mean number of ciliates that were observed to have emerged from each mussel during the 24-day experiment was significantly higher at 21°C (207 ciliates/mussel) than at 14°C (29 ciliates/mussel). Our experiments suggested that *C. acuminatus* have a short survival period outside their host. Although we observed a maximum survival period of 144 hr (6 days), most ciliates died within 48 h.

KEY WORDS: *Conchophthirus acuminatus,* ciliate, commensal, host, bivalve, *Dreissena polymorpha,* zebra mussel, mantle cavity

INTRODUCTION

The ciliate *Conchophthirus acuminatus* (Claparède & Lachmann) (Scuticociliatida: Conchophthiridae) is the most common of 34 endosymbionts associated with zebra mussels (*Dreissena polymorpha* (Pallas)) (Molloy et al. 1997). Although not known from North America, this ciliate is very common in European zebra mussel populations, including in Bulgaria (Raabe 1934), Denmark (Fenchel 1965), Hungary (Raabe 1950), Macedonia (Raabe 1966), Poland (Dobrzanska 1958), and Switzerland (Claparède & Lachmann 1858). Its widespread distribution was recently confirmed by its presence in all 21 zebra mussel populations surveyed in Belarus (Burlakova et al. 1998, Karatayev et al. 2000a). Among all zebra mussel protozoan symbionts, this ciliate typically has the highest prevalence (i.e., percentage of mussels with ciliates) and intensity of infection (i.e., number of ciliates per infected mussel) (Molloy et al. 1997, Burlakova et al. 1998, Karatayev et al. 2000a).

Conchophthirus acuminatus appears to be very specific to *Dreissena* and has never been reported from any other host. Raabe (1950) never observed it in unionid mussels, even though they were sometimes completely covered by *C. acuminatus*-infected zebra mussels. Although its feeding on the sperm cells of *D. polymorpha* has been documented (Laruelle et al. 1999), *C. acuminatus* is likely a commensal organism which ingests a variety of organic particles present on *Dreissena*'s mantle epithelial surfaces (Molloy et al. 1997). *C. acuminatus* is typically found on the epithelial surfaces of the mantle, gills, visceral mass, and labial palps, and within gill water tubes and suprabranchial cavities (Laruelle et al. 1999).

As with other *Conchophthirus* spp., *C. acuminatus* appears to have an obligate association with its bivalve host, with the only free-living phase of its life cycle occurring during its transfer to new hosts. The longer these ciliates can live in open water, the greater their success in reaching new hosts, particularly distant zebra mussel populations. An investigation of this free-living phase in the *C. acuminatus* life cycle was the focus of this study. In a series of laboratory experiments, we quantified the frequency that these ciliates emerged from zebra mussels and measured their survival rate in open water. The results presented herein are part of an extensive investigation that we, as members of the International Research Consortium on Molluscan Symbionts (Molloy 2003), are conducting to characterize the systematics, biology, ecology, and distribution of *Dreissena*'s endosymbionts (Molloy et al. 1996, Molloy et al. 1997, Molloy et al. 2001, Burlakova et al. 1998, Laruelle et al. 1999, Karatayev et al. 2000a, Karatayev et al. 2000b, Karatayev et al. 2002, Laruelle et al. 2002, Fokin et al. 2003). This current study, in particular, will hopefully contribute to a better understanding of the emergence patterns and subsequent free-living phase of *C. acuminatus* and will thereby provide insights into the life cycle of a commensal—a type of symbiont which, relative to parasites and mutualists, has received little research attention.

MATERIALS AND METHODS

Laboratory experiments were conducted during 1998–2002 in the Republic of Belarus using zebra mussels collected at a ca. 1.5 m depth from the Dnieper–Bug Canal (52°06′N, 26°00′E) and the Svisloch River (53°55′N, 27°32′E).

Emergence of C. acuminatus *from* D. polymorpha

To determine the frequency of emergence of *C. acuminatus* from zebra mussels, an experiment was conducted in April 1998 in which 48 mussels from the Dnieper–Bug Canal were placed individually in 20-mL Petri dishes containing a suspension of the alga *Scenedesmus acuminatus* (Lagerheim) in 10 mL of unchlorinated tap water. For 24 days, half of these dishes were held at 14 (±1)°C and half at 21 (±1)°C. Mean mussel lengths in the 14°C and 21°C dishes were, respectively, 13.8 mm and 14.3 mm (Tables 1 and 2). Every 2 to 3 days, the water in each dish was transferred to a plankton counting chamber and fresh, unchlorinated tap water and algae were added to each dish. Water in the counting chamber was examined for *C. acuminatus* using a stereomicroscope (20×), with ciliates counted and discarded.

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TABLE 1.

Pattern of emergence of *C. acuminatus* from *D. polymorpha* at the 14 (±1)°C.

Mussel No.	Mussel Length (mm)	Number of Ciliates Collected Outside Their Host											Infection Intensity on Day 24
		Day 3	Day 5	Day 7	Day 10	Day 12	Day 14	Day 17	Day 19	Day 21	Day 24	Total During Experiment	
1	13.4	6	0	0	1	4	1	1	0	11	7	31	34
2	13.2	1	0	0	1	0	6	1	0	4	6	19	74
3	15.5	1	0	1	2	5	3	0	2	17	24	55	313
4	14.0	3	0	0	1	0	0	1	2	17	6	30	19
5	14.6	2	1	2	3	3	2	2	0	25	28	68	125
6	13.1	2	0	0	1	0	—	1	1	6	1	12	1
7	13.2	0	0	2	1	2	0	2	1	14	5	27	117
8	13.6	0	0	0	0	0	5	1	1	4	4	15	3
9	13.0	0	0	1	0	0	2	0	2	8	24	37	41
10	13.5	1	0	0	3	2	3	2	4	11	7	33	24
11	14.0	1	0	0	2	1	0	1	0	8	8	21	13
12	14.1	4	6	26	19	0	8	13	4	3	12	95	0
13	14.0	1	0	0	3	0	1	0	1	4	6	16	5
14	14.0	0	0	0	0	2	0	2	2	5	29	40	89
15	14.2	1	0	3	3	1	0	2	3	5	1	19	0
16	13.9	0	0	0	1	0	0	0	1	13	6	21	89
17	14.1	0	0	3	0	0	6	9	5	5	6	34	10
18	13.6	3	0	2	1	1	0	0	0	2	10	19	4
19	13.6	0	1	1	1	0	2	0	0	6	3	14	69
20	13.9	1	3	1	1	2	0	—	1	5	7	21	16
21	13.2	0	2	4	2	1	1	0	4	6	18	38	20
22	13.4	1	0	0	1	0	2	0	0	4	17	25	77
23	13.6	1	0	1	2	1	0	0	0	0	1	6	11
24	13.6	0	1	0	0	2	0	1	0	0	5	9	10
Mean	13.8	1.2	0.6	2.0	2.0	1.1	1.8	1.7	1.4	7.6	10.0	29.4	48.5
SE	0.02	0.06	0.06	0.22	0.16	0.06	0.10	0.13	0.06	0.25	0.36	0.83	2.85

To determine infection prevalence and intensity at the beginning of the experiment, we dissected 13 14-mm long mussels from the above-mentioned Dnieper–Bug Canal sample. Infection prevalence and intensity were also calculated at the end of the experiment by dissecting the 48 mussels used in the Petri dishes. During dissection, mussel mantle cavities were repeatedly flushed with unchlorinated tap water using a pipette to remove all ciliates from exposed epithelial surfaces. Because *C. acuminatus* were also present within gill water tubes and suprabranchial cavities, 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×).

Survival of C. acuminatus *Outside* D. polymorpha

Three laboratory experiments were conducted to determine how long *C. acuminatus* survive outside their host in open water. In all experiments, *C. acuminatus* were transferred with a pipette into dishes containing water. Dishes were then covered with lids to prevent evaporation and half of them were held at 14 (±1)°C and the other half at 21 (±1)°C. Using a stereomicroscope (20×), dishes were inspected until all ciliates had died.

Experiment 1

In November 1998, mussels were collected from the Svisloch River and dissected. Ciliates were held in groups of 10 in each of six 10-mL Petri dishes containing 2 mL of unchlorinated tap water and were inspected daily.

Experiment 2

In January 2000, 40 *C. acuminatus* obtained by dissection from zebra mussels collected in Dnieper–Bug Canal were held individually in 10-mL Petri dishes containing 3 mL of unchlorinated tap water. Mortality was scored at 6, 21, 70, and 90 h.

Experiment 3

In July 2002, 20 *C. acuminatus* obtained by dissection from zebra mussels collected from the Svisloch River were held at 14 (±1)°C and 23 (±1)°C in 40 individual 4-mL plastic dishes containing 2 mL of filtered (100-μm mesh net) Svisloch River water. Mortality was scored at 6, 24, 30, 48, and 54 h. During each dish inspection, 1 mL of water in each dish was replaced with fresh filtered water. Since ciliates may be more sensitive to environmental changes than their hosts (Beers 1959), we followed Beers' suggestion to collect mussels as needed and to use the ciliates at once. Therefore, in experiment 3 we repeated the same exact procedure three times, starting on three consecutive days using ciliates from freshly collected mussels.

Data Analysis

The Box–Cox procedure (Krebs 1999) indicated that the best transformation to achieve a normal distribution was $X' = (X + 1)^{0.22}$.

TABLE 2.

Dynamics of the emergence of *C. acuminatus* from *D. polymorpha* at the 21 (±1)°C

Mussel No.	Mussel Length (mm)	Number of Ciliates Collected Outside Their Host										Total During Experiment	Infection Intensity on Day 24
		Day 3	Day 5	Day 7	Day 10	Day 12	Day 14	Day 17	Day 19	Day 21	Day 24		
1	13.1	2	0	0	3	0	0	70	176	15	26	292	0
2	13.1	1	0	17	99	29	9	22	15	16	2	210	0
3	14.0	2	9	2	2	5	3	2	85	171	35	316	7
4	15.5	0	720	186	45	14	5	4	0	12	1	987	63
5	14.0	1	3	6	4	0	3	31	20	12	5	85	1
6	15.5	9	0	6	120	159	87	156	32	24	47	640	143
7	15.8	1	0	1	2	0	0	1	5	5	32	47	49
8	15.2	43	9	22	6	1	4	14	7	4	4	114	129
9	14.6	20	2	0	0	3	9	105	24	37	16	216	114
10	13.0	0	2	0	28	15	9	34	6	9	3	106	168
11	14.3	3	72	3	1	4	11	39	14	24	41	212	732
12	13.5	0	3	10	2	1	2	0	1	1	5	25	262
13	14.5	1	0	0	0	1	3	66	45	15	7	138	331
14	14.5	1	2	1	2	0	5	8	3	6	11	39	158
15	15.2	9	76	1	1	5	0	6	29	9	6	142	1035
16	13.9	5	0	2	0	4	13	4	4	1	1	34	0
17	15.8	2	55	1	3	6	33	61	150	34	61	406	93
18	14.0	0	7	0	1	2	15	200	29	52	6	312	175
19	14.1	1	0	0	0	0	3	3	3	6	11	27	264
20	13.4	0	1	4	7	11	7	26	8	11	3	78	39
21	13.7	0	5	0	0	3	0	1	6	5	5	25	21
22	13.2	0	3	1	0	2	3	9	39	25	133	215	82
23	13.6	5	1	3	11	10	6	20	72	12	0	140	27
24	15.4	0	8	0	19	24	14	81	10	4	3	163	351
Mean	14.3	4.4	40.8	11.1	14.8	12.5	10.2	40.1	32.6	21.3	19.3	207.0	176.8
SE	0.04	0.39	6.10	1.57	1.30	1.34	0.74	2.16	1.91	1.43	1.23	9.17	10.23

To compare transformed data, we used Welch's approximate t test (or t test if variances were homogeneous) in Statistica software (Windows Release 6.0, StatSoft, Inc.). Effects were considered statistically significant at $P < 0.05$.

RESULTS

Emergence of C. acuminatus *from* D. polymorpha

The rate of ciliate emergence from individual mussels varied considerably throughout the experiment at both 14°C and 21°C. It was not uncommon to have a sampling period in which no emergence was observed, immediately followed by a period of high emergence, e.g., at 14°C from 0 to 25 ciliates (Table 1: mussel 5, day 19 vs. day 21) and at 21°C from 0 to 720 ciliates (Table 2: mussel 4, day 3 vs. day 5).

At 14°C, typically ≤3 ciliates were observed outside a host mussel each sampling day, but this pattern was typically interrupted by periods of higher emergence, particularly toward the end of the experiment (Table 1). The mean number of ciliates that were observed outside of the 24 mussels at 14°C ranged from 0.6 to 10.0 ciliates/mussel (Table 1). During the first 19 days of the experiment, a mean of 1.5 ciliates was observed outside the 24 mussels at 14°C (Table 1). Dissection data indicated that infection intensity in the 14°C mussels during the experiment remained constant at about 48 ciliates/mussel (day 0 and day 24 intensities of, respectively 47.3 and 48.5 ciliates/mussel, Table 1). This indicated that during the first 19 days of the experiment on average ca. 3% (i.e., 1.5/49.5) of ciliates were outside their hosts on a sampling day. Emergence rates increased toward the end of the 14°C experiment with a mean emergence of 10.0 ciliates/mussel at the termination of the experiment on day 24 (Table 1). Because the 24 mussels dissected at the end of the 14°C experiment had a mean infection intensity of 48.5 ciliates/mussel (Table 1), this indicated that ca. 17% (i.e., 10.0/58.5) of all ciliates present within the 24 dishes were outside their hosts on day 24.

A similar irregular pattern of ciliate emergence was observed at 21°C (Table 2). Typically ≤15 ciliates were observed outside a host mussel at 21°C, but the majority of mussels also had at least one sampling period during which very high numbers (e.g., 72–720 ciliates) were observed to have emerged. The total mean number of ciliates that were observed to have emerged from each mussel during the 24-day experiment was significantly higher at 21°C than at 14°C (Welch's t test: $t = 6.35$, $P < 0.001$) and was, respectively, 207.0 and 29.4 ciliates/mussel (Tables 1 and 2). The higher number of emerged ciliates in the 21°C dishes was almost certainly related to the significantly higher infection intensity that had developed in mussels at this warmer temperature. Mean infection intensity in the 14°C mussels at the end of the 24-day experiment was 48.5 ciliates/mussel (Table 1) and was not significantly different (t test: $t = 0.06$, $P = 0.95$) from the infection intensity at the beginning of the experiment, i.e., 47.3 ciliates/mussel. In contrast, mean infection intensity in mussels held at 21°C increased to 176.8 ciliates/mussel by the end of the experiment (Table 2) and differed significantly from the initial infection

intensity (Welch's t test: $t = 2.32$, $P = 0.026$) and the infection intensity in mussels held at 14°C (t test: $t = 2.43$, $P = 0.019$). In contrast to the 14°C data, emergence rates at 21°C were not higher toward the end of the experiment. At the termination of the 21°C experiment on day 24, a mean of 19.3 emerged ciliates were observed (Table 2). Because dissections revealed that these 24 mussels had a mean infection intensity of 176.8 ciliates/mussel (Table 2), this indicated that ca. 10% (19.3/196.1) of all the ciliates in the 24 dishes were outside their host on day 24.

Survival of C. acuminatus *outside* D. polymorpha

In experiment 1, *C. acuminatus* exhibited mortality during first 24 h, but 20% were still alive after 96 h at 21°C and after 144 h at 14°C (Fig. 1). During experiment 2, there was a shorter survival period, and all ciliates died by 21 h at 21°C and by 90 h at 14°C (Fig. 2). In experiment 3 ciliates began to die during first 6 h at both temperatures (Fig. 3), and as in previous experiments, ciliates tended to perish faster at higher temperature.

DISCUSSION

Emergence of C. acuminatus *from* D. polymorpha

This is the first study to quantify the periodic emergence of a *Conchophthirus* sp. from its bivalve host. Emergence rates of *C. acuminatus* over the entire 24-day experiment appeared to be correlated with infection intensity. Higher infection intensities led to a higher emergence of ciliates possibly because of higher ciliate reproduction at 21°C compared with 14°C. We hypothesize that these results can explain the seasonal change in zebra mussels infection intensity with *C. acuminatus* that we have observed in the field, i.e., higher intensity in summer and lower in winter (Karatayev et al. 2000b).

The data at both 14°C and 21°C suggested that *C. acuminatus* emergence from an individual zebra mussel does not occur at a constant periodic rate, but is rather an irregular pattern marked occasionally with sudden fluctuations. When data on ciliate emergence was pooled for the entire test group of 24 mussels at either temperature, however, the day-to-day fluctuations in emergence rates were considerably reduced. This suggested that in nature the total number of *C. acuminatus* emerging from a single mussel might fluctuate markedly from day to day, but at the same time the total number emerging from the entire zebra mussel populations would vary far less. Pooling data from all 24 dishes at each temperature provided rough estimates (e.g., 3%, 10%, 17%) of the total *C. acuminatus* outside their hosts, suggesting that a consid-

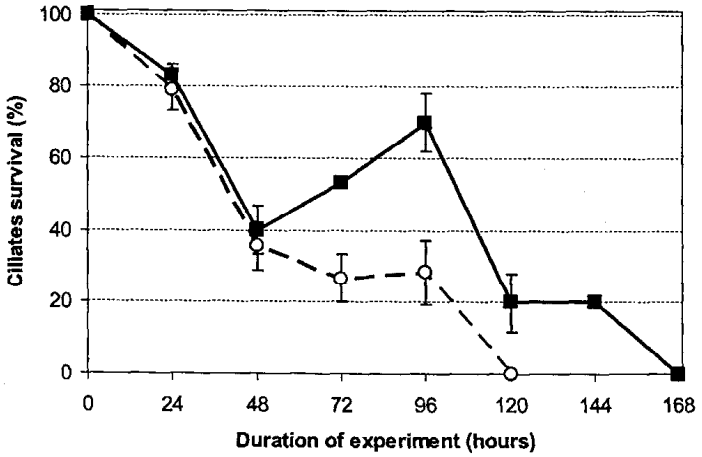

Figure 1. Experiment 1. Mean (±SE) survival of *C. acuminatus* outside its host zebra mussel at 14 (±1)°C (solid line, filled squares) and at 21 (±1)°C (dashed line, open circles).

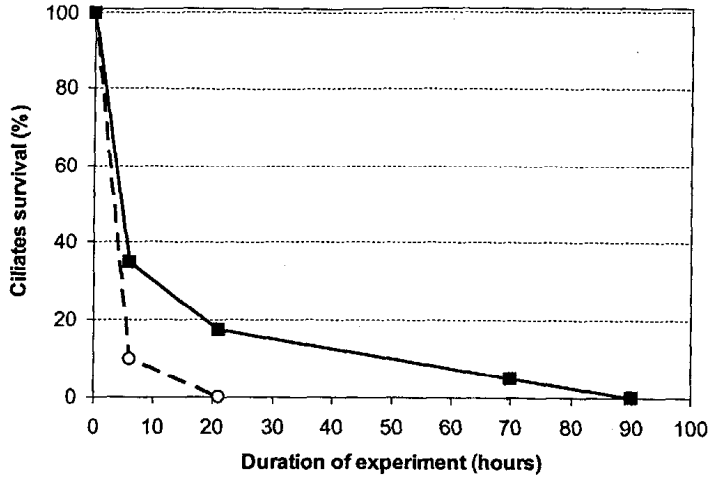

Figure 2. Experiment 2. Survival of *C. acuminatus* outside the host zebra mussel at 14 (±1)°C (solid line, filled squares) and at 21 (±1)°C (dashed line, open circles).

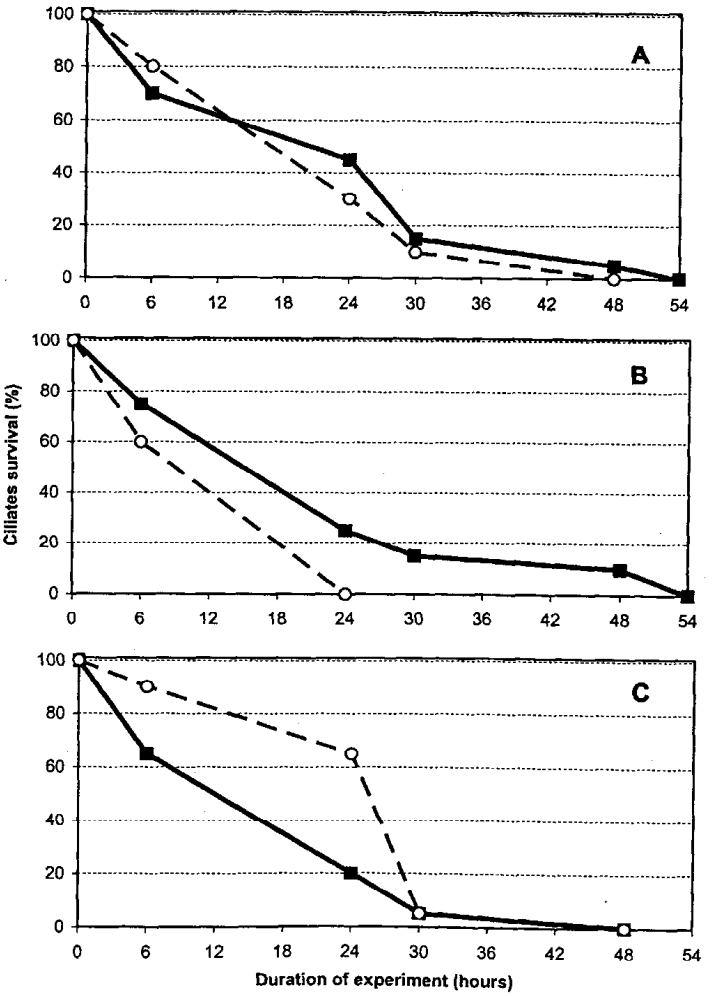

Figure 3. Experiment 3. Survival of *C. acuminatus* outside the host zebra mussel in three consecutive tests (A, B, and C) at 14 (±1)°C (solid line, filled squares) and at 23 (±1)°C (dashed line, open circles).

erable portion of the *C. acuminatus* population might be in open water in search of new hosts. This, in addition to the commensal nature of this symbiont, is likely a key factor explaining why prevalence of this ciliate is typically near 100% in almost all European zebra mussel populations (Molloy et al. 1997, Karatayev et al. 2000a).

Fenchel (1965) observed that *Conchophthirus* spp. in nondreissenid bivalves quickly emerged in large numbers from their damaged or dying hosts. Burlakova et al. (1998) confirmed this same pattern in laboratory trials in which they recorded rapid and massive emergence of *C. acuminatus* from dying zebra mussels. Our present experiment supplements these latter studies by providing information on emergence patterns from live zebra mussels.

Because prevalence of *C. acuminatus* in zebra mussel hosts is frequently 100%, it was surprising, therefore, to observe in our experiment that some infected mussels (i.e., ciliates emerged from them during the experiment) were completely uninfected by the end of the experiment (Table 1, mussels 12 and 15; Table 2, mussels 1, 2, and 16). This suggests that *C. acuminatus* infection can be temporary. In nature, however, mussels are likely infected periodically by *C. acuminatus* from other infected zebra mussels, whereas in our experiment mussels were individually isolated, with transinfection prevented.

Hopefully this experiment has provided some insight into the frequency to which *C. acuminatus* emerge from their host zebra mussels. Future trials, however, may want to expand on its design as follows:

1. *More frequent observations.* We likely underestimated the numbers of ciliates that emerged. Since *C. acuminatus* is a relatively small organism ($L \times W \cong 100 \times 50$ μm), it was extremely difficult to see dead/decomposing individuals using the stereomicroscope. Thus, our counts were almost exclusively based on observation of live ciliates exhibiting movement (i.e., swimming, cilia beating, etc.), and ciliates that emerged and died between the 2- to 3-day sampling periods were likely overlooked. A higher frequency of observations, possibly every 3 h, would be required to address this problem.
2. *Dishes with more than one mussel.* Host density may affect ciliate emergence rates, and this was not accounted for in our experimental design. The possibility exists *C. acuminatus* may be stimulated to emerge from their hosts when chemical cues indicate the presence of other nearby potential host zebra mussels, particularly uninfected juvenile mussels. Our study measured emergence only from isolated zebra mussels (i.e., one mussel per dish).
3. *Mussel siphoning observations.* Is ciliate emergence active (i.e., do they swim out of the mussel) and/or passive (i.e., ejected from the mussel)? Do ciliates emerge through the mussel's inhalant siphon and/or exhalant siphon? Do some ciliates reenter their hosts, and if so, through which siphon? Direct observation, including video recording, would be helpful to shed light on these questions.

Survival of C. acuminatus *Outside the Host*

Our experiments suggest that *C. acuminatus* have a short survival period outside their host. Although we observed a maximum survival period of 144 h (6 days), most ciliates died within 48 h. These results are similar to those of Beers (1959), who studied the survival of *Conchophthirus mytili* DeMorgan (syn. *Peniculistoma mytili* (DeMorgan)) inhabiting the mantle cavity of marine bivalve *Mytilus edulis* Linneaus. He found that a period of 84 h in open water was fatal for the ciliate at 14°C but ciliates died faster at 22°C (48 h) and 30°C (10 h). Fenchel (1965) found that 50% of *Peniculistoma mytili* survived outside their bivalve host for 100 h, *Ancistrum mytili* (Quennerstedt) for about 100 h, and *Ancistrocoma myae* (Kofoid and Busch), *Ancistrum caudatum* Fenchel, and *Thigmophrya saxicavae* Fenchel for ca. 50–100 h. Kidder (1934) studied *Conchophthirus* spp. from nondreissenid bivalves and found them to live not longer than 24 h.

Just because a ciliate is alive does not mean it is capable of reproduction—an essential requirement for establishing a population in a new host. Thus, future trials examining *C. acuminatus* survival should investigate the relationship between duration of time outside a host and the ability of such surviving ciliates to successfully reproduce following entry into a new zebra mussel host.

We set up our survival experiments with ciliates obtained by dissection of zebra mussels. Future trials may want to measure the survival of ciliates that have emerged naturally from their hosts. It is possible that this latter group ciliates may contain greater food reserves and thus may have great longevity in open water.

How does *C. acuminatus* maintain its infection in expanding zebra mussel populations? *Dreissena* spp. often spread to other waterbodies by the downstream dispersal of their planktonic larvae, sometimes being carried hundreds of kilometers from their origin (Stoeckel et al. 1997). These planktonic larvae lack a mantle cavity and are too small to contain *C. acuminatus*. Yet *C. acuminatus* is virtually ubiquitous in all freshwater European zebra mussel populations. Since zebra mussel larvae can stay suspended in downstream currents for more than a week (Hillbricht-Ilkowska & Stanczykowska 1969, Skalskaya 1976), it would appear from our experimental data that *C. acuminatus* would not be able to survive for as long a duration as the zebra mussel larvae that are at the leading edge of the dispersing population. Over time, however, *C. acuminatus* would likely establish itself throughout the entire expanded population by smaller incremental steps of dispersion.

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