(8)

Oikos 20: 189–223. Copenhagen 1969

Ecological energetics of a natural population of the predaceous zooplankter Leptodora kindtii Focke (Cladocera)[1]

KENNETH W. CUMMINS, ROBERT R. COSTA, RUTH E. ROWE, GERALD A. MOSHIRI, RICHARD M. SCANLON and RICHARD K. ZAJDEL
Pymatuning Laboratory of Ecology, University of Pittsburgh

Abstract

Parameters for natural populations of the fluid-feeding predaceous zooplankter *Leptodora kindtii* and probable prey species were followed for three years against a background of limnological monitoring of a shallow lake ecosystem, Sanctuary Lake, Crawford County, Pennsylvania. Due to the shallow, uniform nature of the Fish Hatchery Bay portion of Sanctuary Lake, physical-chemical conditions are quite homogeneous during the *Leptodora* growing season (May through November). Oxygen is normally near saturation, water temperatures follow air temperatures closely and the system is highly productive. Bluegreen algae dominate the phytoplankton during the summer and fall.

The population parameters finite birth, instantaneous birth, instantaneous population change, and instantaneous death rates were estimated from field data for six possible prey species (four cladocerans and two copepods). Also, turnover and production rates were calculated for the prey. The same population data were gathered for *Leptodora*, and predator – prey inferences were drawn by comparing *Leptodora* birth rates with prey death rates. The results indicate that the predator – prey relationships are quite complex, with the *Leptodora* population usually depending on at least two prey species at any given time.

Annual production for the *Leptodora* population was 0.362 g/m^3 (1876.1 cal/m^3) in 1966 and 1.427 g/m^3 (7395.4 cal/m^3) in 1967. Assuming assimilation and production (i.e. growth plus reproduction) efficiencies to be 40% and 30% respectively and calculating yield from estimates of death rate (d), annual energy budgets for *Leptodora* have been proposed for two years.

Резюме

Исследовали параметры естественных популяций *Leptodora kindtii* – хищных представителей зоопланктона, питающихся соками, а также популяций возможных видов их жертв. Наблюдения проводились в течение трех лет в придонных слоях воды лимнологических мониторов экосистемы мелких озер на озере Сэнктуари в Кроуфорд Коунти (Пенсильвания). В мелководной части озера Сэнктуари – Фиш-Хэтчери-Бэй, физико-химические условия довольно постоянны в период роста *Leptodora* (с мая по ноябрь). Концентрация кислорода близка к уровню насыщения, температура воды близка к температуре воздуха, продуктивность системы высока. В фитопланктоне в течение лета доминниуют сине-зеленые водоросли. Параметры популяции определяют сроки появления популяции, массового отрождения особей, одновременных изменений популяции и массовой гибели особей. Эти параметры были определены в полевых опытах с возможными видами жертв (4 вида *Cladocera*, 2 вида *Copepoda*). Для популяций жертв определена продукция и интенсивность обмена. Подобные данные получены и для *Leptodora*. Отношения хищник-жертва были исследованы путем сравнения скорости отрождения *Leptodora* и скорости гибели их жертв. Результаты наблюдений показывают, что отношения хищник-жертва довольно сложны, т.к. популяции *Leptodora* обычно связаны по меньшей мере с двумя видами жертв в каждый данный момент.

Годовая продукция популяций *Leptodora* составляла 0,362г/м^3 (1876.1кал/м^3) – в 1966г. и 1,427г/м^3 (7395.4кал/м^3) – в 1967г. Принимая коэфициент ассимиляции и продукцию (т.е. рост плюс размножение) соттевственной за 40% и 30% при учете скорости гибели (*d*) предположительно подсчитан годичный энергетический баланс для *Leptodora* на ближайщие два года.

[1] This research was supported by contract AT (30-1)-3519 from the Environmental Sciences Branch of the U.S. Atomic Energy Commission. The printing costs have been defrayed by a special grant. Manuscript accepted January 1969.

1. Introduction

The widespread interest in ecological energetics is exemplified by the recent appearance of reviews such as Phillipson (1966) and Englemann (1966) (see also Slobodkin 1962). The collection of data on energy budgets, which constitutes a logical extension of Lindeman's (1942) classical work, has progressed very slowly. Some annual budgets have been prepared for a number of ecosystems (Juday 1940, Odum 1957, Teal 1957, 1962, King and Ball 1967) or portions of ecosystems (Englemann 1961, Mann 1966) but these suffer from the simple lack of data. The few original values which have appeared in the literature have been grossly overworked and overextended; obviously in this area ecologists have more models than data.

Most investigators have approached ecosystem energetics at the level of single populations, the assumption being that the summation of such measurements will eventually allow for model building at the level of entire ecosystems. Some examples of single population energy budgets are represented by the work of Trama (1957), Richman (1958) and Comita (1964). Of particular relevance to the present paper are the budgets prepared for *Daphnia pulex* Leydig (Richman 1958) and *Diaptomus siciloides* Lilljeborg (Comita 1964). The information presented in this paper is intended as an extension of these studies by providing data on a predaceous freshwater zooplankter. The long term objective of the study is to determine an extremely detailed annual energy budget for natural populations of *Leptodora kindtii* (Focke).

Previous investigators have studied various aspects of the biology of *L. kindtii* (Weismann 1874, 1876, Forbes 1886, Kingsley 1886, Weidersheim 1890, Samassa 1891, Samter 1895, 1900, Carlton 1897, Warren 1901, Gerschler 1911, 1912, Guth 1919, Gicklhorn and Keller 1925, Siedentop 1930 a, 1930 b, Sebestyen 1931, 1933, 1949, 1960 a, 1960 b, McDougall and Verzar 1933, Frolich and Zak 1934, Von Saalfield 1936, Andrews 1948, 1949, 1953, Mordukhai-Boltovskaia 1956, 1957, 1958, 1960, Entz and Lukacsovics 1957, Hall 1959, Cheremisova 1960, Scharrer 1964, Wolken and Gallick 1965). Several of these investigations present data on various aspects of population dynamics but none have produced energy budgets.

2. Study location

Pymatuning Reservoir is a large (64.8 km^2) artificial impoundment of the Shenango River in northwestern Pennsylvania and northeastern Ohio. Tryon and Jackson (1952) demonstrated the highly productive nature of this reservoir and showed that it is divided into three distinct portions which are ecologically distinguishable. Sanctuary Lake, the 1013 hectare (2500 acre) eastern arm-like extension of the reservoir, is separated from the remainder of the impoundment by a spillway dam (Fig. 1), and constitutes the shallowest (maximum depth 3 m) and most productive portion (Tryon and Jackson 1952, Hartman and Graffius 1960). The University of Pittsburgh Pymatuning Laboratory of Ecology is located on the west shore of Sanctuary Lake (Fig. 1).

In addition to the studies already cited, various aspects of the ecology of Pymatuning Reservoir have appeared elsewhere (Jackson and McFadden 1954, Orr 1954, Tryon 1954, Verduin 1954, Borecky 1956, Hartman 1958, Hartman and Himes 1961, Dugdale and Dugdale 1965).

Only one area of Sanctuary Lake, Fish Hatchery Bay (station no. 5 in Hartman and Graffius 1960; marked FHB in Fig. 1), was sampled intensively during the quantitative study period, 1965–1967. However, during 1964 and periodically during 1965–1967 comparative samples were taken from other regions of the lake. Since these supplemental collections indicated little difference between zooplankton densities in Fish Hatchery Bay and other regions, we have assumed that the detailed data on the bay reflect conditions in

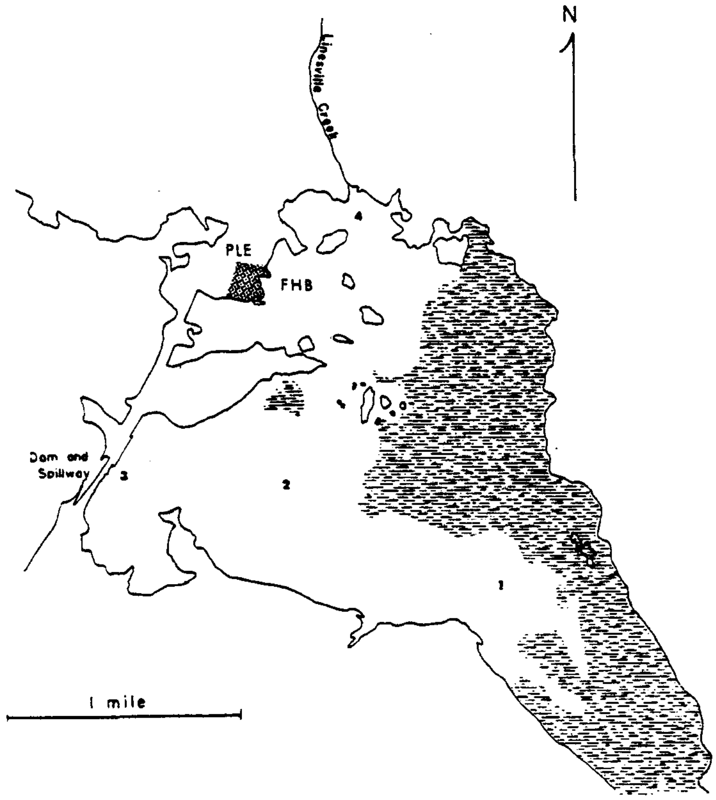


Fig. 1. Sanctuary Lake portion of Pymatuning Reservoir showing sampling location in Fish Hatchery Bay (FHB) and the location of the University of Pittsburgh Pymatuning Laboratory of Ecology (PLE, indicated by cross hatching). (Figure modified from Hartman and Graffius 1960).

the lake as a whole. However, such extensions of the data should be done with caution since Hartman and Graffius (1960) have shown algal differences in various regions of Sanctuary Lake.

Fish Hatchery Bay represents a uniform sampling area; a flat bottom basin with a maximum depth of 3 m and a mean depth of 1.5 m. As shown in Fig. 1, the eastern portion of the lake receives water from an extensive marsh area. In addition to runoff, the other major contribution is from Linesville Creek (Cummins et al. 1965) which enters at the north end (Fig. 1) carrying raw sewage from the town of Linesville, Pennsylvania (population approximately 1200).

3. Methods

A. Physical-chemical limnology

Incident solar radiation was monitored with a Belfort 7 day recording pyrheliometer (Belfort Inst. Co., Baltimore, Md.; sensitivity 3800–7200 Å) and converted to gram calories/cm^2/day (= Langleys) by planimetrically determining the area under each daily tracing. On each sampling date, profiles of the following parameters were determined for the water column by obtaining measurements at four depths (surface, 0.5 m, 1.0 m and 1.5 m): percent light penetration (G. M. submarine photometer, G. M. Mfg. and Inst. Corp., N.Y., 50% sensitivity 4000–6400 Å); temperature (Electronic thermometer, Applied Res. Assoc., Austin, Texas); dissolved oxygen by the P.K.A. modification of the Winkler method, phenolphthalein and total $CaCO_3$ alkalinity, and free CO_2 (Amer. Public Health Assoc. 1965); dissolved solids (Myron dissolved solids meter, Mace Corp., San Gabriel, Cal.). Also, several determinations were made of orthophosphate (1966–1967) by the stannous chloride method (Amer. Public Health Assoc. 1965) and total carbohydrate (1967) by the anthrone reagent method (Hewitt 1958). In addition to the seasonal monitoring of the parameters listed above, extensive physical-chemical data were gathered during round-the-clock studies of *Leptodora* diurnal migration patterns to be reported elsewhere (Costa and Cummins 1969).

B. Plankton sampling

Phyto- and zooplankton samples were collected with a 0.5 m diameter no. 20 mesh (0.076 mm pore size) plankton net, fitted with a metering device (G. M. Instruments, regular gear train counter type), between two marker bouys set 90 m apart in the center of Fish Hatchery Bay. Due to the shallow and uniform nature of the Sanctuary Lake basin, collections could be made at fixed depths. The net hoop was welded to a rod marked at 0.5 m intervals, allowing the net to be positioned at the desired sampling depth and held in place during standard 90 meter tows. During 1965–1967, fixed position plankton net tows were obtained with a 12 ft. aluminum rowboat propelled by a 6 hp. outboard motor. The 1967 season also saw the adoption of a 15 ft. pontoon boat powered by a 20 hp. outboard motor and modified to accomodate the sampling gear.

Other nets on 0.3 m diameter hoops attached to rods and towed at fixed depths the standard 90 m distance were used for additional zooplankton (no. 10 mesh, 0.158 mm pore size) and *Leptodora* (no. 000 mesh, 1.024 mm pore size) collections. In addition, some 1967 collections were taken with an Isaacs-Kidd (G. M. Instruments) high speed plankton sampler lowered to a given depth through a center well in the pontoon boat and supported by a specially designed structure that allowed the sampler to be levelled during collection.

Calibration of the plankton nets was accomplished by two methods. The first involved mounting a metering device outside the net hoop. By comparing the readings obtained on the outside meter during a 90 m tow with those read on the meter recessed in the mouth of the net an efficiency factor was determined. This efficiency factor was then used to correct the theoretical collection volume of 17,640 liters (i.e. (90) $\times$ (efficiency factor) $\times$ $(0.25\,m)^2$ 10,000 = liters) to the actual volume sampled. The second method involved a comparison of meter readings from 90 m tows of the net rigged for sampling with tows after removal of the net. The no. 000 mesh net was used to collect only *Leptodora* and it had an efficiency that was essentially 100%.

The Isaacs-Kidd sampler was calibrated by Dr. Robert Bonn under standard flow conditions (Hydraulics Laboratory, University of Pittsburgh). The resulting calibration curve indicated the relationship between volume processed per meter revolution as determined by the speed of the sample vessel. Comparisons of population estimates obtained with the Isaacs-Kidd sampler and metered nets indicated no significant differences ($P = < 0.05$, Wilcoxon matched-pairs – signed-ranks test: Siegel 1956).

Tests of sampling reproducibility, when replicate tows were compared (three tows at each of two depths on three different dates), on the basis of the 10 taxonomic categories enumerated, indicated no significant differences (variance analysis, F values from 0.32 to 2.66, $P = 99.4$). Comparisons between counts of subsamples from two depths (surface – 0.5 m and 1.0 m–1.5 m) collected on the same date also showed no significant differences ($P = < 0.05$, Wilcoxon matched-pairs – signed-ranks test: Siegel 1956). The high reproducibility of replicate samples taken in Fish Hatchery Bay is undoubtedly due to the uniform, shallow, continuously mixed, and therefore homogeneous, nature of Sanctuary Lake. Sampling of the strata from surface to 0.5 m and from 1.0 m to 1.5 m adequately com-

Tab. 1. Data on sample number and sampling frequency for the years 1965–1967.

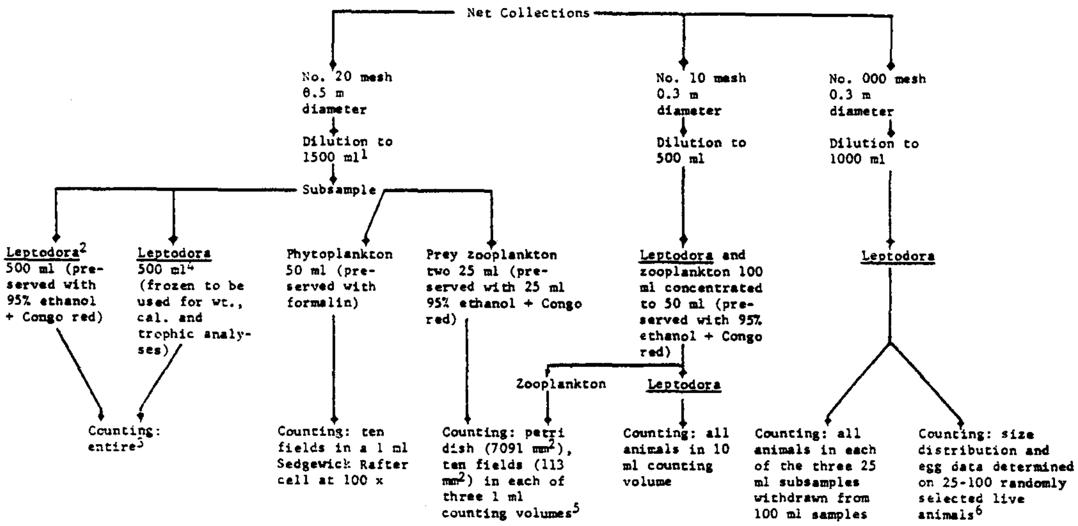
Year	Number of samples: No. 20 mesh 0.5 m net	No. 000 mesh 0.3 m net	No. 10 mesh 0.3 m net	Total	Mean sampling interval (days)[1]	Sampling interval range (days)	Sampling[2] period
1965	39			39	5.2	1–11	18/5– 4/12
1966	36	63		99	2.3	1–11	8/4–26/11
1967	25	88	73	186	1.2	1–11	19/4–19/11

[1] Including all collection methods.
[2] Sampling initiated and concluded to cover the occurrence of *Leptodora.*

pensated for differences in vertical distribution as indicated by extensive studies on *Leptodora* diurnal migration patterns (Costa and Cummins 1969). Furthermore, because most of the sampling was carried out after sunset, differences in density due to depth were not significant. Data on number of net collections, sampling interval and total sampling period for the three years are presented in Tab. 1.

C. Plankton enumeration

Fig. 2 summarizes procedures for quantitative estimates of plankton density which involved separate methods for *Leptodora,* the remainder of the zooplankton and the phytoplankton. Estimates of size distribution for the *Leptodora* population were made from fresh-caught animals obtained with the no. 000 mesh, 0.3 m net. Because of severe and non-uniform



1. In some cases dilution was to 1000 ml
2. Size determinations made on preserved Leptodora (1965) were discarded.
3. In some cases subsampling was necessary due to high Leptodora density.
4. In some cases 350 ml samples frozen.
5. In some cases, counting volumes were 0.5, 1.5 or 2.0 ml.
6. If sample contained less than 25, entire collection was counted.

Fig. 2. Pretreatment, preservation and enumeration procedures for plankton samples collected during the 1965–1967 seasons.

Tab. 2. Calculations of population parameters.

Population Parameters	Formulae	Comments
Mean clutch size ($\hat{E}$)	$\hat{E} = \frac{\text{total no. eggs counted}}{\text{total no. ♀♀ with eggs}}$	An age specific mean clutch size can be employed as an additional refinement.
Embryos/unit volume (E)	E = (% ♀♀ with embryos) (no./unit volume)($\hat{E}$) ($\hat{E}$ = mean clutch size)	Alternate estimates can be obtained by counting all eggs in females from a standard subsample volume removed from a quantitative collection.
Developmental time (D)	Developmental time (from appearance of embryos to brood sac release) determined in laboratory culture at constant temperatures or estimated by using the average lake temperatures over the time period between peaks and lows in mean clutch size or the interval between appearance of smallest egg-bearing females and newborn. Separate times were determined for four morphologically recognizable developmental stages of *Leptodora* (Table 8 and 9).	
Finite birth rate (B)	$B = \frac{E}{(D)(N_o)}$ Where N_o is the population density at a given time (initial time t_o)	B represents the number of newborn per individual female per day. For *Leptodora*: $B = \left(\frac{E_1}{D_1} + \frac{E_2}{D_2} + \frac{E_3}{D_3} + \frac{E_4}{D_4}\right)\left(\frac{1}{N_o}\right)$ where 1–4 are the four morphologically recognizable developmental stages.
Instantaneous birth rate (b)	b = Natural log of (1 + B)	The value of 1 in the equation represents an "initial individual" to which is added the increase/individual/day. Thus, b represents the instantaneous rate at which the populations would increase if it maintained the birth rate B.
change (r)	$\frac{(\text{Natural log } N_t)\text{-}(\text{Natural log } N_o)}{t}$ Where N_o is the initial population density and N_t is the final population density after time t.	the natural log of the equation $N_t = N_o{}^{rt}$
Instantaneous death rate (d)	d = b − r	Death rate, or "total yield", is due to both "natural death" (yield to detrital consumers) and predation (yield to predators). That is, the effect of the observed population change (r) is removed from the predicted population increase (b) to "expose" the death rate (d). If the population is not changing, that is, exists in a steady state condition, death and birth are equal. When the population is increasing, b exceeds d, when it is decreasing d exceeds b; in both cases the values of d are positive. A negative value of d indicates that the observed change (r) exceeds the predicted change based on births (b). This decrease in death is probably associated with increased survival of non-reproductive individuals or other errors in the estimates.
Turnover time in days (T)	$T = \frac{1}{B}$ (% turnover per day = $\frac{1}{T} \times 100$)	Actually the formula is $\frac{N_o}{(N_o)(B)} = \frac{1}{B}$ (Note that $\frac{1}{T} = 1/\frac{1}{B} = B$)

Tab. 2. (continued)

Population Parameters	Formulae	Comments
Production rate (gm/unit vol/day)	(% turnover per day)(N_o) = gm/unit vol/day (Where N_o is expressed in grams)[1]	The values are production rate/day for a given standing crop of size N_o. All values obtained over the growing season can be averaged or monthly averages can be obtained. The procedure employed in the present investigation was to plot daily production for the season and determine the area under the curve planimetrically. Additional refinement can be achieved by estimating size-specific production based on time required to develop from one stage to the next at a given temperature (e.g. see Petrovich et al., 1961).

[1] The dry weight biomass standing crop for a given day is calculated by multiplying the per cent size class information times the standing crop and then each fraction by the mean dry weight of the appropriate size class. For *Leptodora* calculations, dry weight values for animals are without eggs so the egg weight is added to the standing crop by multiplying per cent females with eggs times the female standing crop times the mean clutch size and then times the mean dry weight per egg (summer and winter eggs treated separately).

shrinkage of *Leptodora* when preserved in a wide range of ethanol or formalin concentrations, the size distributions obtained in 1965 were discarded. In addition, during the 1965 season it was discovered that *Leptodora* females dropped significant numbers of eggs even when frozen or preserved in 95% ethanol and therefore 1966 and 1967 egg data were determined using only fresh-caught individuals.

Other zooplankton species exhibited relatively less shrinkage in preservatives and females appeared less inclined to shed their eggs in 95% ethanol. Size distributions for zooplankton species (other than *Leptodora*) were determined on preserved collections in 1966 and 1967. Zooplankton egg data were obtained from preserved samples taken in 1966, while only fresh-caught specimens were examined for eggs during the 1967 season. Counts were made in triplicate (Fig. 2) and in cases where one of the counts fell outside the 95% confidence limits (Crowley and Cohen 1967) one or two additional counts were made.

D. Population parameters and production estimates

Based on measurements of standing crop (numbers per unit volume), mean clutch size, per cent females with eggs, median (or mean) lake temperatures and estimates of development times from field data, a number of population parameters have been calculated for *Leptodora* and the possible prey species. Procedures utilized to calculate the population parameters finite birth rate (B), instantaneous birth rate (b), instantaneous rate of population change (r) and instantaneous death rate (d) have been summarized in Tab. 2. The methods are those described by Deevey (1947), and applied to zooplankton populations by Edmondson (1960), Hall (1964) and Wright (1965).

In addition to some laboratory measurements, several procedures were used in estimating developmental times (D), the time from appearance in the brood sac to the time of hatching, from field data. For prey zooplankton species, this involved two methods: 1) the interval between the peaks and troughs in a plot of mean clutch size by sampling date; 2) one half the period between the low prior to a peak plus one half the period between the peak and the following low. The median (or mean) lake temperature for the period was taken as the developmental temperature. The resulting curves (Fig. 3 and 4) have been corroborated by isolated laboratory measure-

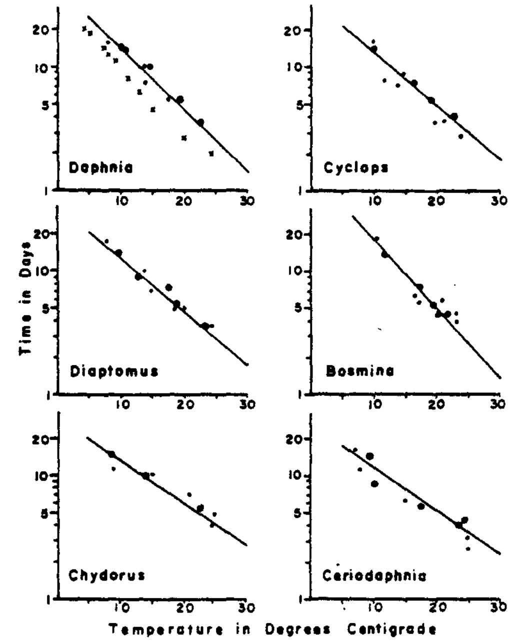


Fig. 3. Zooplankton development times, from the appearance of embryos in the brood chamber to release of young, as determined by temperature (estimates based on time between peaks and lows in mean clutch size; points, ½ time before peak to ½ time after peak; circled points, time from peak to low; × marks: Hall 1964).

ments and compared with data gathered by other investigators (e.g. Hall 1964, see plot for *D. galeata mendotae* in Fig. 3). The range of developmental times for the six species investigated is from 1–3 days to 10–20 days over the range of 30°C to 8°C (Fig. 3). Developmental times for *Leptodora* (Fig. 4) were also determined by the procedure described above supplemented by laboratory observations. In addition, four stages in the development of embryos from their first appearance in the brood sac until just prior to their release as free-swimming young were recognized. Morphological characteristics of these four stages and the relative per cent of the developmental period spent in each have been presented in Tab. 3. The estimated development times for four stages of *L. kindtii* embryos are summarized in Tab. 4. Temperatures are assumed to be medians (or means) over the developmental time period. Estimates of development time for temperatures below 19°C have been taken from the data of Mordukhai-Boltovskaia (1958); these have also been plotted in Fig. 4. The range of total development time from 1°C to 31°C is 17.4 days to 1 day (Tab. 4).

Production estimates were calculated using turnover times derived from field population data. Calculation methods for turnover time, per cent turnover per day and production (grams dry wt/m^3/day and cal/m^3/day) have also been summarized in Tab. 2. The method employed provides an approximation of production based on per cent turnover per day as derived from population birth rate. Production can also be calculated using finite death rate (Heinle 1965, 1967). However, production can be assessed most accurately if, in addition to embryo development times, instar duration times are known. Such data are difficult to obtain for field populations since, unlike embryo development, instar duration times are both temperature and food dependent.

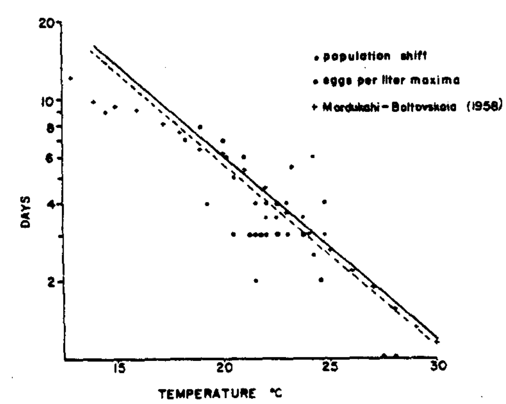


Fig. 4. *Leptodora* development time, from the appearance of embryos (stage I) in the brood chamber to release of young, as determined by temperature. Estimates based on the time between appearance of youngest egg bearing females and new born (2 mm) individuals (population shift) and the time between peaks and lows in eggs per liter (eggs per liter maxima). (Line fit by graphical test of monotonic association, Quenouille 1959.) Data from Mordukhai-Boltovskaia have also been plotted.

Tab. 3. Morphological characteristics and relative duration of *Leptodora* developmental stages (% duration determined in the range 20 to 25°C).

Embryo stage	Morphological description	Approximate size (in microns)	% of total development period (where total period = appearance in brood sac to hatching)
I	Undifferentiated spherical embryo; granular.	250–300 (diameter)	100%
II	Posterior and anterior differentiation; head rounded and with 2 antennae, posterior end slightly tapering.	500 (long)	67%
III	Further differentiation and elongation of anterior and posterior regions. Head still rounded, eye pigmented, antennae 3/4 length of body. Legs present and partially developed.	750–1000 (long)	32%
IV	Elongation of antennae, legs and body. Tail bifurcated. Animals actively moving about in brood sac.	1500–2000 (long)	Hatching (1%)

Investigations are currently underway to permit the use of such a method (Cummins and Costa 1969).

Production per year was estimated by summing the daily production over the growing season. Production values for days on which no samples were taken were calculated by interpolation. Both interpolation and summation to obtain the annual estimate were accomplished by computer programming. The greatest advantage of computer programming in this case is the continual refinement of estimates as more data become available. Since copepod nauplii were not separated to species, the data presented represent non-naupliar copepod production only.

4. Results

A. Physical-chemical limnology of Fish Hatchery Bay

Measurements at Sanctuary Lake of incident solar radiation, obtained for 1965–1967, yielded the following average values in g cal/cm^2/day for the months covering the *Leptodora* growing season: May, 284.7; June, 307.7; July, 320.1; August, 223.7; September, 197.3; October, 121.3; and November, 56.6. Profiles of percent incident radiation indicate a rapid absorption of light with depth due to the large amounts of suspended plankton, detritus and sediment. The general pattern is for less than 1% of incident light to penetrate below a depth of 1 m. This results in an average energy income at a depth of 1 m of 2.4 cal/cm^2/day for the *Leptodora* growing season, of which only 50%, or 1.2 cal/cm^2/day, is presumed to be photosynthetically available. Temperature data summarized in Fig. 5 (1965–1967) show the continuously mixed character of Fish Hatchery Bay water in which the water and air temperatures correspond closely. These data represent instantaneous measurements of the average temperature in the water column. In addition, median temperature measurements (based on maximum and minimum daily temperatures) are available for most dates in 1966 and 1967 courtesy of the Pennsylvania Fish Commission which monitors water temperatures in the bay. When a weak thermal stratification was observed during the summer in the bay, the static period usually prevailed no longer than 24 to 48 hours. Even during such rare occasions, complete oxygen depletion was never observed in the bottom waters.

Tab. 4. Estimated development times in days for four morphologically distinguishable stages of *Leptodora* over the range of 1 °C to 31 °C. Development times for temperatures below 20 °C taken from Mordukhai-Boltovskaya 1958; see also Fig. 4 and Tab. 2.

Temperature °C	Development Times in Days			
	Stage I	Stage II	Stage III	Stage IV
1	17.4	11.5	5.4	0.2
2	16.8	11.1	5.2	0.2
3	16.2	10.7	5.0	0.2
4	15.6	10.3	4.8	0.2
5	15.0	9.9	4.7	0.2
6	14.4	9.5	4.5	0.1
7	13.9	9.2	4.3	0.1
8	13.2	8.7	4.1	0.1
9	12.6	8.3	3.9	0.1
10	12.0	7.9	3.7	0.1
11	11.5	7.6	3.6	0.1
12	10.9	7.2	3.4	0.1
13	10.3	6.8	3.2	0.1
14	9.7	6.4	3.0	0.1
15	9.5	6.3	2.9	0.1
16	9.3	6.1	2.9	0.1
17	8.1	5.3	2.5	0.1
18	7.3	4.8	2.3	0.1
19	6.5	4.3	2.0	0.1
20	6.1	4.0	1.9	0.1
21	5.1	3.4	1.6	0.1
22	4.4	2.9	1.4	0.04
23	3.7	2.4	1.1	0.04
24	3.1	2.0	1.0	0.03
25	2.7	1.8	0.8	0.03
26	2.3	1.5	0.7	0.02
27	1.9	1.3	0.6	0.02
28	1.6	1.1	0.5	0.02
29	1.4	0.9	0.4	0.01
30	1.2	0.8	0.4	0.01
31	1.0	0.7	0.3	0.01

Because of the lack of thermal statification, chemical parameters are quite homogeneous throughout the water column during the *Leptodora* growing season (May–November). Dissolved oxygen is normally at saturation, in fact supersaturation is a common phenomenon in surface waters. The ranges of mean values encountered in three years of sampling were 7 to 12 ppm (80 to 130% saturation). Total alkalinity ranged between 40 and 60 ppm with the majority of measurements yielding values close to 50. Due to the high pH range, 8.0 to 9.5, free CO_2 levels were normally zero or extremely low, the highest levels recorded being 1 ppm on rare occasions. Total dissolved solids (conductivity) were usually above 100 ppm, the total range encountered being 70 to 130 ppm. Other parameters have been monitored from time to time in Sanctuary Lake. Orthophosphate levels are low having an August (1966) mean of 0.0162 ppm. Nitrogen data gathered by Dugdale and Dugdale (1965) indicated rather high levels (0.05 mg/liter NO_3) and suggested extensive nitrogen fixation primarily by large summer populations of bluegreen algae. A few fall (1967) determinations of total carbohydrate had a mean of 7.75 mg/l for six determinations. Assuming a significant proportion to be in the form of glucose, the values are high compared to the data of Hobbie and Wright (1965) on glucose concentrations in some Swedish lakes which ranged from 0.009 mg/l to 0.059 mg/l.

B. Primary producers

As reported by Hartman and Graffius (1960), green algae such as *Pediastrum* spp. dominated the spring phytoplankton community. The summer and early fall communities are com-

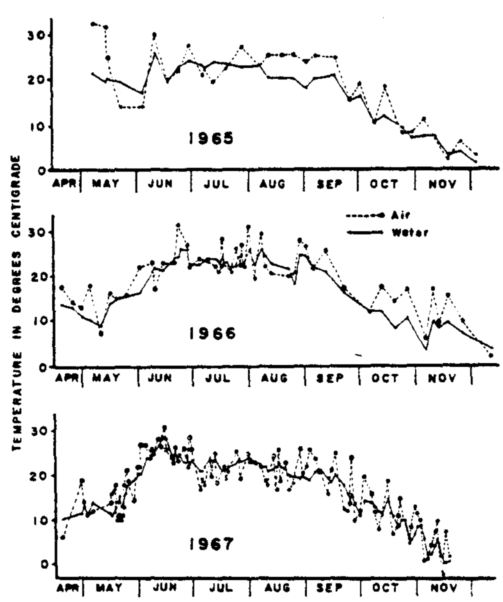


Fig. 5. Air and lake temperatures (mean of four depths) measured for Fish Hatchery Bay, 1965–1967.

posed predominantly of bluegreens, particularly *Microcystis* spp., the late fall community consists of green algae such as *Volvox* and diatoms while the winter community is composed primarily of diatoms, such as *Melosira* spp. Determinations of algal community composition indicated the dominance of bluegreens during the *Leptodora* growing season; for example, *Microcystis* spp. yielded values of per cent occurrence ranging from 60 to 100% (i.e. per cent occurrence in each ten field count made on a given sample).

Microscopic examination of unconcentrated lake water and the close correlation between carbon fixation (as measured by the C^{14} technique: Goldman 1961) and net phytoplankton density, suggest the error incurred by not including nanno- or ultraplankton is probably only significant in the spring. However, since essentially none of the dominant bluegreen algae (*Microcystis*, *Anabaena* and *Aphanizomenon*) have been seen during the examination of the gut contents of Sanctuary Lake herbivorous zooplankters, it seems that unicellular and colonial green algae, ultra phytoplankton, detrital particles and associated (or free) bacteria and fungi probably constitute the primary food sources. The same green algae and diatoms retained by a no. 20 net are normally encountered in zooplankter guts collected in Sanctuary Lake. Other investigators (e.g. Saunders 1967) have demonstrated assimilation of bacteria and detrital particles by grazing zooplankters.

Chlorophyll measurements were made routinely (1966–1967) on 50 ml quantitative samples filtered on 0.45 μ pore diameter Millipore Filters (Millipore Filter Corporation, Bedford, Mass.), extracted in 90% acetone and decanted after overnight refrigeration. A Beckman D.B. spectrophotometer was employed to obtain readings at 480, 510, 630 and 645 μ, and calculations of mg chlorophyll (a, b and c) per liter were obtained following the procedure of Parsons and Strickland (1963). The values were high ranging between 15 and 80 mg/l total chlorophyll (a, b and c). An inverse relationship between mg/l chlorophyll and zooplankton density similar to that reported by Wright (1965) was observed with maximum zooplankton densities associated with reductions in total chlorophyll.

Although photosynthetic carbon fixation was not measured routinely, several experiments were conducted during 1965, 1966 and 1967 using sodium bicarbonate-C^{14}. Measured rates of carbon fixation were fairly high in Fish Hatchery Bay, ranging up to 0.8 mg/l/hr. (approximately 9.6 mg/l/day).

C. Prey population data and production estimates

As yet, the trophic relationships of *Leptodora kindtii* in Sanctuary Lake have not been completely determined, since this predator is a fluid feeder. Extensive data, however, have been gathered on species populations most likely to serve as prey. Detailed studies of ingestion and assimilation by *Leptodora* using radioactive tracer experiments as well as through the employment of chromatography, electrophoresis and immunochemistry, are presently under way. So far, these investigations have implicated *Daphnia* and *Cyclops* as the most important prey species. The information summarized below concerns changes in zooplankter populations which were considered possible prey species (see section on predator-prey relationships below).

a) Daphnia galeata mendotae Birge – Although three species of *Daphnia*, *D. galeata mendotae*, *D. retrocurva* Forbes and *D. pulex* occur in Sanctuary Lake, *D. galeata mendotae* individuals were dominant in the lake during the *Leptodora* growing seasons (1965–1966). *D. pulex* was only encountered in April samples while *D. retrocurva* constituted less than 20% of the population from June through September. (Note: data for 1968 indicate a shift such that *D. galeata mendotae* and *D. retrocurva* are essentially codominants in the system.)

Data on *D. galeata mendotae* population density gathered for the three years are summarized in Fig. 6. Population densities were maximum early in the summer and late in the fall when the *L. kindtii* populations were low. Data on development times, per cent females with eggs, mean clutch size and standing crop

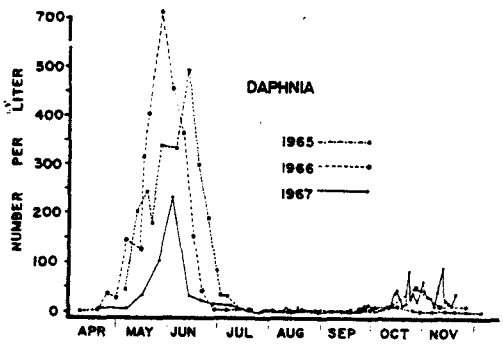


Fig. 6. *Daphnia galeata mendotae* (plus *D. retrocurva* and *D. pulex*, see text), standing crop data.

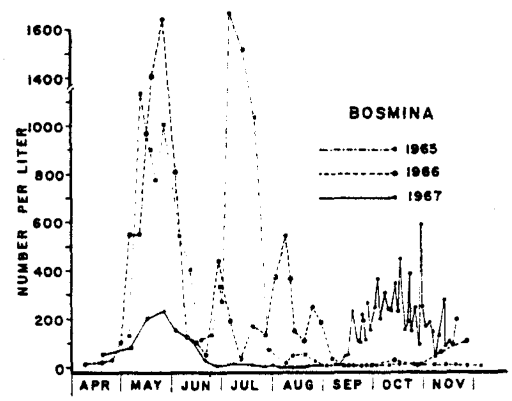


Fig. 7. *Bosmina longirostris – coregoni*, complex standing crop data.

were employed to estimate birth, death, population change, turnover and production rates. Estimates of instantaneous death rates are summarized in Tab. 5. The mean dry weights per individual used to calculate the production rates are presented in Tab. 6. Since the information is processed by computer programming (available, Kellogg Biological Station), as more refined data on any of the parameters (e.g. mean dry weights by size class) become available, better estimates of production can readily be made.

Similarities between standing crop curves for the three seasons (1965–1967) are apparent in Fig. 6, although the range in maximum density was considerable, approximately 230/liter in 1967 to 700/liter in 1966. Based on field data, production during the 1966 and 1967 seasons ranged from 0.061×10^{-3} g/m^3/day to 2.078 g/m^3/day (Table 7).

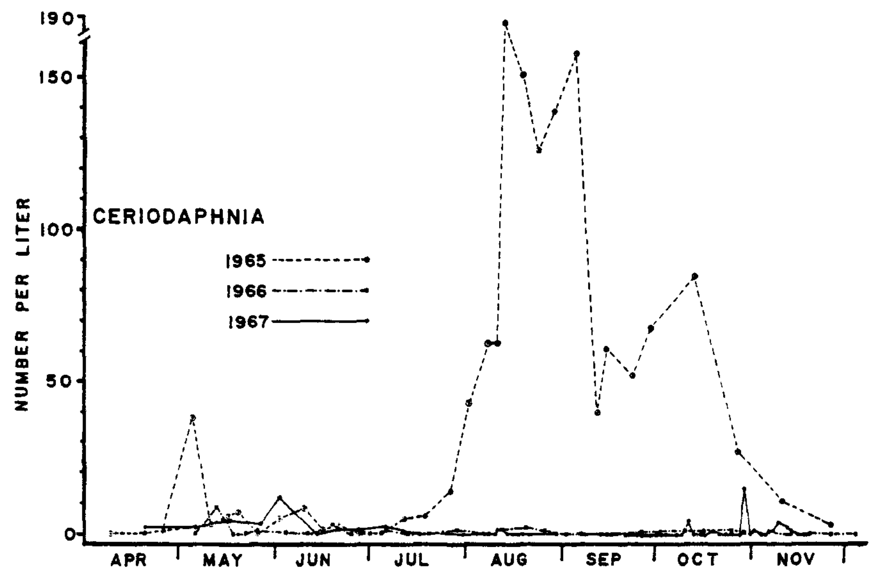


Fig. 8. *Ceriodaphnia reticulata*, standing crop data.

Tab. 5. Estimates of zooplankton instantaneous death rates (d) from field data.
1966

Date	*Daphnia*	*Ceriodaphnia*	*Bosmina*	*Chydorus*	*Cyclops*	*Diaptomus*
May 16	0.128	−0.076	0	0.136	0.131	0.153
19	0.448	0.381	0	0.133	−0.029	0.103
25	0.270	−0.243	0	0.076	0.128	−0.074
June 2	0.318	−0.072	0.209	0.056	0.008	−0.206
9	0.539	0.293	0.069	0.036	0.183	0.327
15	0.592	−0.103	−0.208	−0.004	0.149	0.037
21	1.118	−0.850	0.168	0.032	0.014	0.232
28	−0.086	0	0.287	−0.054	−0.094	−0.192
July 5	0.040	0.767	0.288	0.264	−0.065	0.081
12	0.069	0.024	0.062	0.260	0.599	0.112
19	0.217	0.035	0.143	0.302	−0.306	0.108
27	0.205	−0.059	−0.057	−0.169	0.104	−0.009
Aug 2	0.485	0.103	−0.013	0.018	0.210	0.184
8	0.618	0.178	0.299	−0.146	−0.133	0.401
11	0.876	−0.400	0.316	0.201	0.022	0.821
13	0.129	0.201	0.082	−0.026	0.643	0.139
19	−0.007	0.133	−0.106	−0.042	0.415	−0.095
24	0.217	0.020	0.053	−0.100	0.233	0.051
29	−0.120	0.147	0.257	0.138	−0.332	−0.096
Sept 5	0.479	0.084	−0.088	0.061	0.340	0.184
12	0.135	−0.134	0.592	0.215	−0.266	−0.305
15	−0.179	0.050	0.097	0.124	0.058	0.118
23	0.069	−0.004	0.077	−0.052	−0.161	0.094
29	0.034	−0.006	−0.101	−0.057	−0.092	0.052
Oct 13	−0.100	0.092	0.100	−0.010	0.465	0.078
27	0.139	0.074	−0.113	0.058	0.231	0.056
Nov 10	0.109	0.093	−0.032	0.004	0.225	0.043
May 6	−0.240	0.057	0.029	0.156	0.026	0.003
16	−0.048	0.141	0.004	−0.031	0.033	−0.019
26	0.046	−0.131	0.087	−0.073	0.828	−0.083
June 2	0.236	0.019	0.111	0.094	0.619	0.050
13	0.534	0	0.205	0.366	−0.030	0.648
20	0.123	−0.031	0.526	−0.053	0.727	0.414
27	0.372	0.042	−0.066	−0.301	−0.080	0.067
July 7	0.133	0	0.330	0.348	0.076	0.209
18	0.346	0	0.578	0.170	−0.048	0.693
26	0.402	0	0.381	−0.058	0	−0.271
31	−0.080	0	0.646	0.041	−0.271	0.052
Aug 4	0.095	0	−0.528	−0.027	0.487	−0.442
7	−0.455	0	0.207	−0.030	−0.446	−0.169
11	0.134	0	−0.015	0.019	0.235	−0.235
14	0.249	0	0.934	0.086	0.003	1.142
16	0.361	0	−0.244	0.102	0.093	−0.176
18	−0.306	0	−0.183	0.019	0.072	0.138
21	0.259	0	0.073	0.104	0.072	0.169
Sept 15	0.188	0	−0.668	0.405	−0.008	0.080
17	−0.370	0	0.485	−0.959	−0.240	−0.060
21	−0.420	0	0.311	0.668	0.521	0.127
22	−0.112	0	−0.154	−0.320	−0.459	0.037
24	0.952	0	0.565	0.438	0.392	0.203
25	−0.926	0	−0.799	−0.327	−0.233	−0.517
26	0.544	0	0.355	−0.153	0.029	0.229
28	−0.039	0	−0.107	0.273	−0.143	−0.039
Oct 1	1.318	0	−0.355	−0.466	0.217	−0.054
2	−0.672	0	0.694	0.471	0.127	0.308
3	−0.019	0	−0.063	−0.132	−0.102	−0.013
7	−0.050	0	0.196	0.383	0.504	0.323
9	0.188	0	0.071	−0.018	0.081	−0.024
11	−0.227	0	−0.182	−0.106	−0.231	0.380
13	−0.269	0	0.250	0.373	−0.083	−0.488
15	0.257	0	0.145	−0.070	0.100	0.085
19	0.026	0.527	−0.099	0.045	−0.265	−0.009
21	−0.163	0	0.181	0.285	−0.023	−0.197
23	−0.114	0	−0.265	−0.243	−0.234	0.054
25	0.294	0	0.349	0.293	0.771	0.294
28	−0.626	0	−0.424	−0.321	−0.407	−0.373
30	0.281	0	0.175	0.039	0.067	−0.172
Nov 1	0.177	0	−0.021	0.001	0.025	0.275
3	0.091	0	0.136	0.259	0.505	0.364
5	0.463	0	0.640	0.604	0.193	0.245
7	−0.565	0	−0.605	−0.347	−0.129	−0.645
9	0.196	0.330	0.129	−0.083	0.143	0.159
13	−0.717	0.527	−0.123	0.119	0.307	−0.017
15	−0.108	0	−0.148	0.169	−0.043	−0.068

Tab. 6. Mean dry weights for prey zooplankton species.

Species	Size class[1] range (mm)	Mean dry wt/ individual (µg)	Eggs	Number of individuals
Daphnia galeata mendotae	0.60–1.55	13.6	Mixed	50
	0.60–0.70	10.0	Without	10
	0.80–0.90	11.0	Without	10
	1.00–1.10	11.0	Without	10
	1.20–1.30	12.0	Without	10
	1.40–1.50	15.0	Without	10
	Mean[2]	11.8	Without	50
Ceriodaphnia reticulata	-	6.0	Mixed	*3
Bosmina longirostris	0.25–0.65	7.0	Mixed	50
Chydorus sphaericus	0.20–0.60	1.79	Mixed	*4
Cyclops vernalis	0.44–1.02	8.6	Mixed	50
Diaptomus siciloides	0.69–1.30	7.6	Mixed	50

[1] Total length as measured in a straight line from the base of the spine (Cladocera) or caudal setae (Copepoda) through the eye to the margin of the head.
[2] Mean of 40 females without eggs, 0.60–1.50 mm.
[3] Determined by equivalency of 0.1 mm of body length corresponds to 1.5 µg (based on *Daphnia*).
[4] Determined volumetrically, i.e. a volume containing a calculated number/ml which was dried and weighed; an estimated 1.3×10^6 individuals weighed 2.332 gm.

b) Ceriodaphnia reticulata Jurine – Estimates of *C. reticulata* densities for the three years differ not only in pattern (Fig. 7), but also in magnitude. The midsummer dominance of *Ceriodaphnia* in 1966 was unique for the three year sampling period. The maximum density reached in 1966, about 200/liter, was far greater than the 1965 and 1967 standing crops of 10 to 20/liter. Production estimates for 1966–1967 ranged from 0.003×10^{-1} g/m^3/day to 0.460 g/m^3/day (Tab. 7).

c) Bosmina longirostris (O. F. Müller) – *coregoni* Baird complex. – Although the monospecific nature of the *Bosmina* population had been previously established (Borecky 1956), we discovered in 1967 that *B. coregoni* was present in the lake and probably occurred in 1965–1966 as well. Therefore, the population is referred to in this paper as a co-dominant system. Based on determinations made by Dr. C. E. Goulden (Dept. Limnology, Philadelphia Academy of Science) *B. coregoni* appears to dominate the fall collections.

The maximum standing crop of *Bosmina* was reached earlier in the 1966 season than in 1965 or 1967. In 1965 and 1966, the maximum density attained was more than 1600/liter, while the highest level recorded for 1967 was only 587/liter (Fig. 8). Accordingly, production estimates for 1966 are higher, ranging from 0.001 g/m^3/day to 0.324 g/m^3/day, in contrast to 1967 that ranged from 0.020 g/m^3/day to 0.177 g/m^3/day (Tab. 7).

d) Chydorus sphaericus (O.F.Müller) – *C. sphaericus* reached maximum density peaks of between 1000 and 2000/liter in 1966 and 1967, but the highest recorded density in 1965 was less than 300/liter (Fig. 9). During the 1965 and 1967 seasons, *Chydorus* was abundant in early summer and midfall. Production estimates for *Chydorus* in 1966 and 1967 ranged from 0.002×10^{-1} g/m^3/day to 0.460 g/m^3/day for the two years (Tab. 7).

e) Cyclops vernalis Fischer – In all three years, *C. vernalis*, predominantly a late spring – early summer species, had maximum densities in May and June ranging from 150/liter in 1967 to 1500/liter in 1965 (Fig. 10). Although maximum densities were lower in 1967, the population maintained a higher consistent level throughout the season than in the previous two seasons. Densities of nauplii (lumped with those of *Diaptomus siciloides* Lilljeborg)

Tab. 7. Estimates of production (g/m³/day) for zooplankton species populations from field data. 1966

Date	*Daphnia*	*Ceriodaphnia*	*Bosmina*	*Chydorus*	*Cyclops*[1]	*Diaptomus*[1]
May 16	0.849	0	0.324	0.001	0.023	0.014
19	3.432	0	0.236	0.003	0.089	0.017
25	1.989	0	0.207	0.005	0	0
June 2	1.776	0	0.108	0.003	0.089	0.001
9	2.078	0	0.025	0.004	0	0
15	0.811	0	0.051	0.009	0	0
21	0.238	0	0.040	0.019	0	0.016
28	0.0004	0	0.086	0.008	0	0
July 5	0.006	0	0.019	0.007	0	0.015
12	0.004	0.004	0.017	0.006	0.261	0
19	0.010	0.002	0.134	0.003	0	0
27	0.008	0.012	0.033	0.0002	0	0
Aug 2	0.012	0.046	0.124	0.001	0.018	0.006
8	0.001	0.071	0.410	0.001	0	0
11	0.0002	0.031	0.062	0.0002	0	0
13	0.001	0.207	0.034	0.001	0.082	0.002
19	0.0002	0.093	0.029	0.002	0.030	0
24	0.0002	0.030	0.022	0.004	0	0.003
29	0.061	0.063	0.023	0.019	0	0
Sept 5	0.007	0.025	0	0.010	0	0
12	0	0.003	0	0.010	0	0
15	0.0004	0.013	0.001	0.007	0.005	0.010
23	0.009	0.011	0.001	0.002	0	0.011
29	0.009	0.004	0.001	0.003	0	0.010
Oct 13	0.008	0.003	0.006	0.010	0.014	0.023
27	0.048	0.002	0.001	0.005	0.080	0
Nov 10	0.021	0.0003	0.007	0.005	0.076	0.009
26	0.026	0	0.002	0.009	0.068	0.002
May 6	0	0.002	0.077	0.012	0.033	0
16	0.024	0.003	0.028	0.003	0	0
26	0.212	0.001	0.043	0.005	0.674	0.009
June 2	0.153	0.001	0.085	0.011	0.569	0
13	0.229	0	0.150	0.029	0.045	0.322
20	0.027	0.011	0.052	0.003	0.672	0.089
27	0.090	0.0004	0.002	0.006	0.021	0.068
July 7	0.016	0	0.037	0.004	0	0.157
18	0.006	0	0.017	0.013	0	0.135
26	0.002	0	0.002	0.005	0	0.006
31	0.0001	0	0.002	0.023	0	0.007
Aug 4	0.0005	0	0.0003	0.029	0	0.001
7	0.0001	0	0.003	0.050	0	0.005
11	0.012	0	0.002	0.010	0	0.014
14	0.008	0	0.005	0.001	0.004	0.037
16	0.0004	0	0.001	0.083	0.005	0.005
18	0.0003	0	0.0003	0.069	0.042	0.016
21	0.010	0	0.005	0.074	0.014	0.019
Sept 15	0	0	0.020	0.005	0	0.017
17	0	0	0.282	0.013	0	0.002
21	0	0	0.240	0.051	0	0.019
22	0.007	0	0.117	0.014	0	0.022
24	0.118	0	0.090	0.029	0	0.021
25	0.003	0	0.052	0.007	0	0.006
26	0.028	0	0.179	0.007	0	0.004
28	0.007	0	0.057	0.004	0	0.007
Oct 1	0.005	0	0.051	0.004	0.018	0.003
2	0.003	0	0.088	0.005	0.014	0
3	0.008	0	0.070	0.012	0	0.005
7	0.016	0	0.180	0.002	0	0
9	0.011	0	0.101	0.006	0.006	0.001
11	0.014	0	0.079	0.001	0	0
13	0.012	0	0.126	0.008	0.005	0
15	0.017	0	0.088	0.003	0	0.005
19	0.011	0	0.010	0.001	0	0
21	0.016	0	0.022	0.001	0	0
23	0.013	0	0.573	0.0003	0	0.005
25	0.014	0	0.021	0.005	0.101	0
28	0.010	0	0.019	0.0001	0	0
30	0.074	0	0.017	0.001	0.025	0
Nov 1	0.021	0	0.035	0.003	0.004	0.003
3	0.022	0	0.017	0.001	0.056	0
5	0.025	0	0.014	0.0003	0.011	0.001
7	0.006	0	0.003	0.0001	0	0
9	0.037	0	0.008	0.0001	0.024	0.004
13	0.014	0	0.007	0.007	0.037	0.001
15	0.013	0	0.122	0.0001	0	0.001

[1] Non-naupliar production.

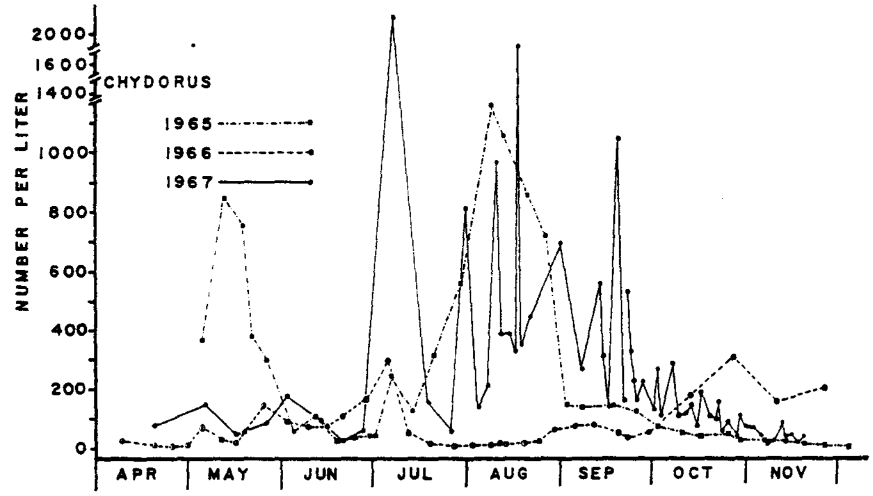


Fig. 9. *Chydorus sphaericus*, standing crop data.

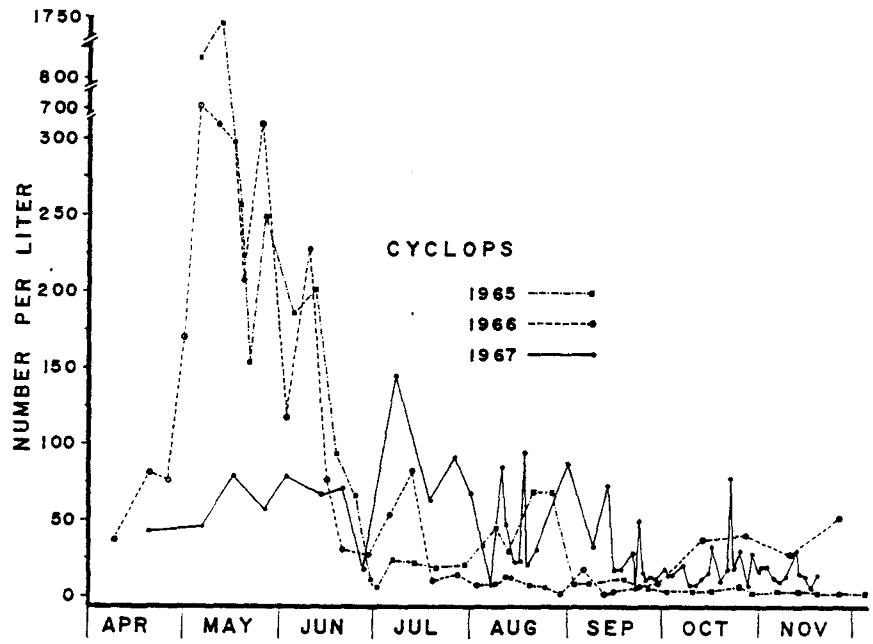


Fig. 10. *Cyclops vernalis*, standing crop data.

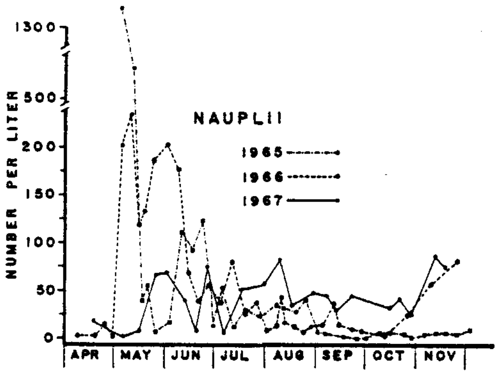


Fig. 11. Copepod nauplii (*Cyclops vernalis* and *Diaptomus siciloides* combined), standing crop.

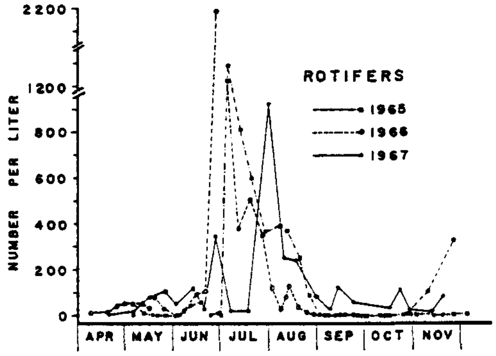


Fig. 13. Rotifer (predominantly *Asplanchna, Keratella* and *Polyarthra*, see text), standing crop.

followed adult copepod densities in all three years (Fig. 11). *Cyclops* non-naupliar production estimates ranged from 0.005 g/m^3/day to 0.706 g/m^3/day during 1966 and 1967 (Table 7).

f) *Diaptomus siciloides* Lilljeborg – *D. siciloides* followed a pattern similar to *C. vernalis* in all three years, but with peak densities, which ranged from 80/liter to 160/liter, observed slightly later in the season (Fig. 12). *Diaptomus* production estimates covered a range of 0.001 g/m^3/day to 0.294 g/m^3/day during the 1966 and 1967 seasons (Tab. 7).

g) *Rotifers*. – Despite the inaccuracies involved in lumping rotifer species together, density patterns were quite similar for the three years. Maximum densities which were approximately 1000 to 2000/liter were observed in June and July in all three seasons (Fig. 13). The sequence of rotifer generic dominance in 1966 and 1967 was *Asplanchna – Keratella – Polyarthra.*

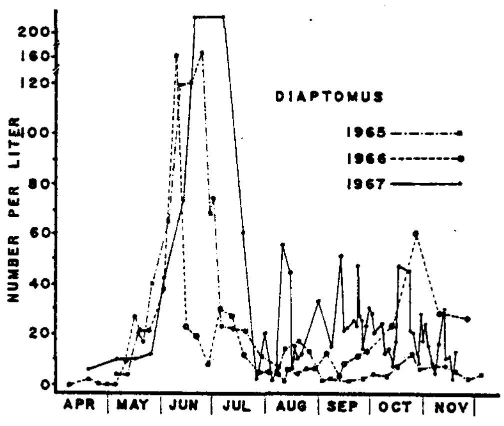


Fig. 12. *Diaptomus siciloides*, standing crop data.

D. Leptodora population data and production estimates

a) *Standing crop*. – Patterns of population density for *L. kindtii* were different for the three seasons (1965–1967). Maximum densities were 1.7/liter in 1965, 4.2/liter in 1966 and 1.8/liter in 1967 (Fig. 14). In 1965, the curve of population growth and decline peaked in early July and again in mid-August. Following both peaks, population density never fell below 0.1/liter, until late September following the second maximum. During the 1966 season the *Leptodora* population increased to a mid-June maximum more than three times greater than either peak observed in 1965. This very high density was followed several days later by a sharp decline to less than 1/liter; the decline continued and the population density remained much lower than in 1965, seldom exceeding 0.02/liter for the remainder of the season. The 1967 pattern (Fig. 14) resembles that of 1966 although the curve is slightly trimodal with declines to about 0.5/liter in mid-July and late August, the latter associated with the first appearance of males. Except for the two brief low periods, the population re-

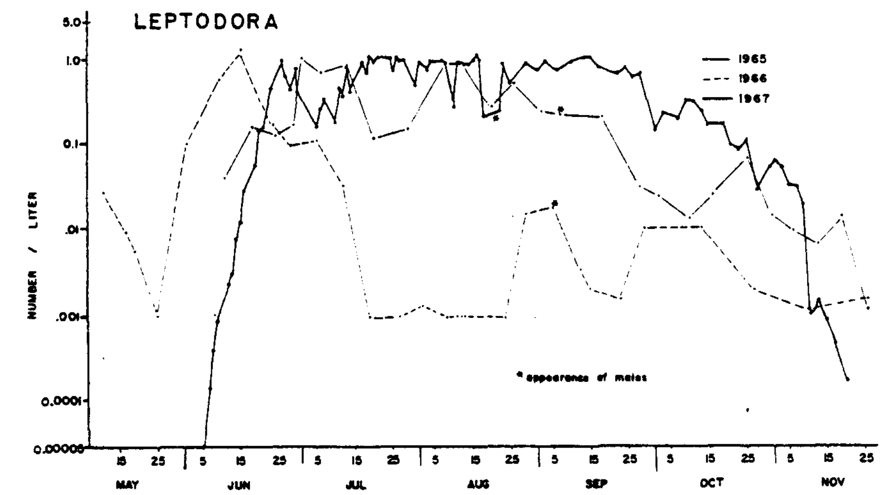


Fig. 14. *Leptodora kindtii*, standing crop.

Table 8. *Leptodora* size class composition (percent in each mm size class).
1966

Date	2	3	4	5	6	7	8	9	10	11	12
May 16	–	8.0	28.0	24.0	16.0	16.0	–	–	–	8.0	–
17, 18	5.0	15.0	5.0	15.0	25.0	15.0	5.0	–	15.0	–	–
19	–	23.5	11.8	–	11.8	–	29.4	23.5	–	–	–
24, 25	3.0	10.7	33.4	13.6	4.5	7.6	4.5	9.1	7.6	3.0	3.0
June 2	–	8.3	14.5	27.0	10.4	12.5	10.4	12.5	6.3	–	–
3	2.0	–	6.0	12.0	20.0	10.0	24.0	10.0	14.0	2.0	–
6	1.8	24.6	29.8	7.0	1.8	5.3	8.7	8.7	10.5	1.8	–
7	–	4.0	10.0	18.0	22.0	10.0	14.0	16.0	4.0	2.0	–
9, 10	1.0	1.8	10.9	13.6	15.5	13.6	19.1	10.9	9.1	2.7	1.8
13	–	6.0	20.0	24.0	12.0	20.0	8.0	8.0	2.0	–	–
14	–	8.0	28.0	24.0	12.0	20.0	4.0	–	4.0	–	–
15	6.0	14.0	22.0	28.0	16.0	10.0	4.0	–	–	–	–
17	–	12.0	24.0	28.0	16.0	20.0	–	–	–	–	–
21	–	2.0	14.0	18.0	28.0	16.0	18.0	4.0	–	–	–
24	–	–	–	6.0	14.0	20.0	26.0	20.0	14.0	–	–
27	–	–	6.0	18.0	18.0	22.0	24.0	8.0	4.0	–	–
28	6.7	24.4	35.6	20.0	11.1	2.2	–	–	–	–	–
July 1	–	–	–	10.0	24.0	44.0	18.0	2.0	–	2.0	–
5	4.0	4.0	20.0	26.0	10.0	28.0	4.0	–	–	–	–
6	–	4.0	10.0	28.0	32.0	22.0	4.0	–	–	–	–
11	–	8.0	8.0	4.0	12.0	36.0	24.0	8.0	–	–	–
12	–	4.4	8.8	13.0	21.7	39.1	13.0	–	–	–	–
14	2.0	2.0	2.0	2.0	14.0	30.0	28.0	20.0	–	–	–
15	–	16.0	14.0	6.0	10.0	22.0	28.0	4.0	–	–	–
16	–	4.0	28.0	32.0	20.0	4.0	12.0	–	–	–	–
17	–	36.0	16.0	20.0	8.0	8.0	8.0	4.0	–	–	–
18	–	–	8.0	8.0	20.0	20.0	32.0	12.0	–	–	–
19	2.0	2.0	11.8	9.7	15.7	31.4	13.7	9.7	2.0	2.0	–
20	–	4.0	8.0	16.0	8.0	52.0	12.0	–	–	–	–
21	–	16.0	12.0	8.0	32.0	16.0	16.0	–	–	–	–
22	–	–	8.0	8.0	20.0	28.0	28.0	8.0	–	–	–
25	–	14.0	10.0	6.0	3.0	18.0	33.0	15.0	1.0	–	–
26	2.0	16.0	14.0	14.0	10.0	18.0	8.0	14.0	4.0	–	–
27	–	–	–	11.5	15.4	38.5	23.1	7.7	38.8	–	–
28	–	–	–	–	8.0	38.0	28.0	16.0	6.0	4.0	–
29	–	4.0	12.0	12.0	14.0	18.0	28.0	12.0	–	–	–
Aug 1, 2	–	–	–	14.8	18.5	11.1	29.6	18.5	5.6	1.9	–
4	–	–	8.0	8.0	12.0	22.0	30.0	10.0	8.0	2.0	–
6	–	–	7.4	7.4	7.4	11.1	22.2	29.7	7.4	–	7.4
8	1.7	8.5	1.7	18.6	8.5	18.6	18.6	17.0	16.8	–	–
9	2.0	12.0	6.0	8.0	12.0	16.0	30.0	10.0	2.0	2.0	–
10	–	12.0	2.0	20.0	8.0	6.0	20.0	10.0	2.0	–	–
11	2.9	22.9	11.4	20.0	20.0	5.7	17.1	–	–	–	–
13	–	–	–	–	3.8	7.7	26.9	34.7	26.9	–	–

Table 8. (Continued)

Date	2	3	4	5	6	7	8	9	10	11	12	13
17, 19	-	3.5	6.8	13.8	6.8	13.8	3.5	34.5	13.8	-	3.5	
23	1.0	10.0	5.0	22.0	23.0	28.0	10.0	1.0	-	-	-	
24	-	1.9	9.2	5.6	11.1	9.2	31.5	27.8	3.7	-	-	
26	-	2.0	-	2.0	-	26.0	20.0	34.0	14.0	2.0	-	
29	1.1	2.2	9.9	15.4	22.0	19.8	15.4	7.6	4.4	2.2	-	
31	-	-	2.0	4.0	8.0	16.0	36.0	26.0	6.0	2.0	-	
Sept 1	-	4.0	-	12.0	36.0	28.0	12.0	8.0	-	-	-	
5	1.5	3.1	27.7	13.9	23.0	20.0	7.8	1.5	-	1.5	-	
12, 15	1.9	16.6	1.9	11.0	16.7	26.0	20.4	5.6	-	-	-	
18	-	8.0	4.0	4.0	12.0	28.0	24.0	20.0	-	-	-	
22	-	-	-	4.0	12.0	28.0	32.0	24.0	-	-	-	
23	-	5.6	-	-	11.1	16.7	16.7	25.0	19.3	5.6	-	
25	-	4.0	4.0	4.0	6.0	20.0	28.0	26.0	8.0	-	-	
29, 30	3.3	1.6	-	6.5	11.4	27.9	23.0	16.4	3.3	3.3	3.3	
Oct 5, 6	-	-	-	4.0	6.0	24.0	26.0	24.0	14.0	2.0	-	
13	-	1.6	3.1	10.9	26.6	20.3	25.0	7.8	3.1	-	1.6	
20	-	2.1	2.1	4.2	27.0	31.3	18.7	2.1	8.3	4.2	-	
27	-	6.1	4.1	8.2	14.2	32.7	28.6	-	6.1	-	-	
Nov 6	-	2.8	2.8	16.6	44.4	25.0	2.8	2.8	2.8	-	-	
10	-	-	-	-	50.0	50.0	-	-	-	-	-	
18	-	-	-	-	-	100.0	-	-	-	-	-	

Table 8. (Continued) Size class composition (percent in each mm size class).
1967

Date	2	3	4	5	6	7	8	9	10	11	12	13
June 5	-	-	-	-	-	-	100.0	-	-	-	-	-
7	-	-	-	-	20.0	-	20.0	20.0	-	20.0	20.0	-
8	-	-	7.7	15.4	38.5	23.1	7.7	7.7	-	-	-	-
9	-	-	5.3	26.3	21.1	15.8	10.5	15.8	-	-	-	-
12	2.8	2.8	3.7	20.6	20.6	11.2	20.6	7.4	3.7	1.9	3.7	0.9
13	3.2	6.4	26.4	21.6	18.4	8.0	4.8	4.8	5.6	8.0	-	-
14	2.2	11.7	16.1	23.9	21.1	12.1	6.7	2.8	1.7	1.7	-	-
15	1.2	10.8	17.2	20.0	22.8	11.2	6.8	6.4	2.4	0.8	-	0.4
16	4.0	14.0	10.0	20.0	22.0	14.0	16.0	-	-	-	-	-
19	-	-	4.0	4.0	24.0	16.0	32.0	8.0	12.0	-	-	-
20	-	4.0	-	4.0	12.0	24.0	12.0	16.0	4.0	12.0	-	-
21	-	4.0	12.0	4.0	12.0	24.0	16.0	24.0	-	4.0	-	-
23	8.0	4.0	12.0	12.0	16.0	8.0	3.0	24.0	-	4.0	-	-
26	4.0	16.0	8.0	24.0	12.0	24.0	8.0	-	4.0	-	-	-
27	-	-	-	8.0	24.0	16.0	20.0	20.0	16.0	-	-	-
28	-	-	4.0	4.0	8.0	32.0	28.0	8.0	12.0	-	-	-
29	-	16.0	12.0	28.0	4.0	4.0	20.0	12.0	4.0	-	-	-
30	-	12.0	8.0	-	4.0	12.0	28.0	12.0	16.0	4.0	4.0	-
July 5	-	8.0	8.0	4.0	4.0	4.0	16.0	24.0	24.0	8.0	-	-
6	8.0	5.0	4.0	-	8.0	16.0	24.0	16.0	4.0	-	-	-
7	4.0	4.0	8.0	4.0	24.0	16.0	20.0	12.0	8.0	-	-	-
10	-	24.0	16.0	20.0	12.0	12.0	12.0	4.0	-	-	-	-
11	-	32.0	26.0	8.0	-	4.0	4.0	12.0	4.0	-	-	-
12	4.0	4.0	16.0	16.0	16.0	12.0	16.0	8.0	4.0	4.0	-	-
13	-	8.0	4.0	16.0	24.0	20.0	12.0	8.0	8.0	-	-	-
14	8.0	16.0	8.0	4.0	20.0	24.0	12.0	4.0	4.0	-	-	-
17	-	4.0	4.0	12.0	12.0	28.0	36.0	4.0	-	-	-	-
18	8.0	32.0	16.0	20.0	-	4.0	12.0	8.0	-	-	-	-
19	4.0	8.0	20.0	12.0	24.0	16.0	20.0	4.0	4.0	-	-	-
20	-	12.0	8.0	8.0	4.0	20.0	28.0	16.0	4.0	-	-	-
21	4.0	8.0	8.0	4.0	12.0	20.0	24.0	20.0	-	-	-	-
24	-	12.0	4.0	32.0	24.0	16.0	8.0	4.0	-	-	-	-
25	-	-	12.0	24.0	24.0	24.0	8.0	8.0	-	-	-	-
26	-	8.0	4.0	12.0	12.0	24.0	20.0	8.0	4.0	-	-	-
27	4.0	4.0	12.0	16.0	16.0	24.0	12.0	12.0	-	-	-	-
28	4.0	16.0	4.0	4.0	20.0	36.0	16.0	-	-	-	-	-
31	-	4.0	8.0	20.0	24.0	20.0	16.0	8.0	-	-	-	-
Aug 1	-	8.0	4.0	4.0	16.0	40.0	28.0	-	-	-	-	-
3	4.0	20.0	4.0	28.0	24.0	16.0	-	4.0	-	-	-	-
4	-	16.0	8.0	12.0	28.0	24.0	8.0	4.0	-	-	-	-
7	4.0	4.0	12.0	8.0	40.0	20.0	12.0	-	-	-	-	-
8	4.0	4.0	20.0	8.0	28.0	20.0	16.0	-	-	-	-	-
10	8.0	4.0	20.0	12.0	24.0	20.0	12.0	-	-	-	-	-
11	8.0	4.0	4.0	-	32.0	36.0	16.0	-	-	-	-	-
14	-	8.0	8.0	12.0	12.0	24.0	36.0	-	-	-	-	-
15	-	8.0	4.0	24.0	4.0	16.0	32.0	12.0	-	-	-	-
16	4.0	-	8.0	12.0	20.0	4.0	20.0	32.0	-	-	-	-
17	4.0	12.0	16.0	12.0	12.0	16.0	28.0	4.0	-	-	-	-
18	-	8.0	4.0	4.0	24.0	24.0	8.0	12.0	8.0	-	-	-
21	-	4.0	4.0	4.0	12.0	24.0	24.0	16.0	12.0	-	-	-

Table 8. (Continued)

Date	2	3	4	5	6	7	8	9	10	11	12	13
22	–	–	4.0	12.0	–	12.0	20.0	40.0	12.0	–	–	–
23	–	8.0	8.0	8.0	16.0	24.0	28.0	4.0	4.0	–	–	–
25	–	7.9	7.9	22.5	19.7	10.5	13.1	6.6	2.6	–	–	–
29	–	5.3	5.3	12.0	10.6	19.1	16.0	21.4	–	–	–	–
Sept 1	–	–	12.0	4.0	24.0	16.0	4.0	16.0	16.0	4.0	4.0	–
3	–	2.0	2.0	10.0	12.0	28.0	20.0	16.0	8.0	2.0	–	–
6	–	20.0	8.0	10.0	8.0	12.0	18.0	12.0	8.0	4.0	–	–
9	–	8.0	20.0	20.0	36.0	4.0	4.0	4.0	4.0	–	–	–
13	–	4.0	4.0	3.0	32.0	28.0	8.0	4.0	8.0	4.0	–	–
15	–	–	8.0	8.0	16.0	40.0	20.0	4.0	4.0	–	–	–
17	–	–	4.0	–	24.0	36.0	36.0	–	–	–	–	–
22	–	4.0	8.0	12.0	28.0	36.0	12.0	–	–	–	–	–
24	–	–	12.0	16.0	16.0	8.0	32.0	16.0	–	–	–	–
26	–	–	16.0	16.0	20.0	8.0	32.0	8.0	–	–	–	–
28	–	–	12.0	12.0	4.0	28.0	20.0	12.0	8.0	4.0	–	–
Oct 1	–	8.0	12.0	20.0	16.0	20.0	20.0	4.0	–	–	–	–
3	–	8.0	4.0	8.0	20.0	24.0	28.0	4.0	4.0	–	–	–
7	4.0	8.0	12.0	12.0	16.0	24.0	12.0	8.0	–	4.0	–	–
9	–	12.0	12.0	8.0	8.0	28.0	8.0	8.0	8.0	8.0	–	–
11	–	12.0	4.0	16.0	12.0	20.0	16.0	4.0	8.0	8.0	–	–
13	–	–	4.0	8.0	28.0	12.0	12.0	20.0	8.0	8.0	–	–
15	–	–	–	28.0	4.0	28.0	20.0	8.0	8.0	4.0	–	–
19	–	–	–	–	32.0	28.0	16.0	12.0	4.0	4.0	4.0	–
21	–	–	–	4.0	8.0	56.0	28.0	–	4.0	–	–	–
23	–	–	8.0	4.0	12.0	24.0	24.0	20.0	4.0	4.0	–	–
25	–	–	8.0	–	8.0	40.0	32.0	8.0	4.0	–	–	–
28	–	–	–	–	8.0	36.0	36.0	16.0	4.0	–	–	–
30	–	4.0	16.0	12.0	20.0	28.0	4.0	12.0	–	4.0	–	–
Nov 1	–	–	–	12.0	–	12.0	28.0	28.0	4.0	–	4.0	–
3	–	–	4.0	4.0	12.0	24.0	32.0	20.0	4.0	–	–	–
5	–	–	4.0	8.0	16.0	36.0	20.0	12.0	–	4.0	–	–
7	–	–	–	–	12.0	16.0	36.0	16.0	4.0	12.0	4.0	–
9	–	–	–	4.0	20.0	8.0	20.0	20.0	16.0	4.0	–	–
11	–	–	–	4.0	20.0	36.0	32.0	–	8.0	–	–	–
13	–	–	4.0	12.0	20.0	24.0	28.0	4.0	4.0	4.0	–	–
15	–	–	4.0	20.0	20.0	28.0	8.0	16.0	4.0	–	–	–
17	–	–	46.2	30.7	15.4	7.7	–	–	–	–	–	–
19	–	–	–	25.0	25.0	25.0	25.0	–	–	–	–	–

mained about 1/liter from late June through late September.

b) Size distribution and sex ratio. – The size distribution in the *Leptodora* population was determined at frequent intervals in 1966 and 1967 (Tab. 8). The general pattern was for the largest individuals to be present at low population densities and for dense populations to be composed predominatly of small individuals, especially 6 and 7 mm females.

Male-female percentages were determined for each sampling date, when males were present, for all three years. The first males were observed about the same time, early September, in 1965 and 1966 while they were detected by mid-August in 1967. During the 1967 season males constituted 50% or more of the population from mid-September on. In 1965 and 1966 the 50% level was not reached until late October.

c) Population parameters. – Estimates of finite birth, instantaneous birth, death and population change rates are summarized in Tab. 9 for 1966 and 1967. Based on the field population data, estimates of turnover time ranged from 1.5 to 200 days. The highest calculated rate of population increase was + 0.822 and the highest rate of decline, − 2.708.

Mean clutch size, including all ages of embryos, varied from 0.8 to 16.0 for the two seasons. When mean clutch size was calculated by embryo age class (see Tab. 3), the ranges for ages I to IV were as follows: I, 1–13; II, 1–17; III, 3–5; and IV, 2–7. Although these values indicate embryo mortality, unequal developmental rates among clutch members coupled with gradual release of the clutch as free swimming young is undoubtedly of primary significance.

Following the disappearance of summer embryos in the fall (Tab. 10), the winter eggs,

Tab. 9. Estimates of population parameters for *Leptodora kindtii*. 1966

Date	Median temp.	Standing crop: No. per liter	Standing crop: mg per cubic meter	Kcal per cubic meter	Fecundity and recruitment: Per cent females with embryos	Mean clutch size ($\bar{E}$)	Embryos per liter (E)	Development time (days)(D)[1]	Finite birth rate (B)	Inst. birth rate (b)	Inst. rate of population change (r)	Turnover time (days)	Yield: Inst. death rate (d)
May 11	8.9	0.043	1.08	0.006	(Metanauplii)								
16	13.9	0.009	0.91	0.005	0	0	0	–	0	0	−0.059	–	0.059
18	14.5	0.008	0.73	0.004	0	0	0	–	0	0	−0.134	–	0.134
19	14.9	0.007	1.00	0.005	0	0	0	–	0	0	0.152	–	−0.152
24	15.3	0.015	1.72	0.009	0	0	0	–	0	0	−2.708	–	2.708
25	15.5	0.001	0.11	0.001	0	0	0	–	0	0	0.822	–	−0.822
June 2	16.4	0.139	17.60	0.091	0	0	0	–	0	0	0.542	–	−0.542
3	17.5	−0.239	34.32	0.179	0	0	0	–	0	0	0.250	–	−0.250
7	20.0	1.536	213.71	1.108	6.0	4.0	0.36864	6	0.040	0.039	−0.037	25.0	0.076
9	21.5	1.430	206.43	1.070	24.0	4.5	1.54440	6	0.180	0.166	0.270	5.6	−0.104
13	21.5	4.209.	519.26	2.691	8.0	4.0	1.34688	6	0.053	0.049	−0.779	18.9	0.828
14–15	21.4	0.886	97.07	0.503	12.0	3.0	0.31896	6	0.060	0.058	−0.152	16.7	0.210
21–24	26.1	0.356	42.53	0.220	20.0	3.3	0.35244	3	0.330	0.285	−0.129	3.0	0.414
27–28	26.0	0.144	15.50	0.080	8.0	2.5	0.28800	3	0.667	0.513	0.033	1.5	0.479
July 5–6	25.4	0.182	23.44	0.121	10.0	2.4	0.04368	3	0.080	0.770	−0.031	12.5	0.108
11–12	25.1	0.054	7.18	0.037	0	0	0	–	0	0	−0.713	–	0.713
19	24.2	0.001	0.13	0.001	2.0	1.0	0.00002	4	0.005	0.010	0	200.0	0.010
27	24.5	0.001	0.15	0.001	10.0	5.6	0.00056	4	0.140	0.131	0.116	7.6	0.016
August 1–2	23.4	0.002	0.30	0.002	2.0	2.0	0.00008	5	0.008	0.010	−0.115	125.0	0.125
8	25.9	0.001	0.12	0.001	4.0	5.5	0.00022	3	0.073	0.068	0	13.7	0.068
11	23.7	0.001	0.10	0.001	0	0	0	–	0	0	0	–	0
13–15	22.8	0.001	0.19	0.001	4.0	16.0	0.00064	5	0.128	0.122	0	7.8	0.122
17–19	23.8	0.001	0.17	0.001	8.0	3.0	0.00024	4	0.060	0.058	0	16.7	0.058
24	20.0	0.001	0.15	0.001	6.0	6.0	0.00036	6	0.060	0.058	0.480	16.7	−0.421
29	24.8	0.011	1.65	0.009	16.0	7.6	0.01338	4	0.304	0.262	0.062	3.3	0.200
September 5	22.0	0.017	2.01	0.010	4.0	9.0	0.00612	5	0.072	0.068	−0.149	13.9	0.216
12	21.2	0.006	0.72	0.004	0	0	0	–	0	0	−0.135	–	0.135
15	19.2	0.004	–	–	–	–	–	–	–	–	−0.036	–	0.036
23	15.9	0.003	0.59	0.003	16.0[2]	5.5[2]	0.00264[2]	9	0.106	0.104	1.117	9.4	−1.013
25	15.3	0.028	5.00	0.026	8.0[2]	5.0[2]	0.01120[2]	9	0.047	0.049	−0.154	21.3	0.203
29–30	14.3	0.014	2.25	0.012	–	–	–	–	–	–	0.021	–	−0.021
October 5–6	12.3	0.016	3.34	0.017	8.0[2]	6.5[2]	0.00832[2]	11	0.066	0.068	−0.084	15.2	0.152
13	12.0	0.012	2.02	0.010	12.0[2]	6.7[2]	0.00965[2]	11	0.139	0.131	−0.077	7.2	0.208
20	8.2	0.007	1.40	0.007	0	0	0	–	0	0	−0.121	–[3]	0.121
27	10.7	0.003	0.45	0.002	4.0[2]	14.0[2]	0.00168[2]	–	0	0	−0.141	–[3]	0.141
November 6	3.4	0.002	0.27	0.001	4.0[2]	12.0[2]	0.00096[2]	–	–	–	−0.173	–	0.173
10	10.0	0.0003	0.04	0.210	0	0	0	–	–	–	0	–	0
18	9.4	0.0003	0.05	0.233	0	0	0	–	–	–	0	–	0
26	7.1	0	–	–	0	0	0	–	–	–	–	–	–

Tab. 9. (Continued). Estimates of population parameters for *Leptodora kindtii*.
1967

Date	Median temp.	Standing crop No. per liter	Standing crop mg per cubic meter	Kcal per cubic meter	Fecundity and recruitment: Per cent females with embryos	Mean clutch size ($\bar{E}$)	Embryos per liter (E)	Development time (days)(D)[1]	Finite birth rate (B)	Inst. birth rate (b)	Inst. population change (r)	Turnover time (days)	Inst. death rate (d)
June 5	20.1	0.0002	0.03	0.166	0	0	0	–	0	0	0.284	–	−0.284
7	21.2	0.0002	0.04	0.197	0	0	0	–	0	0	1.012	–	−1.012
8	21.8	0.001	0.13	0.668	0	0	0	–	0	0	0.375	–	−0.375
9	22.9	0.001	0.13	0.001	0	0	0	–	0	0	0.576	–	−0.576
12	27.2	0.005	0.85	0.004	4.6	8.0	0.00199	1.9	0.205	0.186	0.144	4.9	0.042
13	28.0	0.006	0.71	0.004	0	0	0	–	0	0	0.378	–	−0.378
14	29.0	0.009	1.02	0.005	0	0	0	–	0	0	0.836	–	−0.836
15	28.5	0.021	2.26	0.012	2.0	3.1	0.00130	1.4	0.044	0.043	0.926	22.7	−0.883
16	27.8	0.053	5.90	0.031	0	0	0	–	0	0	0.137	–	−0.137
19	24.0	0.080	18.27	0.095	32.0	4.9	0.12544	3.1	0.506	0.409	1.050	2.0	−0.641
20	23.4	0.028	50.60	0.262	20.0	1.6	0.00896	3.7	0.086	0.082	2.420	11.6	−2.338
21	24.0	0.315	46.95	0.243	4.0	1.0	0.01260	3.1	0.013	0.013	0.731	77.9	−0.718
23	20.9	0.073	96.22	0.499	0	0	0	–	0	0	1.008	–	−1.008
26	20.6	1.500	143.91	0.746	0	0	0	–	0	0	−0.568	–	0.568
27	21.8	0.850	131.16	0.680	0	0	0	–	0	0	−0.189	–	0.189
28	22.3	0.704	112.42	0.583	0	0	0	–	0	0	0.293	–	−0.293
29	21.8	0.944	127.56	0.661	8.0	4.0	0.27974	4.1	0.060	0.058	−0.328	–	0.386
30	20.6	0.680	129.30	0.670	28.0	2.3	0.43792	5.1	0.126	0.110	−0.157	7.9	0.267
July 5	21.8	0.310	53.99	0.280	4.0	5.0	0.06200	4.4	0.045	0.044	0.498	22.2	−0.454
6	21.8	0.510	84.04	0.435	16.0	2.5	0.20400	4.4	0.091	0.087	0.174	11.0	−0.087
7	21.8	0.607	83.80	0.434	0	0	0	–	0	0	−0.165	–	0.165
10	23.4	0.370	39.64	0.205	0	0	0	–	0	0	0.697	–	−0.697
11	22.9	0.743	74.00	0.383	0	0	0	–	0	0	−0.173	–	0.173
12	23.7	0.625	84.07	0.436	4.0	3.0	0.07500	3.1	0.039	0.038	0.428	–	−0.390
13	24.3	0.959	127.80	0.662	0	0	0	–	0	0	−0.341	–	0.341
14	20.6	0.682	82.45	0.427	4.0	1.0	0.02728	5.1	0.008	0.008	0.174	125.0	−0.166
17	21.8	1.148	159.38	0.826	0	0	0	–	0	0	−0.255	–	0.255
18	21.8	0.890	85.27	0.442	0	0	0	–	0	0	0.684	–	−0.684
19	20.6	1.763	238.34	1.235	0	0	0	–	0	0	−0.466	–	0.466
20	21.8	1.106	173.35	0.898	16.0	2.3	0.40701	4.4	0.084	0.081	0.376	11.9	−0.295
21	21.8	1.610	218.93	1.135	0	0	0	–	0	0	−0.016	–	0.016
24	22.3	1.534	176.74	0.916	0	0	0	–	0	0	−0.539	–	0.539
25	22.8	0.895	136.13	0.705	4.0	13.0	0.46540	3.7	0.141	0.132	0.646	7.1	−0.514
26	24.0	1.708	261.10	1.353	24.0	4.2	1.72166	3.1	0.325	0.281	0.098	3.1	0.383
27	25.1	1.548	196.67	1.019	12.0	4.0	0.74304	2.7	0.178	0.164	−0.012	5.6	0.176
28	24.8	1.529	187.18	0.970	0	0	0	–	–	–	−0.234	–	0.234
31	24.5	0.758	99.80	0.517	4.0	2.0	0.06064	2.9	0.028	0.028	0.358	35.7	−0.330
August 1	24.5	1.084	160.65	0.832	12.0	2.0	0.26016	2.9	0.083	0.080	−0.066	12.0	0.146
3	24.5	0.950	99.90	0.518	0	0	0	–	–	–	0.154	–	−0.154
4	23.3	1.108	170.94	0.886	8.0	9.0	0.79776	3.7	0.195	0.134	0.016	5.1	0.158
7	22.3	1.162	147.96	0.767	12.0	0.8	0.10458	4.4	0.020	0.020	0.270	50.0	−0.250
8	24.5	1.052	125.82	0.652	4.0	1.0	0.04208	2.9	0.014	0.014	−0.517	71.4	0.527
10	23.4	0.541	65.51	0.355	8.0	3.5	0.15148	3.7	0.076	0.073	0.810	13.2	−0.733
11	22.7	1.216	254.34	1.318	40.0	4.0	1.94560	3.7	0.432	0.366	−0.058	2.3	0.424

Table 9. (Continued). Estimates of population parameters for *Leptodora kindtii*.
1967 (continued)

Date	Median temp.	Standing crop: No. per liter	Standing crop: mg per cubic meter	Kcal per cubic meter	Fecundity and recruitment: Per cent females with embryos	Mean clutch size ($\bar{E}$)	Embryos per liter (E)	Development time (days)(D)[1]	Finite birth rate (B)	Inst. birth rate (b)	Inst. rate of population change (r)	Turnover time (days)	Inst. death rate (d)
14.......	21.8	1.022	161.21	0.835	20.0	2.6	0.53144	4.4	0.118	0.112	0.270	8.5	−0.158
15.......	22.9	1.339	318.14	1.649	40.0	5.1	2.73156	3.7	0.551	0.439	0.325	1.8	0.114
16.......	22.9	1.854	423.64	2.195	32.0	5.5	3.26304	4.4	0.400	0.336	−0.334	2.5	0.670
17.......	22.9	1.372	261.48	1.355	24.0	6.5	2.07012	3.7	0.422	0.352	−1.139	2.4	1.491
18.......	23.4	0.425	86.65	0.449	28.0	4.4	0.52360	3.7	0.333	0.288	0.028	3.0	0.260
21.......	21.5	0.462	82.93	0.430	20.0	1.7	0.15708	4.4	0.077	0.074	0.057	13.0	0.017
22.......	22.0	0.489	123.34	0.639	36.0	4.8	0.84499	4.4	0.393	0.331	0.758	2.5	−0.427
23.......	20.0	1.043	153.39	0.795	8.0	3.0	0.25032	6.1	0.039	0.038	−0.186	25.6	0.224
25.......	20.0	0.791	141.79	0.735	17.0	4.8	0.64546	6.1	0.134	0.126	0.113	7.5	0.013
29.......	18.9	1.134	216.94	1.124	27.0	3.3	0.99917	6.5	0.136	0.128	0.025	7.4	0.153
September 1.....	20.6	0.931	145.80	0.756	4.0	2.0	0.07448	6.5	0.012	0.012	0.015	83.3	−0.003
3.....	21.8	1.324	302.74	1.569	10.0[2]	2.8[2]	0.49803[2]	6.5	0.072	0.070	−0.076	13.9	0.146
6.....	20.6	0.949	57.86	0.300	2.0[2]	3.0[2]	0.05403[2]	6.5	0.012	0.012	0.060	83.3	−0.048
9.....	20.9	1.260	138.03	0.715	0	0	0	–	–	–	0.092	–	−0.092
13.....	19.5	1.820	118.95	0.616	16.0[3]	3.0[2]	0.87360[3]	–	–	–	−0.016	–	0.016
15.....	17.9	1.764	114.01	0.591	4.0[2]	3.0[2]	0.37340[2]	7.3	0.052	0.051	−0.266	19.2	0.317
17.....	20.4	0.965	86.19	0.447	4.0[2]	2.0[2]	0.07450[2]	6.1	0.029	0.030	−0.029	34.4	0.059
22.....	18.4	0.895	53.65	0.278	4.0[2]	2.0[2]	0.07160[2]	7.3	0.011	0.011	0.040	90.9	0.030
24.....	16.0	0.969	61.76	0.320	0	0	0	–	–	–	−0.056	–	0.056
26.....	16.0	0.867	66.10	0.343	4.0[3]	5.0[3]	0.17340[3]	–	–	–	0.018	–	−0.018
28.....	14.0	0.899	72.94	0.378	4.0[3]	2.0[3]	0.07327[3]	–	–	–	0.342	–	−0.342
October 1.......	10.6	0.454	8.58	0.044	0	0	0	–	–	–	0.027	–	−0.027
3.......	14.4	0.479	53.25	0.276	8.0[3]	8.0[3]	0.30656[3]	–	–	–	−0.030	–	0.030
7.......	13.8	0.425	9.48	0.049	0	0	0	–	–	–	0.079	–	−0.079
9.......	13.0	0.498	56.32	0.292	4.0[3]	11.4[3]	0.21912[3]	–	–	–	0.017	–	−0.017
11.......	11.8	0.515	41.51	0.215	4.0[3]	8.0[3]	0.16480[3]	–	–	–	−1.593	–	1.593
13.......	11.0	0.022	14.52	0.075	0	0	0	–	–	–	−0.120	–	0.120
15.......	12.9	0.018	9.32	0.048	0	0	0	–	–	–	0.032	–	−0.032
19.......	11.0	0.019	7.92	0.041	0	0	0	–	–	–	−0.499	–	0.499
21.......	9.0	0.007	3.78	0.020	0	0	0	–	–	–	1.309	–	−1.309
23.......	10.0	0.096	3.10	0.016	0	0	0	–	–	–	0.359	–	−0.359
25.......	10.0	0.197	5.05	0.026	0	0	0	–	–	–	−0.478	–	0.478
28.......	6.0	0.047	4.39	0.023	0	0	0	–	–	–	0.285	–	−0.285
30.......	7.0	0.083	0.69	0.004	0	0	0	–	–	–	0.029	–	−0.029
November 1.....	8.6	0.088	2.84	0.015	4.0	1.0[2]	0.00100	–	–	–	−0.041	–	0.041
3.....	9.0	0.081	6.61	0.034	0	0	0	–	–	–	−0.126	–	0.126
5.....	5.9	0.063	5.56	0.029	0	0	0	–	–	–	−0.024	–	0.024
7.....	2.5	0.061	8.47	0.044	0	0	0	–	–	–	−0.178	–	0.178
9.....	2.5	0.042	3.19	0.017	0	0	0	–	–	–	−3.350	–	3.350
11.....	4.5	0.001	0.09	0.0004	0	0	0	–	–	–	0.575	–	−0.575
13.....	5.0	0.004	0.25	0.001	4.0[3]	6.0[3]	0.00094[3]	–	–	–	−0.471	–	0.471
15.....	2.0	0.002	0.08	0.0004	0	0	0	–	–	–	0.040	–	−0.040
17.....	0.5	0.001	0.01	0.0001	0	0	0	–	–	–	−0.206	–	0.206
19.....	1.0	0.0002	0.03	0.137	0	0	0	–	–	–	–	–	–

[1] Development times are for stage I embryos (see Table 4).
[2] Overwintering eggs excluded.
[3] Owerwintering eggs only (i.e. no summer embryos observed).

Tab. 10. Relationship of lake temperature and date to some changes in *Leptodora* populations.

Year	First detection in the spring		First detection of males		First detection of over-wintering eggs		Last detection of summer embryos		Last detection in the fall		Total time span for the population (days)
	Date	Lake temp. °C	Date	Lake temp. °C	Date	Lake temp. °C	Date	Lake temp. °C	Date	Lake temp. °C	
1965	June 11	24.0	Sept. 7	20.1	–	–	–	–	Nov. 26	3.9	168
1966	May 11	8.9	Sept. 5	22.0	Sept. 23	15.4	Oct. 13	12.0	Nov. 18	9.4	191
1967	June 5	24.0	Aug. 21	21.0	Sept. 3	19.1	Sept. 22	18.0	Nov. 19	1.0	167
Means		19.0		21.0		17.3		15.0		4.8	175

Tab. 11. Dry and wet weights in micrograms for *Leptodora kindtii.*

Size Class (mm)	Females without eggs		Females with eggs		Males		Males and Females (without eggs)		Percent Water
	wet	dry	wet	dry	wet	dry	wet	dry	
2	–	50	–	–	–	–	–	50	–
3	240	60	–	–	–	–	240	60	75.0
4	720	80	–	–	650	80	690	80	88.4
5	1370	100	–	–	1370	150	1370	130	90.5
6	2210	120	2400	200	2360	140	2290	130	94.3
7	3200	150	3600	220	3310	150	3260	150	95.4
8	4420	160	4720	250	4220	190	4320	180	95.8
9	5480	180	5730	290	5240	180	5360	180	96.6
10	6620	210	7130	400	6200	–	6410	210	96.7
11	7960	240	8100	400	–	–	7960	240	97.0
12	9540	250	–	–	–	–	9540	250	97.4
Means	418	14.5	528	29.3	334	14.8	414	15.1	96.1

Summer eggs: dry wt. 51 µgm, water 61.0%.
Winter eggs: dry wt. 110 µgm.

which appear only after males are present in the population, reached a maximum mean clutch size of 14 in 1966 and 11 in 1967. The winter eggs result from sexual fertilization and overwinter to produce the first generation of the next year. The eggs hatch as nauplii, molt to metanauplii within a few hours, then molt to 2 mm females in about one day.

Production estimates based on standing crop information (Tab. 9) and data on mean weight per individual (Tab. 11) have been calculated for a number of dates in 1966 and 1967 (Tab. 12). Production estimates ranged from zero (lowest positive value was 0.007 g/m^3/day or 0.0036 Kcal/m^3/day) to a high of 0.1753 g/m^3/day (0.9085 Kcal/m^3/day) measured in August, 1967. Monthly and annual production measured by planimetry of curves of daily production against time are summarized in Tab. 13. Monthly values ranged from 0.003 g/m^3/yr (Aug., Sept., 1966) to 1.087 g/m^3/yr (Aug., 1967), while annual production was estimated as 0.362 g/m^3/yr in 1966 and 1.427 g/m^3/yr in 1967.

d) Predator – prey relationships. – Previous studies implicated *Leptodora* in the control of zooplankton populations. Hall (1964) suggested that *Leptodora* played a significant role in the control of *Daphnia galeata mendotae* populations in Base Line Lake, Michigan. Comparing *Leptodora* standing crop and *Daphnia schrodleri* Sars instantaneous death rates calculated from field data in Canyon Ferry Reservoir, Montana, Wright (1965) inferred that a predator – prey rela-

Tab. 12. Daily production rates of *Leptodora kindtii* based on estimates of per cent turnover per day and dry weight biomass standing crop.

Date	% Turnover per day	Standing Crop in gm/m^2	Production in $gm/m^2/day$	Production in $Kcal/m^2/day$[1]
1966				
June 7	4	.21371	.0085	.0441
9	18	.20643	.0372	.1928
13	5	.51926	.0275	.1425
14–15	6	.09707	.0058	.0301
21–24	33	.04253	.0140	.0726
27–28	67	.01550	.0103	.0534
July 5–6	8	.02344	.0019	.0098
19	0.5	.00013	$.0007 \times 10^{-3}$	$.0036 \times 10^{-3}$
27	9	.00015	$.0210 \times 10^{-3}$	$.1088 \times 10^{-3}$
Aug. 1–2	0.8	.00030	$.0024 \times 10^{-3}$	$.0124 \times 10^{-3}$
8	7	.00012	$.0088 \times 10^{-3}$	$.0456 \times 10^{-3}$
13–15	13	.00019	$.0243 \times 10^{-3}$	$.1259 \times 10^{-3}$
17–19	6	.00017	$.0102 \times 10^{-3}$	$.0529 \times 10^{-3}$
24	6	.00015	$.0090 \times 10^{-3}$	$.0466 \times 10^{-3}$
29	30	.00165	.0005	.0026
Sept. 5	7	.00201	.0001	.0005
23	19	.00059	$.0625 \times 10^{-3}$	.0003
25	14	.00500	.0002	.0010
Oct. 5–6	11	.00334	.0002	
13	12	.00203	.0003	
1967				
June 12	20.5	.00085	.0002	.0010
15	4.4	.00226	.0001	.0005
19	50.6	.01827	.0092	.0477
20	8.6	.05060	.0044	.0228
21	1.3	.04695	.0006	.0031
29	6.0	.12756	.0077	.0399
30	12.6	.12930	.0163	.0845
July 5	4.5	.05399	.0024	.0124
6	9.1	.08404	.0076	.0394
12	3.9	.08407	.0033	.0171
14	0.8	.08245	.0007	.0036
20	8.4	.17335	.0146	.0757
25	14.1	.13613	.0192	.0995
26	32.5	.26110	.0849	.4400
27	17.8	.19667	.0350	.1814
31	2.8	.09980	.0028	.0145
Aug. 1	8.0	.16065	.0129	.0669
4	19.5	.17094	.0333	.1726
7	2.0	.14796	.0030	.0155
8	1.4	.12582	.0018	.0093
10	7.6	.06851	.0052	.0269
11	43.2	.25434	.1099	.5696
14	11.8	.16121	.0190	.0985
15	55.1	.31814	.1753	.9085
16	40.0	.42364	.1695	.8784
17	42.2	.26148	.1028	.5328
18	33.3	.08665	.0289	.1498
21	7.7	.08293	.0064	.0332
22	39.3	.12334	.0485	.2513
23	3.9	.15339	.0060	.0311
25	13.4	.14179	.0193	.1000
29	13.6	.21694	.0295	.1529
Sept. 1	12.0	.14580	.0018	.0093
3	7.2	.30274	.0218	.1130
6	1.2	.05786	.0007	.0036
15	5.2	.11401	.0059	.0306
17	2.9	.08619	.0025	.0130
22	1.1	.05365	.0006	.0031

[1] A caloric conversion of 5182.5 cal/gm dry wt (Cummins 1967) was used.

Tab. 13. Comparison of *Leptodora* production and ingestion estimates to production of probable prey species on a monthly basis as gm/m³/month. Calculations are for the time periods in which *Leptodora* was found in the lake. Astricies mark probable prey based on comparisons of *Leptodora* birth rates and prey death rates, see Tab. 9.

1966

Month	Days	*Leptodora* Production	*Leptodora* Ingestion	Prey Production: *Daphnia*	*Cerio-daphnia*	*Bosmina*	*Chydorus*	*Cyclops*[1]	*Diaptomus*[1]	Total Prey	*Leptodora* Ingestion as % Total Prey Production[2]
May	20	0	0	41.800	0	5.100	0.060	0.740	0.200	(47.900)	–
June	30	0.327	2.725	29.418*	0	1.860*	0.270*	0.510*	0.090*	32.148	8.5
July	31	0.025	0.208	0.217*	0.155	1.581	0.0001*	2.015	0.0001	3.968	5.2
Aug.	31	0.003	0.025	0.341*	2.387	3.100	0.124*	0.589	0.062	7.183	0.3
Sept.	30	0.003	0.025	0.540	0.330	0.0003	0.180*	0.00003	0.180	1.230	2.0
Oct.	31	0.004	0.033	0.868	0.093	0.0001	0.248	1.457	0.372	3.038	1.1
Nov.	18	0	0	0.432	0.004	0.126	0.126	1.296	0.108	(2.092)	–
Totals	191	0.362	3.018	73.616	2.969	11.767	1.008	6.607	1.012	47.567[3]	6.3[3]
1967											
June	25	0.049	0.408	3.125*	0.075	1.800	0.300*	8.175*	3.000	16.475	2.5
July	31	0.211	1.758	0.190*	0	0.449	0.359*	0	2.373	3.371	52.1
Aug.	31	1.087	9.058	0.137*	0	0.074*	1.395*	0.286*	0.471	2.363	383.3
Sept.	30	0.080	0.668	0.612*	0	3.891	0.488*	0	0.366	5.357	12.5
Oct.	31	0	0	0.495	0	3.203	0.106	0.376	0.043	(4.223)	–
Nov.	19	0	0	0.380	0	0.551	0.038	0.361	0.038	(1.368)	–
Totals	167	1.427	11.893	4.939	0.075	9.968	2.686	0.198	6.291	27.566[3]	43.1[3]

[1] Non-naupliar production.
[2] Production does not include rotifers.
[3] Total does not include values shown in parentheses.

tionship existed and *Leptodora* was responsible for a significant mid-summer decline in *D. schrodleri* density. Mordukhai-Boltovskaia (1958) concluded, based on laboratory observations, that the *Leptodora* population in Rybinsk Reservoir (Russia) was supported chiefly by predation on *Bosmina* and *Ceriodaphnia*.

Our observations indicated that *Leptodora* in culture will feed on a wide variety of organisms, including brine shrimp (*Artemia*), hardly to be considered a natural food. Since *Leptodora* is a fluid ingesting predator, microscopic gut analyses yield little or no information. For the present, it is possible to infer predator – prey relationships by comparing such parameters as *Leptodora* birth rates (b) and suspected prey death rates (d) calculated from field data (see also Wright 1965).

Investigations reported elsewhere (Costa 1967, Moshiri 1968, Moshiri et al. 1969) have demonstrated that the 2–5 mm size classes and the 6–12 mm size classes constitute two distinct groups. For example, less than 0.01 % of the 2–5 mm females collected have been observed carrying eggs. Field investigations showed that the two groups have inverse diurnal migration patterns, the larger animals being found at the surface at night and the smaller ones occupying the upper strata in the daytime (Costa and Cummins 1969). Tracer studies on ingestion and assimilation together with determinations of RQ (respiratory quotient) values show only the larger size class group (6–12 mm) to be predaceous. The smaller animals (2–5 mm) probably depend upon bacteria, algae and detrital particles (This size category can be fed yeast in the laboratory). Therefore, only that per cent of the population in the 6–12 mm size classes probably should be considered predaceous on any given sampling date. This means that if *Leptodora* standing crop data are used in the future to infer predator – prey relationships, only the larger size classes should be included.

The relationship between *Leptodora* instantaneous birth rate (b) and prey instantaneous death rate (d) estimates is expressed in Tab. 14. Correlation coefficients have been calculated to express the degree of relationship for various time intervals during the 1966 and 1967 seasons. Early in the 1966 season, during the period of rapid population increase, the data suggest a dependence by the *Leptodora* population on five prey: *Daphnia*, *Ceriodaphnia*, *Chydorus*, *Cyclops* and *Diaptomus*. *Bosmina* was apparently an important prey organism in June and early July with *Chydorus* and *Cyclops* carrying the *Leptodora* population through the later summer and fall. The suggested 1967 pattern differs from 1966 in that the dominant prey were apparently *Daphnia* and *Cyclops*, and possibly *Chydorus*, throughout the *Leptodora* growing season with an August dependence upon *Bosmina* also indicated. Naturally such correlations are weak, showing only that *Leptodora* birth rates and various prey death rates are responding similarly either to each other or independently to some other factor or combination of factors. Since instantaneous death rates were not determined for rotifer populations, total rotifer standing crop was compared with *Leptodora* birth rate. The resulting correlations indicate possible predator – prey relationships between *Leptodora* and rotifer populations in June and July both years and in August in 1966.

Data have been gathered on fish predation on the *Leptodora* population in Sanctuary Lake. The results are similar to those obtained by other investigators (Entz and Lukacsovics 1957, Mordukhai-Boltovskaia 1958, Sebestyen 1960 a). Of the nine fish species examined, only four, Lake chub (*Squalius cephalus* L.), golden shiner (*Notemigonus chrysoleucas* Mitch.), black and white crappie (*Pomoxis nigromaculatus* de S. and *P. annularis* Raf.), ingested *Leptodora*. By employing Ivlev's (1961) method of calculating a selection index, it appears that feeding on *Leptodora* was selective; that is, this large predator was taken in preference over other zooplankters by those species which fed upon it. On occasion small lake chub, golden shiner and white crappie were collected in quantitative plankton tows (on occasion a 0.75 m diameter no. 000 mesh net was used for this purpose). When such rough quantitative data were available, fish

OIKOS 20, 2 (1969)

Tab. 14. Correlations between field estimates of *Leptodora* birth rate (b; independent variable) and prey death rates (d; dependent variable). The dates used to obtain the Pearson correlation coefficients given at the bottom of each column are indicated by crosses (N = the sum of crosses for any given column).

1966

Date	*Daphnia*					*Ceriodaphnia*				*Bosmina*			*Chydorus*			*Cyclops*				*Diaptomus*			
May 16	×		×		×	×			×						×	×	×		×	×		×	×
19	×		×		×	×			×					×	×	×	×		×	×		×	×
25	×		×		×	×		×	×						×	×	×		×	×		×	×
June 2	×		×		×	×		×	×		×	×			×	×	×		×	×		×	×
9	×		×		×	×		×	×	×		×	×	×	×	×	×		×	×		×	×
15	×		×		×	×		×	×	×		×	×	×	×	×	×		×	×		×	×
21	×		×		×				×	×		×	×	×	×			×	×	×		×	×
28				×	×				×	×		×			×			×	×				×
July 5				×	×				×	×		×			×			×	×				×
12				×	×				×		×	×		×	×		×		×				×
19		×	×		×			×	×		×	×			×		×		×			×	×
27		×	×		×			×	×		×	×			×		×		×			×	×
Aug 2		×	×		×			×	×		×	×	×	×	×		×		×			×	×
8		×	×		×			×	×		×	×	×	×	×			×	×			×	×
11		×	×		×				×		×	×			×		×		×				×
13		×	×		×		×	×	×		×	×	×	×	×		×		×			×	×
19				×	×		×	×	×		×	×	×	×	×		×		×			×	×
24			×		×		×	×	×		×	×	×	×	×		×		×			×	×
29				×	×		×	×	×		×	×	×	×	×			×	×				×
Sept 5			×		×		×	×	×		×	×	×	×	×		×		×		×	×	×
12			×		×		×	×	×			×			×			×	×		×	×	×
15				×	×		×	×	×		×	×			×		×		×		×	×	×
23				×	×		×	×	×		×	×	×	×	×			×	×		×	×	×
29				×	×		×	×	×		×	×	×	×	×			×	×		×	×	×
Oct 13				×	×		×	×	×		×	×	×	×	×		×		×		×	×	×
27			×		×		×	×	×		×	×	×	×	×		×		×		×	×	×
Nov 10			×		×		×	×	×		×	×			×		×		×		×	×	×
Coefficients	.90	−.09	.65	.27	−.13	.93	.40	.45	.28	.85	.19	.30	.41	.71	.27	.62	.60	.39	−.09	.66	.47	.25	−.03

1967

Date	*Daphnia*					*Ceriod.*	*Bosmina*				*Chydorus*				*Cyclops*				*Diaptomus*				
June 13	×		×		×	×	×	×		×			×	×	×			×	×		×		×
20	×		×		×	×	×	×		×			×	×				×	×		×		×
27	×		×		×	×	×	×		×	×		×	×	×			×	×		×		×
July 7	×		×		×		×	×		×	×			×	×			×	×		×		×
18	×		×		×		×	×		×				×	×			×	×		×		×
26			×	×	×		×	×		×		×	×	×	×			×	×		×	×	×
31			×	×	×		×	×		×		×	×	×	×			×	×		×	×	×
Aug 4			×	×	×				×	×		×	×	×				×				×	×
7			×	×	×			×		×		×	×	×	×	×		×			×	×	×
11				×	×				×	×		×	×	×	×	×	×	×				×	×
14			×	×	×			×		×		×	×	×	×	×	×	×			×		×
16				×	×				×	×		×	×	×	×	×	×	×				×	×
18					×				×	×		×	×	×	×	×	×	×				×	×
21		×	×		×			×	×	×		×	×	×	×	×	×	×		×	×	×	×
Sept 15		×	×		×				×	×				×	×	×	×	×		×	×	×	×
17		×	×	×	×			×		×			×	×	×	×		×		×	×	×	×
21		×	×	×	×			×		×	×			×				×		×	×		×
22		×	×	×	×			×		×			×	×	×			×		×	×		×
24					×			×		×	×			×				×		×	×		×
25					×				×	×			×	×	×				×	×	×		×
26			×		×			×		×			×	×				×		×	×		×
28			×		×			×		×	×			×				×		×	×		×
Oct 1					×			×		×			×	×				×		×	×		×
2				×	×			×		×	×			×				×		×	×		
Coefficients	.79	.72	.48	.80	.22	−.54	−.04	.20	.61	−.14	0	−.06	.52	.13	.62	.72	.28	.78	−.30	.35	.19	−.39	−.13

ingestion could be compared to estimates of loss to the *Leptodora* population (d). On four sampling dates when comparisons were possible, fish predation was roughly of the same order of magnitude as the estimated death rate of the *Leptodora* population. Of course, the difficulty with such comparisons lies in the need for information on the rate of fish feeding on *Leptodora*, although the data do suggest that non-predatory loss from the *Leptodora* population may be negligible.

5. Discussion and conclusions

The physical-chemical homogeneity of the Sanctuary Lake ecosystem, due to continuous mixing in the shallow basin, together with its generally high biological productivity, constitutes a situation which allows *Leptodora kindtii* to reach densities as high as any previously reported. In all three years (1965–1967), there were similarities in the overall population growth patterns of *Leptodora*. Variation in the date and lake temperature of earliest detection of the new spring population was observed. Males appeared and the population disappeared at about the same lake temperature and time of year in all three seasons. A mean lake temperature of at least 9°C was required for overwintering eggs to hatch, while temperatures below 9°C terminated the population. The total time span of the population had a mean of 175 days for the three years. Thus, the general pattern was for *Leptodora* to appear in the spring after lake temperatures reached 10°C, to disappear in the fall after temperatures fell below 10°C and for males to appear in the fall when declining median temperatures fell to near 20°C (Tab. 10).

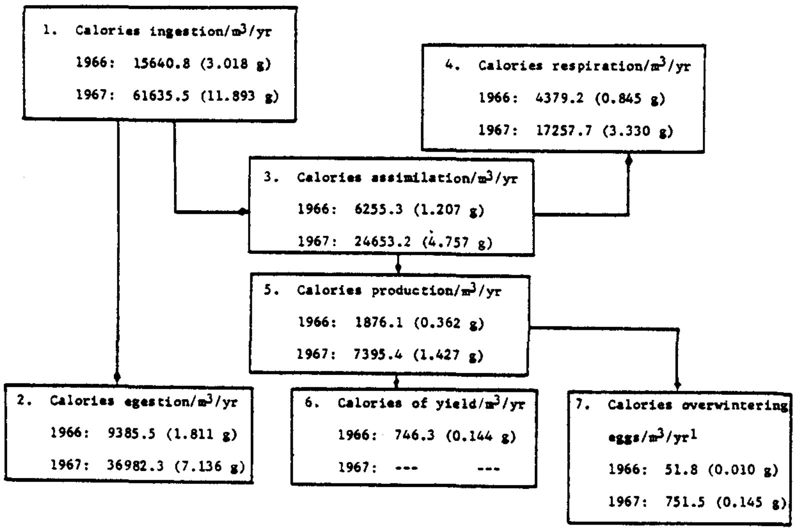
Given the size-specific differences in food habits of the *Leptodora* population, such that only 6–12 mm individuals are predaceous, the energy processing by the population is quite complex. Once young *Leptodora* reach egg-bearing and predaceous-feeding size (6 mm), presumably by eating algae, bacteria and organic detritus, feeding is probably primarily opportunistic. The predator crops the most readily available prey (this is usually, but not always, the most abundant prey zooplankter). Naturally, the dominant size class in the *Leptodora* population and the dominant size classes in the prey population will dictate certain limits with regard to food intake by the predator population as a whole. Based on available data, the pattern is one in which the predaceous size classes of the *Leptodora* population depend upon a variety of prey species throughout the growing season. In addition, the patterns differ between years, probably as a function of the differences in relative abundance of suitable prey species. The production estimates ($g/m^3/day$) obtained in the present study for *Leptodora* and a number of probable prey species are compared with selected data from the literature in Tab. 15. Although there are significant differences in the lake ecosystems compared, the estimates are roughly of the same order of magnitude for similar temperature regimes and portions of the growing season. The highest values given for zooplankters other than *Leptodora* were obtained by Patalas (1968) for Lake Lichenskie, an artificially heated Polish reservoir. Production estimates for *Leptodora* are higher in Lichenskie than Sanctuary Lake in 1966. The *Leptodora* values are essentially the same for the two systems, when the 1967 Sanctuary Lake data are compared, indicating the comparatively high productivity of Sanctuary Lake *Leptodora* in 1967.

The annual production by the *Leptodora* population in 1966 and 1967 (Fig. 15) was 0.362 g/m^3 (1876.1 cal/m^3) and 1.427 gm/m^3 (7395.4 g/m^3) respectively. This would result in a total assimilation by the population of 1.207 $g/m^3/yr$ (6255.3 cal/m;) in 1966 and 4.757 g/m^3 (24653.2 cal/m^3) in 1967, assuming production (growth and reproduction) to account for 30% of assimilation. If an assimilative efficiency of 40% is assumed, then total annual ingestion would be 3.018 g/m^3 (15640.8 cal/m^3) for 1966 and 11.893 g/m^3 (61635.5 cal/m^3) for 1967. This approximates the actual intake required by the *Leptodora* population annually and, therefore, represents the impact of predator upon prey. In all instances, except August 1967, the production of the proposed prey is greater than this

Tab. 15. Comparison of mean daily zooplankton production estimates (g/m^3) determined in the present study with selected values from the literature.

Species	Source	Location	Median temperature °C	Sampling period	Number of sample days	Mean production gm/m^3/day
Leptodora kindtii	Present study	Sanctuary Lake, Pa	15.0	May–Nov, 1966	37	0.003
" "	" "	" " "	14.0	June–Nov, 1967	57	0.013
" "	" "	" " "	23.0	July–Aug, 1966	9	0.001
" "	" "	" " "	22.7	July–Aug, 1967	34	0.021
" "	Patalas 1968	Lake Mikorzynskie, Poland	21.6	July–Aug, 1966	6	0.006
" "	" "	Lake Lichenskie, Poland	27.4	July–Aug, 1966	6	0.013
Daphnia galeata mendotae	Present study	Sanctuary Lake, Pa	15.0	May–Nov, 1966	28	0.407
" " "	" "	" " "	14.0	May–Nov, 1967	47	0.030
" " "	Wright 1965	Canyon Ferry Reservoir, Mont.	–	Apr–Sept, 1958	23	0.114
D. schodleri	" "	" " " "	–	Apr–Sept, 1958	23	0.227
D. cucullata	Petrovich et al. 1961	Lake Naroch, Russia	13.5	Apr–Nov, 1960	211[1]	0.016
D. galeata mendotae	Present study	Sanctuary Lake, Pa	23.0	July–Aug, 1966	11	0.009
" " "	" "	" " "	22.7	July–Aug, 1967	11	0.005
D. cucullata and *D. longispina hyalina*	Patalas 1968	Lake Mikorzynskie	21.6	July–Aug, 1966	6	0.128
" " " " " "	" "	Lake Lichenskie	27.4	July–Aug, 1966	6	1.547
Bosmina longirostris and *B. coregoni*	Present study	Sanctuary Lake, Pa	15.0	May–Nov, 1966	28	0.183
" " " " "	" "	" " "	14.0	May–Nov, 1967	47	0.067
Bosmina coregoni	Petrovich et al. 1961	Lake Naroch	13.5	Apr–Nov, 1960	211[1]	0.006
Bosmina longirostris and *B. coregoni*	Present study	Sanctuary Lake, Pa	23.0	July–Aug, 1966	11	0.082
" " " " "	" "	" " "	22.7	July–Aug, 1967	11	0.007
Bosmina coregoni	Patalas 1968	Lake Mikorzynskie	21.6	July–Aug, 1966	6	0.060
" "	" "	Lake Lichenskie	27.4	July–Aug, 1966	6	1.547
Ceriodaphnia reticulata	Petrovich, et al. 1961	Sanctuary Lake, Pa	16.3	July–Nov, 1966	20	0.031
" "	Present study	" " "	19.1	June, 1967	4	0.003
" "	Petrovich et al. 1961	Lake Naroch	13.5	Apr–Nov, 1960	211[1]	0.004
Chydorus sphaericus	Present study	Sanctuary Lake, Pa	23.0	July–Aug, 1966	11	0.004
" "	" "	" " "	22.7	July–Aug, 1967	11	0.047
" "	Patalas 1968	Lake Mikorzynskie	21.6	July–Aug, 1966	6	0.007
" "	" "	Lake Lichenskie	27.4	July–Aug, 1966	6	0.347
Cyclops vernalis	Present study	Sanctuary Lake Pa	21.3	June, 1966	1	0.089[2]
" "	" "	" " "	19.1	June, 1967	4	0.327[2]

[1] Since number of sample days not given, total days in sample period used.
[2] Non-naupliar production.



1. Estimated by plotting number of winter eggs/liter from first detection until disappearance of the population (Table 10) and summation of peak amounts over the period.

Fig. 15. Proposed 1966 and 1967 annual energy budgets for *Leptodora kindtii*. Year defined as the period from first detection of *L. kindtii* in the spring to the last in the fall: Tab. 9).

amount estimated to be required by the *Leptodora* population. The impact of predator on prey over the season was much greater in 1967 (43.1%) than in 1966 (6.3%) (Tab. 13). The calculated intake by the *Leptodora* population in August, 1967, was nearly four times greater than the measured prey production. The difference, 6.695 g/m³, is undoubtedly accounted for by the naupliar portion of copepod production, rotifer production and algal-bacterial-detrital feeding by 2–5 mm *Leptodora*. In future studies, an attempt will be made to assess production by all prey (prey identity being determined by immunochemistry) and to partition *Leptodora* production into non-predatory (2–5 mm) and predatory (< 6 mm) portions.

Other investigations are necessary to measure respiration and assimilation and ingestion directly (Moshiri and Cummins 1969). Proposed 1966 and 1967 annual energy budgets for *L. kindtii* are presented in Fig. 15. Only production and yield have been estimated directly, for the present the other values have been obtained by proportionality and difference.

Estimates of yield, or harvest by predators, from the production portion of the energy budget have been made using field measurements of instantaneous death rate (d). A yield of 0.144 g/m³/yr (746.3 cal/m³) leaves 0.436 g/m³/yr (2259.6 cal/m³) unaccounted for in 1966. A small fraction is accounted for by overwintering eggs, 0.010 g/m³/yr (51.8 cal/m³), but the majority of the difference is undoubtedly due to the present level of refinement whereby harvest is calculated. We expect that as more information is processed, the estimate will balance production on an annual basis. Preliminary data also indicate that fish predation is sufficient to account for loss to (yield from) the population throughout the season. Thus, "natural death", that is non-predatory loss, is probably insignificant. Therefore, it seems that although the general effect of *Leptodora* on its prey may be minimal, during periods of maximum predator production the impact can be extremely significant. The effect of fish predators on the *Leptodora* population is also quite significant. This is to be expected since the herbivorous zooplankters have other predators, such as fish and *Chaoborus* larvae, while all predation on *Leptodora* is accounted for by relatively few fish species.

6. Acknowledgements

We would like to thank Drs. W. T. Edmondson, D. J. Hall, J. C. Wright, O. Sebestyen, G. W. Saunders, G. R. Marzolf and A. Robertson for critical suggestions concerning portions of the study. In addition we wish to thank Drs. C. A. Tryon and R. T. Hartman for the use of various equipment and for encouragement throughout the study, Dr. R. Bonn for calibration of sampling gear, Dr. J. H. Graffius for the identification of algae and Drs. D. J. Hall, A. Robertson, C. E. Goulden and J. L. Brooks (in conjunction with a previous study by Borecky, 1956) for identifications of zooplankters. We are also indebted to Mr. John C. Wuycheck, Mr. Thomas Zaret, Mr. Jeffry Huberman and Mr. Jeffrey Lawhead for assistance with various aspects of laboratory and field studies. Mr. Fred Mauk provided valuable advice on computer programming. A special debt of gratitude is due Mr. Warren Grieser for aid in the construction and maintenance of numerous items of equipment.

References

American Public Health Association, American Water Works Association and Water Pollution Control Federation. 1965 (12th ed.). Standard methods for the examination of water and wastewater including bottom sediments and sludges. – Amer. Publ. Health Assn. N.Y. 640 pp.

Andrews, T. F. 1948. The parthenogenetic reproductive cycle of the cladoceran, *Leptodora kindtii*. – Trans. Amer. Micro. Soc. 68: 54–60.

— 1949. The life history, distribution, growth, and reproduction of *Leptodora kindtii* (Focke) in western Lake Erie. – Abstracts of Doctoral Dissertations, No. 57. The Ohio State University Press.

— 1953. Growth studies on parthenogenetically produced male and female *Leptodora kindtii* (Focke). – Trans. Amer. Micro. Soc. 72: 9–17.

Borecky, G. W. 1956. Population density of the limnetic Cladocera of Pymatuning Reservoir. – Ecology 37: 719–727.

Carlton, E. P. 1897. The brain and optic ganglion of *Leptodora hyalina*. – Anat. Anz. 13: 293–304.

Cheremisova, K. A. 1960. Observations of the biology of *Bythotrephes longimanus* Leydig and *Leptodora kindtii* (Focke). – Tr. Belorussk. Nauchno-Issled. Inst. Rybn. Khoz. 3: 131–137.

Comita, G. W. 1964. The energy budget of *Diaptomus siciloides*, Lilljeborg. – Verh. Internat. Verein. Limnol. 15: 646–653.

Costa, R. R. 1967. Population dynamics and ecology of *Leptodora kindtii* (Focke). – Unpubl. Ph. D. Dissertation, Univ. Pittsburgh. 219 pp.

— and Cummins, K. W. 1969. Diurnal vertical migration of *Leptodora kindtii* (Focke) (Crustacea: Cladocera) in a shallow eutrophic reservoir. – In manuscript.

Cummins, K. W., Coffman, W. P. and Roff, P. A. 1966. Trophic relationships in a small woodland stream. – Verh. Internat. Verein. Limnol. 16: 627–638.

— 1967. Calorific equivalents for studies in ecological energetics. – Publ. Pymatuning Lab. Ecol. 52 pp.

Cummins, K. W. and Costa, R. R. 1969. Comparative calculations of production rates for natural populations of *Leptodora kindtii* (Focke) (Crustacea: Cladocera). – In preparation.

Crowley, F. J. and Cohen, M. 1967. Basic facts of statistics. – Macmillan Co., New York. 64 pp.

Deevey, E. S., Jr. 1947. Life tables for natural populations of animals. – Quarterly Review of Biology 22: 283–314.

Dugdale, V. A. and Dugdale, R. C. 1965. Nitrogen metabolism in lakes III. Tracer studies of the assimilation of inorganic nitrogen sources. – Limnol. Oceanogr. 10: 53–67.

Edmondson, W. T. 1960. Reproductive rates of rotifers in natural populations. – Mem. Ist. Ital. Idrobiol. 12: 21–77.

Engelmann, M. D. 1961. The role of soil arthropods in the energetics of an old-field community. – Ecol. Monog. 31: 221–238.

— 1966. Energetics, terrestrial field studies, and animal productivity. – In: Advances in Ecological Research. Vol. 3, pp. 73–115. Academic Press, N.Y. 324 pp.

ENTZ, B. and LUKACSOVICS, F. 1957. Untersuchungen im Winterhalbjahr an einigen Balatonsee-Fischen zwecks Feststellung ihrer Ernährungs-, Wachstums- und Vermehrungsumstände. – Annal. Biol. Tihany 24: 85–86.

FORBES, S. A. 1886. *Leptodora* in America. – Amer. Nat. 20: 1057.

FRÖHLICH, A. and ZAK, G. 1934. Pharmakologische Untersuchungen am Herzen und am Verdauungskanal von *Leptodora kindtii*. I. Die Wirkungen von Alkaloiden, Glykosiden und einigen andren Mitteln. – Arb. Ung. Biol. Forsch. Inst. 7: 267–274.

GERSCHLER, M. W. 1911. Monographie der *Leptodora kindtii* (Focke). I. Teil. – Arch. Hydrobiol. u. Planktonkunde 6: 415–466.

— 1912. Monographie der *Leptodora kindtii* (Focke). II. Teil. – Arch. Hydrobiol. u. Planktonkunde 7: 63–117.

GICKLHORN, J. and KELLER, R. 1925. Bau und Funktion des Haftorganes von *Daphnia*, bzw. des Kopfschildes von *Leptodora* und *Polyphemus* auf Grund vitaler Elektivfarbung. – Zool. Anz. 64: 217–234.

GOLDMAN, C. R. 1961. The measurement of primary productivity and limiting factors in freshwater with Carbon-14. – In: Proc. Conf. of Prim. Productivity Measurement. U.S.A.E.C. Report TIDO7633. Washington 25, D.C. 237 pp.

GUTH, G. 1919. Über den Kopfschild von *Leptodora* und *Polyphemus*. – Zool. Anz. 50: 285–286.

HALL, D. J. 1959. Preliminary observations on the biology and population dynamics of *Leptodora kindtii* (Focke). – Unpublished report of work completed under Woods Hole Oceanographic Institution's Summer Fellowship Program.

— 1964. An experimental approach to the dynamics of a natural population of *Daphnia galeata mendotae*. – Ecology 45: 94–112.

HARTMAN, R. T. 1958. Studies of plankton centrifuge efficiency. – Ecology 39: 374–376.

— and GRAFFIUS, J. H. 1960. Quantitative seasonal changes in the phytoplankton communities of Pymatuning Reservoir. – Ecology 41: 333–340.

— and HIMES, C. L. 1961. Phytoplankton from Pymatuning Reservoir in downstream areas of the Shenango River. – Ecology 42: 180–183.

HEINLE, D. R. 1965. Growth rates, turnover times, and production of a population of *Acartia tonsa*, Dana, in Chesapeake Bay. – Unpubl. M. S. Diss., Univ. Maryland.

— 1966. Production of a calanoid copepod, *Acartia tonsa*, in the Patuxent River Estuary. – Chesapeake Sci. 7: 59–74.

HEWITT, B. R. 1958. Spectrophotometric determination of total carbohydrate. – Nature 182 (4630): 246–247.

HOBBIE, J. E. and WRIGHT, R. T. 1965. Bioassay with bacterial uptake kinetics: Glucose in freshwater. – Limnol. Oceanogr. 10: 471–474.

IVLEV, V. S. 1961. Experimental ecology of the feeding of fishes. – (Translated from Russian by D. Scott). Yale Univ. Press, New Haven. 302 pp.

JACKSON, D. F. and MCFADDEN, J. 1954. Phytoplankton photosynthesis in Sanctuary Lake, Pymatuning Reservoir. – Ecology 35: 1–4.

JUDAY, C. 1940. The annual energy budget of an inland lake. – Ecology 21: 438–450.

KING, D. L. and BALL, R. C. 1967. Comparative energetics of a polluted stream. – Limnol. Oceanogr. 12: 27–33.

KINGSLEY, J. S. 1886. *Leptodora* in America. – Amer. Nat. 20: 896.

LINDEMAN, R. L. 1942. The trophic-dynamic aspect of ecology. – Ecology 23: 399–418.

MANN, K. H. 1966. The pattern of energy flow in the fish and invertebrate fauna of the river Thames. – Verh. Internat. Verein. Limnol. 15: 485–495.

MCDOUGALL, E. J. and VERZAR, F. 1933. Untersuchungen über die Resorption von Farbstoffen aus dem Darm von *Leptodora kindtii*. – Arb. Ung. Biol. Forsch. Inst. 6: 201–206.

MOORE, R. J. 1965. Productivity and standing crop of vascular hydrophytes. – Ph. D. Dissertation, Univ. Pittsburgh. 186 pp.

MORDUKHAI-BOLTOVSKKAIA, E. D. 1956. Some aspects of the biology of *Leptodora kindtii*(Focke)and *Bythotrephes* Leydig as found in the Rybinsk Reservoir. – Doklady Akad. Nauk. SSSR., Biol. Sci. Sect., 110: 688–691.

— 1957. Parthenogenetic breeding of *Leptodora kindtii* and *Bythotrephes*. – Doklady Akad. Nauk. SSSR., Biol. Sci. Sect., 112: 123–125.

— 1958. Preliminary notes on the feeding of the carnivorous cladocerans *Leptodora* and *Bythotrephes*. – Doklady Akad. Nauk. SSSR., Biol. Sci. Sect., 122: 828–830.

— 1960. The nutrition of the carnivorous Cladocerae *Leptodora* and *Bythotrephes*. – Biull. Inst. Biologie Vodokr. 6: 21–22.

MOSHIRI, G. A. 1968. Energetics of the predaceous zooplankter *Leptodora kindtii* (Focke) and selected prey species. – Unpubl. Ph. D. Dissertation, Univ. Pittsburgh. 148 pp.

MOSHIRI, CUMMINS, K.W. and COSTA, R. R. 1969. Annual respiratory energy expenditure by a natural population of the predaceous zooplankter *Leptodora kindtii* (Focke) (Crustacea: Cladocera). – Limnol. Oceanogr. In press.
ODUM, H. T. 1957. Trophic structure and productivity of Silver Springs, Florida. – Ecol. Monog. 27: 44–112.
ORR, H. D. 1954. Quantitative studies of protozoan populations from two areas of Pymatuning Lake, Pennsylvania. – Ecology 35: 332–334.
PARSONS, T. R. and STRICKLAND, J. D. H. 1963. Discussion of spectrophotometric determination of marine-plant pigments, with revised equations for ascertaining chlorophylls and caratenoids. – J. Mar. Res. 21: 115–163.
PATALAS, K. 1968. The assessment of plankton production in a lake heated by the thermal power plant. – In manuscript.
PETROVICH, P. G., SUSHKINA, E. A. and PECHEN, G. A. 1961. Evaluating zooplankton production. – Doklady Akad. Nauk. SSSR. 139: 1235–1238.
PHILLIPSON, J. 1966. Ecological energetics. – New York, St. Martin's Press. 57 pp.
QUENOUILLE, M. H. 1959. Rapid statistical calculations. – Hafner Publ. Co., N.Y. 44 pp.
RICHMAN, S. 1958. The transformation of energy by *Daphnia pulex*. – Ecol. Monog. 28: 273–291.
SAMASSA, P. 1891. Über eigentümliche Zellen im Gehirn von *Leptodora*. – Anat. Anz. 6: 54–56.
SAMTER, M. 1895. Die Veränderung der Form und der Lage der Schale von *Leptodora hyalina* während der Entwicklung. – Zool. Anz. 36: 483–484.
— 1900. Studien zur Entwicklungsgeschichte der *Leptodora hyalina* Zeilf. – Zool. 68: ???
SAUNDERS, G. W. 1967. Zooplankton nutrition. – International Symposium on Eutrophication. June 11–16, 1967. Univ. Wisc.
SCHARRER, E. 1964. A specialized trophospongium in large neurons of *Leptodora* (Crustacea). – Zeitschrift für Zellforschung 61: 803–812.
SEBESTYEN, O. 1931. Contributions to the biology and morphology of *Leptodora kindtii*. – Arb. Ung. Biol. Forsch. Inst. 4: 9–20.
— 1933. The daily vertical migration of *Leptodora kindtii*. – Arb. Ung. Biol. Forsch. Inst. 6: 112.
— 1949. On the life method of the larva of *Leptodora kindtii* (Focke). – Hungarica Acta Biologica 1: 71–81.
— 1960 a. On the food niche of *Leptodora kindtii* Focke (Crustacea, Cladocera) in open water communities of Lake Balaton. – Int. Revue Hydrobiol. 45: 277–282.
— 1960 b. Quantitative plankton studies of Lake Balaton. X. Notes on the distribution of *Leptodora kindtii* Focke. – Annal. Biol. Tihany 27: 131–138.
SIEDENTOP, W. 1930 a. Physiologische Beobachtungen an *Leptodora kindtii*. – Arb. Ung. Biol. Forsch. Inst. 3: 79–82.
— 1930 b. Über die Darmatmung von *Leptodora kindtii*. – Arb. Ung. Biol. Forsch. Inst. 3: 82–87.
SIEGEL, S. 1956. Nonparametric statistics. – McGraw-Hill Book Co. 312 pp.
SLOBODKIN, L. B. 1962. Energy in animal ecology. – In: Advances in Ecological Research. Vol. I: pp. 69–101. Academic Press. New York. 203 pp.
TEAL, J. M. 1957. Community metabolism in a temperature cold spring. – Ecol. Monog. 27: 283–302.
— 1962. Energy flow in the salt marsh ecosystem of Georgia. – Ecology 43: 614–624.
TRAMA, F. B. 1957. The transformation of energy by an aquatic herbivore, *Stenonema pulchellum* (Ephemeroptera). – Unpublished Ph. D. Dissertation, University of Michigan.
TRYON, C. A. Jr. 1954. The effect of carp exclosures on growth of submerged aquatic vegetation in Pymatuning Lake, Pennsylvania. – J. Wildlife Management 18: 251–254.
— and JACKSON, D. F. 1952. Summer plankton productivity of Pymatuning Lake, Pennsylvania. – Ecology 33: 342–350.
VERDUIN, J. 1954. Phytoplankton and turbidity in western Lake Erie. – Ecology 35: 550–561.
VON SAALFIELD, E. 1936. Untersuchungen über den Blutkreislauf bei *Leptodora hyalina*. – Zeit. vergl. Physiol. 24: 58–70.
WARREN, E. 1901. A preliminary account of the free-swimming nauplius of *Leptodora hyalina* (Lillj.). – Proc. Roy. Soc. London 86: 210–218.
WEIDERSHEIM, R. 1890. Bewegungserscheinungen im Gehirn von *Leptodora hyalina*. – Anat. Anz. 5: 673–679.
WEISMANN, A. 1874. Über Bau und Lebenserscheinungen von *Leptodora hyalina* Lilljeborg. – Z. wiss. Zool. 24: 349–418.
— 1876. Zur Naturgeschichte der Daphniden. I. Über die Bildung von Wintereiern bei *Leptodora hyalina*. – Z. wiss. Zool. 27: 51–112.

WOLKEN, J. J. and GALLICK, G. J. 1965. The compound eye of a Crustacean, *Leptodora kindtii* (Focke). – J. Cell. Biol. 26: 968–973.
WRIGHT, J. C. 1965. The population dynamics and production of *Daphnia* in Canyon Ferry Reservoir, Montana. – J. Limnol. Oceanogr. 10: 583–590.

K. W. Cummins
Kellogg Biological Station
Michigan State University
Hickory Corners, Mich. 49060
U.S.A.

R. R. Costa
Dept. of Biological Sciences
State University of New York
Brockport, New York 14420
U.S.A.

G. A. Moshiri
Institute of Ecology
University of California
Davis, California 95616
U.S.A.