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Chaetogaster limnaei (Annelida: Oligochaeta) as a parasite of the zebra mussel *Dreissena polymorpha*, and the quagga mussel *Dreissena bugensis* (Mollusca: Bivalvia)

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Abstract Dreissenid mussels, *Dreissena polymorpha* and *D. bugensis*, were found to be infected by the naidid oligochaete *Chaetogaster limnaei* at four sites in the St. Lawrence River. This is the first report of this species infecting dreissenids anywhere in the world. Most worms inhabited the mantle cavity, where they caused erosion of the mantle and gill epithelia as determined by histopathological examination. Others penetrated various tissues; one had invaded the ovary and was feeding on oocytes and ovarian tissues. Of 606 mussels examined, 166 (27.4%) harbored at least 1 *C. limnaei*. The prevalence varied between 1% and 80%, depending on the collection site and date. The worms were slightly but significantly more prevalent in *D. bugensis* than in *D. polymorpha*. The intensity ranged from 1 to 18 worms per infected host. Variations in prevalence and intensity were not related to the size or sex of the host, but the data did suggest some seasonality.

Introduction

The zebra mussel *Dreissena polymorpha* and the quagga mussel *D. bugensis* are dreissenid bivalve molluscs that are native to freshwater habitats throughout Europe and western Asia. They were introduced into North America in the 1980s, presumably by accidental transport of their planktonic larvae (Conn et al. 1993) in ballast water of ships navigating the St. Lawrence Seaway (Griffiths et al. 1991; Hebert et al. 1989). The mussels have since spread throughout eastern and midwestern North America, where they have cost billions of dollars in damage caused by their biofouling of hard submerged substrates (Hebert et al. 1991; Ludyanskiy et al. 1993).

The introduction of a nonindigenous (exotic) species raises many questions regarding its impact on native biota. Among the most interesting of these is whether such introductions will result in the introduction of new parasites or alter the composition of native parasite fauna by making a new host available. In their native European range, the adult mussels serve as hosts for several parasites (Davids and Kraak 1993), none of which has been reported from the veliger larvae. Thus, because the mussels were introduced to North America as veligers, none of their native parasites was introduced along with them. However, some parasite species that occur on both continents might be expected to colonize the introduced mussels in North America (Conn and Conn 1993). This has important practical implications inasmuch as some parasites of *Dreissena* spp., such as bucephalid (Davids and Kraak 1993) and echinostomatid (Conn and Conn 1995) trematodes that are pathogenic to wild fishes and birds, might become more widely distributed or infest a larger percentage of their vertebrate hosts. Alternatively, some parasites might damage the mussels, thus serving as agents for natural biological control.

Considering these possibilities, we have conducted preliminary studies of parasites associated with zebra and quagga mussels in recently established populations in the St. Lawrence River (Conn and Conn 1993; Conn et al. 1994). The present study involved a more detailed examination of one of the more commonly encountered parasites, the naidid oligochaete annelid *Chaetogaster limnaei*. The results reported herein are a compilation of data from what began as two independent studies, one conducted in the state of New York and the other carried out in the province of Quebec.

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Materials and methods

Histopathology

A total of 179 *Dreissena polymorpha* collected at the Snell Lock site (see below) in 1993 and 1994 were examined for evidence of histopathology associated with infection by *Chaetogaster limnaei*. Immediately upon tranfer to the laboratory, all organs of the mantle cavity and visceral mass were removed, carefully teased apart, and examined as tissue presses with a compound light microscope to determine the exact location of *C. limnaei*.

The shells were removed from 40 mussels, and each entire deshelled animal was fixed intact in Lillie's 10% neutral buffered formalin for examination of potential histopathology. Fixed mussels were dehydrated in an ethanol series, cleared in Shandon Xylene Substitute (Shandon Inc., Pittsburgh, Pa., USA), embedded in Paraplast, sectioned at 10 µm on a rotary microtome, stained in Harris' hematoxylin and eosin, dehydrated in ethanol, cleared in xylene, and mounted on glass slides with gum damar. All slides were examined with an Olympus Vanox AHBT-3 compound light microscope using bright-field and differential interference-contrast optics.

Several *C. limnaei* specimens were removed from their hosts and photographed alive. Others were fixed in ethanol/formalin/acetic acid (AFA), stained in Semichon's acetocarmine, dehydrated in ethanol, cleared in methyl salicylate, and mounted whole in gum damar. Some of the latter were deposited as voucher specimens in the United States National Parasite Collection, United States Department of Agriculture (USDA), Beltsville, Maryland (Accession number 85282).

Epizootiology

Dreissenid mussels and some associated benthic macroinvertebrates were collected from four sites along the St. Lawrence River. Collection methods appropriate for each site differed between sites as described below. The shell length of each mussel was measured to the nearest 0.1 mm using a hand-held digital caliper. Mussels were taken to the laboratory and either monitored while alive for emergence of *C. limnaei* or dissected under a dissecting microscope to determine the prevalence (i.e., percentage of hosts infected) and intensity (i.e., number of parasites per infected host) of infection by *C. limnaei*. Specific identification of parasites was made after examination with a compound light microscope. The study sites are given below in an upstream-downstream sequence.

Cape Vincent

In Cape Vincent, New York state, near the St. Lawrence River's outflow from Lake Ontario (44°08´N, 76°20´W), dreissenids were first encountered in 1991 (Conn et al. 1992a,b). Collections were made on 9 and 30 July 1993 by removing dreissenids from rocks, sticks, and the shells of living unionid clams dredged from depths of 10–12 m using an oceanographic dredge operated from a research trawler.

Snell Lock

In Snell Lock, between Massena, New York, and Cornwall, Ontario (44°59´N, 74°46´W), dreissenids were first encountered in 1989 (Conn et al. 1991). Between 6 July and 3 August 1993, five weekly collections were made by scraping adult dreissenids from submerged steel columns using a hand-held scraping basket at less than 1.5 m depth. Specimens from this site were grouped by sex to determine whether *C. limnaei* occurred more commonly in one sex than in the other.

Soulanges Canal

In Soulanges Canal, Quebec province (45°20´N, 73°58´W), dreissenids were first encountered in 1990 (Mills et al. 1993; unpublished observations). Collections were made on 2 July, 28 July, 26 August, and 27 October 1993 by hand-picking adult dreissenids from submerged concrete walls at depths of 2–5 m using scuba gear. A similar follow-up collection was made on 9 May 1994. In addition to the dreissenids, unionid clams (2 July 1993 – 10 *Lampsilis radiata*, 10 *Elliptio complanata*, and 5 *Pyganodon cataracta*; 26 August 1993 – 10 *L. radiata* and 12 *E. complanata*) were collected from within 5 m of the walls at this site and examined for the presence of *C. limnaei*.

Lac St. Louis

In Lac St. Louis, Montréal, Quebec, near the outflow from the Ottawa River (45°26´N, 73°42´W), dreissenids were first encountered in 1991 (Mills et al. 1993; unpublished observations). Collections were made on 11 September 1992 by hand-picking adult dreissenids from submerged substrates at depths of <2 m using scuba gear.

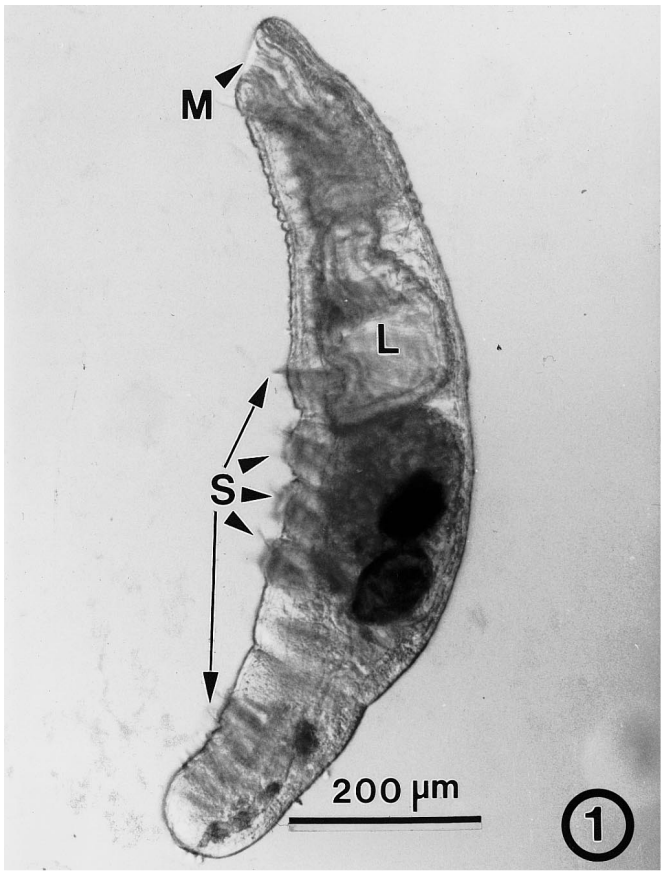
Comparisons of parasite prevalence in relation to host sex and host species were tested using the chi-square 2 × 2 contingency method. Variation in parasite prevalence among the four study sites was tested using the chi-square test for independence. Comparisons of parasite prevalence in relation to host size and of parasite intensity in relation to host species and host sex were tested by Student's *t*-tests. The relationship between parasite intensity and host size was tested using regression analysis. The relationship between prevalence and mean intensity of infection was tested using linear regression (Proc GLM, SAS procedures), with prevalence being variable normalized using the standard transformation for proportion data (Zar 1984).

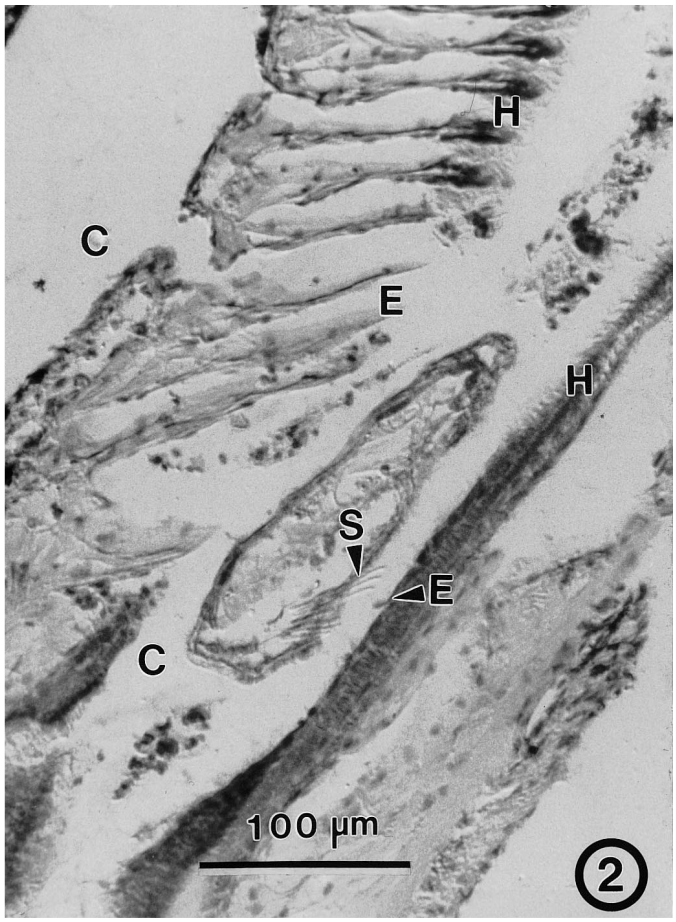
Results

Histopathology

Chaetogaster limnaei (Fig. 1) occurred in dreissenid mussels throughout the St. Lawrence River. The vast majority of *C. limnaei* inhabited the mantle cavity of the dreissenids. Of these, most occurred between the gill lamellae, but some occurred between the gills and mantle or on the surface of the foot. No gross pathology was evident in these locations. However, histological sections revealed some evidence of erosion of the gill and mantle epithelia in areas adjacent to the worms (Fig. 2).

Fig. 1–4 Differential interference-contrast light micrographs of *Chaetogaster limnaei* from *Dreissena polymorpha*. **Fig. 1** Living, unstained *C. limnaei* showing the gut lumen (*L*), large mouth (*M*), and prominent bundles of setae (*S*). **Fig. 2** Histological section showing the location of *C. limnaei* between the gills and within the mantle cavity (*C*) of *D. polymorpha*. Note that the host's gill epithelium is highly eroded (*E*) in areas adjacent to the *C. limnaei* but is healthy (*H*) elsewhere. The parasite's prominent setae (*S*) are closely apposed to part of the eroded gill epithelium. **Fig. 3** Living, unstained tissue squash preparation showing a *C. limnaei* within the ovary of *D. polymorpha*. The parasite has left a large migration track (*T*) through the host's ovarian tissue (*Ov*) and is ingesting host oocytes (*O*) with its large mouth (*M*). **Fig. 4** Higher magnification of the specimen illustrated in Fig. 3, showing the whole oocytes (*O*) of *D. polymorpha* within the gut lumen (*L*) of *C. limnaei*. Also note the parasite's prominent setae (*S*) and gut wall (*W*)


M
L
S
200 µm
1


H
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E
H
S
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C
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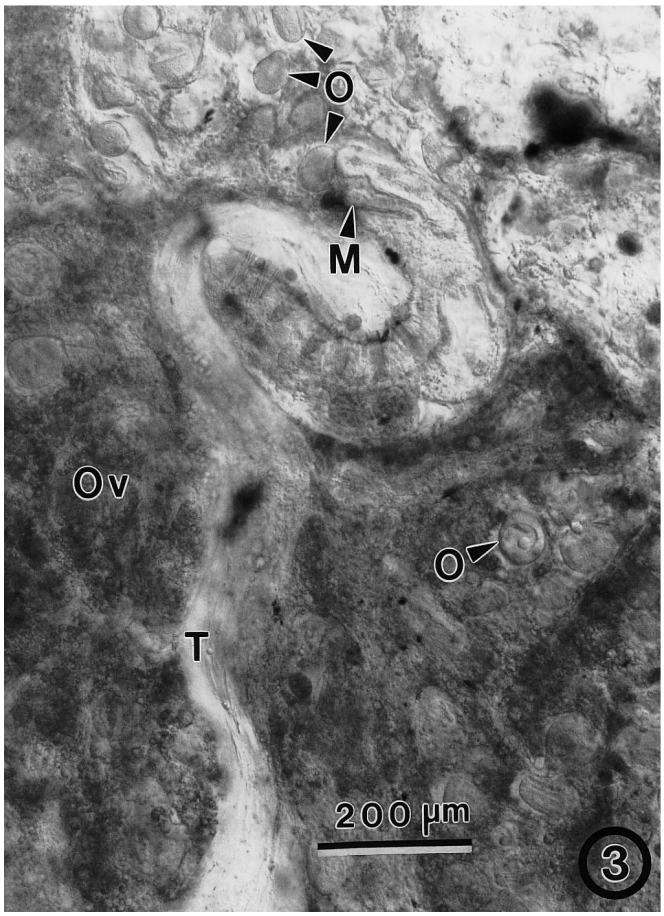
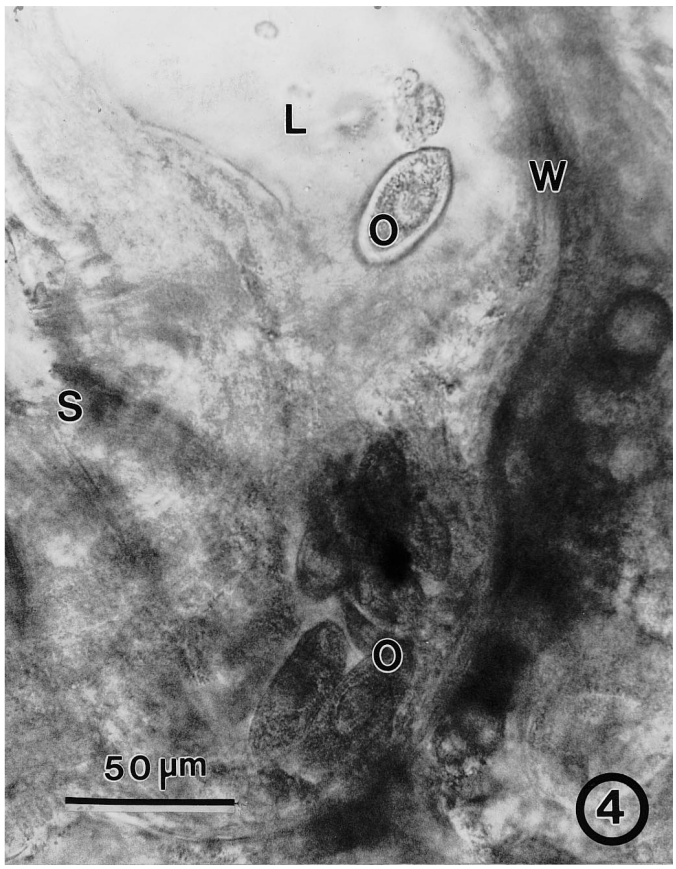
2


O
M
Ov
O
T
200 µm
3


L
W
O
S
O
50 µm
4

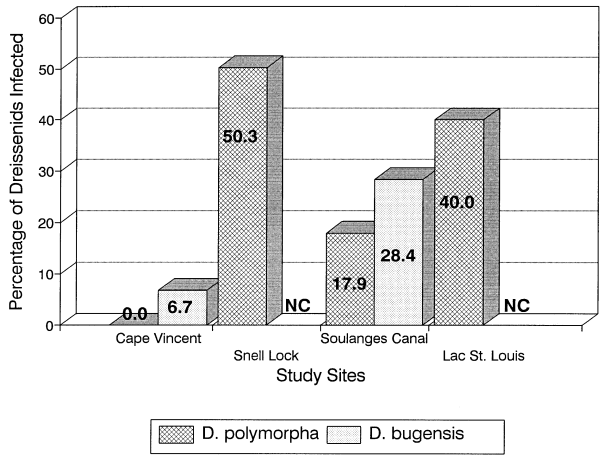


Fig. 5 Histogram comparing the prevalence of infection of *Dreissena polymorpha* and *D. bugensis* by *Chaetogaster limnaei* at 4 sites in the St. Lawrence River between 1992 and 1994 (*NC D. bugensis* was not collected at Snell Lock or Lac St. Louis)

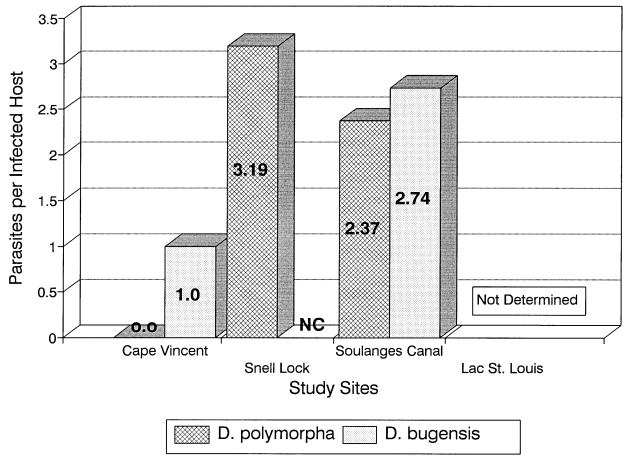


Fig. 6 Histogram comparing the intensity of infection of *D. polymorpha* and *D. bugensis* by *C. limnaei* at 4 sites in the St. Lawrence River between 1992 and 1994 (*NC D. bugensis* was not collected at Snell Lock or Lac St. Louis). Intensity was not determined for *D. polymorpha* at Lac St. Louis, but the species was collected at this site

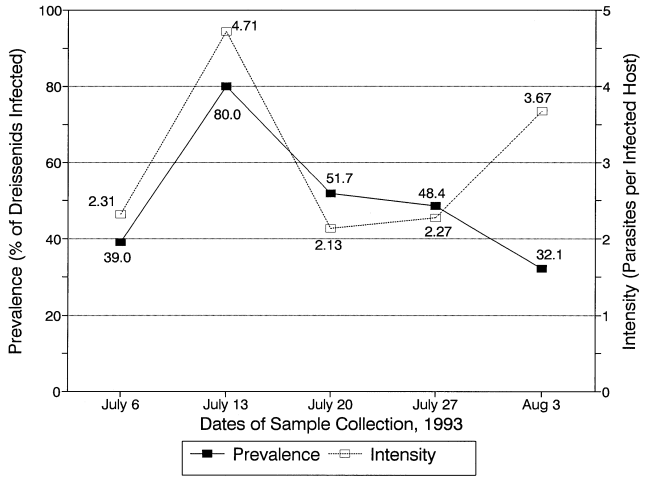


Fig. 7 Line graph showing temporal trends in the prevalence and intensity of infection of *D. polymorpha* by *C. limnaei* during 5 consecutive weeks at Snell Lock, New York, in the St. Lawrence River. *D. bugensis* was not collected at this site

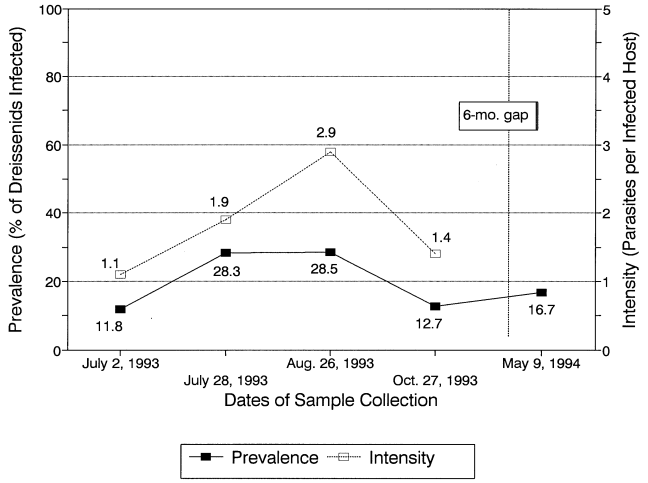


Fig. 8 Line graph showing temporal trends in the combined prevalence and intensity of infection of *D. polymorpha* and *D. bugensis* by *C. limnaei* at 5 unevenly spaced dates at Soulanges Canal, Quebec, in the St. Lawrence River

A few *C. limnaei* were more invasive, penetrating the siphonal tissues of the mantle or the gonadal tissues of the visceral mass. In one female mussel, a single *C. limnaei* was observed migrating through the ovary, causing some damage to the ovarian tissue (Fig. 3). This worm was observed ingesting the host's oocytes within the ovarian acini (Figs. 3, 4). Oocytes were ingested whole such that they appeared intact within the worm's gut lumen (Fig. 4). No *C. limnaei* occurred in the nephridium, hepatopancreas, or other organs of the visceral mass.

Epizootiology

Of 606 dreissenids (496 *Dreissena polymorpha* and 110 *D. bugensis*) examined, 166 (27.4%) were found to harbor *C. limnaei*. In all, 28 (25.5%) *D. bugensis* and 138 (27.8%) *D. polymorpha* were infected. Among all sites and dates, the prevalence in both host species ranged from 0 to 80%. The mean intensity of infection (i.e., number of parasites per infected host) was 2.68 for *D. bugensis* and 2.86 for *D. polymorpha*. Among all sites and dates, the intensity ranged from 1 to 18. At the two sites where *D. polymorpha* and *D. bugensis* co-occurred, the prevalence (i.e., percentage of hosts infected) of *C. limnaei* was higher in *D. bugensis* (Fig. 5; chi-square with Yates correction = 3.99, $P < 0.05$), but the intensity of infection did not differ significantly between these two host species (Fig. 6; *t*-test, $P > 0.05$). No *C. limnaei* was found among the unionids examined from Soulanges Canal.

There was no relationship between the host's size and the prevalence of infection by *C. limnaei* ($t = 1.02$;

$P < 0.2$). The host's size was not correlated linearly with the intensity of infection ($r = 0.06$; $P < 0.64$). Among the *D. polymorpha* examined by sex from Snell Lock, 42 (58.3%) of 72 males and 31 (43.1%) of 72 females harbored *C. limnaei*. This difference was not significant (chi-square with Yates correction = 2.78; $P > 0.05$). The intensity of infection in males ($\bar{x} = 2.48$; SD = 1.92) was lower than that in females ($\bar{x} = 3.19$; SD = 3.34), but this difference also was not significant ($t = 1.16$; $P > 0.2$). There was a significant variation among the four study sites (Fig. 5) with respect to the prevalence of *C. limnaei* in *D. polymorpha* alone (chi-square = 65.64; $P < 0.0001$) and in both dreissenids combined (chi-square = 65.42; $P < 0.0001$), but not in *D. bugensis* alone (chi-square = 2.19; $P > 0.1$). Temporal trends in the prevalence and intensity of infection of dreissenids by *C. limnaei* at Snell Lock and Soulanges Canal are shown in Figs. 7 and 8. The combined prevalence and intensity at Snell and Soulanges were positively correlated ($r = 0.77$; $P < 0.016$).

Discussion

The present data demonstrate that *Chaetogaster limnaei*, by eroding gill and mantle epithelia and ingesting ovarian tissue, is at least mildly pathogenic to *Dreissena polymorpha*. Thus, it qualifies as a true parasite. This is consistent with the report of Gamble and Fried (1976), who presented histological evidence that *C. limnaei* disrupted the mantle epithelium of the pulmonate gastropod *Physa acuta*. However, the nature of the symbiotic relationship between *C. limnaei* and its host has often been questioned. Eng (1976) reported that among asiatic clams introduced into North America, *C. limnaei* caused no tissue damage in *Corbicula manilensis*, but Sickel (1981) provided some inconclusive evidence that *C. limnaei* induced lesions in the mantle tissues of *Corbicula fluminea*. In Europe, two subspecies of *C. limnaei* from snails are recognized (Buse 1971, 1972, 1974; Gruffydd 1965). *C. l. limnaei* is considered to be commensalistic, living on the outside of the shell and causing no damage to the host; conversely, *C. l. vaghini* is considered to be parasitic, living in the kidney and causing damage by ingesting renal tissue. Whether the worms found to be living in the mantle cavity and the gonad in the present study were two subspecies is not clear. Some authors have considered *C. limnaei* to be somewhat mutualistic in snails, because the worms occasionally eat trematode miracidia and cercariae that would otherwise be pathogenic to the host (Khalil 1961; Wagin 1941). Adding to this complex symbiotic relationship, miracidia and cercariae have been shown to provide a major food source for *C. limnaei* associated with snails that are infected with these digenean larvae (Fernandez et al. 1991). The clear evidence of pathogenicity to *D. polymorpha* found in the present study suggests that *C. limnaei* might exert some suppressive effect on dreissenid populations, thereby effecting some level of natural biological control. Further physiology and ecology studies will be necessary to determine whether this is actually the case.

This is the first report of *C. limnaei* infecting *Dreissena* spp. in any part of the world, although *C. limnaei* has long been known to infect gastropod hosts in Europe, throughout the mussels' native range (Buse 1974; Gruffydd 1965; Streit 1974). European infections may have been simply overlooked, but this would be surprising given the considerable amount of work that has been done on other helminth parasites of the mussels (Davids and Kraak 1993). The lack of previous reports from North America undoubtedly is related to the observation that the mussels were first discovered on this continent in 1988 (Hebert et al. 1989), only 5 years prior to the initiation of the present study. In addition to the St. Lawrence River sites that received detailed examination in the present study, we observed numerous *C. limnaei* in water exhaled from the siphons of dreissenids that we handpicked from rocks in shallow (<0.5 m depth) water at Port Stanley, Lake Erie, on 10 October 1991 (unpublished observations). Thus, it appears that *C. limnaei* has quickly become a common parasite of dreissenids throughout the St. Lawrence River-Great Lakes system.

C. limnaei has been reported from native populations of several molluscs in North America. Infected gastropods include the pulmonates *P. acuta* from tributaries of the Delaware River (Gamble and Fried 1976) and *P. gyrina* from ponds in Michigan (Kenk 1949), the pulmonate *Helisoma anceps* from a pond in North Carolina (Fernandez et al. 1991), and the prosobranch *Amnicola limosa* from Douglas Lake, Michigan (Eggleton 1952). Infected bivalves include the pill clams *Sphaerium transversum*, *S. striatinum*, and *S. securis* from the Mississippi River (Gale 1973) and *S. corneum*, *S. striatinum*, and *S. securis* from Cayuga Lake and Lake Ontario (Barbour 1977). Despite the absence of *C. limnaei* in the unionids examined in the present study, unionids from other areas of North America have been reported as hosts (Coker et al. 1921). Given the widespread and common occurrence of *C. limnaei* in native molluscs in other North American rivers and lakes, it is likely that this species will be a major parasite of dreissenids as they spread throughout their new range.

The higher prevalence of *C. limnaei* in *D. bugensis* relative to *D. polymorpha* may reflect a true difference in host specificity, such as that shown by Buse (1974) for 21 species of British gastropods. Alternatively, it is possible that some ecological factor might increase the chances that *D. bugensis* will become colonized. For example, *D. polymorpha* is more likely to occur on unionid substrates (Conn and Conn 1993) and at shallower depths (Mills et al. 1993) than is *D. bugensis*. Thus, these two sympatric congeners exhibit ecological differences that might affect their relative vulnerability to different parasites. Such possibilities warrant further study.

The overall prevalence and intensity found in the present study was similar to that reported for other hosts in other localities. However, several authors have reported peak prevalences ranging between 95% and 100%

(Buse 1971; Eggleton 1952; Gale 1973; Gruffydd 1965). Furthermore, some authors have reported intensities as high as 30 (Barbour 1977), 50 (Gruffydd 1965), or 70 parasites/host (Gamble and Fried 1976) at peak seasons. Because of the large variations in habitat, host density, host population stability, and other factors, it is not possible to determine whether these differences reflect real and permanent variations in the population dynamics of *C. limnaei*. In any case, *C. limnaei* is clearly among the dominant symbionts of many freshwater molluscs.

The present finding of no relationship between the host size and the prevalence or intensity of infection is contrary to the findings of several authors. Buse (1971), working with lymnaeid snails, and Streit (1974), working with ancylid snails, reported that the intensity of *C. limnaei* infection was positively correlated with the host size. Similarly, Gruffydd (1965) reported higher intensities in larger lymnaeids. Gale (1973) and Barbour (1977) reported that sphaeriid clams under 4.5 mm were not infected by *C. limnaei*, whereas larger specimens of the same species were; both authors noted a trend toward higher intensities among larger clams. However, the latter three authors did not provide statistical analysis of these relationships. These authors have speculated that larger hosts simply provide more space and resources, thus supporting larger parasite populations. However, variations in intensity and prevalence may reflect temporal changes in the relative proportions of hosts of different size classes throughout the season (Gruffydd 1965).

No previous author has examined possible differences in the prevalence and intensity of *C. limnaei* infection in different host sexes. The absence of host sex preference demonstrated in the present study may be related to the observations that male and female dreissenids are comparable in size and most natural gastropod hosts of *C. limnaei* are hermaphroditic.

The present data demonstrated differences in the prevalence of *D. polymorpha* among the study sites (Fig. 5); however, these data should be interpreted with caution inasmuch as the four sites differed in many characteristics (e.g., depth, substrate, associated biota) and different methods were used to collect mussels at each site. That the prevalence of *D. bugensis* did not show statistically significant variation among the sites may have been influenced by the failure to collect this species at two of the four sites. Gruffydd (1965) compared prevalences of *C. limnaei* infecting the gastropod *Lymnaea pereger* in a reservoir and a stream in Wales but found little variation between these two sites.

Temporal patterns of the prevalence and intensity of *C. limnaei* infecting dreissenids were examined at only two sites in the present study. These data are probably of limited value inasmuch as the Snell site was monitored for only 5 consecutive weeks (Fig. 7) and the Soulanges site was monitored on an irregular schedule (Fig. 8). However, the present data do seem to indicate peaks in prevalence and intensity during July and August. Furthermore, the positive correlation found between prevalence and intensity at these sites suggests that most mussels were infected at similar rates. These data are generally consistent with the study by Gale (1973), who observed a peak prevalence of *C. limnaei* in sphaeriids in the upper Mississippi River during July, with dramatic reductions occurring during the fall. Similarly, Gamble and Fried (1976) reported high populations of *C. limnaei* in physid snails in the Delaware River in the spring and summer, with marked declines being noted during the winter months. Fernandez et al. (1991) reported that the prevalence and intensity of *C. limnaei* infecting the planorbid snail *H. anceps* declined during the winter in a small pond in North Carolina. Eng (1976) reported that nearly 87% of *C. maniliensis* from California harbored *C. limnaei* from March to May, but fewer than 3% were infected during other months. Among European populations of lymnaeid (Buse 1971; Gruffydd 1965) and ancylid (Streit 1974) snails, *C. limnaei* has been shown to peak between May and July and remain low throughout the fall, winter, and early spring. Thus, the general patterns of seasonality appear to be consistent in all cases; variations in specific peak months are probably related to variations in local conditions.

Because the dreissenid invasion of North America is relatively new, little has been learned regarding which parasites native to North America will be capable of infecting the mussels. In addition to the *C. limnaei* reported herein, newly established dreissenid populations have been reported as hosts for plagiorchioid metacercariae (trematodes) in Lake Erie (Toews et al. 1993); various nematodes, a hydracarinid, and other naidid oligochaetes in the St. Lawrence River (Conn et al. 1994); and *Paratanytarsus* sp. larvae (chironomid midges) in the St. Lawrence River (Conn et al. 1994; Ricciardi 1994). Furthermore, Conn and Conn (1995) obtained experimental infections of *D. polymorpha* by metacercariae of the avian fluke *Echinoparyphium* sp. collected from naturally infected *Physa* sp. snails in New York state. From these studies, it is apparent that further research on symbiotic associations between introduced dreissenid mussels and native animals promises to be a fruitful line of investigation; such studies will be essential if we are to understand the full impact of the dreissenid invasion of freshwater ecosystems in North America and other sites where they have been or might be introduced.

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