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Movement, Growth, and Density of Stagnicola
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Control of Cercarial Dermatitis

presented by

James Barrett Saxton

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MOVEMENT, GROWTH, AND DENSITY OF STAGNICOLA EMARGINATA (LYMNAEIDAE) IN HIGGINS LAKE, MICHIGAN IN RELATION TO LIMNOLOGICAL VARIABLES: IMPLICATIONS FOR CONTROL OF CERCARIAL DERMATITIS

By

James Barrett Saxton

AN ABSTRACT OF A THESIS

Submitted to
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ABSTRACT

Stagnicola emarginata (Sowerby), the blue snail, is one of the most common intermediate hosts for Trichobilharzia stagnicolae (Talbot), a parasite the causes cercarial dermatitis (swimmer's itch). Because relatively little was known about the biology of the blue snail, the objective of this study was to document the prevalence of infected S. emarginata at four stations over time and to better describe its growth, density, and movements in Higgins Lake, Michigan, in relation to water depth, water temperature, dissolved oxygen, and food resources. The percentage of snails shedding T. stagnicolae cercariae increased with snail size and was similar between years. The Columbine Lane site had significantly more snails shedding T. stagnicolae than the other three sites. Densities of S. emarginata varied spatially and temporally and greatest densities were associated with relatively shallow water, higher concentrations of benthic algae, and lower concentrations of benthic organic matter. Snails in water greater than 1 m deep were significantly larger than those in shallower water. No relationship between snail density and dissolved oxygen concentrations or water temperature were detected. The blue snail migrated towards deep water in late July. Growth of S. emarginata was greatest at 20°C in light conditions that simulated the summer environment. The results of this study have important implications for the control of swimmer's itch in Michigan lakes. S. emarginata in water greater than 1 m deep may be a significant source of cercariae and densities of S. emarginata may increase if nutrient pollution is not controlled. Because abundance of S. emarginata is known for several water depths from May through August, maximum densities can now be targeted for molluscicide application.

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CHAPTER ONE

PREVALENCE OF TRICHOBILHARZIA STAGNICOLAE (TALBOT) IN STAGNICOLA EMARGINATA (SOWERBY)

Introduction

The common beach or blue snail (Stagnicola emarginata (Sowerby)) is a freshwater pulmonate snail belonging to the family Lymnaeidae which is primarily distributed from Maine west to Minnesota and in the southern Canadian Interior Basin (Burch 1988). In Michigan, the distribution includes numerous lakes in the northern part of the lower-peninsula and the southern portion of the upper-peninsula (Wall 1968). Within these lakes the organism is generally found in exposed littoral regions, often wave-swept beaches with a low angle of repose (Baker 1928; Harman 1972). Because of its characteristic distribution and its predisposition to certain types of avian parasitic infections, S. emarginata also is among the more common intermediate hosts of Trichobilharzia stagnicolae (Talbot), a trematode blood fluke parasite belonging to the Schistosomidae family that causes cercarial dermatitis, commonly known as swimmer's itch (Burton et al. 1999; Cort et al. 1937; Cort et al. 1940; Brackett 1940).

The life cycle of *T. stagnicolae* involves one of a large number of aquatic birds or mammals as the primary host and one of several species of snails as the intermediate host. Adult flukes live in blood vessels of the digestive tract of final bird or mammal hosts until reproduction is completed. Newly hatched eggs move through the intestinal wall and are excreted with feces into the surrounding water (Blankespoor 1991). Once in the water, eggs hatch into a larval stage called a miracidium, which seeks out *S.*

emarginata or another species of snail intermediate host. Once the miracidium comes into contact with the snail, it penetrates the skin and seeks out the liver. The parasite then develops into mother sporocysts, which mature over time to produce daughter sporocysts. These daughter sporocysts continue to develop and, when conditions are correct, produce cercariae, which move out of the snail and seek the final avian or mammalian host so that the life cycle can be completed (Blankespoor 1991; Burton et al. 1998). Swimmer's itch is an inflammatory immune response produced as a result of accidental penetration of cercariae into the skin of a human (Cort et al. 1940). This disease is characterized by pusfilled pimples that cause a painful and irritating itch which may last for several days to over a week (Burton et al. 1998).

A substantial amount of behavioral information is known about cercariae of *T. stagnicolae*. Brackett (1940) concluded that these cercariae swim towards light and during summer in northern Michigan lakes, they emerge from their snail intermediate hosts at approximately 4:30 AM. He also concluded that emergence from snail hosts may be triggered by sudden changes in ambient temperature, both in dark and lighted conditions, and that emergence was inhibited when the snail was malnourished. Brackett (1940) also found that cercariae of *T. stagnicolae* vigorously swim towards shadows when placed in a lighted container, indicating a search response for their final avian hosts.

Data are also available describing the prevalence of *T. stagnicolae* in their snail intermediate hosts over both time and space in northern Michigan lakes (Table 1). It is well documented that the incidence of *T. stagnicolae* in *S. emarginata* varies anywhere from 1.1% to 10.3% from studies conducted in Douglas Lake, Lake Leelanau, and

Lake	Site	Year of Collection	Prevalence (% Infected)
Douglas Lake	Phragmites Flats	1936	4.8
		1957	1.1
		1994	1.9
	Nutting Bay	1935 - 1936	1.9
		1994	4.8
	North Fishtail Bay	1935 - 1936	10.3
		1994	2.3
Higgins Lake		1992	1.5
		1998	1.4
North Lake Leelanau		1990	1.2
South Lake Leelanau		1990	2.1

Table 1. Prevalence of *T. stagnicolae* in *S. emarginata* collected in northern Michigan. Modified from Keas and Blankespoor (1997). Higgins Lake data from Blankespoor (1992) and Nyman (1998).

Higgins Lake, Michigan (Cort et al. 1937; Cort et al. 1960; Keas and Blankespoor 1997; Nyman 1998). Parasitic infections of S. emarginata also vary both by sampling site and by year (Cort et al. 1937; Cort et al. 1940). Broad trends were apparent as they found that snails were most heavily infected with parasites near the end of July and into early August, and they attributed this to warmer water temperatures during this portion of the summer.

Although this literature is valuable for understanding cercarial dermatitis in Michigan lakes, the data are generally outdated and the literature states that prevalence of schistosome infections in *S. emarginata* varies both spatially and temporally. Also, little work has been completed in Higgins Lake, Michigan. Therefore, the goal of this study was to document the seasonal prevalence of *T. stagnicolae* in *S. emarginata* at several sites in a northern Michigan lake. Based on the literature, I hypothesized that the

percentage of S. emarginata shedding T. stagnicolae cercariae would vary both among sites and at any one site from May through August.

Description of Study Site

The study was conducted in Higgins Lake, a 4130 hectare cold-water lake located in Roscommon County in the northern portion of the lower peninsula of Michigan (Figure 1). The lake, which is Michigan's tenth largest inland lake (Jones 1990), was formed approximately 11,000 years ago as a result of a melting glacial ice block from the Pleistocene era which was isolated by marginal moraines at the current north and south ends of the lake (Schultz and Fairchild 1984). As a result of the geological processes that formed Higgins Lake, most of the lake's 8940 hectare watershed is glacial outwash plain while the soils are a mixture of gravel, sand, and clays (Limno-Tech, Inc. 1992). Averaging 13.7 meters in depth, the deepest part of the lake is nearly 41 meters deep and it holds 5.64 x 10⁸ cubic meters of water (Schultz and Fairchild 1984). The water body has a hydraulic residence time of 12.4 years (Limno-Tech, Inc. 1992) and is characterized by a shoal area that encompasses nearly one-third of the entire area of the lake (Jones 1990). Higgins Lake is also primarily groundwater fed as approximately 50% of the water volume within the lake comes from beneath the surface of the earth (Jones 1990). Higgins Lake discharges via the Cut River to Houghton Lake and is part of the Muskegon River drainage basin.

Because of the two state parks located on both the north and south ends of the lake and the large number of permanent and summer homes located around the lake, Higgins Lake is one of the most heavily used inland lakes in Michigan (Jones 1990).

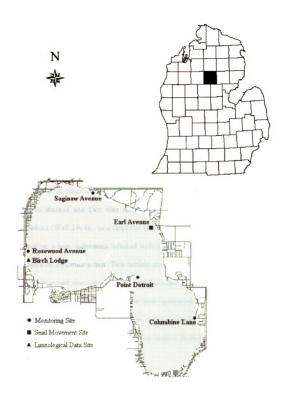


Figure 1. Higgins Lake, Michigan showing locations of studies monitoring prevalence of T. stagnicolae in S. emarginata, snail movement, and snail densities in relation to limnological variables.

Adding to this popularity is a Michigan Department of Natural Resources public access site on the west side of the lake, three township parks scattered around the shoreline, and approximately seventy-five public roads ends (Limno-Tech, Inc. 1992). The water body has traditionally been classified as an oligotrophic lake, but because of the tremendous recreational demand placed on the lake in the summer months, Higgins Lake could be classified as mesotrophic water body, depending on the specific limnological variable quantified (Limno-Tech, Inc. 1992).

Cercarial dermatitis seems to be a concern for many residents and visitors to Higgins Lake, as well as many other lakes in northern Michigan. Operators of resorts have reported that at times their beaches had to be closed because of the concern for contracting the disease and they also feel that this disease limits the appeal of their facility to visitors (Wall 1968). As a response to this concern, residents on Higgins Lake operate a hotline where individuals infected with the disease are encouraged to call to report incidents of swimmer's itch. This hotline yielded over 400 calls in 1999 and the numbers have increased since then. Although these calls do not represent a scientifically valid measurement of number of persons who have contracted the condition and cercarial dermatitis can be confused with other diseases, it is reasonable to assume that swimmer's itch is a major problem in Higgins Lake for at least a portion of the individuals that recreate in the lake from June through August.

Methods

Four sites (Saginaw Avenue, Point Detroit, Columbine Lane, and Rosewood Avenue) were chosen in Higgins Lake for intensive bimonthly monitoring from the

middle of May through the middle of August, 1999 and 2000 (Figure 1). These sites were selected because previous research indicated that a relatively high percentage of *S. emarginata* were infected with *T. stagnicolae* at these particular locations (Burton *et al.* 1999; Nyman 1998). Two of these sites were located in the northern sub-basin of the lake while the other two sampling sites were located in the southern portion of the lake. Each of these sites was relatively similar, characterized by a predominately sand substrate with a small number of scattered cobbles. An additional site (Birch Lodge) was also examined only in 2000 (Figure 1).

At each sampling area, S. emarginata and Physa integra (another snail known to host the dermatitis producing parasite Trichobilharzia physellae) were collected along an approximate 100 m long stretch for two hours or until at least 400 snails were gathered. To locate snails, a diving mask or a glass-bottom bucket was utilized and collection was accomplished by directly picking snails off of the substrate or by using a cooking strainer mounted to a wooden dowel rod. Once collected, organisms were placed in a bucket and brought to the laboratory where identification of the organism was confirmed according to Burch (1988). Snails collected from the monitoring sites were then measured with a metric ruler and sorted into size classes based on shell length. The size classes were as follows: one (0.0 - 4.9 mm), two (5.0 - 9.9 mm), three (10.0 - 14.9 mm), four (15.0 - 19.9 mm), five (20.0 - 24.9 mm), and six (25.0 - 29.9 mm).

Once measured, snails collected from the four monitoring stations were isolated in 1 oz. plastic cups and exposed to white fluorescent light for at least two hours to stimulate emergence of cercariae (Blankespoor and Reimink 1998). Each of the plastic cups was then observed under a dissecting microscope to determine the presence of

cercariae. Cercariae were identified under 10-40X magnification using a compound microscope and procedures developed by Schell (1970). Snails collected in 2000 from the Birch Lodge site were extracted from their shells and examined for *T. stagnicolae* cercariae under 10-40X magnification (Cort *et al.* 1940).

Results

A total of 554 *P. integra* were assayed in 1999 and 2000, and 4 (0.72%) were shedding *T. physellae* cercariae in the light box assay. The majority of *P. integra* were collected during May and early June when water temperatures were low and therefore when few residents swim in Higgins Lake. Additionally, only 3.0% of snails collected throughout 1999 and 2000 were *P. integra*. Thus, *P. integra* were deemed unimportant for transmission of cercarial dermatitis in Higgins Lake.

A total of 7,166 *S. emarginata* were collected from the monitoring sites and assayed in 1999, of which 64 (0.89%) were shedding *T. stagnicolae* (Table 2) in the light box assay. In 2000 at the monitoring stations, a total of 10,633 *S. emarginata* were examined and 60 (0.56%) were shedding the parasite that causes cercarial dermatitis (Table 3) in the light box assay. At the Birch Lodge site, 5,898 *S. emarginata* were dissected to determine presence of *T. stagnicolae* cercariae and 6 (0.10%) were infected. Although these results seem to indicate a higher prevalence in 1999, there were no significant differences in percentage of snails shedding *T. stagnicolae* in the light box assay between 1999 and 2000 at the four monitoring stations ($\chi^2=1.94$, p=0.16). Data collected from May 2000 were not included in this analysis because no snails were collected in May of 1999. The highest prevalence in each year was at the Columbine

Point Detroit			
	No.	No.	Percentage
Collection Date	Collected	Infected	Infected
3-Jun-99	210	0	0.00%
14-Jun-99	259	0	0.00%
28-Jun-99	395	0	0.00%
12-Jul-99	347	6	1.73%
26-Jul-99	300	2	0.67%
9-Aug-99	321	0	0.00%
TOTAL	1832	8	0.44%
Saginaw Avenue			
	No.	No.	Percentage
Collection Date	Collected		Infected
4-Jun-99	292	0	0.00%
15-Jun-99	299	ì	0.33%
29-Jun-99	313	0	0.00%
13 - Jul-99	283	i	0.35%
27-Jul-99	309	ī	0.32%
10-Aug-99	318	2	0.63%
TOTAL	1814	5	0.28%
1			
Columbine Lane			
	No.	No.	Percentage
Collection Date	Collected	Infected	Infected
Collection Date 7-Jun-99	Collected 203	Infected 2	Infected 0.99%
Collection Date 7-Jun-99 21-Jun-99	Collected 203 315	Infected 2 1	Infected 0.99% 0.32%
Collection Date 7-Jun-99 21-Jun-99 7-Jul-99	203 315 276	2 1 10	Infected 0.99% 0.32% 3.62%
Collection Date 7-Jun-99 21-Jun-99 7-Jul-99 19-Jul-99	Collected 203 315 276 385	2 1 10 10	Infected 0.99% 0.32% 3.62% 2.60%
Collection Date 7-Jun-99 21-Jun-99 7-Jul-99 19-Jul-99 2-Aug-99	Collected 203 315 276 385 301	2 1 10 10 8	Infected 0.99% 0.32% 3.62% 2.60% 2.66%
Collection Date 7-Jun-99 21-Jun-99 7-Jul-99 19-Jul-99 2-Aug-99	Collected 203 315 276 385 301 214	2 1 10 10 8 8	Infected 0.99% 0.32% 3.62% 2.66% 2.66% 3.74%
Collection Date 7-Jun-99 21-Jun-99 7-Jul-99 19-Jul-99 2-Aug-99	Collected 203 315 276 385 301	2 1 10 10 8	Infected 0.99% 0.32% 3.62% 2.60% 2.66%
Collection Date 7-Jun-99 21-Jun-99 7-Jul-99 19-Jul-99 2-Aug-99 16-Aug-99 TOTAL	Collected 203 315 276 385 301 214	2 1 10 10 8 8	Infected 0.99% 0.32% 3.62% 2.66% 2.66% 3.74%
Collection Date 7-Jun-99 21-Jun-99 7-Jul-99 19-Jul-99 2-Aug-99	Collected 203 315 276 385 301 214 1694	2 1 10 10 8 8 39	Infected 0.99% 0.32% 3.62% 2.60% 2.66% 3.74% 2.30%
Collection Date 7-Jun-99 21-Jun-99 7-Jul-99 19-Jul-99 2-Aug-99 16-Aug-99 TOTAL Rosewood Avenue	Collected 203 315 276 385 301 214 1694	Infected 2 1 10 10 8 8 8 39	Infected 0.99% 0.32% 3.62% 2.60% 2.66% 3.74% 2.30% Percentage
Collection Date 7-Jun-99 21-Jun-99 7-Jul-99 19-Jul-99 2-Aug-99 16-Aug-99 TOTAL Rosewood Avenue Collection Date	Collected 203 315 276 385 301 214 1694 No. Collected	Infected 2 1 10 10 8 8 8 39 No.: Infected	Infected 0.99% 0.32% 3.62% 2.60% 2.66% 3.74% 2.30% Percentage Infected
Collection Date 7-Jun-99 21-Jun-99 7-Jul-99 19-Jul-99 2-Aug-99 16-Aug-99 TOTAL Rosewood Avenue Collection Date 8-Jun-99	Collected 203 315 276 385 301 214 1694 No. Collected 206	Infected 2 1 10 10 8 8 8 39 No.: Infected 0	Infected 0.99% 0.32% 3.62% 2.60% 2.66% 3.74% 2.30% Percentage Infected 0.00%
Collection Date 7-Jun-99 21-Jun-99 7-Jul-99 19-Jul-99 2-Aug-99 16-Aug-99 TOTAL Rosewood Avenue Collection Date 8-Jun-99 22-Jun-99	Collected 203 315 276 385 301 214 1694 No. Collected 206 308	Infected 2 1 10 10 8 8 8 39 No.: Infected 0 0	Infected 0.99% 0.32% 3.62% 2.60% 2.66% 3.74% 2.30% Percentage Infected 0.00% 0.00%
Collection Date 7-Jun-99 21-Jun-99 7-Jul-99 19-Jul-99 2-Aug-99 16-Aug-99 TOTAL Rosewood Avenue Collection Date 8-Jun-99 22-Jun-99 8-Jul-99	Collected 203 315 276 385 301 214 1694 No. Collected 206 308 325	Infected 2 1 10 10 8 8 8 39 No. Infected 0 0 2	Infected 0.99% 0.32% 3.62% 2.60% 2.66% 3.74% 2.30% Percentage Infected 0.00% 0.00% 0.62%
Collection Date 7-Jun-99 21-Jun-99 7-Jul-99 19-Jul-99 2-Aug-99 16-Aug-99 TOTAL Rosewood Avenue Collection Date 8-Jun-99 22-Jun-99 8-Jul-99 22-Jul-99	Collected 203 315 276 385 301 214 1694 No. Collected 206 308 325 318	Infected 2 1 10 10 8 8 8 39 No.: Infected 0 0 2 7	Infected 0.99% 0.32% 3.62% 2.60% 2.66% 3.74% 2.30% Percentage Infected 0.00% 0.00% 0.62% 2.20%
Collection Date 7-Jun-99 21-Jun-99 7-Jul-99 19-Jul-99 2-Aug-99 16-Aug-99 TOTAL Rosewood Avenue Collection Date 8-Jun-99 22-Jun-99 8-Jul-99 22-Jul-99 3-Aug-99	Collected 203 315 276 385 301 214 1694 No. Collected 206 308 325 318 349	Infected 2 1 10 10 8 8 8 39 No.: Infected 0 2 7 1	Infected 0.99% 0.32% 3.62% 2.60% 2.66% 3.74% 2.30% Percentage Infected 0.00% 0.00% 0.62% 2.20% 0.29%
Collection Date 7-Jun-99 21-Jun-99 7-Jul-99 19-Jul-99 2-Aug-99 16-Aug-99 TOTAL Rosewood Avenue Collection Date 8-Jun-99 22-Jun-99 8-Jul-99 22-Jul-99	Collected 203 315 276 385 301 214 1694 No. Collected 206 308 325 318	Infected 2 1 10 10 8 8 8 39 No.: Infected 0 0 2 7	Infected 0.99% 0.32% 3.62% 2.60% 2.66% 3.74% 2.30% Percentage Infected 0.00% 0.00% 0.62% 2.20%

Table 2. Number of S. emarginata shedding T. stagnicolae at four monitoring stations in 1999.

Point Detroit			
	No.	No.	Percentage
Collection Date	Collected	Infected	Infected
10-May-00	303	0	0.00%
23-May-00	341	0	0.00%
5-Jun-00	438	0	0.00%
19-Jun-00	450	1	0.22%
5-Jul-00	485	0	0.00%
17-Jul-00	485	3	0.62%
2-Aug-00	485	2	0.41%
14-Aug-00	485	1	0.21%
TOTAL	3472	7	0.20%
Saginaw Avenue			
	No.	No.	Percentage
Collection Date	Collected	Infected	Infected
11-May-00	285	0	0.00%
24-May-00	324	0	0.00%
6-Jun-00	427	1	0.23%
20-Jun-00	447	0	0.00%
6-Jul-00	483	2	0.41%
18-Jul-00	300	0	0.00%
3-Aug-00	485	0	0.00%
TOTAL	2751	3	0.11%
Columbine Lane	No.	Ma	Damaantana
Collection Date		No.	Percentage Infected
Collection Date	Collected 131	Infected 0	0.00%
15-May-00 30-May-00	111	0	0.00%
12-Jun-00	463	2	0.43%
26-Jun-00	236	4	1.69%
10-Jul-00	308	4	1.30%
24-Jul-00	308 477	31	6.50%
	2032	70	2.2470
Rosewood Avenue	No	No	Percentage
Collection Date			_
_			
		ì	0.32%
25-Jul-00		ī	
	485	0	0.00%
TOTAL	2358	4	0.17%
8-Aug-00	326 2052 No. Collected 113 254 231 481 309 485 485	1	0.21% 0.00%

Table 3. Number of S. emarginata shedding T. stagnicolae at four monitoring stations in 2000.

Lane site. Prevalence at the other three sites was relatively low (Tables 2 and 3).

In 1999, few snails assayed in June were shedding *T. stagnicolae* in the light box assay and the greatest percentage of shedding snails occurred in July (Table 2 and Figure 2). At Point Detroit, the majority of *S. emarginata* which were shedding cercariae occurred in mid to late July and none of the assayed snails were shedding cercariae before July 12. Prevalence at the Rosewood Avenue monitoring station peaked in late July while the prevalence of shedding snails peaked in middle August at Columbine Lane. The prevalence of *S. emarginata* that were shedding *T. stagnicolae* remained relatively small from June through August at Saginaw Avenue (Table 2 and Figure 2).

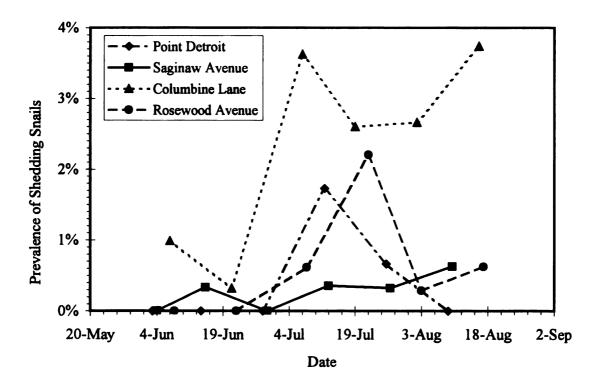


Figure 2. Prevalence of S. emarginata shedding T. stagnicolae in Higgins Lake, 1999.

The year 2000 was characterized by a different pattern in prevalence as the percentage of shedding snails remained relatively constant from May through August at three of four monitored sites, including sites at Point Detroit, Saginaw Avenue, and Rosewood Avenue (Table 3 and Figure 3). Conversely, cercarial shedding rates from snails peaked in July of 2000 at the Columbine Lane station just as in 1999 (Figures 2 and 3). When all stations were combined and averaged over two-week periods, the percentage of *S. emarginata* shedding cercariae peaked in July, just as in 1999 (Figure 4). In 2000, Columbine Lane had a higher prevalence of shedding snails from May through August (2.17%) and prevalence peaked on July 24 at 6.5 %, which was greater than for any other site or sampling date in 1999 or 2000 (Tables 2 and 3). At no time after

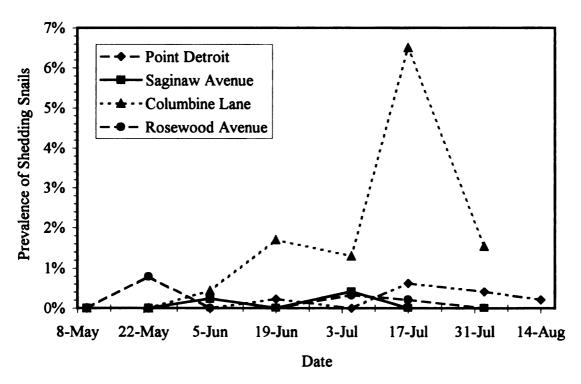


Figure 3. Prevalence of *S. emarginata* shedding *T. stagnicolae* in Higgins Lake, 2000.

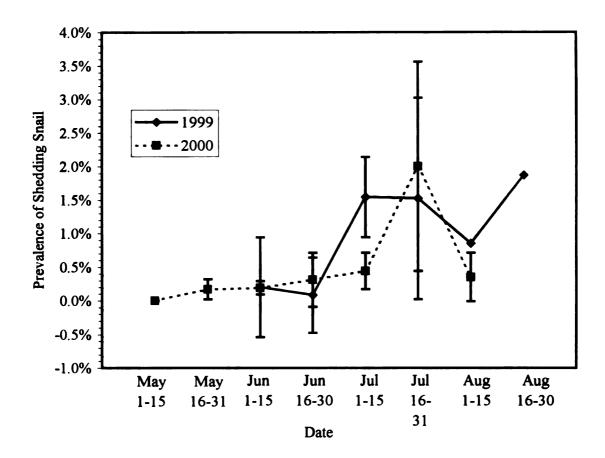


Figure 4. Prevalence of S. emarginata shedding T. stagnicolae in 1999 and 2000.

June 26, 2000, did prevalence fall below 1.3% at Columbine Lane and in 1999 prevalence never fell below 2.6% after July 7. Including both years, Columbine Lane had significantly more S. emarginata infected with T. stagnicolae than the other three monitoring stations (χ^2 =41.86, p<0.01). There was no significant difference in prevalence of shedding snails at the other three stations during this same time period (χ^2 =0.18, p=0.67).

As size of S. emarginata increased, the percentage of snails shedding T. stagnicolae also increased (Table 4). Snails with a shell length between 20.0 and 24.9

mm were the largest size class of snails collected in large enough numbers to be able to detect rate of cercarial shedding with statistical confidence. 1.75% of snails in this large size class were shedding cercariae in the light box assay. 0.89% of snails with a shell length between 15.0 and 19.9 mm long and 0.29% of snails between 10.0 and 14.9 mm long were shedding cercariae. No *S. emarginata* less than 10.0 mm long ever shed cercariae. Too few snails greater than 24.9 mm long were collected to detect percent shedding. These data suggest that snails less than 10.0 mm long were either not infected with the parasite or that they do not shed cercariae until they grow to a larger size.

Size Class	No. Examined	No. Infected	Percentage Infected
0.0 – 4.9 mm	12	0	0.00%
5.0 – 9.9 mm	438	0	0.00%
10.0 – 14.9 mm	7,566	22	0.29%
15.0 – 19.9 mm	10,265	91	0.89%
20.0 – 24.9 mm	1,200	21	1.75%
25.0 – 29.9 mm	14	0	0.00%
Total	19495	134	0.69%

Table 4. Percentage of S. emarginata shedding T. stagnicolae in six size classes collected from Higgins Lake in 1999 and 2000.

Discussion

Over both years, the mean percentage of *S. emarginata* infected with *T. stagnicolae* was 0.69% according to the light box assay and there was no significant difference between 1999 and 2000 (Tables 2 and 3). 0.10% of *S. emarginata* were infected with *T. stagnicolae* in 2000 at the Birch Lodge site. This prevalence at these five sites is slightly lower than reported in other studies (Table 1) conducted in Higgins Lake (Blankespoor 1992; Nyman 1998) and in other northern Michigan lakes (Keas and

Blankespoor 1997; Cort et al. 1960; Blankespoor 1984). However, these results should be expected because studies by other authors did not examine infections of S. emarginata throughout May and early June, when the percentage of infected snails tends to be extremely low. Thus, it appears that the prevalence recorded for Higgins Lake in this study is very similar to other studies.

The rate of cercarial shedding by S. emarginata peaked during late July and early August at the four monitoring stations (Figures 2, 3, and 4), supporting the hypothesis that the percentage of snails infected with T. stagnicolae would vary from May through August. These results are consistent with other studies that documented an increase in the percentage of S. emarginata infected with parasites in July (Cort et al. 1937; Cort et al. 1940). An increase in the prevalence of T. stagnicolae is generally associated with an increase in water temperature, accelerating development in larval stages of the parasite (Brackett 1940). Indeed, water temperatures in Higgins Lake increased from $9 - 11^{\circ}C$ in mid-May to $> 21 - 24^{\circ}C$ in mid-July (See Figure 13, Chapter 2).

Consistent with the hypothesis that the percentage of snails infected with T. stagnicolae varied spatially, S. emarginata were significantly more infected with T. stagnicolae at the Columbine Lane site than at the other three monitored stations (Figures 2 and 3 and Tables 2 and 3). The reasons for this are unclear. Although not directly measured in this study, one hypothesis may be that final avian hosts of the parasite find this area of Higgins Lake more satisfactory than other examined areas, increasing the likelihood that snail intermediate hosts become infected. Also, because the outlet for the Cut River is relatively close to this site, water flow in the lake may be bringing a large number of miracidia to the area, infecting a higher percentage of S. emarginata.

As the size of *S. emarginata* increased, the percentage that were shedding *T. stagnicolae* cercariae also increased, and no snails smaller than 10.0 mm shed cercariae (Table 4). One explanation for this may be that parasite development time in the snail results in shedding only after small snails have grown to lengths greater than 10 mm. Alternatively, parasitic infections in many types of snails leads to an increase in growth rates in intermediate host organisms (Esch and Fernandez 1994).

These data have implications for controlling cercarial dermatitis in Michigan lakes. A majority of *S. emarginata* shed *T. stagnicolae* during July and early August. Thus, swimmers susceptible to cercarial dermatitis are evidently more likely to contract the disease during this portion of summer. This agrees with reports of swimmer's itch reported to the swimmer's itch hotline for Higgins Lake. However, the paper by Lindblade (1998) for Walloon Lake suggests that reports of swimmer's itch for this lake peak in early July. Even though not directly measured, it also appears that percentage of snails infected with *T. stagnicolae* is correlated with water temperature, at least to some degree. Therefore, an intense warming trend may lead to an outbreak of cercarial dermatitis within a lake (Brackett 1940; Cort *et al.* 1937).

CHAPTER TWO

DISTRIBUTION OF STAGNICOLA EMARGINATA (SOWERBY) IN RELATION TO LIMNOLOGICAL VARIABLES

Introduction

Numerous studies have documented the complete life cycle of *T. stagnicolae* including morphological characteristics of each life stage, length of time required for each stage to develop, and the incidence of snails infected with the parasite (Brackett 1940; Cort *et al.* 1940). The effects of temperature on emergence of cercariae, swimming power of larval stages of the parasite, and activities of cercariae in normal habitats have been described (Brackett 1940). Cort (1950) described effects of cercariae on the liver of snail intermediate hosts.

Relatively little is known about life history traits and behavior of the snail S. emarginata. To better understand occurrence and distribution of cercaria in lakes and occurrence of cercarial dermatitis in swimmers, abundance, distribution, and movements of S. emarginata should be better documented. Such documentation is a necessary step in effectively developing methods to control snail intermediate hosts of the parasite that causes swimmer's itch (Brackett 1940; Laman et al. 1984).

The amount of calcium carbonate in water has been described as the variable that most influences distribution and abundance of freshwater snails in temperate regions. Boycott (1936) and Macan (1950) found a significant positive correlation between concentrations of calcium and abundance of snails in European lakes. Okland (1983) found this same relationship in Norway and concluded that taxonomic diversity of

gastropods declined significantly in lakes with extremely low calcium concentrations.

These conclusions were based on lakes in a homogenous region and did not explain variation in abundance and distribution of several species of snails in the same lake.

Variables that may influence distribution and abundance of gastropods in an individual lake include size and type of substrate, water depth, temperature and dissolved oxygen fluctuations, and availability of food resources, among other things (Lodge et al. 1987). Little attention has been paid to the effects of these variables on S. emarginata. The majority of studies have instead focused on the entire Lymnaeidae family rather than on S. emarginata specifically. Each of these variables is covered in more detail below.

Distribution and abundance of snails may be influenced by size and type of substrate in lakes (Harman 1972). Clampitt (1973) attempted to determine characteristics of substrates that most influenced distribution of several pulmonate snails, including S. emarginata in Douglas Lake, Michigan. He concluded that S. emarginata exhibited a complex and varied pattern of distribution in regards to substratum and was found on both cobbles and sand. Because these conclusions were based on a small number of field observartions, Clampitt (1973) performed laboratory studies to confirm that S. emarginata was a generalist in regard to preferred substratum size. These results were similar to earlier findings by Baker (1928) who concluded that blue snails were usually found in exposed littoral regions clinging tightly to rocks or buried in sand or muck. Therefore, substrate type and size may not be an effective indicator of distribution and abundance of S. emarginata in a lake.

Water depth may influence distribution and abundance of S. emarginata. Burton et al. (1999) were unable to determine whether significant differences existed in the

distribution of blue snails at three depths in Higgins Lake, Michigan because of small sample sizes and high variance in data. Their data were suggestive, however, because S. *emarginata* was more common in water depths of 60 and 90 cm than at 30 cm. Laman *et al.* (1984) believed that the population density of Lymnaeidae snails in a northern Michigan lake varied spatially and temporally and was influenced by water depth. However, these individuals did not focus specifically on density and distribution of S. *emarginata*. The influence of water depth on snail distribution has also been documented in laboratory studies (Boag 1981).

In a study examining diversity of the aquatic biota on a wave swept sandy beach in a northern Michigan lake, Moffett (1943) determined that *S. emarginata* were relatively rare compared to other species of snails and were most common in depths between 2.4 and 3.0 m. Moffett (1943) suggested that the blue snail was unable to cope with the intensity of disturbances commonly present in wave-swept shoals of lakes, but were able to survive in deeper water in reduced numbers where disturbance was less. Moffett's (1943) results supported the general conclusions of Cheatum (1934) who stated that *S. emarginata* numbers tended to be greatest in depths greater than one meter. Cheatum (1934) measured the distribution of blue snails qualitatively at one point in time rather than over a long period of time. While these studies suggest that density of *S. emarginata* varies with depth, the quantitative relationship between depth and snail distribution needs to be determined more definitively both spartially and temporally in relation to other limnological variables such as temperature, substrate, and food availability.

The abundance and distribution of *S. emarginata* in a lake may be influenced by ambient water temperature and dissolved oxygen levels (Lodge *et al.* 1987). Cheatum (1934) conducted laboratory and field studies on respiration of pulmonate snails common to northern Michigan and concluded that snails, including the blue snail, were influenced by amounts of dissolved oxygen in water. McMahon (1983) also concluded that distribution of many species of prosobranch snails was influenced by the amount of oxygen in water. Some snails even utilize macrophytes to move to the surface to acquire adequate oxygen (Lodge *et al.* 1987).

The amount of oxygen dissolved in water is, in part, a function of temperature (Horne and Goldman 1994), so water temperature may influence oxygen availability to S. emarginata. Water temperature may also influence reproductive success, growth, and other life history traits of snails (Russell-Hunter 1978), and snails may move to temperatures which are more favorable for development. Van der Schalie and Berry (1973) concluded that high ambient temperatures may limit geographic distribution of snails.

The amount and type of food resources available may influence distribution and abundance of snails (Lodge et al. 1987). Little is known specifically about food preferences of S. emarginata. Based on laboratory and field studies, Kesler et al. (1986) concluded that filamentous green algae was one of the most common food resource utilized by Lymnaeidae snails. Lindblade (1998) suggested that higher levels of algae could result in higher populations of snails in a given area. Others documented that Lymnaeidae snails utilize periphyton, including bacteria, fungi, and other organic matter (Barnese et al. 1990; Bovbjerg 1968; and Lodge 1986). Weber and Lodge (1990)

concluded from a field study that more *S. emarginata* colonized rocks with periphyton than colonized rocks without periphyton. Therefore, literature about food preference in snails is inconsistent and focuses on the entire Lymnaeidae family rather than specifically on *S. emarginata*.

Objectives

Because of deficiencies and inconsistencies in literature in regards to factors that influence abundance and distribution of *S. emarginata* in lakes, the overall goal of this study was to document the snail's distribution in relation to depth and to identify other limnological variables that influence abundance and distribution of *S. emarginata*. Specific objectives were to:

- 1. Document the density of different sizes of *S. emarginata* from mid-May through mid-August at three water depths
- 2. Determine the degree to which limnological variables identified from the literature, including water depth, oxygen levels, food availability, and water temperature, influence abundance and distribution of *S. emarginata*

Based on the literature, I hypothesized that density of S. emarginata would differ between three measured depths and would change from May through August. I also hypothesized that greater densities of S. emarginata in summer months would be associated with higher oxygen levels, lower water temperatures, and increased food resources.

Methods

Establishment of Sampling Sites

In order to correlate limnological variables with abundance and distribution of S. emarginata, two transects were established perpendicular to the shoreline near Birch Lodge during the summer of 2000 (Figure 1). This area was located along the western portion of the northern sub-basin of Higgins Lake in an area that supported a greater density of snails than other areas of the lake (Chapter 1; Burton et al. 2000). The sampling area was characterized by a sandy substrate from shoreline to approximately 90 m out from this point and then was dominated by sand covered with silt as the water depth increased beyond this point. Depth increased gradually from the shoreline outwards at the rate of about 0.5 m for each 10 m horizontal distance.

Along the transects, three water depths were used to categorize the snail population: 0.0 - 0.5 m, 0.51 - 1.0 m, and greater than 1 m. HOBO temperature data loggers were placed in sealed plastic chambers and attached to cinder block anchors at each of these depths. These data loggers measured water temperature at one-hour intervals. They were placed in the lake on the first snail sampling date (May 12, 2001) and were recovered after the last sampling date (August 9, 2001). Each HOBO was examined weekly to ensure that they were working properly and that their location had not been changed by swimmers.

At water less than 1 m deep, glass-bottomed buckets were used initially to examine distribution and density of the snails to ensure that each sampling area contained at least one hundred blue snails. The sampling area needed for obtaining one hundred snails varied from 2 x 2 m to 10 x 10 m plots. Once the dimensions of an adequate

sampling area were established, a metric tape rule and metal stakes were used to mark the corners of the sampling area. Brightly colored masonry line was attached to the stakes and used to define the boundaries of the sampling areas. All *S. emarginata* on the substrate surface in the sampling area were collected using a glass bottomed-bucket and a strainer attached to a wooden dowel rod. Snails "on the line" were included in the sample. Sampling in any given area was terminated when no new *S. emarginata* were discovered in a five-minute period. An additional sampling station located ten meters away from the first area at the same water depth was marked out and sampled so that variances in the measured parameters could be determined. To avoid re-sampling the same area, areas that had been previously sampled were referenced to land structures and were not sampled again for at least five weeks.

Limnological Data Collection

Dissolved oxygen, chlorophyll a, and organic matter concentrations were measured on each snail sampling date. A YSI Model 51B dissolved oxygen meter was used to document the amount of oxygen in the water. To do this, the meter was calibrated according to the manufacturer's recommendations and the probe was placed in water just above the substrate in the middle of the sampling area. The probe was agitated for at least one minute before the oxygen concentration was recorded. All measurements were recorded between 8:30 and 11:00 AM.

Using a 1.5 m long piece of schedule 30 PVC pipe, a wooden broom handle, a wood screw, and a disc of plastic with a diameter (3.81 cm) the inside diameter of the PVC, a coring device was constructed to collect a known volume of sand (45.6 cm³) for chlorophyll and organic matter analyses (Figure 5). To do this, the open end of the coring

device was gently placed on the substrate surface and the broom handle, which was attached to the plastic disc with a screw, was slowly pulled upwards, creating a vacuum to extract a 4 cm long core for each sample. This technique was utilized to randomly collect three chlorophyll samples and three separate organic matter samples for each sampling area. Three samples of each parameter were collected to minimize effects of patchiness in the sampling area. Once collected, all six sand cores were transferred into six separate plastic bags and placed in a cooler. As soon as possible after initial collection, sand samples were frozen in the dark to prevent degradation.

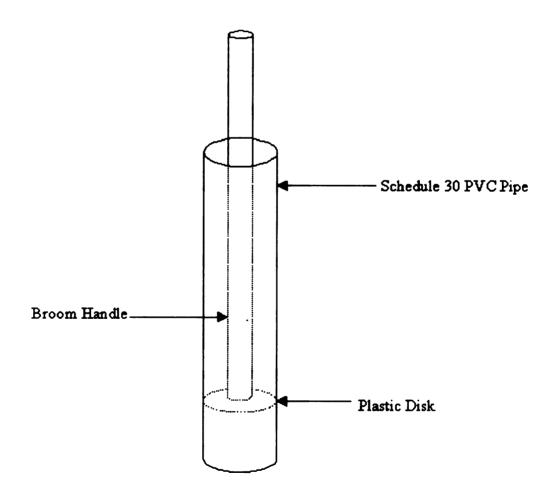


Figure 5. Coring device used to collect sand samples for food availability analyses.

The same general techniques were used at water depths greater than 1 m, except that SCUBA techniques were employed to collect *S. emarginata*. Sampling stations were prepared in the same manner, with the exception that small diameter PVC pipes were used to anchor four corners of the sampling area to increase visibility of the corners. Each *S. emarginata* was collected directly from the substrate by the diver and placed in fine meshed bags. Again, sampling stopped when no new blue snails were seen in a five-minute period. Dissolved oxygen was collected with the dissolved oxygen meter using the same method except that the probe was suspended from the side of the boat. Chlorophyll and organic matter samples were collected in the same manner, but a 2.5 m long piece of PVC was used as a corer rather than the shorter corer used in shallower water. This additional length in the PVC pipe prevented water from entering the top of the apparatus, destroying the vacuum needed to collect sand cores.

Laboratory Analysis

In the laboratory, all S. emarginata were counted, measured with calipers, and placed in size classes based on shell length as follows: class one (0.0 - 4.9 mm), class two (5.0 - 9.9 mm), class three (10.0 - 14.9 mm), class four (15.0 - 19.9 mm), and class five (20.0 - 24.9 mm).

To estimate food availability for *S. emarginata*, chlorophyll a was quantified as a surrogate of algal abundance (American Public Health Association *et al.* 1985). To prevent degradation of pigments, all collected chlorophyll samples were quantified within thirty days after collection using fluorometry as proposed by American Public Health Association *et al.* (1985) using a Turner Designs fluorometer. One modification to this procedure, which is specific for planktonic chlorophyll measurements, was required. The

modification consisted of extracting chlorophyll a from the sand by soaking the sand in 90% buffered acetone in a freezer for twenty-four hours. After twenty-four hours, the sand was shaken vigorously for thirty seconds. The acetone and chlorophyll solution was filtered with a Whatman #4 filter to remove the sand and used to determine chlorophyll a concentrations. Because phaeophyton and other pigments found in natural communities of algae affect determination of chlorophyll a concentrations, samples collected before July 12 were acidified (American Public Health Association et al. 1985). Chlorophyll samples collected on or after July 12 were analyzed using a Turner Designs 436 nm excitation filter installed in the fluorometer to negate the additive effects of phaeophyton on chlorophyll a concentrations. The fluorometer was calibrated using standardized methods (American Public Health Association et al. 1985) before initial samples were analyzed and immediately after the filter was installed. Chlorophyll a concentrations measured with the fluorometer were converted to mg chlorophyll a m² by the following equation:

Chlorophyll a (mg m⁻³) X volume of extract (L) 0.0011395 m⁻² (area of substrate collected with core sampler)

The amount of organic matter, an additional food source for the blue snail (Barnese et al. 1990; Bovbjerg 1968; and Lodge 1986), was quantified by drying the three remaining sand samples to a constant weight at 100 °C prior to ashing at 500 °C in a Fisher Isotemp Model 186 muffle furnace for 24 hours. Loss on ignition was used as a measurement of the ash-free dry mass (AFDM) of organic matter (American Public Health Association et al. 1985). AFDM of organic matter was converted to mg m⁻² by the following equation:

organic matter lost on ignition (mg) 0.0011395 m⁻² (area of substrate collected with core sampler)

Statistical Analysis

All statistical analyses were performed according to the guidelines of Younger (1998) and Neter *et al.* (1996) utilizing SAS version 8.0. Scatter plots and residual plots were used to assess normality in the data. Data were considered significant at α =0.05.

Results

Snail Size and Density

The 0.0 - 0.5 m water depth was sampled on twelve dates with two plots sampled per date (24 plots) from May 12 through August 9 and a total of 2,736 snails were collected (Table 5). A total of 2,973 *S. emarginata* were collected from the 0.51 - 1.0 m water depth on 11 dates (22 plots) from May 22 through August 9. Water greater than one meter in depth was sampled a total of six times (12 plots) from May 26 through August 1, yielding a total of 2,531 *S. emarginata* (Table 5). In water greater than 1 m deep, mean water depth sampled was 2.1 m. Depth ranged from 1.4 to 2.4 m.

Including snails from all dates and depths, *S. emarginata* between 10.0 and 14.9 mm long comprised over 70% of collected snails (Figure 6). Snails between 5.0 and 9.9 mm long were the next most common size class of snails collected. Snails with shell length between 15.0 and 19.9 mm were even less common while *S. emarginata* greater than 20 mm in shell length were rare and comprised about 1% of the total number of blue snails collected. No organisms with a shell length less than 5 mm were collected during this study. Snails first start shedding cercariae when they are longer than 9.9 mm

(Chapter 1; Burton et al. 2000). Thus, a significant number of snails were too small to shed cercariae at any point in time.

S. emarginata between 5.0 and 9.9 mm represented 20% to 25% of collected individuals at the shallowest two water depths but only 4.2% in water greater than one meter deep (Table 5). Snails with shell lengths between 15.0 and 19.9 mm made up approximately 9% of snails collected in depths less than 0.5 m and only about 5% of snails collected from water between 0.51 and 1.0 m deep. In water greater than a meter

Water Depth	Snail Size	Number of Snails	Percent Frequency
0.0 - 0.5 m	0.0 - 4.9 mm	0	0.0%
	5.0 - 9.9 mm	498	18.2%
	10.0 - 14.9 mm	2001	73.1%
	15.0 - 19.9 mm	237	8.6%
	20.0 - 24.9 mm	0	0.00%
0.51 - 1.0 m	0.0 - 4 .9 mm	0	0.0%
	5.0 - 9.9 mm	766	25.7%
	10.0 - 14.9 mm	2060	69.2%
	15.0 - 19.9 mm	147	4.9%
	20.0 - 24.9 mm	0	0.0%
> 1 m	0.0 - 4.9 mm	0	0.0%
	5.0 - 9.9 mm	108	4.2%
	10.0 - 14.9 mm	1744	68.9%
	15.0 - 19.9 mm	677	26.7%
	20.0 - 24.9 mm	2	0.0%

Table 5. Number of S. emarginata collected per shell length for three sampled water depths.

deep, however, snails between 15.0 and 19.9 mm long made up 27% of snails collected. Because of this, larger S. emarginata were significantly more common in depths greater than one meter than in the other two water depth categories examined in this study (F=52.34, p<0.001), suggesting that snails at depths greater than 1 m may be particularly important as vectors of swimmer's itch.

Densities of S. emarginata varied anywhere from 1.3 snails m⁻² in early June to over 18 snails m⁻² in the later portion of July with the mean density of blue snail collected during 2000 being 6.4 snails m⁻². The greatest mean density of snails per unit area over the season were found at the 0.51 - 1.0 m water depth category with 8.2 snails m⁻². The

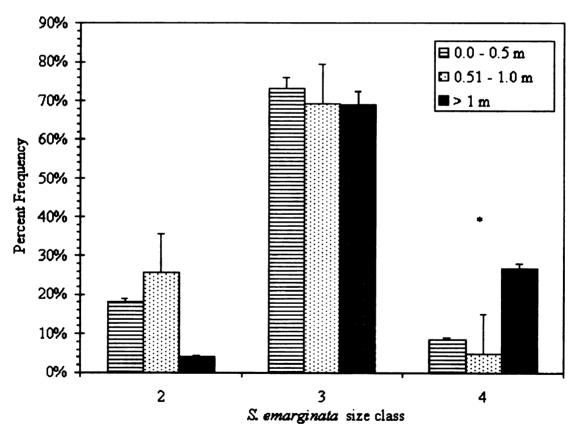


Figure 6. Frequency distribution of S. emarginata size classes collected in 2000 at three water depths. Size class 2 = 5.0 - 9.9 mm, 3 = 10.0 - 14.9 mm, 4 = 15.0 - 19.9 mm. Bars equal standard errors and * is significant at p<0.05.

next highest mean seasonal density of snails occurred at water depths greater than 1 m and averaged 5.2 snails m⁻² while 5.0 snails m⁻² occurred in the shallowest water depth category. Thus, there was no significant difference in snail density at the two shallowest depths. Even though there was a significant difference in density of *S. emarginata* at three measured depths over the summer (F=7.37, p<0.001), the major difference was between the deepest depth examined and the two shallow depths.

The greatest density of S. emarginata at depths less than 1 m occurred from early June through early July (Figure 7). The density of the blue snail was relatively low before

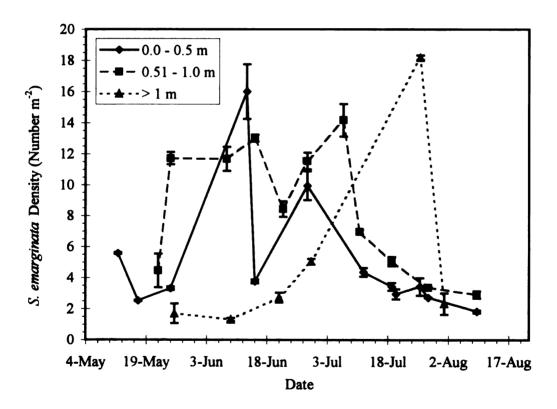


Figure 7. S. emarginata density versus sampling date at three water depths. Bars equal standard errors.

late May/early June (Figure 7). The number of snails in a given area decreased from late June/early July through mid-August (Figure 7). At water depths greater than 1 m, conversely, the density of *S. emarginata* increased after mid-June and peaked in late July at approximately 18.2 snails m⁻², only to fall after this date (Figure 7).

At the 0.0 - 0.5 m water depth, S. emarginata between 10.0 and 14.9 mm long were the most common size class during the summer (Figure 8). The density of snails in this size class increased in mid to late June and then decreased gradually over the rest of the summer, although there was a reduction in the density of S. emarginata on June 15. In early May, there were more snails between 5.0 and 9.9 mm long than in the other two size classes, although this was no longer true by early June (Figure 8). The density of this

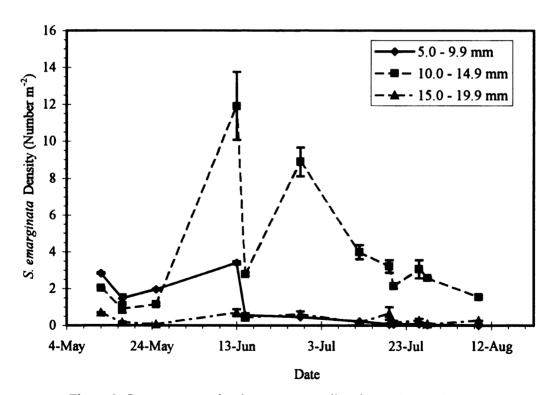


Figure 8. S. emarginata density versus sampling date at 0.0 - 0.5 m water depth for three size classes. Bars equal standard errors.

size class of snails peaked on June 13 and then declined after this date. The density of 15.0 - 19.9 mm long S. emarginata remained relatively constant from May through August at 0.0 - 0.5 m water depths (Figure 8).

At 0.51 - 1.0 m water depths, the largest snails (15.0 - 19.9 mm long) remained at a relatively constant density except for a slight peak in early July while density of 5.0 - 9.9 mm long snails peaked on May 25 and gradually declined thereafter (Figure 9). The density of S. emarginata between 10.0 and 14.9 mm long increased from May to July 7, after which the density of these snails decreased. There was always a higher density of S.

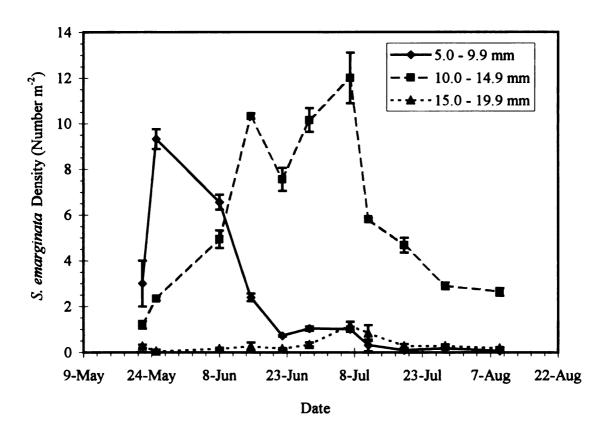


Figure 9. S. emarginata density versus sampling date at 0.51 - 1.0 m water depth for three size classes. Bars equal standard errors.

emarginata between 10.0 and 14.9 mm long than in the other two size classes after June 8, while blue snails between 5.0 and 9.9 mm dominated in late May (Figure 9).

In water deeper than one meter, densities of *S. emarginata* in the smallest and largest size classes stayed relatively constant over the sampling season with very small numbers of individuals collected. Snail densities in the 10.0 - 14.9 mm and 15.0 - 19.9 mm size classes increased until July 26, after which density of the blue snail decreased (Figure 10). Snails between 10.0 and 14.9 mm in shell length were always more common in this water depth than were snails in other size categories. *S. emarginata* between 15.0 and 19.9 mm long were always the next most abundant size class after early June (Figure 10). Thus, almost all snails in water greater than 1 m deep were approaching or in the size

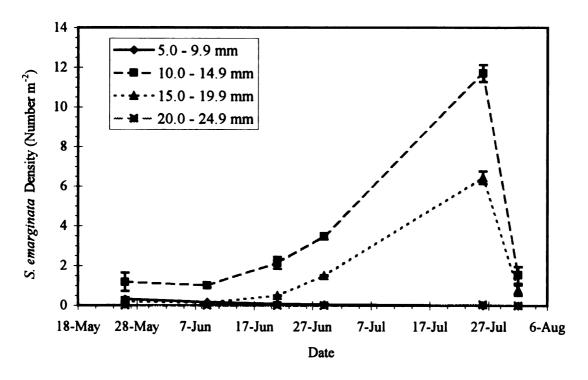


Figure 10. S. emarginata density versus sampling date at > 1 m water depth for four size classes. Bars equal standard errors.

classes known to shed cercariae (Chapter 1).

Dissolved Oxygen

Dissolved oxygen concentrations ranged from 10.6 mg/L at its highest to 8.4 mg/L at its lowest and were always near saturation or slightly under saturated (Table 6).

Water	Sampling	Mean Dissolved	Percent	Standard
Depth	Date	Oxygen (mg/L)	Saturation	Error
0.0 - 0.5 m	12-May-00	9.3	90	0.30
	17-May-00	10.2	95	0.05
	25-May-00	10.4	100	0.15
	13-Jun-00	9.0	97	0.10
	15-Jun-00	9.3	98	0.10
	28-Jun-00	10.6	115	0.05
	12-Jul-00	9.5	108	0.05
	19 -Jul- 00	8.8	104	0.10
	20-Jul-00	8.8	104	0.05
	26-Jul-00	8.9	103	0.00
	28-Jul-00	8.9	103	0.05
	9-Aug-00	8.6	100	0.10
0.51 - 1.0 m	22-May-00	9.9	96	0.00
	25-May-00	10.4	100	0.10
	8-Jun-00	9.9	103	0.05
	15-Jun-00	9.1	99	0.00
	22-Jun-00	9.4	102	0.15
	28-Jun-00	10.6	115	0.00
	7-Jul-00	9.5	110	0.05
	11-Jul-00	9.2	109	0.00
	19-Jul-00	8.7	103	0.00
	28-Jul-00	8.7	103	0.00
	9-Aug-00	8.4	97	0.00
> 1 m	26-May-00	10.4	105	0.15
	9-Jun-00	9.2	100	0.05
	21-Jun-00	8.8	99	0.10
	29-Jun-00	9.5	107	0.05
	26-Jul-00	8.6	100	0.00
	1-Aug-00	8.7	100	0.05

Table 6. Mean dissolved oxygen concentrations with percent saturation and standard errors at three water depths.

The concentration of dissolved oxygen fell from May through August at all three water depths, although changes were very gradual (Figure 11) and appeared to simply reflect increases in temperature since warmer water holds less oxygen at saturation (Horne and Goldman 1994). The mean dissolved oxygen concentration from May through August for the shallowest through the deepest water depth categories, respectively, were: 9.3 mg/L, 9.4 mg/L, and 9.2 mg/L. As a result, there was no significant difference in dissolved oxygen concentrations over the summer at the three measured depths (F=0.57, p=0.5703) and dissolved oxygen concentrations were always well above any level known to cause stress for aquatic organisms (McKee and Wolf 1963).

Including all three water depths from May through August, density of S. emarginata was not correlated with the concentration of dissolved oxygen in water (p=0.1053) as indicated by a correlation coefficient of 0.21. Snail densities in water

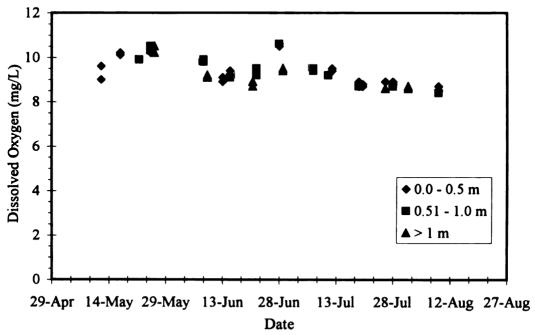


Figure 11. Dissolved oxygen versus sampling date at three water depths.

between 0.51 and 1.0 m deep were significantly correlated with oxygen concentrations (p=0.0047). Snail densities in water less than 0.5 m deep were not significantly correlated with dissolved oxygen concentrations (p=0.4967). Higher densities of *S. emarginata* in water greater than 1 m deep were not significantly correlated (p=0.1700) with dissolved oxygen levels (Figure 12).

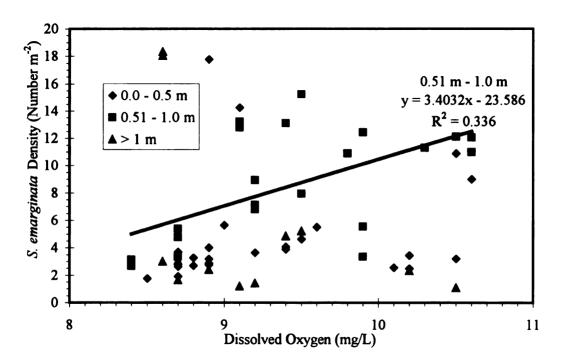


Figure 12. S. emarginata density versus dissolved oxygen at three water depths.

Water Temperature

Water temperatures recorded by HOBO data loggers varied from May through August. The lowest mean daily temperature recorded was 9.3 °C in water between 0.51 and 1.0 m deep and the highest temperature recorded (24.5 °C) was in water less than 0.51 m deep (Figure 13). From May through August, mean daily water temperature for

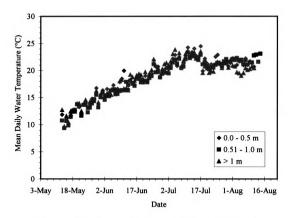


Figure 13. Mean daily water temperature versus sampling date at three water depths.

both the shallowest and middle water depths was 18.5 °C while the mean temperature in water greater than 1 m deep was 18.9 °C. Mean daily water temperatures at all three depths increased from May through August until mid-July, after which temperatures fell, only to recover in early August (Figure 13). Thus, there was no significant difference in water temperature between the three measured depths from May through August (F=0.06, p=0.9463).

There was no significant correlation between density of *S. emarginata* and mean daily water temperature (p=0.6234) as indicated by the correlation coefficient of -0.07 (Figure 14). This was also true when depths were considered individually.

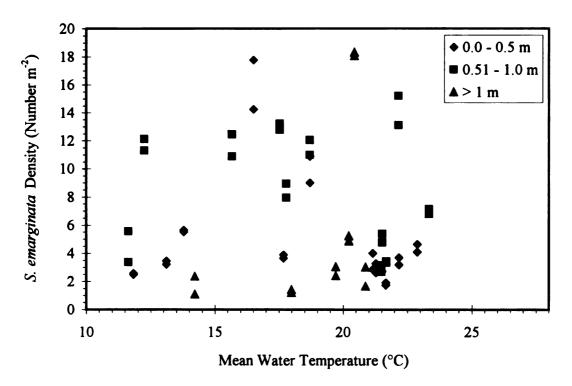


Figure 14. S. emarginata density versus mean daily water temperature at three water depths.

Chlorophyll a

Chlorophyll a concentrations ranged from 2.5 mg m⁻² in late May to 22.5 mg m⁻² when concentrations peaked near late June and early July (Figure 15). Chlorophyll a concentrations tended to increase from May through August at all three water depths (Figure 15). Water greater than 1 m deep had a significantly lower chlorophyll a concentration (F=25.37, p<0.001) and averaged 5.5 mg m⁻² from May through August. Water between 0.51 and 1.0 m deep had the highest mean chlorophyll a concentration

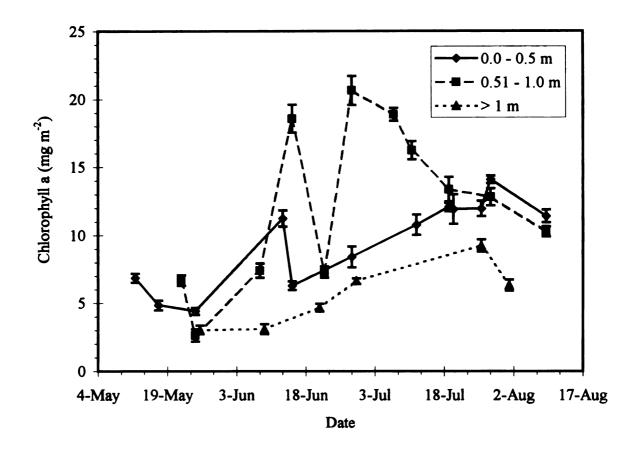


Figure 15. Mean benthic chlorophyll a concentration versus sampling date at three water depths. Bars equal standard errors.

(12.2 mg m⁻²) and the shallowest water depth averaged 9.5 mg m⁻² chlorophyll a from May through August.

Considering all water depths, greater densities of *S. emarginata* were significantly correlated (p=0.0038) with higher chlorophyll a concentrations (Figure 16). This relationship was not significant in water between 0.0 and 0.5 m deep (p=0.5128) and water between 0.51 and 1.0 m deep (p=0.2139). Snail densities in water greater than 1 m deep were significantly positively correlated with chlorophyll a concentrations (p=0.0005).

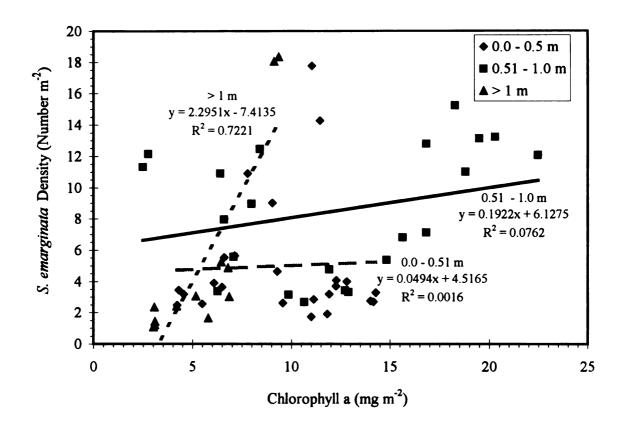


Figure 16. S. emarginata density versus benthic chlorophyll a concentration at three water depths.

Organic Matter

The amount of organic matter present on the substrate in the form of AFDM varied from 224 mg m⁻² to 439 mg m⁻² (Table 7). AFDM organic matter concentrations remained relatively constant from May through August at all three water depths (Figure 17). Water between 0.0 and 0.5 m deep had a mean AFDM organic matter concentration of 315 mg m⁻² from May through August and water between 0.51 and 1.0 m deep had a mean AFDM organic matter concentration of 323 mg m⁻². Organic matter present in water greater than one meter deep averaged 287 mg m⁻² from May through August. There

was no significant difference in organic matter concentrations from May through August at the three measured depths (F=2.35, p=0.0982).

Water	Sampling	Mean	Standard
Depth	Date	AFDM (mg m ⁻²)	Error
0.0 m - 0.5 m	12-May-00	267	22.70
	17-May-00	332	29.36
	25-May-00	340	29.41
	13-Jun-00	235	20.96
	15-Jun-00	273	22.49
	28-Jun-00	297	36.07
	12-Jul-00	324	11.29
	19-Jul-00	271	16.45
	20-Jul-00	349	28.08
	26-Jul-00	400	29.37
	28-Jul-00	366	23.46
	9-Aug-00	324	59.75
0.51 m - 1.0 m	22-May-00	299	45.96
	25-May-00	305	46.87
	8-Jun-00	271	32.96
	15-Jun-00	272	18.17
	22-Jun-00	270	25.55
	28-Jun-00	329	34.29
	7-Jul-00	207	24.60
	11 -Jul-00	359	28.22
	19-Jul-00	370	22.55
	28-Jul-00	439	42.19
	9-Aug-00	432	35.99
> 1 m	26-May-00	281	29.08
	9-Jun-00	322	45.77
	21-Jun-00	297	41.36
	29-Jun-00	229	28.01
	26-Jul-00	224	16.32
	1-Aug-00	343	29.46

Table 7. Mean AFDM organic matter concentrations with standard errors at three water depths.

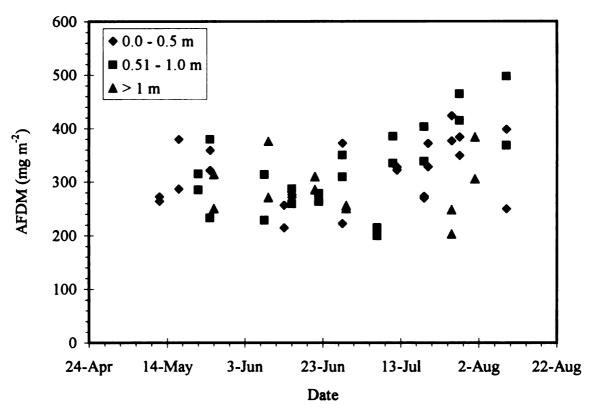


Figure 17. Mean benthic AFDM organic matter concentration versus sampling date at three water depths.

From May through August, there was a highly significant negative correlation (-0.43) between density of *S. emarginata* and the amount of organic matter on the substrate of the lake (p<0.001). This relationship was significant at the 0.0 - 0.5 m (p=0.0271), the 0.51 - 1.0 m (p=0.0002), and the > 1 m (p=0.0354) water depths (Figure 18).

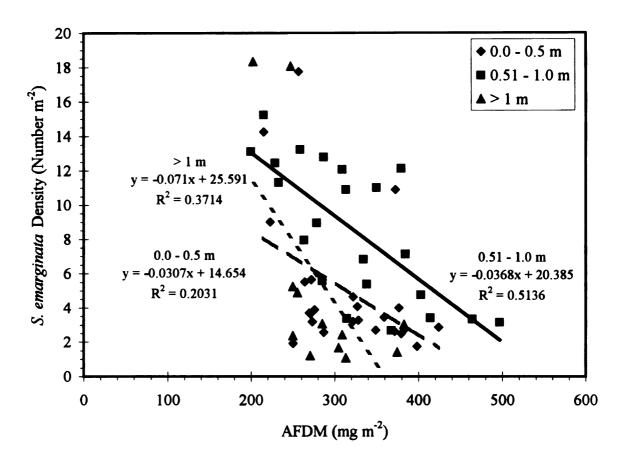


Figure 18. S. emarginata density versus benthic AFDM organic matter concentration at three water depths.

Discussion

S. emarginata between 10.0 and 14.9 mm long were most common from May through August at each of the three measured depths (Figure 6 and Table 5), indicating that this is the most common size of snail in this portion of the lake. According to other studies (Chapter 1; Burton et al. 1999, 2000), S. emarginata were considerably larger at these same depths in other areas of Higgins Lake, especially towards the end of June and the first of July when snails between 15.0 and 19.9 mm long were most prevalent. The reasons for this are unclear, but these results may be a function of food availability in this area of the lake. Chlorophyll a concentrations were not quantified in other portions of the

lake, so little can be said to support this argument. Also, other areas of the lake have considerably more cobbles as part of the substrate. Because increased predation pressure tends to decrease foraging time in snails (Weber and Lodge 1990), cobbles present in other portions of the lake may be acting as a refuge for snails from their predators. This refuge would allow more time for snails to forage for food and to increase the amount of energy allocated for growth.

Larger S. emarginata were significantly more prevalent in water greater than 1 m deep than those snails collected in shallower water (Table 5). One explanation for this phenomenon may be that larger snails have stronger shells and can better resist predation than can smaller snails (Brown and Devries 1985). Thus, larger snails may have an advantage over smaller snails in water depths greater than 1 m because they are better able to resist predation by fish or crayfish predators than are smaller snails in shallower water (Slootweg 1987; Turner et al. 2000). This hypothesis agrees with the model proposed by Lodge et al. (1987), who found that predation is the most important factor structuring distribution of freshwater snails in permanent water bodies. This relationship is difficult to document in this study, however, because the depth distributions of sunfish and crayfish, the main predators of many snails (Lodge et al. 1987), were not known.

The final possible explanation for the fact that *S. emarginata* were significantly larger in water greater than 1 m deep may be that this depth of water may have a higher proportion of snails infected with a parasite, which tends to increase growth rates of gastropods (Esch and Fernandez 1994). Although Burton *et al.* (1999) refuted this by concluding that more snails infected with schistosomes were present in the shallowest depth of water (30 cm), they concluded that their results may have been an artifact of

sample size and this data did not include other types of parasitic infections. Because Burton et al. (1999, 2000) and the results from Chapter 1 indicate that S. emarginata were increasingly more heavily infected with schistosome parasites as the size of snail increased, their results (along with these data) do imply that water greater than 1 m deep may harbor a disproportionably higher prevalence of S. emarginata infected with T. stagnicolae. Attempts were made to document this relationship in this study, but only six assayed snails were infected with this parasite and therefore little can be concluded from these results.

These data have important implications for the control of swimmer's itch in Higgins Lake. There were significantly more large snails in water greater than 1 m deep than in shallower water and large snails are more likely to shed cercariae of schistosome parasites (Burton et al. 1999, 2000; Chapter 1), suggesting that snails in water greater than 1 m deep are a significant source of cercariae. Efforts to control swimmer's itch have often emphasized treatment of shallow beach areas with copper sulfate (Howard et al. 1964; Novy et al. 1973). Therefore, managers may need to focus on controlling S. emarginata in water greater than 1 m deep more than on snails in a shallower water depths to control the disease.

Consistent with the proposed hypothesis, densities of *S. emarginata* from May through August varied by water depth. Overall, the lowest density of *S. emarginata* was present in water less than 0.5 m deep (Figure 7). These data were consistent with the results of Nyman (1998), who concluded that densities of *S. emarginata* were lowest in water 0.3 m deep and greatest in water depths of 0.6 and 0.9 m. One possible explanation for these results may be related to the amount of disturbance in the shallowest water

depth. Lodge et al. (1987) concluded that waves on exposed lakeshores may reduce snail numbers because of increased habitat disturbance. Lodge and Kelly (1985) also concluded that Lymnae peregra, a member of the same family of snails that includes S. emarginata, exhibited low resistance to habitat disturbance and were not present in areas of lakes with high disturbance regimes. Moffett (1943) concluded that S. emarginata was not present in large numbers in shoal areas of Douglas Lake, which were dominated by a high number of waves.

The greatest mean summer density of *S. emarginata* was in the 0.51 - 1.0 m depth category (Figure 7), indicating that this depth was most suitable for this particular organism. This depth of water also supported the highest standing crop of chlorophyll a (Figure 15) and AFDM of organic matter (Figure 17 and Table 7), although differences in AFDM organic matter were not significant. Another explanation for this relationship may be that predation pressure was lowest in this area, although this was not documented in this study.

Densities of S. emarginata varied both spatially and temporally, supporting the hypothesis that densities of S. emarginata would change from May through August at each of three water depths. The peak in density at the two shallowest depths occurred in June and early July (Figures 8 and 9). The density of blue snails in water greater than 1 m deep peaked towards the end of July (Figure 10). These data suggest that a large group of snails present in the shallowest two water depths during June and early July may have moved to water greater than 1 m deep in late July. This movement coincided with a decrease in water temperature (Figure 13). A similar pattern was described by Cheatum (1934), who concluded that S. emarginata underwent an annual movement in spring and

autumn to avoid hazards in the littoral zone in the winter and to take advantage of resources in shallower water in the summer. This phenomenon was investigated in this study and will be reported in chapter three.

These results imply that treatments to kill snails to control cercarial dermatitis in Higgins Lake should occur in late June and early July in water less than 1 m deep and in mid to late July in water greater than 1 m deep. Additionally, water greater than 1 m deep should be treated throughout the summer because this is the depth of water where S. emarginata large enough (larger than 9.9 mm long) to consistently shed cercariae are found (Figure 6). Since peak density of snails tends to be greatest in water between 0.51 and 1.0 m deep from May through August, this is the depth where managers should apply molluscicides most heavily.

The densities of *S. emarginata* in this study tended to be greater than those reported by Nyman (1998) for Higgins Lake and by Clampitt (1973) for Douglas Lake, Michigan. The lowest density I observed was 1.3 snails m⁻², while Nyman (1998) found anywhere from 0.37 – 0.70 snails m⁻² and Clampitt (1973) did not find any *S. emarginata* in mid-May. I consistently found densities of the blue snail greater than 4 snails m⁻² in this study while this was the maximum density found by Clampitt (1973). The difference in snail densities between the three studies indicates that the habitat analyzed by Cheatum (1973) and Nyman (1998) was not conducive to a high density of *S. emarginata*, as was the case at the one site examined in Higgins Lake.

The concentration of dissolved oxygen (D.O.) in the lake was relatively high and at or near saturation from May through August (Table 6). These D.O. values were similar to those recorded by Limno-Tech, Inc. (1992). The concentration of dissolved oxygen

decreased slightly over time (Figure 11), perhaps reflecting the fact that the amount of oxygen in saturated water is in part a function of water temperature (Horne and Goldman 1994), which increased from May through August at all three water depths (Figure 13).

There were no significant differences in D.O. concentrations between the three measured depths from May through August. D.O. concentrations did not significantly correlate with density of *S. emarginata* (Figure 14), disputing the hypothesis that higher densities of snails would be associated with higher D.O. concentrations. These data suggest that these organisms were not influenced greatly by the oxygen concentrations observed in Higgins Lake. Cheatum (1934) concluded that *S. emarginata* decreased intervals between breathing periods when water warmed because there was less available oxygen, and that they were able to survive 62 days in an experimentally induced desiccation state. Therefore, the relatively small variability in dissolved oxygen concentrations observed in this study from May through August was not great enough to correlate with a response in the density of *S. emarginata*.

Mean daily water temperatures recorded by HOBO data loggers increased from May through mid-July at all three water depths (Figure 13), which correlated with warming air temperatures during this same period of time. There was no significant difference in water temperature between the three water depths, which could be explained by the fact that the lake tends to stratify at water depths between 12 and 15 m (Limno-Tech 1992), which is much deeper than depths examined in this study. Therefore, temperature differences in water depths examined in this study would not be expected to be different in the well-mixed epilimnion of the lake.

Refuting the hypothesis that abundance of *S. emarginata* would be negatively correlated with water temperature, snail densities did not significantly correlate with mean daily water temperatures (Figure 14). There was no significant difference in mean daily water temperatures between the three water depths (Figure 13), suggesting that water temperature differences were not great enough to cause a response in densities of *S. eamrginata*. However, the data do indicate that snails were affected by water temperature to some degree because densities of snails in water between 0.0 and 1.0 m deep decreased when mean daily water temperature fell in late July (Figure 13). This relationship may indicate that *S. emarginata* migrate and that this movement may be triggered by a change in water temperature (Cheatum 1934).

Algal biomass, recorded as chlorophyll a, increased from May through August at all three water depths (Figure 15). This relationship was likely due to the fact that productivity in a water body tends to increase as temperatures increase because of higher metabolic rates (Horne and Goldman 1994). There was a significant difference in chlorophyll a concentrations between the three measured depths. Water greater than 1 m deep had the lowest mean concentration and water between 0.51 and 1.0 m deep had the highest concentration from May through August. This suggests that the algal community in water greater than 1 m deep may have been light inhibited because light extinction does increase as a function of water depth (Horne and Goldman 1994). Algae in water less than 0.5 m deep were likely disturbed by increased wave action in the lake (Horne and Goldman 1994), causing a decrease in algal biomass.

Greater chlorophyll a concentrations were overall significantly associated with greater densities of S. emarginata (Figure 16), although the relationship was not

significant in water less than 1 m deep. This relationship supported the original hypothesis and indicated that *S. emarginata* may be influenced by algal biomass, which is a food source for the snail (Kesler *et al.* 1986). Densities of *S. emarginata* were highly correlated with chlorophyll a concentrations in water greater than 1 m deep (Figure 16), implying that algae may be increasingly more important for the blue snail as water depth increases.

These results have great implications for controlling swimmer's itch in Higgins Lake. Because increased algae biomass is associated with nitrogen and phosphorus pollution, increases in nutrient levels may lead to increased algae in the lake (Dillon and Rigler 1974). Thus, managers should focus on controlling pollution in Higgins Lake because greater densities of *S. emarginata* are associated with a greater algal biomass. Greater densities of the blue snail provide more intermediate snail hosts for *T. stagnicolae*, the parasite that causes cercarial dermatitis.

Organic matter in the form of AFDM increased from May through August (Table 7 and Figure 17), suggesting an accumulation due to settling of organic sediments from the water column (Horne and Goldman 1994). There was no significant difference in organic matter concentrations between the three water depths, likely due to a relatively small difference in water depth examined in this study.

There was a significant negative relationship between density of blue snails and organic matter on the lake substrate (Figure 18), refuting the hypothesis that greater densities of *S. emarginata* would be associated with higher levels of organic matter. This relationship was unexpected because *S. emarginata* utilize detritus as a staple in their diets (Barnese *et al.* 1990; Bovbjerg 1968; and Lodge 1986). The negative relationship

between snail density and organic matter could indicate that snail grazing pressure is great enough to reduce organic matter biomass at high snail densities. The negative relationship could also be explained by the fact that blue snails are often found on wave swept beaches (Baker 1928) where, because of disturbances caused by waves, organic matter does not accumulate (Horne and Goldman 1994). This hypothesis is supported by the fact that *S. emarginata* were never found in depths greater than 9 m while SCUBA diving, where the lake substrate is dominated by fine organic matter (Limno-Tech, Inc. 1992).

CHAPTER THREE

MOVEMENT OF STAGNICOLA EMARGINATA (SOWERBY)

Introduction

Many groups of animals undergo regular movements within their environment. Salmon migrate between saltwater and freshwater to mature and complete reproduction (Moyle and Cech 2000), phytoplankton regularly move vertically through the water column to avoid predators and to absorb light for photosynthesis (Horne and Goldman 1994), zooplankton move to collect prey and avoid predation (Dini and Carpenter 1991), and *Chaoborus* midges migrate to obtain food resources (Roth 1968). These migrations are influenced by a large number of variables, including food acquisition, predator avoidance, and physiochemical changes. Regular movements have been documented in snail populations, although data presented in these studies were not quantitative and were based on anecdotal evidence (Cheatum 1934; Brackett 1940). These studies also did not focus on *S. emarginata* but rather on several other species of snails in the same family. Other studies shed doubt on movements in snail populations (Morrison 1932).

Cheatum (1934) concluded that snails move during spring and autumn in Douglas Lake, Michigan. He attributed movements towards deeper water in autumn to avoidance of hazards in the littoral zone as water temperatures decrease and migration to shallow water in spring to the snail seeking food resources. These conclusions were drawn from several studies completed during winter where Cheatum (1934) filled aquaria with water at room temperature and placed several species of snails in the tanks. He then measured water temperature and placed the aquaria on a window ledge. After two days, aquaria

were taken from the window ledge and water temperature was recorded. He noticed that a majority of snails had moved to the bottom of the tank, which corresponded with a decrease in water temperature. Cheatum (1934) also stated that when he observed snails in the lake, snails were facing towards the center of the lake as water temperatures decreased. When water temperatures began to increase, snails oriented themselves towards the shoreline. Cheatum (1934) attributed this regulated movement to respiration requirements of snails and to water temperature changes.

Objectives

Because of the importance of *S. emarginata* as a host of *T. stagnicolae* and its implications for better understanding cercarial dermatitis, the specific objective of this study was to document movement of *S. emarginata* in Higgins Lake. Based on the literature, I hypothesized that *S. emarginata* would move towards shallow water in spring and deep water in autumn.

Methods

To determine movement patterns of *S. emarginata*, a circular area was established in water approximately 0.50 m deep in Higgins Lake near the Earl Avenue road end, located along the northeast shoreline of the lake (Figure 1). The substrate of this area, dominated by sand, cobbles, and small numbers of macrophytes, is typical of other areas in the lake and is characterized by a low angle of repose. Although not directly measured, this area appeared to have *S. emarginata* densities that were typical of other areas in the lake (Chapter 1).

To construct the circle, a wooden broomstick was colored with surveyor's paint and driven into the substrate approximately 50 m from the shoreline. A metric tape rule, metal stakes, and brightly colored masonry line were then used to establish a 0.5 m radius circle around the broom pole. Four quadrants were constructed so that one quadrant faced the shoreline, one faced towards deep water, and the other two quadrants faced in a direction parallel to the shoreline (Figure 19). To ensure an adequate size range of snails,

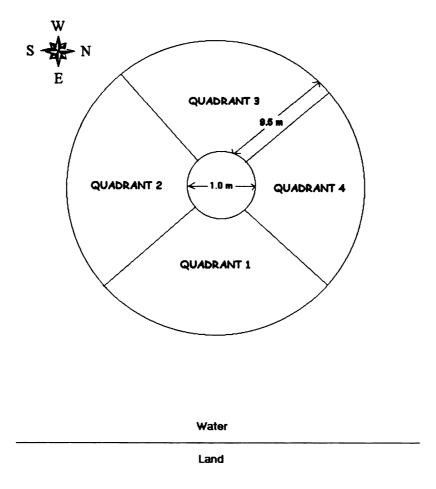


Figure 19. Experimental design of *S. emarginata* movement study showing quadrant relationship to the shoreline. Center circle (0.5 m radius) used for release of snails. Movements recorded when snails moved out of center circle (distance greater than 1.0 m from center plot).

S. emarginata were randomly collected from several areas of Higgins Lake and placed into size classes based on shell length: class three (10.0 – 14.9 mm), class four (15.0 – 19.9 mm), and class five (20.0 – 24.9 mm). Thirty snails per size class were painted with a different color of Testor's paint (90 total snails) and placed in a small volume of water until the paint had dried.

All S. emarginata were then placed in a bucket and transported to the lake where they were randomly released within 0.5 m of the center of the circle. Every 24 ± 2 hours after this point, a metric tape rule was anchored to the broomstick with a nail so that distance the snails had traveled could be measured by category: in the center circle, 1-2 m from center, 2-3 m from center, 3-4 m from center, 4-5 m from center, 5-6 m from center, 6-7 m from center, 7-8 m from center, 8-9 m from center, 9-10 m from center, and > 10 m from the center circle. The number of snails belonging to each size class was recorded for each quadrant to determine directional movement. This procedure was completed for a trial running from June 9 through June 23 and for another trial running from July 21 through August 4.

Results

The number of snails in the center circle decreased through both studies (Tables 8 and 9). Snails were greater than 10 m from the center circle during the last seven days of the first trial and no snails were greater than 10 m from the center at any time during the second trial, so *S. emarginata* in the first trial traveled greater distances than in the second trial (Tables 8 and 9). At the end of the first study, there were more snails 2 to 4 m from the center area than in the other remaining categories. This pattern was not observed

	No. in	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.
Date	Center	1-2m	2-3m	3-4m	4-5m	S-6m	6-7m	7-8m	8 -9m	9-10m	>10m
00-unf-6	06										
10-Jun-00	70	\$	9	6							
11-Jun-00	54	14	10	6	7	-					
12-Jun-00	35	19	17	7	8	4	_	2			
13-Jun-00	34	20	17	7	2	3	-	8			
14-Jun-00	24	56	19	10	9	7	0	-	7		
15-Jun-00	21	24	15	13	2	4	1	4	7	-	
16-Jun-00	17	15	17	10	7	9	4	5	7	7	
17-Jun-00	14	14	17	6	6	5	4	4	00	4	7
18-Jun-00	13	15	18	10	10	ю	4	4	7	4	7
19-Jun-00	12	14	17	12	12	4	2	8	8	3	3
20-Jun-00	111	13	17	13	15	ю	4	3	4	4	3
21-Jun-00	∞	10	15	10	11	∞	7	\$	2	9	2
22-Jun-00	∞	00	13	12	10	6	9	∞	9	4	9
23-Jun-00	∞	7	13	13	10	6	5	6	9	4	6

Table 8. Total S. emarginata in each category for trial 1 of the movement study conducted in Higgins Lake, June 9-23, 2000.

	No. in	No.	No.	No.	No.	Z.	No.	No.	No.	No.	No.
Date	Center	1-2m	2-3m	3-4m	4-5m	5-6m	6-7m	7-8m	8-9m	9-10m	>10m
21-Jul-00	06										
22-Jul-00	78	7	2								
23-Jul-00	74	∞	7	_							
24-Jul-00	\$	12	6	ю	7						
25-Jul-00	09	13	10	4	7	-					
26-Jul-00	28	13	11	\$	7	,					
27-Jul-00	54	14	13	9	7	_					
28-Jul-00	47	17	15	7	7	-	-				_
29-Jul-00	34	22	17	6	4	-	7	-			
30-Jul-00	32	21	18	10	4	7	7	1			
31-Jul-00	31	22	18	11	3	7	-	1	1		
1-Aug-00	24	70	22	13	4	3	7	1	-		
2-Aug-00	19	14	23	17	\$	3	4	7	7	-	
3-Aug-00	17	15	24	18	2	4	3	1	7	1	
4-Aug-00	15	16	24	19	9	3	2	1	2	2	

Table 9. Total S. emarginata in each category for trial 2 of the movement study conducted in Higgins Lake, July 21 - August 4, 2000.

in the second trial because relatively few blue snails were farther than 4 m from the center circle (Tables 8 and 9).

Because there was a relatively large difference in numbers of snails that changed categories between both trials (Tables 8 and 9), mean daily wind speed and predominant wind direction were retrieved from the Houghton Lake weather station (http://www.noaa.gov), slightly south of Higgins Lake. A significant relationship existed (p<0.01) between the number of snails changing categories in a twenty-four hour period and mean daily wind speed (Figure 20). Because predominant wind was from the east,

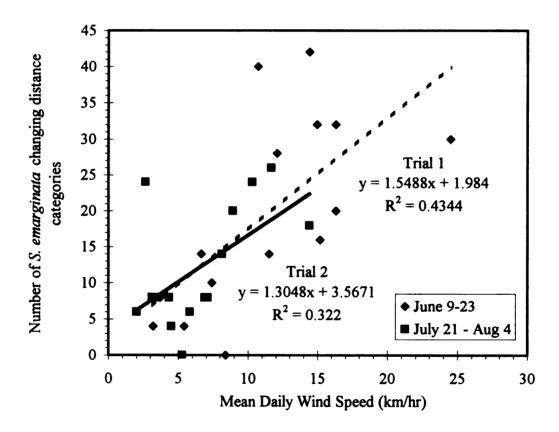


Figure 20. Mean daily wind speed versus number of *S. emarginata* changing categories in a twenty-four hour period for the movement experiment.

northeast, or southeast during a major portion of trial two and many snails accumulated in the leeward quadrant (quadrant three) during this same trial (Table 10), wind direction

Trial 1 Jun 9 -	23, 2000				
Date	Quadrant 1 (East)	Quadrant 2 (South)	Quadrant 3 (West)	Quadrant 4 (North)	Predominant Wind Direction
9-Jun-00	23	24	23	18	SW
10-Jun-00	21	24	22	19	SW
11-Jun-00	22	23	21	24	SE
12-Jun-00	25	23	20	22	E
13-Jun-00	27	22	20	22	E
14-Jun-00	24	25	20	22	SW
15-Jun-00	25	23	21	21	SW
16 -Jun- 00	23	21	26	18	SW
17-Jun-00	25	22	20	20	NW
18-Jun-00	25	24	17	22	S
19-Jun-00	25	23	18	23	W
20-Jun-00	24	24	21	21	SE
21-Jun-00	28	23	21	18	W
22-Jun-00	25	25	22	19	W
23-Jun-00	25	23	22	20	S

Trial 2 Jul 21 -	Aug 4, 2000				
	Quadrant 1	Quadrant 2	Quadrant 3	Quadrant 4	Predominant
Date	(East)	(South)	(West)	(North)	Wind Direction
21-Jul-00	25	21	26	18	NW
22-Jul-00	20	22	30	19	NW
23-Jul-00	18	19	31	23	W
24-Jul-00	18	20	31	21	SE
25-Jul-00	16	20	32	20	S
26-Jul-00	16	20	31	20	S
27-Jul-00	13	21	33	20	SE
28-Jul-00	13	21	36	20	E
29-Jul-00	8	22	38	20	E
30-Jul-00	10	23	44	19	NE
31-Jul-00	8	25	44	17	SE
1-Aug-00	9	22	44	18	NE
2-Aug-00	8	18	44	21	NW
3-Aug-00	5	20	45	19	N
4-Aug-00	6	19	47	18	S

Table 10. Total *S. emarginata* in four quadrants and predominant wind direction for two movement trials. Data include all snail size classes. Predominant wind direction data from National Oceanic and Atmospheric Administration.

did influence numbers of *S. emarginata* in each quadrant. This was also true in trial one because wind direction varied by date, just as did the number of snails in each quadrant (Table 10).

There was no significant difference in snail size between the four quadrants after one day in either trial (t=2.57, p=0.642). There was also no significant difference in snail size between the four quadrants after seven days (t=3.14, p=0.784) or at the end of the experiment (t=1.64, p=0.241) in both trials. Numbers of *S. emarginata* in each of four quadrants were not significantly different (t=1.98, p=0.175) at the end of trial one (Table 10 and Figure 21). In trial two, the quadrant facing deeper water had significantly more S.

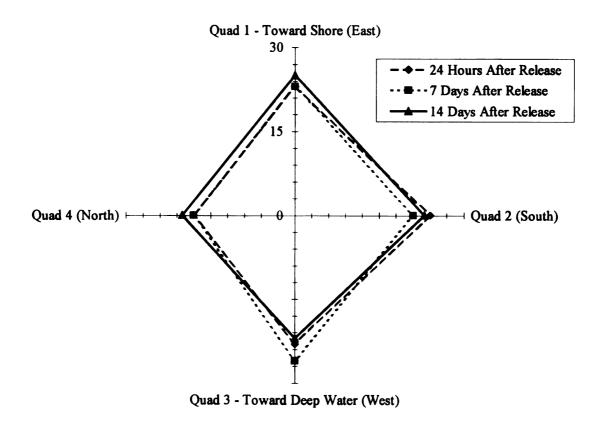


Figure 21. Number of S. emarginata in each of four quadrants throughout trial 1 of the movement study.

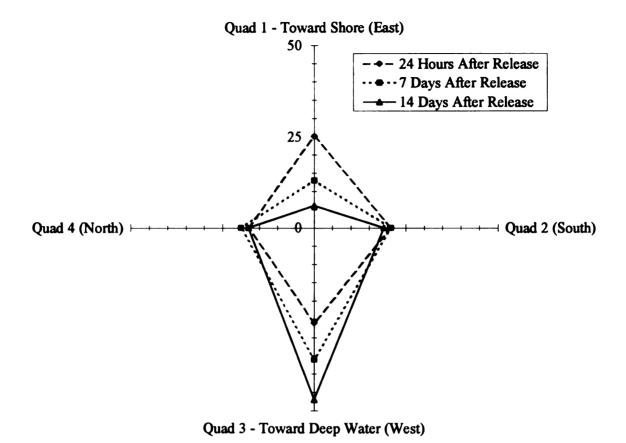


Figure 22. Number of S. emarginata in each of four quadrants throughout trial 2 of the movement study.

emarginata than did the first quadrant (t=5.61, p<0.01), which was facing the shoreline (Table 10 and Figure 22). There was no significant difference in snail numbers between the second and fourth quadrants during trial two (t=2.01, p=0.098).

Discussion

There was a significant difference in the number of *S. emarginata* between the first and third quadrants in trial two (Figure 22). Blue snails showed a preference towards the quadrant facing deep water in late July and early August, corresponding with results of Cheatum (1934), who concluded that snails exhibit a regular movement in spring and

early autumn as a response to changes in dissolved oxygen levels and water temperature. Brackett (1940) attributed snail movement to acquisition of previously unusable areas in spring. Because of these data and patterns observed in Chapter 2, S. emarginata seem to move towards deep water in late July/early August, consistent with my original hypothesis.

There was no significant difference between numbers of snails in the four quadrants at the end of the trial conducted from June 9 through June 23 (Figure 21). Cheatum (1934) concluded that blue snails move towards shallow areas of the littoral zone when water thaws in spring. Thus, *S. emarginata* may move in spring, but movement was not detected in this study because snails had already moved to shallow water by June 9.

These data may explain results from other studies. Burton et al. (1999, 2000) concluded that Lake Leelanau and Walloon Lake saw a reduction in S. emarginata numbers in shallow areas during late July and early August. Assuming that movements of snails in Higgins Lake are similar to those in Lake Leelanau and Walloon Lake, researchers may have seen reduced snail numbers in shallow areas because of a movement pattern in the snail population.

S. emarginata movement is influenced by wind (Table 10 and Figure 20). Laman et al. (1984) found that when wind speeds increased, snails became unattached from the substrate and were consequently moved by water movement. Although this correlation was significant at water 0.5 m deep, the relationship may not exist in deeper water. Because the maximum wavelength that a wave can obtain is partially a function of water depth (Horne and Goldman 1994), snails in water greater than 0.5 m deep may be less

influenced by wind because deep water inhibits the depth to which a surface wave can penetrate the water column. Conversely, snails in water less than 0.5 m deep may be more affected by air movements.

Each of these results has implications for controlling swimmer's itch in lakes. Because S. emarginata exhibit regular movements during autumn and early spring, it would be unwise for managers to apply molluscicides during this time unless they knew exact depths at which large numbers of snails were located. Winds also affect movements of S. emarginata. Thus, management should consider wind speed when applying copper sulfate because snails may be blown into or out of areas treated for swimmer's itch.

CHAPTER 4

GROWTH OF STAGNICOLA EMARGINATA (SOWERBY)

Introduction

Water temperature greatly influences behavioral and physiological traits of aquatic organisms. Biochemical reactions in aquatic organisms are extremely sensitive to water temperature, as all enzymes function best at an optimal temperature and any deviation from this temperature may cause inefficiencies in the organism (Hickman and Roberts 1994). When ambient temperatures are lowered in poikilotherms, metabolic processes slow and organisms have less energy for normal activities (Hickman and Roberts 1994). Increases in temperature cause proteins to become denatured, destroying the efficacy of proteins and possibly leading to negative effects on the organism. Within an optimal temperature range, lowered ambient temperatures may negatively affect growth and reproduction of the organism (Hickman and Roberts 1994).

Little is known about growth of *S. emarginata* in the natural environment. Burton et al. (1999, 2000) and Chapter 1 have performed intensive studies in three northern Michigan lakes and have concluded that shell lengths of *S. emarginata* vary over time at the same site and between sites on the same date. The majority of *S. emarginata* in Higgins Lake are between 10.0 and 24.9 mm in length (Burton et al. 1999, 2000; Chapter 1; Chapter 2). Cort et al. (1940) concluded that *S. emarginata* live from thirteen to sixteen months, although this conclusion was based on anecdotal evidence and was not measured quantitatively. Brackett (1940) concluded that Lymnaeidae snails live for a year or less. With these data and mathematical calculations, *S. emarginata* grow, on

average, from 0.63 to 1.9 mm per month. Because of this tremendous variation in growth rate of *S. emarginata*, the objective of this study was to determine the degree to which differing environmental conditions alter growth of *S. emarginata* and to better understand the life span of the snail. Based on the literature, I hypothesized that *S. emarginata* would grow fastest in summer conditions and slowest in winter conditions.

Methods

During mid-August 1999, buckets of sand, cobbles, and a large number of S. emarginata were collected from several areas around Higgins Lake (Figure 1). Once collected, an artificial stream filled with de-chlorinated tap water chilled to water temperatures in Higgins Lake was filled with the sand, cobbles, and snails. All items were stored in this stream to prevent desiccation while the remaining portion of the experiment was assembled.

Four 10-gallon aquaria were filled with nine gallons of de-chlorinated tap water and 25 mm of sand and two equally sized cobbles taken from the artificial stream. All four tanks were placed in one of three environmental chambers: "winter" conditions with a temperature of 4°C and light cycle of 9 hours of light and 15 hours of darkness, "spring" conditions with a temperature of 12°C and light cycle of 12 hours of light and 12 hours dark, and "summer" conditions with a temperature of 20°C and light cycle of 14 hours of light and 10 hours of dark. Thus, there were a total of four aquaria for each of three treatments. Air stones were connected to an air pump and placed into each of twelve tanks to ensure an adequate dissolved oxygen concentration throughout the study.

Ten S. emarginata of an approximate equal size were collected from the artificial stream and both maximum shell width and shell length were measured with calipers. Each S. emarginata was dried with paper towels and distinctively marked with Testor's paint. Snails were then weighed with a Mettler balance to quantify wet mass and placed into one of the aquaria. This procedure was completed for all twelve tanks so that forty snails were exposed to each of three treatments.

Throughout the sixty-day experiment, consistent water levels were maintained in all tanks by adding de-chlorinated tap water as needed. Once sixty days had passed, shell length, maximum shell width, and wet mass were recorded for all 120 snails.

Results

Because *S. emarginata* in "winter" conditions (4°C; 9 L:15 D) had the smallest increase in shell length and maximum shell width, these snails grew at the slowest rate. On average, snails in "winter" conditions gained approximately 0.7 mm in shell length, 0.13 mm in maximum shell width, and 0.3 g during the experiment (Table 11). Snails in "summer" conditions (20°C; 14 L:10 D) gained approximately 3 mm in shell length and 0.6 mm in maximum shell width (Table 11). *S. emarginata* exposed to "spring" conditions (12°C; 12 L:12 D) grew slower than in "summer" conditions and faster than "winter" conditions in all three growth measurements (Table 11). Both "spring" and "summer" conditions had, on average, a smaller increase in wet mass than in the "winter treatment" (Figure 23).

There was a significant difference (F=4.20, p<0.01) in maximum shell length changes between "summer" and the other two conditions after the sixty-day experiment

(Figure 24). Maximum shell width change was significantly greater (F=7.36, p<0.01) in "summer" conditions (Figure 25) and wet mass changes were significantly greater (F=4.11, p<0.01) in "winter" conditions than in the other two treatments (Figure 23).

	Mean Change in		Mean Change in		Mean Change in	
	Length (mm)	SE	Width (mm)	SE	Wet Mass (g)	SE
Winter Conditions						
(4°C; 9 hr. light: 15	hr. dark)					
Tank 1	0.22	0.07	0.02	0.01	0.40	0.01
Tank 2	0.71	0.25	0.03	0.01	0.50	0.01
Tank 3	0.16	0.08	0.10	0.04	0.30	0.04
Tank 4	1.67	0.73	0.38	0.09	0.10	0.01
Spring Conditions						
(12°C; 12 hr. light:	12 hr. dark)					
Tank 1	0.85	0.02	0.53	0.08	0.27	0.01
Tank 2	0.46	0.01	0.08	0.01	0.04	0.01
Tank 3	0.28	0.01	0.11	0.01	0.02	0.01
Tank 4	0.47	0.01	0.10	0.01	0.03	0.01
Summer Conditions	3					
(20°C; 14 hr. light:	10 hr. dark)					
Tank 1	3.03	0.11	0.72	0.14	0.08	0.01
Tank 2	4.10	0.12	0.66	0.20	0.05	0.01
Tank 3	1.67	0.07	0.39	0.12	0.05	0.01
Tank 4	2.21	0.07	0.64	0.14	0.00	0.00

Table 11. Mean change in S. emarginata size in four aquaria at winter, spring, and summer temperature and light conditions.

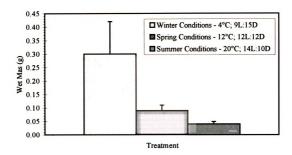


Figure 23. Mean difference between initial and final measurements in wet mass of S. emarginata for three treatments. Bars equal standard errors.

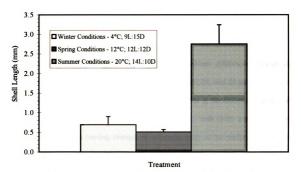


Figure 24. Mean difference between initial and final measurements in shell length of *S. emarginata* for three treatments. Bars equal standard errors.

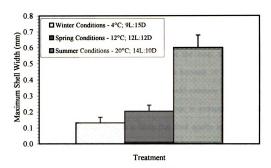


Figure 25. Mean difference between initial and final measurements in maximum shell width of *S. emarginata* for three treatments. Bars equal standard errors.

Discussion

Consistent with the hypothesis, there were significant differences between the three treatments in all three measured variables (Figures 23, 24, and 25 and Table 11). S. emarginata in "summer" conditions grew longer and wider at the fastest rate and snails exposed to "winter" conditions grew at the slowest rate, both likely a result of water temperature differences causing changes in metabolic rates of the snails (Hickman and Roberts 1994).

Snails in "winter" conditions added significantly more mass than did S.

emarginata in the other two conditions (Figure 23). This result may be due to food
quality in the tanks because the algal community in "winter" were likely different than in
the other two conditions due to differences in light and water temperature (Horne and

Goldman 1994) or to snails putting most of their energy into increases in weight rather than to increases in shell length.

Based on mean growth rates from this experiment, *S. emarginata* would add approximately 8 mm year⁻¹ in shell length. Because the most common size of *S. emarginata* found in Higgins Lake had a shell length between 10 and 14.9 mm long (Chapters 1 and 2; Burton *et al.* 1999, 2000), one could conclude that blue snails live slightly over one year. However, one must be cautious in extrapolating results from laboratory studies to field conditions. It is likely that food quality in laboratory aquaria were different than in the lake because of use of artificial lights, less water movement than would occur on the wave-swept lake shore, and greater probability of nutrient limitation in laboratory aquaria. Even so, growth rates measured in the laboratory do support other estimates (Cort *et al.* 1940; Brackett 1940) that blue snails live slightly more than one year in lakes.

Based on these data and on anecdotal evidence gained from field studies, it appears that adult *S. emarginata* reproduce and deposit eggs on hard substrates throughout June. Eggs hatch throughout June and early July. By the early portion of August, newly hatched *S. emarginata* are approximately 4.0 to 10.0 mm long. In late September and early October, large numbers of adult snail shells are seen on the shoreline of the lake. Development of young snails continues during this same time period and throughout winter and spring months. In June, adult snails reproduce and the life cycle is initiated once again. Thus, it appears that *S. emarginata* live from late June to early July through September and October of the following year.

SUMMARY AND CONCLUSIONS

The overall goal of these studies was to better understand the biology of Stagnicola emarginata because of its role as a major host of Trichobilharzia stagnicolae, one of the parasites that causes cercarial dermatitis (swimmer's itch) in northern Michigan lakes. From May through August of 1999 and 2000, studies were performed in Higgins Lake, Michigan to determine variation in the percentage of shedding snails over time and space, to identify limnological variables that influence abundance and distribution of S. emarginata, and to determine whether S. emarginata exhibit regular movement during portions of the year. Growth of snails in several different environmental conditions was also examined in the laboratory.

The overall percentage of *S. emarginata* shedding *T. stagnicolae* cercariae according to the light box assay was 0.69% over both summers, although prevalence varied spatially and temporally. The greatest prevalence occurred during July and August of both years, and the Columbine Lane site had significantly more shedding snails according to the light box assay than did the other three sites. Larger snails were more likely to be shedding *T. stagnicolae* cercariae, and snails less than 10.0 mm long never shed cercariae.

At the Birch Lodge site, snails with a shell length between 10.0 and 14.9 mm were most common, and snails were largest in water greater than 1 m deep. The density of *S. emarginata* varied by water depth from May through August and the greatest density of blue snails was in water between 0.51 and 1.0 m deep. The lowest mean density from May through August was in water less than 0.5 m deep. *S. emarginata* were

most dense between early June and early July in water less than 1 m deep and in late July in water greater than 1 m deep, indicating a movement towards deep water.

Water temperature increased from May to early July and was not significantly correlated with density of S. emarginata. Dissolved oxygen concentrations were also not correlated with density of S. emarginata and tended to decrease slightly from May to early July as temperatures increased. Percent saturation of dissolved oxygen was at or near 100% from May through August. At all three water depths, density of blue snails was positively correlated with benthic chlorophyll a and there was a negative association between density of S. emarginata and benthic organic matter, whose concentrations stayed relatively constant from May through August.

Movement experiments conducted in the lake, along with density changes at three depths from May through August, documented the fact that *S. emarginata* do move towards water greater than 1 m deep in late July. Movement was likely initiated by a drop in water temperature and was influenced by wind speed and direction. Different sized snails did not prefer to move in one particular direction. Growth experiments showed that changes in both shell length and maximum shell width of snails were positively associated with increasing water temperatures and changes in wet mass were negatively associated with increasing water temperatures. Extrapolations from the growth experiment indicate that *S. emarginata* live slightly over one year.

These results have implications for controlling swimmer's itch in Higgins Lake. Because most snails were shedding cercariae in July and early August, this should be a time to focus on controlling the disease. Water greater than 1 m deep had significantly larger snails than shallower water and larger snails were more likely to shed T.

stagnicolae cercariae, so water greater than 1 m deep may be a significant source of cercariae. Densities of S. emarginata varied over time and space, so managers should target maximum densities of snails for molluscicide control. Greater densities of snails were associated with higher concentrations of algae, indicating that nutrient pollution should be controlled to inhibit increases in algal biomass. By doing so, managers may be able to alleviate the swimmer's itch problem in Higgins Lake to a certain degree.

APPENDICES

Appendix A - 1. Snail density data collected over 2000 at 0.0 - 0.5 m water depth.

	Quadrant	Total	No. Size	No. Size	No. Size	No. Size
Date	Size	No. Snails	Class 2 Snails	Class 3 Snails	Class 4 Snails	Class 5 Snails
12-May-00	5 x 5 m	141	72	52	17	<u> </u>
12-May-00	5 x 5 m	138	70	90	18	0
17-May-00	5 x 5 m	49	31	28	\$	0
17-May-00	5 x 5 m	62	42	17	8	0
25-May-00	0 x 6 m	115	69	44	7	0
25-May-00	0 x 6 m	112	72	38	7	0
13-Jun-00	4 x 4 m	228	53	161	14	0
13-Jun-00	2 x 2 m	71	14	55	7	0
15-Jun-00	0 x 6 m	131	15	104	12	0
15-Jun-00	0 x 6 m	140	24	16	19	0
28-Jun-00	3 x 3 m	81	4	73	4	0
28-Jun-00	3 x 3 m	86	4	87	7	0
12-Jul-00	5 x 5 m	116	\$	109	2	0
12-Jul-00	5 x 5 m	102	9	06	9	.3 m
19-Jul-00	4 x 4 m	51	0	46	ς.	0
19-Jul-00	4 x 4 m	75	2	57	15	0
20-Jul-00	w 9 x 9	118	1	102	16	0
20-Jul-00	7 x 7 m	128	я	112	13	0
26-Jul-00	4 x 4 m	49	1	57	9	0
26-Jul-00	4 x 4 m	49	1	- 1	57	

1						
	Quadrant	Total	No. Size	No. Size	No. Size	No. Size
	Size	No. Snails	Class 2 Snails	Class 3 Snails	Class 4 Snails	Class 5 Snails
26-Jul-00	7 x 7 m	140	9	126	∞	0
28-Jul-00	0 x 6 m	26	-	91	\$	0
28-Jul-00	0 x 6 m	66	7	95	7	0
9-Aug-00	$10 \times 10 \mathrm{m}$	161	0	164	27	0
9-Aug-00	$10 \times 10 \mathrm{m}$	174		146	27	0

Appendix A - 2. Snail density data collected over 2000 at 0.51 - 1.0 m water depth. Class 5 Snails No. Size Class 4 Snails No. Size Class 3 Snails No. Size 113 129 118 154 50 171 34 39 48 92 94 4 92 80 Class 2 Snails No. Size 142 100 156 28 62 9 No. Snails Total 165 139 119 176 118 114 194 112 127 143 193 137 109 181 86 Quadrant $3 \times 3 \text{ m}$ 4 x 4 m 4 x 4 m $3 \times 3 \text{ m}$ $3 \times 3 \text{ m}$ 3 x 3 m 4 x 4 m 4 x 4 m 4 x 4 m 4 x 4 m 3 x 3 m $3 \times 3 m$ 4m x 4m Size 22-May-00 22-May-00 25-May-00 25-May-00 15-Jun-00 15-Jun-00 22-Jun-00 22-Jun-00 28-Jun-00 28-Jun-00 11-Jul-00 8-Jun-00 8-Jun-00 7-Jul-00 11-Jul-00 19-Jul-00 7-Jul-00 Date

Appe		A -	2. (0	cont'	d)	
No. Size	Class 5 Snails	0	0	0	0	0
No. Size	Class 4 Snails	S	∞	13	7	12
No. Size	Class 3 Snails	109	110	66	121	138
No. Size	Class 2 Snails	8	8	∞	е	4
Total	No. Snails	119	123	120	131	154
Quadrant	Size	5 x 5 m	0 x 6 m	0 x 6 m	7 x 7 m	7 x 7 m
	Date	19-Jul-00	28-Jul-00	28-Jul-00	9-Aug-00	9-Aug-00

Appendix A	- 3. Snail dens	ity data coli	lected over	2000 at > 1	m water der	oth.
S						

	Quadrant	Total	No. Size	No. Size	No. Size	No. Size
Date	Size	No. Snails	Class 2 Snails	Class 3 Snails	Class 4 Snails	Class 5 Snails
26-May-00	10 x 10 m	107	22	73	12	<u>3. Snai</u>
26-May-00	10 x 10 m	243	41	164	29	0
00 -un f-6	10 x 10 m	141	13	110	18	0
00-unf-6	10 x 10 m	119	17	92	10	0
21-Jun-00	10 x 10 m	240	∞	184	48	0
21-Jun-00	5 x 5 m	76	7	61	13	0
29-Jun-00	m 9 x 9	175	0	120	55	<u>o at ≥1</u>
29-Jun-00	0 x 6 m	188	4	131	53	0
26-Jul-00	5 x 5 m	458	0	303	153	7
26-Jul-00	5 x 5 m	451	0	282	169	0
1-Aug-00	5 x 5 m	41	0	28	13	0
1-Aug-00	10 x 10m	301	1	196	104	0

Appendix A - 4. Limnological data collected over 2000 at 0.0 - 0.5 m water depth.

	Dissolved	Chlorophyll a	
Date	Oxygen (mg/L)	(mg m ⁻²)	AFDM (mg m ⁻²)
12-May-00	9.0	6.01	197
		8.23	328
		7.12	289
12-May-00	9.6	6.18	295
		7.12	199
		6.46	297
17-May-00	10.1	5.56	297
		5.99	325
		4.87	236
17-May-00	10.2	3.73	414
		4.01	420
		4.89	302
25-May-00	10.5	3.67	412
		4.61	223
		5.33	328
25-May-00	10.2	3.88	345
		4.77	312
		4.20	419
13-Jun-00	9.1	11.12	210
		10.79	184
		12.44	249
13-Jun-00	8.9	13.49	203
		10.14	328
		9.50	236
15-Jun-00	9.2	5.66	299
		6.13	256
		7.66	256
15-Jun-00	9.4	5.95	197
		5.56	363
		6.72	266
28-Jun-00	10.6	6.78	214
		9.45	236
1		10.88	217
28-Jun-00	10.5	8.00	423
		9.45	322
		5.90	371

Appendix A - 4. (cont'd)

	Dissolved	Chlorophyll a	AFDM
Date	Oxygen (mg/L)	(mg m ⁻²)	(mg m ⁻²)
12-Jul-00	9.5	8.19	311
		9.19	298
		10.45	355
12-Jul-00	9.4	11.49	319
		12.19	362
		13.12	299
19- Jul -00	8.9	12.49	305
		12.45	217
		10.79	295
19-Jul-00	8.7	11.49	311
		12.49	229
		12.78	268
20-Jul-00	8.8	13.49	229
		14.19	399
		15.13	355
20-Jul-00	8.7	9.08	402
		10.46	312
		9.17	399
26-Jul-00	8.9	12.50	375
		12.46	299
		13.45	455
26-Jul-00	8.9	9.80	501
		12.79	411
		10.79	359
28-Jul-00	8.8	14.79	322
		13.49	401
		14.19	322
28-Jul-00	8.9	14.12	311
		14.76	455
		13.15	384
9-Aug-00	8.7	12.19	315
		13.14	236
		10.13	197
9-Aug-00	8.5	10.45	554
		11.79	442
		10.79	197

Appendix A - 5. Limnological data collected over 2000 at 0.51 -1.0 m water depth.

	Dissolved	Chlorophyll a	AFDM
Date	Oxygen (mg/L)	(mg m ⁻²)	(mg m ⁻²)
22-May-00	9.9	6.85	341
		5.96	302
		6.00	295
22-May-00	9.9	5.98	453
		6.75	105
		8.49	295
25-May-00	10.5	4.72	328
		1.65	519
		1.89	289
25-May-00	10.3	2.49	198
		2.00	221
		2.99	277
8-Jun-00	9.8	5.91	276
		7.57	249
		5.73	414
8-Jun-00	9.9	7.99	164
		8.46	256
		8.76	264
15-Jun-00	9.1	18.23	249
		19.99	236
		22.67	289
15-Jun-00	9.1	18.50	256
		16.20	247
		15.79	355
22-Jun-00	9.5	5.46	249
		6.79	374
		7.49	210
22-Jun-00	9.2	7.49	302
		8.46	210
		7.99	276
28-Jun-00	10.6	25.40	394
		20.49	256
		21.49	276
28-Jun-00	10.6	18.49	452
		19.46	352
		18.47	244

Appendix A - 5. (cont'd)

	Dissolved	Chlorophyll a	AFDM
Date	Oxygen (mg/L)	(mg m ⁻²)	(mg m ⁻²)
7-Jul-00	9.4	18.50	282
		20.49	124
		19.46	190
7-Jul-00	9.5	17.13	155
		18.19	244
		19.47	244
11-Jul-00	9.2	16.80	309
		15.49	445
		18.18	399
11 -Jul- 00	9.2	13.91	344
		17.82	257
İ		15.19	401
19-Jul-00	8.7	15.46	304
		12.50	322
		16.49	388
19-Jul-00	8.7	10.49	355
		12.79	455
		12.49	397
28-Jul-00	8.7	14.94	282
		10.79	401
		12.46	559
28-Jul-00	8.7	12.99	377
		13.99	502
		11.72	511
9-Aug-00	8.4	10.74	445
		9.79	335
		11.44	322
9-Aug-00	8.4	10.99	544
		9.45	446
		9.16	499

Appendix A - 6. Limnological data collected over 2000 at > 1 m water depth.

	Dissolved	Chlorophyll a	AFDM
Date	Oxygen (mg/L)	(mg m ⁻²)	(mg m ⁻²)
26-May-00	10.5	2.45	361
-		3.45	249
		3.15	328
26-May-00	10.2	1.91	236
		4.18	335
		3.13	177
9-Jun-00	9.2	1.57	368
		3.98	460
		3.76	295
9-Jun-00	9.1	3.78	344
		2.47	122
		3.00	344
21-Jun-00	8.9	4.12	401
		3.49	276
		4.99	249
21-Jun-00	8.7	4.98	184
		5.50	230
		5.01	440
29-Jun-00	9.4	6.12	243
		7.13	256
		7.12	266
29-Jun-00	9.5	6.18	243
		6.19	92
		6.99	276
26-Jul-00	8.6	10.13	177
		9.45	212
		8.50	217
26-Jul-00	8.6	10.92	199
		8.45	253
		7.99	288
1-Aug-00	8.7	5.13	355
_		6.47	312
		5.79	246
1-Aug-00	8.6	8.13	311
		6.45	459
		5.99	377

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