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Diurnal Vertical Migration Patterns of *Leptodora kindtii* (FOCKE) (Crustacea: Cladocera) in a Shallow Eutrophic Reservoir

Contents

1. Introduction

In 1933 SEBESTYEN provided the first quantitative evidence of a daily vertical migration pattern for *Leptodora kindtii* (FOCKE). Other workers, although not specifically involved in determining the precise pattern of vertical movements, have provided further records of diurnal migrations. (ANDREWS, 1948; MORDUKHAI-BOLTOVSKAIA, 1956; HALL, 1959; CHEREMISOVA, 1960). SEBESTYEN reported (1960) that a "definite diurnal vertical migration" occurred in *Lepto dora* populations, but did not detail the pattern.

During an intensive four-year sampling (1965—1968) of Sanctuary Lake (Crawford Co., Pa.), differences were encountered in *Leptodora* population densities at various depths, demonstrating a vertical migration pattern for this predaceous zooplankter. Sanctuary Lake is a 1,000 hectare body of water which is a highly productive eutrophic lake forming an eastern armlike extension of an artificial impoundment known as Pymatuning Reservoir. Sanctuary Lake has a maximum depth of three meters, but most of the flatbottomed basin is two meters or less. Because of this shallow and rather uniform morphometry, physical-chemical conditions are quite homogeneous during ice-free periods (CUMMINS et al., 1969).

Preliminary investigation showed the general pattern of diurnal migration to be one in which more individuals were found at the surface during the evening and early morning while lesser numbers were observed at the surface after midmorning and in the afternoon. A difference in vertical movements between the smaller and larger animals was also observed.

2. Methods

Specific details regarding the exact patterns of migration in Sanctuary Lake were obtained for selected sampling periods. These special collections included:

(1) a preliminary 24-hour study consisting of collections taken every two hours at three depths (surface, 0.5 and 1.0 meter);
(2) a 21-hour study in which three samples each were obtained every three hours from the three depths (Aug. 23—24, 1965);
(3) a six-day sampling period in which three samples were taken from each of the three depths every six hours for a total of 216 collections (Aug. 2—7, 1965); and,
(4) a surface-only collection over a period of 16 hours involving daylight samples every two hours and including samples one hour after sunset (Aug. 23, 1966).

For these studies the data obtained, either as actual counts or converted to numbers per liter, were analyzed by various means. Because of the large amount of data to be processed, results were analyzed by computer programming. This was done, not only to obtain output concerning a vertical migrational pattern, but also to provide information relative to pattern differences between nonegg-bearing young females (2—5 mm) and egg-bearing females (6—12 mm). Size class data were based on the measurement of 3,871 individuals; these provided the relative percent size class composition for each collection of each day and depth for the entire period.

All samples were obtained with a 0.3 meter diameter, no. 000 mesh (1.024 mm) net which was mounted on a rod and towed a marked distance of 90 meters at a fixed depth. Continuous temperature and light records were also kept during sampling periods in order to correlate their possible roles with the diurnal migratory activity.

3. Results

Table 1 shows changes in relative numbers of *Leptodora* over a 21-hour sampling period with counts made of animals taken during replicate tows entered at the designated times. It can be seen that significant changes in the relative percent at a given depth did occur with time.

Changes at the surface were of much greater magnitude than either the 0.5 or 1.0 meter depths. An analysis of variance of *Leptodora* counts made at time intervals of three hours over this 21-hour period showed that highly significant differences existed at the three depths when the effect of time was considered. Variance analysis yielded highly significant F values for all depths, especially those counts made from surface tows. (F: Surface $= 303.3$, $0.5\,M = 6.3$, $1.0\,M = 6.3$).

The relative percentage of animals collected at the surface, 0.5 and 1.0 meter depths over a six-day period (Aug. 2—8, 1965) are shown in Table 2. The changes in the percent of animals present at the three depths every six hours are listed for each day. Changes at 0.5 m and 1.0 m levels were rather uniform while those at the surface were much more variable. Four of the six dates show lowest population densities at the surface at noon. On the two dates when surface numbers were quite high, August 2 and 4, the day was overcast. This is substantiated by the measurements of total incident solar radiation for the dates (Belfort recording pyrheliometer, Belfort Inst. Co., Baltimore, Md.; sensitivity 3800—7200 Å). The values (gram calories/cm^2/day) were as follows: Aug. 2, 323.5; Aug. 3, 1738.9; Aug. 4, 525.7; Aug. 5, 1779.4; Aug. 6, 1213.2; Aug. 7, 1415.4.

Table 1. Changes in the relative numbers of *Leptodora* over a 21-hour period; August 23—24, 1965

Time	Total Collection (3 replicate tows)	Mean ± SD (3 replicate tows)	Relative % of Total Collection for Given Depth
		Surface	
9:00 AM	506	168.7±18.8	11.6
12:00 N	117	39.0±12.2	2.7
3:00 PM	144	48.0±10.2	3.3
6:00 PM	296	98.7±15.9	6.8
9:00 PM	1085	361.7± 5.0	24.9
12:00 M	1693	564.3±13.9	38.9
6:00 AM	515	171.7±32.3	11.8
		0.5 meter	
9:00 AM	37	12.3± 4.7	3.2
12:00 N	140	46.7± 4.9	12.1
3:00 PM	230	76.7±10.3	19.8
6:00 PM	253	84.3±12.5	21.8
9:00 PM	202	67.3±15.3	17.4
12:00 M	136	45.3±22.4	11.7
6:00 AM	164	54.7±12.1	14.2
		1.0 meter	
9:00 AM	298	99.3± 4.1	23.0
12:00 N	129	43.0±11.2	9.9
3:00 PM	162	54.0± 8.5	12.5
6:00 PM	175	58.3±14.7	13.5
9:00 PM	175	58.3±13.1	13.5
12:00 M	134	44.7± 6.2	10.3
6:00 AM	225	75.0±15.3	17.3

This pattern was influenced by differences in migration patterns of the immature and mature animals. It had been noted in preliminary studies that quite often the animals collected at different depths and times were either all small, ranging in size from 2 to 5 mm, or large, 6 to 12 mm. This was verified by measuring 3,781 specimens and determining the relative percent of each size class at the time of collection at the surface. These results, shown in Fig. 1, indicate differences in pattern between size classes 2 mm through 5 mm and 6 mm through 12 mm animals. It is interesting to note that 5 mm and 6 mm class females do not quite conform to their respective patterns as precisely as the others. The transition from immature to mature, egg-bearing females occurs in this size range (5 mm to 6 mm).

In order to further clarify the diurnal vertical migration behavior pattern, an experimental design using the very pronounced changes at the surface was employed to provide more detailed information. Samples were taken at ten-minute intervals during designated hours (Table 3) along with light and temperature readings. Special attention was given to sampling periods immediately

Table 2. Percentage distribution of *Leptodora* at three depths over a six-day period grouped according to time of collection

Date (Aug., 1965)	Surface	0.5 m	1.0 m
	12:00 midnight		
2	46.8	21.4	31.8
3	34.7	28.2	37.1
4	33.8	35.7	30.5
5	45.9	22.6	31.5
6	24.7	28.4	47.0
7	33.3	33.4	33.3
Means	36.8	28.4	34.8
	6:00 A. M.		
2	54.0	13.6	32.4
3	42.5	25.3	32.2
4	26.5	20.7	52.8
5	40.1	27.1	32.8
6	38.4	32.1	29.6
7	39.6	23.9	26.6
Means	41.7	23.5	34.8
	12:00 Noon		
2	68.6	8.8	22.6
3	22.4	27.0	50.6
4	42.5	19.6	37.8
5	10.5	43.9	45.6
6	17.8	52.6	29.7
7	22.3	23.1	54.6
Means	30.6	29.6	39.8
	6:00 P. M.		
2	42.3	27.3	30.4
3	34.1	19.3	46.7
4	30.3	23.4	46.2
5	15.1	50.9	34.1
6	43.4	28.8	27.8
7	33.6	20.3	46.1
Means	34.5	28.9	36.6

before and after sunrise and sunset. The pattern clearly shows the response to light (Fig. 2). Within one hour after sunrise, there is a reduction to one-half that of the lowest value observed at noon. At sunset the increase is 30 times greater than that measured at noon.

In addition to *Leptodora,* data on *Chaoborus* (*flavicans* and *punictipennis*) and various chironomids (predominately *Chironomus plumosus*) are included for comparison (Table 3). The rapid response of *Chaoborus* can be seen in changes

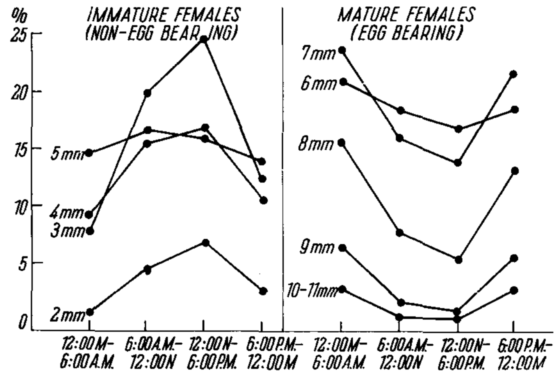

Fig. 1. Relative percent of various size classes of *Leptodora* collected in the surface waters of Sanctuary Lake over a 24-hour period.

occurring around sunset. Ten minutes before sunset only 10 animals were counted in the sample, but at sunset 452 were collected while 10 minutes later their numbers had increased to over 700 (Table 3).

A number of diurnal oxygen determinations were made in Sanctuary Lake and these always indicated dissolved oxygen levels at or near saturation. In only three instances, out of 30 determinations of oxygen profiles, was saturation less than 90% (COSTA, 1967; CUMMINS et al., 1969). The relationship between oxygen concentration and *Leptodora* numbers has been summarized in Table 4.

In six of eight sampling periods the greatest number of animals occurred at the depth having the lowest oxygen concentration. For seven of the eight sampling periods, the smallest number of animals was associated with the highest oxygen concentration. However, the difference in oxygen concentration at the various depths for each time period averaged only 0.6 ppm and ranged from 0.2 to 1.2 ppm and, even when oxygen concentrations were nearly identical, the numbers of animals varied considerably. In one case the numbers were virtually equal (514 and 515), while in the other instances they varied from 40 to 70 percent.

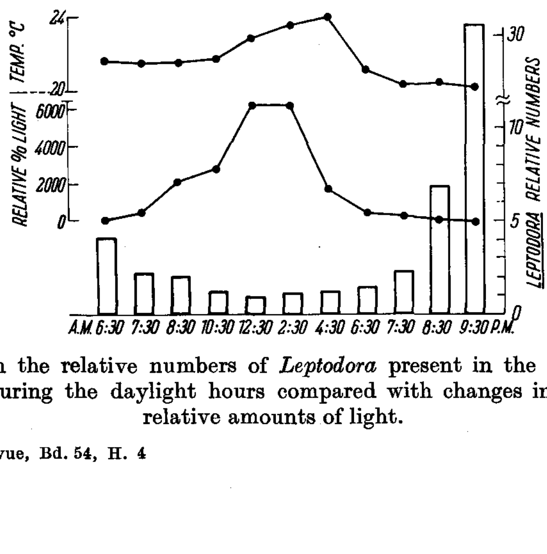

Fig. 2. Changes in the relative numbers of *Leptodora* present in the surface waters of Sanctuary Lake during the daylight hours compared with changes in temperature and relative amounts of light.

Table 3. Changes in the number of animals at the surface in three collections made at 10 minute intervals. Samples consisted of 90 meter tows taken Aug. 23, 1966

Starting Time	*Leptodora* collected			*Chaoborus* Collected			Chironomidae Collected		
	First	Second	Third	First	Second	Third	First	Second	Third
6:30 AM	148	133	122	0	0	0	0	0	0
7:30 AM	91	76*	42	0	0*	0	0	0*	0
8:30 AM	85	79	39	0	0	0	0	0	0
10:30 AM	39	32	39	0	0	0	0	0	0
12:30 PM	30	39	31	0	0	0	0	0	0
2:30 PM	29	51	21	0	0	0	0	0	0
4:30 PM	30	31	51	0	0	0	0	0	0
6:30 PM	54	36	52	0	0	0	0	0	0
7:30 PM	66	72	89	0	0	0	0	0	0
8:30 PM	167	220**	251	10	452**	739	0	0**	2
9:30 PM	1120	1010	1090	3660	2714	3030	80	90	220

* Sunrise: 7:25 AM
** Sunset: 8:40 PM

Table 4. Changes in the relative numbers of *Leptodora* compared to oxygen concentration, August 22—23, 1967

Time	Depth	Oxygen Concentration (p.p.m.)	*Leptodora* Counts	Relative Percent for each Depth
4:30 PM	Surface	10.4	120	14.15
	0.5 M	10.0	216	25.47
	1.0 M	10,0	512	60.38
7:00 PM	Surface	8.2	371	48.69
	0.5 M	9.2	70	9.19
	1.0 M	8.8	321	42.12
8:30 PM	Surface	7.4	452	51.89
	0.5 M	8.6	254	29.16
	1.0 M	8.2	165	18.95
10:30 PM	Surface	8.0	459	53.87
	0.5 M	8.0	198	23.24
	1.0 M	9.0	195	22.89
5:30 AM	Surface	7.0	223	34.05
	0.5 M	6.8	279	42.59
	1.0 M	7.4	153	23.36
7:00 AM	Surface	7.2	230	33.43
	0.5 M	7.4	189	27.47
	1.0 M	7.4	269	39.10
9:00 AM	Surface	7.4	275	36.47
	0.5 M	8.0	75	9.95
	1.0 M	7.6	404	53.58
12:30 PM	Surface	8.8	50	4.63
	0.5 M	8.4	515	47.73
	1.0 M	8.4	512	47.64

4. Discussion

In Sanctuary Lake the light penetration into the water column is poor (Fig. 3) with normally more than 50 percent reduction in incident solar radiation at the 0.5 meter depth during the ice-free period. In the summer and early fall less than 1 percent of incident illumination reaches a depth of one meter (Costa, 1967).

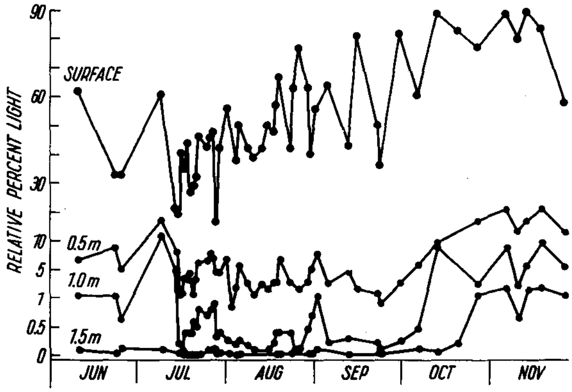

Fig. 3. Percent of incident solar radiation penetrating to four depths in Sanctuary Lake, 1966. (Surface percent of incident radiation measured several mm under water surface.)

Because of the rapid extinction of light through the water column, the vertical migration pattern exhibited by *Leptodora kindtii* in Sanctuary Lake is striking. This is true even though the lake's maximum depth is only three meters, and for the most part only two meters. Yet, not only did differences in population density at various depths occur with time, but differences in the migration pattern of various size groups were also encountered.

The changes in density were most obvious at the surface, exhibiting a pattern in which more individuals were observed during the late afternoon and evening with lesser numbers present at other times, reaching their lowest density a few hours before the afternoon. The response to light changes (Fig. 2) was most striking with respect to the differences encountered immediately prior to and after sunrise and sunset (Table 3). Within ten minutes after sunrise the relative numbers at the surface were about 50 percent less than for the ten minute period before sunrise. In the ten minute period following sunset, the numbers increased by 1.5 times over that of the period before sunset. A gradual, but continuous, increase in numbers started from 7:30 P. M. continuing until 9:30 P.M. when the relative numbers were about 30 times greater than the noon sampling period. It is of interest that even though the faint light after 8:30 P. M. was not measurable with a G. M. Submarine Photometer, the animals were still reacting to it.

As shown above, diurnal migration behavior was found to be influenced by size differences of the animals. The smaller immature females (2—5 mm) responded in a fashion opposite to that of the larger mature (6—12 mm) ones. In general, the smaller animals reach their maximum numbers at the surface between 6:00 A. M. and 6:00 P. M. while the larger females during this same period were at their lowest density (Fig. 1). This difference may be explained partially by the immature nature of the smaller animals and the lesser sensitivity of their eye to light (WOLKEN and GALLICK, 1965). This hypothesis is supported by the behavior of 5 mm and 6 mm size class animals which exhibit patterns like their respective groups but not nearly as pronounced (Fig. 1). As noted above, the transition from immaturity to maturity occurs when, upon moulting, the 5 mm animals become egg-bearing 6 mm females.

In their diurnal vertical migrations, *Leptodora*, particularly the larger size classes (6—12 mm) avoid strong light. On bright and sunny days they were not found in surface waters; if the day was overcast they were found at the surface in higher numbers, even at noon.

Other studies (CUMMINS et al., 1969; MOSHIRI et al., 1969) have treated differences in trophic relations, assimilation and respiration between the two size categories. Thus, it is clear that the young (2—5 mm) and adult (6 mm and >) females constitute two portions of the population that are fairly well isolated with respect to ecology, physiology and behavior. The observed size group specific diurnal migration patterns serve to minimize contacts between the predatory *Leptodora* size classes (6—12 mm) and the immature, less predatory individuals (2—5 mm), thus insuring that other species populations will constitute the predominant prey sources.

Little, if any, correlation between oxygen concentration or temperature differences at various depths, and the quantitative presence of *Leptodora* was observed. Table 4 reinforces the hypothesis that the diurnal migration pattern is primarily related to light. An examination of changes in *Leptodora* densities, especially at the surface, substantiates this.

In Table 4 it can also be seen that the total numbers collected for all three depths varies (655—1079). A significant portion of the difference can be accounted for by a migration into deeper waters below the 1.0 meter depth. Sampling for quantitative population estimates has shown that animals collected at a depth of 1.5 meters or greater may account for as much as 11 to 38 percent of the total sample.

The daytime migration of *Leptodora* from the surface to the deeper strata according to MOSHIRI (1968) is not related to a decrease in the rate of respiratory metabolism. He also states that the nightly presence of high concentrations of *Leptodora* should not be equated with a high rate of respiratory activity. The abundance of oxygen production in Sanctuary Lake (COSTA, 1967) indicates that daytime oxygen production, together with almost continuous circulation, is more than sufficient to compensate for high levels of nighttime community respiration.

The attempt to correlate behavior of organisms with a single factor is extremely difficult. However changes, especially physical-chemical ones, are often reflected in living populations (MACARTHUR and CONNELL, 1966). It appears that of the three factors examined, light plays the dominant role in affecting the diurnal vertical migratory behavior of the two size groupings of *Leptodora kindtii* (FOCKE) females.

5. Summary

The diurnal vertical migration pattern of *Leptodora kindtii* (FOCKE) in Sanctuary Lake, a section of Pymatuning Reservoir (Crawford County, Pa.) was examined over a four year

period (1965—68). Changes in the relative numbers of animals at three specific dephts (Surface, 0.5 and 1.0 Meter) occur with time. Surface changes appear to be of much greater magnitude, although highly significant differences exist at all three sampling depths. The pattern is influenced by differences in migration of immature, nonegg-bearing females (2—5 mm) and mature, egg-bearing females (6—15 mm).

Temperature, light and oxygen concentration were examined as factors relating to the quantitative presence of *Leptodora* and depth of their occurrence. Of the three factors evaluated, light appears to play the dominant role.

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