THE INFLUENCE OF FLATWORM PREDATION ON ZOOPLANKTON INHABITING SMALL PONDS

Edward J. MALY*, Stephen SCHOENHOLTZ** & Michael T. ARTS***

* Biology Dept., Concordia University, Montreal, Québec H3G 1M8; ** Rocky Mountain Laboratory, Crested Butte, Colorado 81224; *** Biology Dept., Concordia University, Montreal, Québec H3G 1M8

Received January 29, 1980

Keywords: *Mesostoma ehrenbergii, Daphnia middendorffiana,* flatworm predation, feeding rate, seepage pond

Abstract

Experiments were performed in 1977 to determine which large zooplankton in a series of high altitude ponds can be consumed by the predatory flatworm *Mesostoma ehrenbergii.* This predator consumes *Daphnia* at a high rate and the fairy shrimp *Branchinecta* at a low rate, but does not consume *Diaptomus.* Experiments were performed in 1978 and 1979 to determined the rate of predation on *Daphnia* in 30 liter tubs and to determine if predation rate is correlated with surface to volume ratio of experimental containers. There is a clear correlation between surface to volume ratio and predation rate. Determinations of *Mesostoma* and *Daphnia* densities were made in a series of eight high altitude ponds, and pond surface to volume ratios were determined. Examination of these parameters lends credence to the argument that *Mesostoma* predation affects *Daphnia* dynamics in some circumstances. The results suggest that benthic invertebrate predators may affect zooplankton dynamics, especially in shallow ponds.

Introduction

This paper examines the influence of predation by *Mesostoma ehrenbergii* on zooplankton in small pond ecosystems and presents evidence that this flatworm may in some circumstances influence the dynamics of some zooplankton.

It is fairly well established that some flatworms consume zooplankton: rhabdocoel flatworms can eat many zooplankton species (Pennak, 1978; Jennings, 1957, 1964), and triclad flatworms feed upon cladocerans when the latter are abundant (Pickavance, 1971). Reynoldson and his co-workers (see Reynoldson, 1974) have studied distribution and competitive relationships among triclads; they find that both intra- and interspecific competition regulate populations (Bellamy & Reynoldson, 1971). Although these studies suggest that triclad food supply may be limiting, feeding rates and the extent to which flatworms influence prey density are unknown.

The impact of predation on zooplankton abundance and distribution has received considerable attention in the past 15 years. Size-selective predation may alter relative abundance of zooplankton species in some situations (Hall *et al.,* 1976). Many detailed studies examine the impact of predators on cladocerans, particularly *Daphnia* species; typical interactions studied include the predators: *Chaoborus* (Dodson, 1972), *Leptodora* (Hall, 1964), *Salmo* (Galbraith, 1967) and *Alosa* (Brooks, 1968). No study reports on the possible importance of benthic invertebrate predators in affecting zooplankton populations.

Our study is designed to answer these questions: can a predatory flatworm noticeably affect zooplankton abundance, and what factors might affect flatworm feeding rate or diet?

This work was supported by NSERC grant A9883, by a grant from the Penrose Fund of the American Philosophical Society, and by a grant from the Marsh Fund of the U.S. Academy of Sciences, all to E.J.M. We thank the Nature Conservancy for setting aside ponds studied for research purposes. We thank M. J. McElhone, M. P. Maly, and numerous graduate and undergraduate students for advice and criticism.

Materials and methods

This work was carried out in ponds at Mexican Cut in western Colorado. All are seepage ponds, ranging in size from 0.01 to about 0.50 ha. Maximum depths of the ponds range between 0.2-2m in July although most are <1 m in depth. Ice clears in June or early July and water temperature rapidly rises to approximately 20°C. The altitude of the ponds is approximately 3350 m. The ponds have been the subjects of studies by Dodson (1970, 1974), Sprules (1972), and Maly (1976, 1978).

The density of the flatworm *M. ehrenbergii* was obtained in two ponds (L8 and L11) in 1978 and in 8 ponds (L6, L8,

Hydrobiologia 76, 233-240 (1980). 0018-8158/80/0763-0233$01.60.

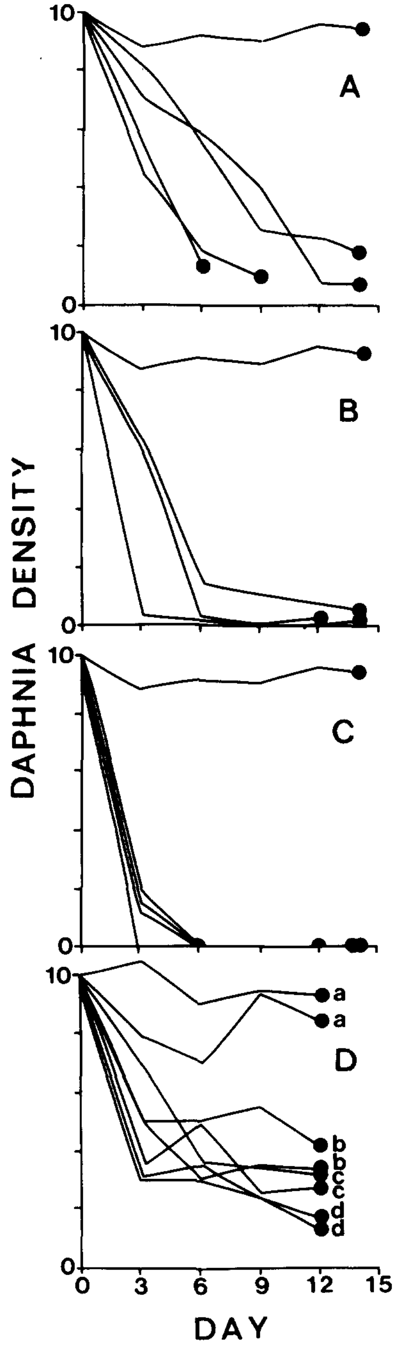

Fig. 1. *Daphnia* remaining in tub experiments after various lengths of time. In graph A, there were 20 flatworms; in B, 60 flatworms; and in C, 100 flatworms. The top line in A-C is the control. Graph D depicts the number of *Daphnia* remaining with 25 flatworms present but with different surface to volume ratios: a are controls (no flatworms), b are experiments at a surface to volume ratio of 16.67; c, at a surface to volume ratio of 17.67; and d, 19.67. The y axis is the number of *Daphnia* per liter.

L9, L10, L11, U2, U4, U5) in 1979. These were obtained by setting out 25 x 25 cm pieces of cheesecloth covered with approximately 1 cm of pond bottom detritus (gravel, silt, and decaying wood) in 1978; in 1979, 15 x 15 pieces of screen were used. These were left in ponds for 7-10 days and were then carefully lifted from the pond, complete with substrate, and placed in white enamel trays. Flatworms were removed and counted. Qualitative estimates of *M. ehrenbergii* density were obtained in 1977 by determining approximate numbers that were attracted by 'traps', plastic ice cream containers into which several 5 x 5 cm holes had been cut and which contained approximately 5 gm of pig liver.

Experiments to ascertain prey consumed by *M. ehrenbergii* were carried out in 1000 ml beakers into which were placed flatworms with various numbers of *Daphnia middendorffiana, Branchinecta coloradensis, Diaptomus shoshone*, or *Diaptomus coloradensis*. Experiments persisted 8-48 hr. Remaining prey were counted to ascertain how many were consumed by the predator. Since *Daphnia middendorffiana* was the only prey consumed at a high rate, further experiments were conducted with only this prey.

A second set of feeding experiments was carried out in situ in 1978, using tubs (75 x 60 x 37.5 cm) containing 30 l of water. The tubs had a 6 x 8.5 cm hole cut into each end; these were covered with 263 micron nylon mesh. Various members of *M. ehrenbergii* (0, 20, 60, or 100) were placed into these tubs with 300 *D. middendorffiana* and were left in pond L8 for 6-14 days. These were anchored with a rock. The tubs were sampled for prey at 3 day intervals by mixing and removing three 1 liter samples, counting the prey, and then returning these to the tubs. These were taken to determine if there was exponential disapperance of prey. All introduced predators and prey were counted on the day the experiment was terminated. In some experiments, *D. middendorffiana* offspring were also counted on the terminal day. Prey were greater than 1 mm in lenght and were reproductively mature.

A third set of feeding experiment was carried out in 1979, similar to the 1978 set, except that the surface to volume ratio of the tubs was altered by installing 30 x 15 cm or 15 x 10 cm pieces of plastic. Using these pieces of plastic, surface to volume ratios of 16.67, 17.67, 19.67, 21.67, and 30.67 (m^2 of bottom surface divided by m^3 volume) were created. The initial number of *M. ehrenbergii* was always 25, experiments all lasted 4-12 days, and the tubs were placed in L10 rather than in L8, and a rock was not used to anchor the tubs.

Mesostoma ehrenbergii feeding rates were calculated using the following formula:

$$D_t/D_o = e^{(r - ac)\,t} \tag{1}$$

where D_o and D_t are the initial and final *D. middendorffiana* densities, r is *D. middendorffiana's* rate of change in control tubs, a is predator density (per m^3 of water to facilitate comparison with ponds), t is time in days, and c is feeding rate.

Pond bottom areas and volume were calculated in eight ponds (Table 5) in mid August 1979. Transects were taken at one or two meter intervals along the longest axis of the ponds, and 10 cm depth intervals were determined. The length of each transect along the bottom of the pond was determined, and the bottom surface area between adjacent transects was determined. Surface areas were summed to give an estimate of bottom surface. The volume was determined by measuring the vertical areas bounded by the bottom and top lengths of adjacent transects and multiplying the mean of these by the distance between transects. These volumes were summed to provide an estimate of volume. Some information about pond surface to volume ratios and evaporation rates was drawn from a previous study (Maly 1976).

Daphnia middendorffiana densities were determined in 1979 by sampling with a 2.1 l Van Dorn sample bottle. Each pond was sampled on five days during a seven week period (Table 6); six samples were taken on each day, either at three locations and two depths or at two locations and three depths. Numbers of *Daphnia* were corrected by percentage of volume of ponds found at each of the two or three depths using:

$$\text{Density} = \Sigma_i x_i p_i \tag{2}$$

where x_i is the mean number of *Daphnia* at the i^{th} depth an p_i is the proportion of total volume at the i^{th} depth. The depths sampled were usually 0-20 cm, 20-40 cm, and greater than 40 cm, but the precise figures varied, dependent upon the pond profiles.

Table 1. Flatworm densities per m^2 in several ponds in 1979. The numbers in parentheses are standard errors of the mean; every value is derived from 15 x 15 cm quadrats (n = 20).

Pond	July 28-31	August 12-14	August 22-23
L6	20.0 (7.54)	48.9 (14.38)	0
L8	15.6 (9.27)	31.1 (9.17)	71.1 (13.06)
L9	0	0	0
L10	331.1 (72.12)	720.0 (27.75)	1137.8 (120.48)
L11	15.6 (6.67)	280.0 (49.17)	195.6 (43.90)
U2	408.9 (136.35)	2644.4 (328.25)	1442.2 (81.78)
U4	0	104.4 (19.69)	104.4 (24.40)
U5	117.8 (74.45)	331.1 (74.03)	337.8 (44.36)

Densities determined in 1978 were found simply by taking the mean of eight Van Dorn samples on each of five days over a six week period.

Results

Distribution and abundance

Of the ponds studies extensively at Mexican Cut (Dodson 1970, Maly 1976), *M. ehrenbergii* is found only in the shallower ponds which contain *Diaptomus shoshone, Daphnia*

Table 2. Trap record for flatworms in several Mexican Cut ponds in 1977. Symbols are as follows: 0, none found at trap; 1, 1-10 found; 2, 10-25 found; 3, over 25 found; -, not tested, D, dry pond. Multiple readings in columns indicate more than one trap.

Pond	June 24-29	July 2-6	July 24-27	August 1-8	August 12-16
L1	-	0,0	0	0	0
L5	0	0	0	0,0	-
L6	1,1	-	0	0,0	D
L8	2,3,1,3	0,0	0	0,0	D
L9	0,0	0,0	-	0,0	0,0
L10	3,3	3,2,3	-	3	3
L11	2,3,3	3,1	3	3	3
L12	0,0	0,0,0	0	-	0,0

Table 3. Percentage mortality of *Diaptomus shoshone* (DS) and *D. coloradensis* (DC) in experiments where 5-25 prey were placed in 1000 ml beakers with varying numbers of *M. ehrenbergii*. Experiments persisted approximately 48 hr.

Prey	Number of flatworms	Percent mortality	S.D.	n
DS	0	7.1	9.6	30
DS	2	3.7	5.0	31
DS	5	4.3	6.2	15
DC	0	8.5	10.5	31
DC	2	13.2	13.2	30
DC	5	14.6	12.6	12

middendorffiana, and which lack the 'axolotl' from of *Ambystoma tigrinum*. Table 1 summarizes abundance in 1979; in 1978, the density of the flatworm in L8 was found to be 91 m^{-2} (SE = 21, n = 8) and in L11, 623 m^{-2} (SE = 106, n = 11) in late July. The large standard deviations are evidence of clumping. Table 2 shows the qualitative distribution of *M. ehrenbergii* among several of the L series ponds in 1977.

Mesostoma ehrenbergii individuals are found shortly after the ice disappears from ponds in June or early July. In 1979, ice disappeared from the L series on approximately July 6 and flatworms were observed a few days later. They appear at approximately the same time that *Daphnia* appear: in 1970 and 1976, they were found on the first day that *Daphnia* were taken in plankton tows; in 1978, they were found a few days after the appearance of *Daphnia*. Early in the season, individuals tend to spend time off the bottom; one of us saw numerous flatworms in surface tension in early July 1979, and in other years (1970, 1976), they were found in plankton tows only within the first two weeks after ice disappeared from ponds. Individuals grow rapidly from 1-2 mm to 5-6 mm and become sexually mature about four weeks after their appearance. The may disappear from some ponds (Tables 1, 2); this disappearance was especially obvious in 1977 (Table 2) which was a dry year.

Experimental determination of feeding rates

Experiments (Tables 3, 4) show that *Mesostoma ehrenbergii* does not consume either *Diaptomus shoshone* or *D. coloradensis* when these prey are alive (Table 3). The flatworm might consume *Branchinecta coloradensis* at a low rate, and definitely consumes *Daphnia middendorffiana* at a high rate (Table 4).

In 1978, experiments were performed in which 3-6 mm *M. ehrenbergii* and greater than 1 mm *D. middendorffiana* persisted together in tubs for 6-14 days. These were done to determine removal rates at different flatworm densities. Figures 1a, 1b, and 1c plot surviving *D. middendorffiana* against day at flatworm densities of 0, 670, 2000, and 3333 m^{-3}. In some tubs, offspring production of the prey was determined. Offspring production in the control tub was 0.068 per adult per day, while values in the experimental tubs ranged from 0.015-0.066, with a mean of 0.042 per

Table 4. Number of *Daphnia* (D) and *Branchinecta* (B) surviving after several time intervals in experiments with *Mesostoma*.

Prey	Number of flatworms	Number surviving and S.D. after 0 hr	2 hr	4 hr	6 hr	8 hr	n
D	0	20	19.5(1.1)	15.8(2.9)	14.5(1.8)	13.9(4.2)	10
D	5	20	8.8(3.0)	4.2(2.3)	3.0(2.4)	1.6(2.6)	5
D	10	20	5.2(2.4)	2.8(2.4)	2.0(0.7)	1.0(1.2)	5
B	0	10	10	10	10	10	10
B	5	10	9.2(0.5)	9.2(0.5)	9.0(0.0)	9.0(0.0)	5
B	10	10	8.8(0.5)	8.8(0.5)	8.6(0.6)	8.6(0.6)	5

Table 5. Feeding rates calculated from tub experiments at different surface to volume ratios.

Surface/volume	Feeding rate ($\times 10^{-5}$)	Maximum error ($\times 10^{-5}$)
16.67	8.5	7.1 - 10.3
17.67	11.2	10.6 - 12.7
19.30^{a}	21.0	17.4 - 24.6^{c}
19.67	18.6	16.5 - 20.5
21.67	53.3	31.8 - 86.9
27.67	86.9	62.5 -128.5
30.67	104.1	86.9 -128.5
53.00^{b}	90.0	63.0 -117.0

a - From 1978 tub experiments
b - From experiments in Table 4
c - Standard error

adult per day.

In 1979, additional tub experiments were performed to ascertain the effect of surface to volume ratio on removal rates by a constant density (833 m^{-3}) of flatworms. Figure 1d plots the number of prey surviving in 12 day experiments. Some experiments with larger baffles were terminated on day 4, because few prey were found, but the estimates of prey remaining on day 2 are utilized below. The disappearance of *D. middendorffiana* appears to be related to surface to volume ratio.

Both 1978 and 1979 experiments were utilized to obtain a relationship between feeding rate and surface to volume ratio. In calculating feeding rate from the 1978 experiments (Equation 1), the number of *D. middendorffiana* remaining in control tubs is the mean of three replicates; the control r value obtained is -0.004 day^{-1} (equation 1). If t is the duration of the experiment in days and a is the predator density, the mean feeding rate calculated from Figs. 1a, 1b, and 1c is 21.0×10^{-5} day^{-1} (SD = 12.3×10^{-5}). The surface to volume ratio in these experiments is 19.30. The same equation was used to calculate feeding rate between day 0 and day 3, to ascertain if there was an initial high feeding rate. The value for c obtained with these numbers is 24.8×10^{-5} (SD = 16.47×10^{-5}), not much above the first estimate.

The same procedure was used to calculate feeding rates from the 1979 set of experiments. The feeding rates

Table 6. Surface areas, volumes, surface to volume ratios, *Daphnia* densities, feeding rates (c of equation 1), and theoretical rates of removal of *Daphnia* by flatworms (ac of equation 1) in several Mexican Cut ponds.

Pond	Surface (m^2)	Volume (m^3)	Surface to volume	Daphnia density ($\times 10^4 m^{-3}$)					Feeding rate ($\times 10^{-5}$)	Removal Rate		
				7/11	7/17	7/26	8/6	8/21		7/28	8/12	8/22
L6	199	71	2.82	0.72	0.54	3.34	9.43	4.57	1.20	.001	.002	0
L8	724	300	2.41	0.64	2.56	9.06	3.65	0.37	1.03	.001	.001	.002
L9	480	252	1.90	0.79	4.57	10.22	7.86	7.96	0.80	0	0	0
L10	251	77	3.27	0	0.21	0.21	2.11	4.11	1.39	.015	.033	.052
L11	177	37	4.80	3.45	0.06	4.33	9.70	25.53	2.04	.002	.027	.019
U2	520	83	6.26	0	0	0	0	0.50	2.67	.068	.442	.241
U4	884	241	3.66	0	0	0	2.16	3.11	1.56	0	.006	.006
U5	404	99	4.08	0	0.24	0.40	2.37	41.26	1.74	.008	.024	.024

calculated are shown in Table 5; the maximum possible errors are determined by calculating each experimental *D. middendorffiana* density against each control, using equation 1. An estimate of c at a surface to volume ratio of 53 was also obtained from experiments presented in Table 4.

When plotting feeding rate against surface to volume ratio, these data suggest a predator type III functional response. The feeding rate is fairly flat at high surface to volume ratios presumably because flatworms are limited by satiation. The feeding rate is low at low surface to volume ratios, presumably because prey are generally unavailable to the predator. We postulate that the curve passes through the origin because there must be some chance collision of predator and prey, resulting in prey capture, even at extremely low surface to volume ratios.

Predation in natural conditions

In this section, results from the feeding rate experiments (Table 5) are combined with field estimates of density (Table 1, Table 6) to determine if *M. ehrenbergii* predation could affect *D. middendorfinna* densities.

Table 6 summarizes information on surface to volume ratios of eight ponds, and presents information on *D. middendorffiana* densities calculated according to equation 2.

Let us assume that *M. ehrenbergii* feeding rate increases linearly from 0 at a surface to volume ratio of 0 to 7.1×10^{-5} (Table 5) at a surface to volume ratio of 16.67. The value of 7.1×10^{-5} is the most conservative estimate of feeding rate at this surface to volume ratio. The effective rate of reduction of the prey population by the predator population (ac of equation 1) is then calculated using flatworm densities from Table 1 converted to number per cubic meter and surface to volume ratios in Table 6. These values are shown in Table 6.

The removal rates calculated suggest that the existence of *D. middendorffiana* is precarious in U2 and that the population in L10 might be affected by flatworms. Examination of *D. middendorffiana* densities in Table 6 tends to confirm this prediction – the peak densities in these ponds are 5-30% of those found in several other ponds. (The *Daphnia* density in U4 is also low, but is connected to U5 by a fairly substantial stream, and both predator and prey populations are probably immigrants from U5.)

There might be some impact of flatworm predation in ponds U5 and L11, but the affect is probably masked by high evaporation rates in these (Maly 1976). We return to this issue in the Discussion. However, in 1978, L11 had a flatworm density of 623 m^{-2} in late July, and in that year, the maximum *D. middendorffiana* density observed was 1.82×10^4 m^{-3}.

There is some evidence which suggests that *M. ehrenbergii* may be more effective than suspected on the basis of the above calculations; they may be attracted to congregations of *D. middendorffiana*. Cage experiments were performed in 1976 for another purpose; zooplankton was placed in cages at approximately triple the pond densities measured. *Mesostoma* were able to invade several of these 1.7 liter cages which were suspended near the surface of pond L8 by a styrofoam float and anchored to the bottom by a single string. Thirty-five of 84 cages contained *D. middendorffiana* (41% of the cages); *M. ehrenbergii* invaded 13 of the 84 cages (15%). But 10 of the 13 cages invaded contained *D. middendorffiana* A total of 23 flatworms invaded cages, and 20 of the 23 invasions were into cages with *D. middendorffiana*. Possibly this flatworm is attracted to high prey concentrations; they certainly were attracted to pig liver used in traps (Table 2).

Discussion

These results suggest that predation by *M. ehrenbergii* may be an important influence on *Daphnia* populations in ponds that have a high surface to volume ratio and a moderately high (over 2-300 m^{-2}) flatworm density. Predation by those or other predatory flatworms might be commonplace; there are numerous kinds of small lakes, including kettle lakes, cryogenic lakes, and solution lakes in limestone (Hutchinson 1967) and flatworms can be fairly abundant in small bodies of water (Young 1970, 1973, Mack-Fira 1974, Mitchell 1974, Pennak 1978). V. J. Dodson (pers. comm.) suspects that a flatworm may exert influence on zooplankton in tundra ponds. Any effect of these predators would be insignificant in larger lakes, unless both predators and prey are restricted to small sections of these lakes for other reasons.

Our calculations demonstrate only that predation by *M. ehrenbergii* might influence *Daphnia* dynamics; numerous other factors, such as predation by other organisms, mortality, natality, increases in density due to pond evaporation, must be quantified before the degree of impact can be ascertained. In 1976, peak population densities in ponds L8, L9, and L11 were 12.5, 12.0, and 2.5×10^4 m^{-3} respectively; clutches of *Daphnia* from several individuals in these ponds are: L8, 3.00 (SD = 1.05), L9, 3.09 (SD = 1.81), and L11, 5.60 (SD = 2.27). The clutches in pond L11 tend to be higher (although not significantly higher), suggesting that something other than natality is holding this population in check. Other predators are numerous in some ponds, especially the L series: *Diaptomus shoshone, Ambystoma tigrinum* tadpoles, several dytiscids, and these could affect population size of *D. middendorffiana* dramatically. The tadpoles feeding rate could be governed by factors similar to those governing flatworm feeding rate, since both tend to remain on the bottom.

Our results suggest that evaporation can play a significont role in affecting plankton density, especially in small seepage ponds where snowmelt and rainfall are major sources of water. For instance, pond L11 has an evaporation rate which increases from about 1% per day to 7% per day as the pond becomes smaller (Maly 1976). Such high evaporation rates late in the season might give the appearance that population size in a pond is increasing rapidly (Such as those found in U5 and L11 in 1979) even when a substantial number of individuals have formed ephippia and predation rate by various predators may be high. Increases in density due to evaporation might also lead to a considerable amount of inter- or intraspecific competition on occasion.

Hall *et al.* (1976) review invertebrate predators commonly believed to affect zooplankton; they include *Chaoborus, Mesocyclops, Epishura, Leptodora,* and some other copepod species. These invertebrates are small zooplankters quite unlike *Mesostoma. Mesostoma* can be attracted in large numbers to a food source, and can produce mucous capable of entrapping prey. Thus, it is probably not a tactile mechanism which results in predators finding prey (Dodson 1974); it appears that flatworms are attracted by chemical substances.

We were not able to determine why *M. ehrenbergii* did not eat any living diaptomid. Perhaps, since copepods are more powerful swimmers than cladocerans, they may be able to move away from disturbance more quickly (Lehman 1977) and they may be able to free themselves from mucous with relative ease. From the laboratory experiments (Tables 3, 4), it is clear that one of the major mechanism for entrapping prey was through the production of mucous.

Summary

Experiments performed in 1977 reveal that the predatory flatworm, *Mesostoma ehrenbergii,* consumes *Daphnia middendorffiana* in laboratory beakers, might consume *Branchinecta coloradensis,* and does not consume either *Diaptomus shoshone* or *D. coloradensis.* Experiments performed in 30 liter tubs show that *Daphnia* can be eliminated by the flatworm; experiments performed in 1979 show that the rate of consumption by *M. ehrenbergii* is dependent upon the surface to volume ratio of the experimental container. The 1978 and 1979 experiments are utilized to obtain estimates of *M. ehrenbergii* feeding rate.

Determinations of *M. ehrenbergii* density were made in eight ponds in 1979 and in two ponds in 1978. Densities may be as high as 2644 m^{-2}. Determinations of *D. middendorffiana* densities were also made, and pond surface to volume ratios were calculated. Utilizing feeding rates determined from experiments, it is shown that predation by the flatworm may account for low *D. middendorffiana* densities in at least two of the ponds studied.

Results also show that *M. ehrenbergii* may be attracted to regions of high prey density. The results suggest that benthic invertebrate predators may often affect zooplankton dynamics in small ponds.

References

Bellamy, L. S. & Reynoldson, T. B. 1971. Intraspecific competition in lake-dwelling triclads in a laboratory study. Oikos 22: 315-328.

Brooks, J. L. 1968. The effects of prey size selection by lake planktivores. Syst. Zool. 17: 272-291.

Dodson, S. I. 1970. Complementary feeding niches sustained by size selective predation. Limnol. Oceanogr. 15: 131-137.

Dodson, S. I. 1972. Mortality in a population of Daphnia rosea. Ecology 53: 1011-1023.

Dodson, S. I. 1974. Zooplankton competition and predation: an experimental test of the size-efficiency hypothesis. Ecology 55: 605-613.

Edmondson, W. T. (ed.) 1959. Freshwater Biology. Second edition. Wiley. 1248 pp.

Galbraith, M. G. 1967. Size-selective predation on Daphnia by rainbow trout and yellow perch. Am. Fish. Soc. Trans. 96: 1-10.

Hall, D. J. 1964. An experimental approach to the dynamics of a natural population of Daphnia galeata mendotae. Ecology 45: 94-112.

Hall, D. J., Threlkeld, S. T., Burns, C. W. & Crowley, P. H. 1976. The size-efficiency hypothesis and the size structure of zooplankton communities. Ann. Rev. Ecol. Syst. 7: 177-208.

Hutchinson, G. E. 1967. A treatise on limnology II. Wiley. 1115 pp.

Jennings, J. B. 1957. Studies on feeding, digestion and food storage in free-living flatworms. Biol. Bull. 112: 63-80.

Jennings, J. B. 1974. Digestive physiology of the Turbellaria. pp. 173-197 in: Riser, N.W. & M. P. Morse (eds.) Biology of the Turbellaria. McGrow Hill. 530 pp.

Lehman, J. T. 1977. On calculating drag characteristics for decelerating zooplankton. Limnol. Oceanogr. 22: 170-172.

Mack-Fira, V. 1974. The Turbellarian fauna of the Romanian littoral waters of the Black Sea. pp. 248-290 in: Riser, N. W. & M. P. Morse (eds) Biology of the Turbellaria. McGraw Hill. 530 pp.

Maly, E. J. 1976. Resource overlap between co-occurring copepods: effects of predation and environmental fluctuation. Canadian J. Zool. 54: 933-940.

Maly, E. J. 1978. Some factors influencing size of Diaptomus shoshone. Limnol. Oceanogr. 23: 835-837.

Mitchell, R. W. 1974. The cave-adapted flatworms of Texas; systematics, natural history, and responses to light and temperature. pp. 402-430 in:Riser, N. W. & M. P. Morse (eds.) Biology of the Turbellaria. McGraw Hill 530 pp.

Pennak, R. W. 1978. Fresh-water invertebrates of the United States. (Second editon) Wiley. 803 pp.

Pickavance, J. R. 1971. The diet of the immigrant planarian D. tigrina in the field. J. Anim. Ecol. 40: 637-650.

Reynoldson, T. B. 1974. Ecological separation of British triclads (Turbellaria) with a comment on two American species. pp. 213-228 in: Riser, N. W. & M. P. Morse (eds.) Biology of the Turbellaria. McGraw Hill. 530 pp.

Sprules, W. G. 1972. Effects of size-selective predation and food competition on high altitude zooplankton communities. Ecology 53: 375-386.

Young, J. O. 1970. British and Irish freshwater Microturbellaria: historical records, new records and a key for their identification. Arch. Hydrobiol. 72: 333-355.

Young, J. O. 1973. The occurrence of Microturbellaria in some British lakes of diverse chemical content. Arch. Hydrobiol. 75: 202-224.