

Vertical migration of microcrustacea (Cladocera) in Long Lake, Gogebic County, Michigan

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Abstract. Vertical migration was monitored this summer for a full day in a two h. interval on Daphnids (fine-scale study) and five days, twice daily (long-term study) among three species in Long Lake. *Daphnia pulex* and *D. rosea* migrated significantly for the first four sampling periods, but the last day the migration was not significant. The difference between the mean modal depth of *Daphnia pulex* and *D. rosea* was not significant in any of the five sampling periods. The migration of *Holopedium gibberum* was not significant in any of the five sampling periods.

Introduction

Vertical migration of zooplankton is a widespread phenomenon occurring in oceans as well as in freshwater lakes, and involving a large number of zooplankton species (Enright, 1977). Most organisms perform nocturnal migration, migrating to the surface at night and back to deep water during the day. Variations include reversed migration, where the movement is the opposite (up at day, down at night), or a twilight migration where the organisms move upward at dusk and sunset and descend at midday and midnight (Hutchinson, 1967). There are some species that do not migrate at all, others start migrating after reaching a particular developmental stage and others that migrate only during particular seasons of the year (Hutchinson, 1967).

Many hypotheses have been proposed to explain the ultimate causes of this phenomenon. The major ones are: the energetic hypothesis (McLaren, 1974), the algal quality hypothesis (Enright, 1977) and the predation avoidance hypothesis (Hutchinson, 1967; Zaret and Suffern, 1976). McLaren showed that in cold waters the development rate (change from egg to adult) of copepods decreased while their growth (body length) increase. As length increases, fecundity increases with it. Therefore, organisms that migrate should have a greater chance to proliferate and persist.

The algal quality hypothesis (Enright, 1977) is a metabolic model that states that nighttime grazing by herbivores, coupled with vertical migration could, under a certain range of conditions, permit grazing zooplankton to obtain a greater net gain in energy for growth and reproduction than could be obtained by continuous feeding in warm waters.

The predation avoidance hypothesis (Hutchinson, 1967; Zaret and Suffern, 1976), states that upward migration enables more abundant food resources in the upper strata of water to be exploited at night, while predators can be avoided during the day by descent to depths where the light intensity is too low for planktivorous fishes to see prey items.

This work was done to characterize vertical migration among the cladocerans in this lake. The major focus was on the migration differences between *Daphnia rosea* and *D. pulex*. The migratory behavior of *Holopedium gibberum* was also analyzed. Nocturnal migration was commonly performed by *Daphnia rosea* and *D. pulex* and the extent of migration was the same for the two species. *Holopedium gibberum* performed significant vertical migration on only one occasion out of five.

Materials and methods

Fine-scale study

The study was conducted during summer 1988 on Long Lake, a moderately stained seepage kettle lake at the University of Notre Dame Environmental Research Center, T45N R42W, Gogebic Co., MI. The depth below which few crustacean zooplankton occurred was determined over the deepest part of the west basin on June 1 at midday by making progressively deeper casts with a 28-L Schindler-Patalas trap equipped with an 125- μ m mesh plankton net. The zooplankton composition of the pelagic zone of the lake was determined from samples taken on June 7 with a 125- μ m mesh plankton net at midday. Two horizontal and two vertical tows were made. Horizontal tows were done at three and six meters; the length of these tows was about ten meters. The vertical tows were made in the deepest part of the basin from thirteen meters to the surface. Zooplankton composition was determined using a dissecting microscope; animals that required greater magnification to be identified to species were removed from the dissecting microscope to an inverted microscope where they could be differentiated.

Sampling was performed on June 8 by eight people. Samples were collected over the deepest part of the west basin at two different stations 4 m apart along a cross-lake transect line.

Samples from 0800 to 1800 h. were collected at 2-h. intervals with duplicate casts of a 12-L Schindler-Patalas trap; samples from 2000 to 0800 h. were collected with single casts of a 28-L Schindler-Patalas trap. Each station was sampled at 0.25, 1, 3, 6, 9 and 12 meters and samples were immediately preserved in buffered sugared formalin for later analysis.

Chaoborids and daphnids were counted by the same eight people, using a dissecting microscope (7 x). Samples containing more than 600 individual zooplankters were subsampled. Subsampling was accomplished by pouring the sample into a 100 ml graduated cylinder and adding water. The sample was evenly distributed by swirling and a fraction poured off into a square counting dish. Zooplankters in this fraction were counted and the resulting number was multiplied by the dilution factor (the reciprocal of the dilution volume divided by the total volume of the cylinder).

Long-term study

This study was done on June 10 and 21, and on July 1, 21 and 30, twice daily (at midday and midnight) and sampling was completed within 1.5 h. Samples were collected with single casts of a 28-L Schindler-Patalas trap at three different stations 2 m apart along the same cross-lake transect line of the fine-scale study. Each station was sampled at the previously mentioned depths and samples were immediately preserved in buffered sugared formalin for later analysis.

The cladocerans *Daphnia pulex*, *D. rosea* and *Holopedium gibberum* were chosen from among the other microcrustacea--rotifers and copepods--because they were easily identifiable and were known to undergo migration in nearby lakes (Dini and Carpenter, 1988). Samples containing about 600 individual cladocerans were subsampled as previously described.

Student's t-test was used to determine if the migrations of the individual species were significant, as well as to compare differences in migration between the three species. Tests were conducted using two measures representing the central tendency of the population at each sampling session: mean average depth (MAD) and mean modal depth (MMD) of the population. These were calculated from vertical profiles constructed for each of the three horizontal stations. Because of problems with replicates in the last two sampling periods, MAD could only be

determined for the first three sampling periods whereas MMD could be determined on all sampling periods. The results given by MMD for the first three sampling periods were identical to those that MAD gave, so I have assumed that I can rely on only MMD to characterize migrations on the last two sampling periods.

Results

Fine-scale study

Vertical migration of daphnids was very strong on the day of the fine-scale study, performing a typical nocturnal vertical migration (Fig. 3). At 0 and 1 m depths, there were no daphnids between 0800 and 1800 h. At 6, 9 and 12 m the proportion of daphnids remained constant during the full 24 h period (except for 6 m at 0400 h) suggesting some non-migrating organisms or some organisms migrating up, while others migrated down. The first sign of an organized migration was a peak of daphnids at 1600 h at 3 m suggesting ascent. The next major peak of daphnids occurred at midnight at 0 and 1 m--the highest percentage of daphnids found during the study period. In addition, at 0200 h a peak of daphnids was found at 3 m and at 0400 h another peak of daphnids occurred at 6 m suggesting descent by the group well before any possible stimulus from increasing light levels.

Chaoborids showed a normal nocturnal vertical migration (Fig. 3). The major clusters were found at 0, 1 and 3 m during the night (2200 to 0200 h) being absent during the rest of the time at these depths. At 6, 9 and 12 m there was a constant number of organisms, also suggesting that some organisms of this population were not migrating vertically or some organisms migrating up, while others migrated down.

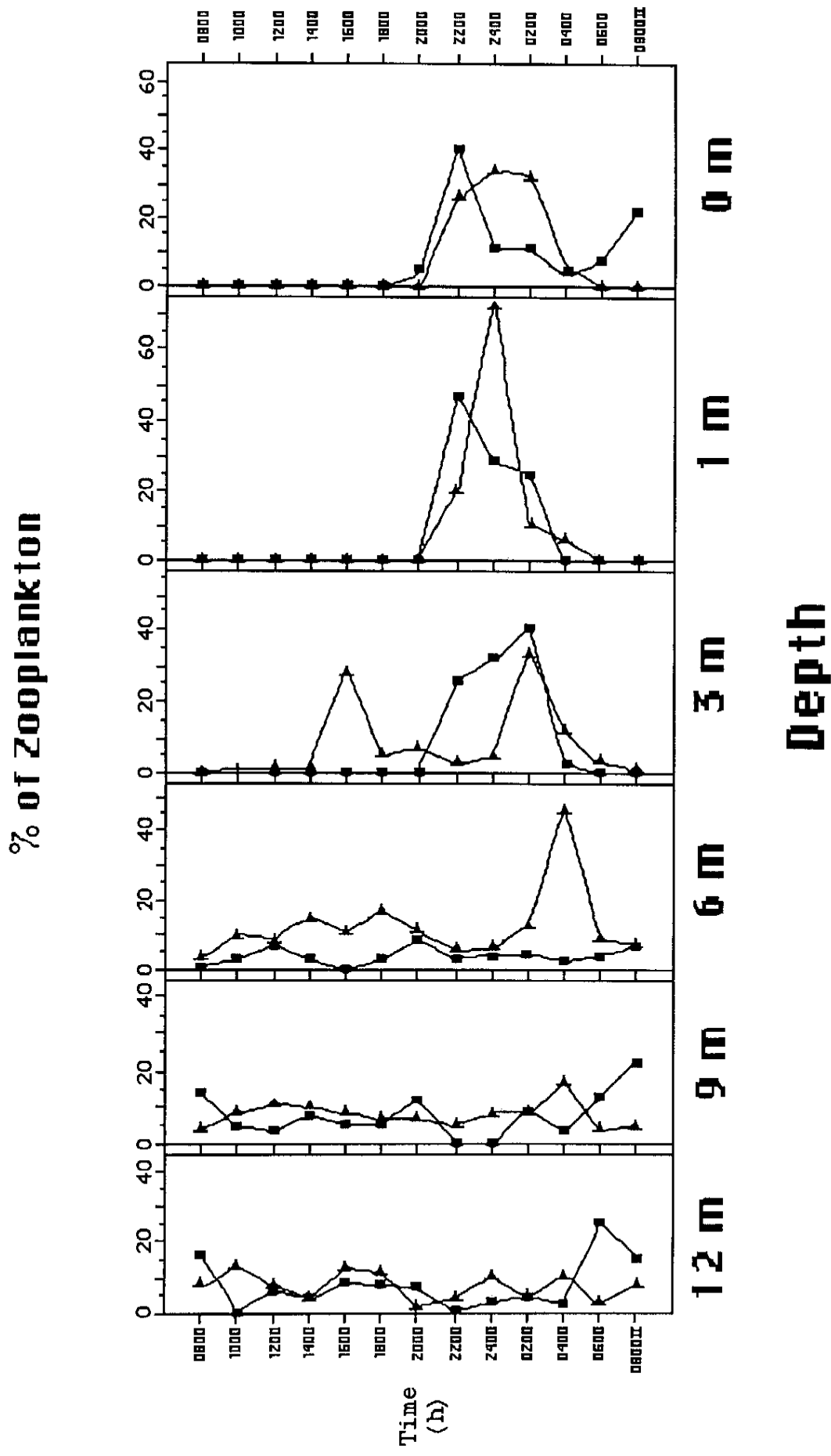


Fig. 3 % of Zooplankton collected at each sampling session (top axis), depth (bottom axis), time of day (vertical axis), Dephrids (\blacktriangle) and Cheoborids (\blacksquare).

Long-term study

Diel vertical migration was significant ($p < 0.05$) over the first four sampling periods (June 10, 21 and July 1, 21) for *Daphnia pulex* and *D. rosea* (Fig. 1). On the last sampling period (July 30), the migration of neither daphnid species was significant. The vertical migration of *Holopedium gibberum* was only significant on the first sampling period (Fig. 1).

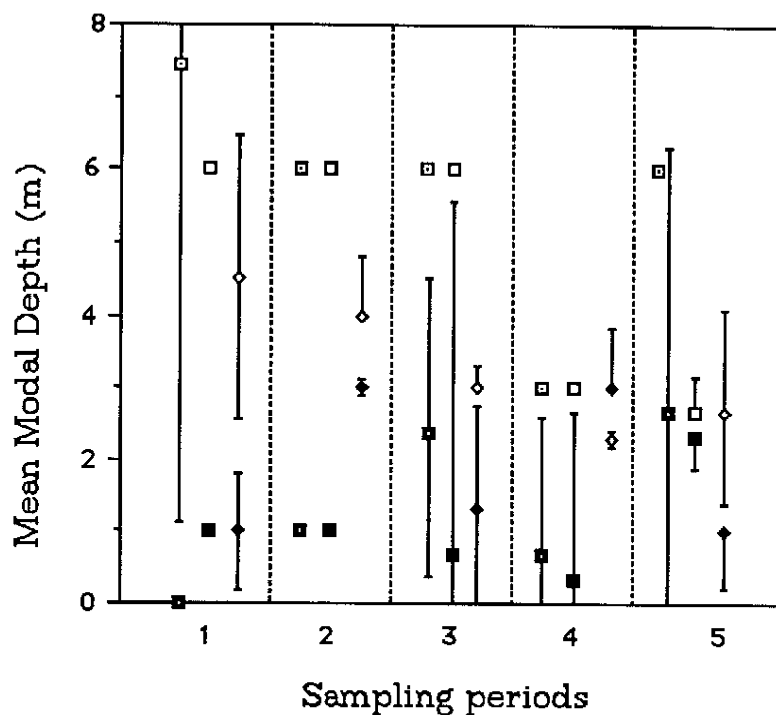


Fig. 1. Mean modal depth (in meters) between midday (open symbols) and midnight (shaded symbols) on the five days sampled. *Daphnia rosea* = square with dot, *D. pulex* = simple square and *Holopedium gibberum* = diamond, between 95% confidence intervals.

The difference between the vertical migration of *Daphnia pulex* and *D. rosea* was not significant on any of the five sampling periods as indicated by the overlap of the 95% confidence intervals. The amplitude of the vertical migration in both daphnid species declined significantly as summer progressed (Fig. 2).

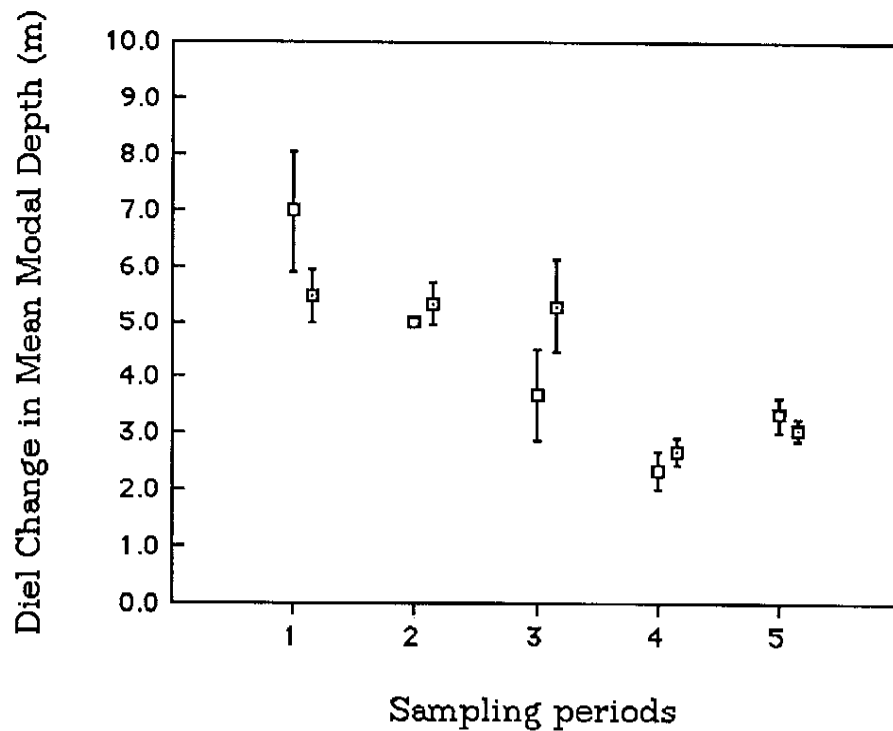


Fig. 2. Difference in mean modal depth (m) between midday and midnight on the five sampling periods between 95% confidence intervals. Symbols same as in Fig. 1.

Discussion

In the fine-scale study, several questions can be raised according to the ascent and descent performed by daphnids. Why was the descent better defined than the ascent? An explanation for this could be that the stimuli that controlled the descent were stronger than the ones acting on the ascent. Another important fact was the way the mode dropped (descent) between 2400 and 0400 h. Many explanations could be proposed to explain it. The lunar cycle could be influencing it, but no correlation was found between phase of the moon and timing of migration on the day sampled. Another explanation could be satiation (Pearre, Jr., 1979). After grazing for 4 h in the epilimnion where food quality and often food quantity are higher than at other depths (Stich and Lampert, 1981), daphnids migrated to deep waters after being satiated, independent of other factors. Finally, an internal clock could be setting a particular time for the descent of chaoborids probably

stayed at 0, 1 and 3 m to prey on the smaller daphnids at these depths. There is evidence that small daphnids do not perform vertical migration (Dini *et al.*, 1987), staying at the depths mentioned above. An optimal depth for chaoborids that can only prey on the small daphnids.

The results of the long-term study for daphnids could be explained by a decrease in the size structure of the population. The amplitude of migration by small daphnids is less than that of larger ones (Hutchinson, 1967; Dini *et al.*, 1987) which might explain the observed decrease in the vertical migration. As summer passes by, the predation of the new year classes of yellow perch as well as of small and largemouth bass (zooplanktivorous stage) increases (S.R. Carpenter, pers. comm.). They eat the larger *Daphnia* (Keast, 1985), so the smaller ones remain, resulting in a decrease in the size structure of the population (Brooks and Dodson, 1965). Unfortunately, there are no data available yet on the size structure of Long Lake daphnids over this time.

Another explanation for the decline in migratory amplitude could be a change in the food content of the lake. One hypothesis states that if the food supply is too low, zooplankton will not migrate because, to avoid starvation, they need to spend all of their time feeding in the (relatively) food-rich surface waters. They do not have the luxury of migrating (Johnsen and Jakobsen, 1987). A second hypothesis claims that if food is high, zooplankton does not migrate because energy is available to compensate, through increased rate of reproduction, the loss that would occur by predation during the day (Geller, 1986). Another hypothesis proposes that there is no necessity to pay the energetic costs of vertical migration when food is well distributed throughout the water column (Pijanowska and Dawidowicz, 1987), therefore, vertical migration is not necessary. Unfortunately, there are no data available yet on the quantity and food distribution in Long lake to evaluate the certainty of these hypothesis.

An explanation for the results of *Holopedium gibberum* could be due to the migration type that *Holopedium gibberum* presents. *Holopedium gibberum* tends to migrate horizontally. These zooplankters aggregate into patches that move horizontally from low food areas to rich ones (Tessier, 1983). If the low food availability hypothesis has any merit, vertical migration may not

be necessary for this species to avoid starvation since horizontal migration continually introduces them to unexploited algal resources.

There is a strong genetic component to vertical migration in natural *Daphnia* populations. Not only different species (Stich and Lampert, 1981), but different clones can have different migratory behaviors (Weider, 1984). These two species seemed to have the same genetic constellation controlling vertical migration in this lake at this time. Due to the fact that *Daphnia pulex* and *D. rosea* usually co-occur (Brooks, 1957), they are subjected to many of the same pressures from the environment, similar pressures thereby resulting in similar migratory behavior.

This study created more questions than answers. A way to solve some of these questions would be to correlate the distribution of food throughout the water column with vertical migration. Chlorophyll would be measured throughout the water column and a gut fullness analysis would be done in some organisms to determine how much food they eat. Another way would be to monitor the size structure of the zooplankton population as the summer progresses.

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Appendix-1

Stations: E for "east", M for "middle" and W for "west".

Species: R for *Daphnia rosea*, P for *Daphnia pulex* and H for *Holopedium gibberum*.

Numbers in organisms found per 28-L Schindler-Patalas trap, and "-" represents sample lost.

										6/10/88											
										1200			2400			1200			2400		
Stations:	E			M			W			E			M			W					
Species:	R	P	H	R	P	H	R	P	H	R	P	H	R	P	H	R	P	H			
D 0m	0	0	0	0	1	0	0	1	0	-	-	6	43	186	6	36	69	2			
E 1m	0	0	0	0	0	0	0	0	0	-	-	6	36	165	3	43	91	14			
P 3m	0	0	1	0	0	2	0	0	1	-	-	3	18	21	6	23	13	0			
T 6m	2	4	0	15	120	6	2	14	1	-	-	1	2	8	0	7	11	0			
H 9m	6	5	0	13	2	0	10	10	0	0	0	2	6	7	1	2	5	5			
12m	-	-	-	0	1	0	0	3	0	-	-	-	28	8	0	0	7	1			
										6/21/88											
										1200			2400			1200			2400		
Stations:	E			M			W			E			M			W					
Species:	R	P	H	R	P	H	R	P	H	R	P	H	R	P	H	R	P	H			
D 0m	0	0	1	0	0	0	0	0	0	-	-	-	57	48	6	48	36	0			
E 1m	0	1	2	0	0	0	0	0	1	129	84	3	96	66	0	69	63	0			
P 3m	0	1	0	0	0	16	0	0	17	12	12	4	10	3	71	11	9	17			
T 6m	6	3	11	5	6	0	7	11	0	0	0	0	1	3	0	1	4	2			
H 9m	0	0	1	1	1	2	3	3	0	5	4	1	2	1	1	2	1	1			
12m	1	2	1	4	1	2	3	2	0	5	2	1	1	0	0	1	0	0			
										7/01/88											
										1200			2400			1200			2400		
Stations:	E			M			W			E			M			W					
Species:	R	P	H	R	P	H	R	P	H	R	P	H	R	P	H	R	P	H			
D 0m	0	0	1	0	2	0	0	1	1	72.5	60	0	107.5	62.5	14.5	125	95	10			
E 1m	0	0	0	0	0	4	1	2	1	85	65	0	215	105	7	130	110	18			
P 3m	1	1	24	1	0	16	3	4	6	86.6	38.3	5	47.5	10	0	180	60	2			
T 6m	90	45	0	132	39	0	108	66	0	6	12	2	6	4	0	9	3	0			
H 9m	7	4	5	19	17	2	5	6	1	4	3	1	12	9	2	11	8	0			
12m	10	8	1	12	19	0	1	1	2	5	0	0	12	11	0	5	1	0			
										7/21/88											
										1200			2400			1200			2400		
Stations:	E			M			W			E			M			W					
Species:	R	P	H	R	P	H	R	P	H	R	P	H	R	P	H	R	P	H			
D 0m	-	-	-	3	3	19	-	-	-	345	200	22	210	95	46	195	90	20			
E 1m	3	2	34	3	1	127	4	1	33	325	185	13	220	85	25	365	115	26			
P 3m	54	39	60	57	17	20	138	24	99	168	9	110	110	25	48	150	5	48			
T 6m	11	1	8	30	0	12	18	2	9	15	4	-	15	1	8	16	4	3			
H 9m	3	1	6	11	5	13	24	4	40	11	4	33	17	10	20	17	4	32			
12m	7	3	5	4	5	3	48	17	36	6	4	6	65	29	29	6	3	7			
										7/30/88											
										1200			2400			1200			2400		
Stations:	E			M			W			E			M			W					
Species:	R	P	H	R	P	H	R	P	H	R	P	H	R	P	H	R	P	H			
D 0m	5	6	7	3	8	4	16	24	11	110	270	60	130	290	105	-	-	-			
E 1m	36	60	50	22	52	24	21	21	42	190	740	10	210	360	60	175	505	35			
P 3m	24	27	3	57	132	6	55	105	15	57	48	35	-	-	-	171	485	60			
T 6m	90	24	18	114	6	30	63	6	9	282	750	48	54	39	21	10	24	2			
H 9m	10	24	0	18	27	1	52	24	4	27	38	4	34	32	6	30	51	9			
12m	7	2	1	36	16	8	29	17	7	34	65	7	2	7	4	24	60	6			

Appendix-2

Stations: E for "east", W for "west".

Zooplankton: C for Chaoborids, D for Daphnids.

Numbers in organisms found per Schindler-Patalas trap, and "-" represents sample lost.

* half of this sample was not collected due to problems with the 12-L Schindler-Patalas.

Stations:	Depth												
	0 m		1 m		3 m		6 m		9 m		12 m		
	E	W	E	W	E	W	E	W	E	W	E	W	
800	C	0	0	0	0	0	0	1	0	11	9	4	5
	D	1	2	0	0	11	6	30	51	19	17	32	15
1000	C	8	0	0	0	0	0	0	2	3	3	0	1
	D	0	3	1	0	60	6	172	79	41	40	46	27
1200	C	0	-	0	-	0	0	2	3	2	2	16	1
	D	0	-	0	-	48	6	124	97	37	75	17	25
1400	C	0	-	0	-	0	0	0	2	7	2	9	4
	D	0	-	0	-	54	17	155	244	76	30	18	4
1600	C	0	0	0	0	0	0	0	0	2	4	16	5
	D	0	0	0	1	115	30	155	119	46	36	29	37
1800	C	0	*	0	-	0	-	1	-	3	-	10	-
	D	2	-	0	-	120	-	226	-	34	-	30	-
2000	C	0	1	0	0	-	0	3	3	9	7	10	8
	D	0	1	1	0	-	192	120	143	50	18	3	7
2200	C	0	11	10	5	35	26	1	1	0	0	1	-
	D	515	400	410	276	15	87	83	69	25	25	11	-
2400	C	1	2	2	7	31	48	1	3	0	0	6	2
	D	960	220	1480	668	165	53	61	30	48	34	27	28
200	C	1	2	-	4	53	46	1	8	4	7	9	4
	D	410	713	-	160	71	99	64	55	62	18	18	4
400	C	1	0	0	0	4	1	8	25	2	-	3	3
	D	197	9	154	27	305	295	42	19	84	-	47	8
600	C	1	1	0	0	0	0	3	3	9	7	-	35
	D	2	1	0	2	84	54	60	41	17	23	-	8
800II	C	6	0	0	0	0	0	1	4	14	-	20	-
	D		0	3	0	1	48	45	134	29	23	-	20