

Effects of predation and food on the population dynamics of the raptorial cladoceran *Leptodora kindtii*

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Abstract

We assessed the trophic status of *Leptodora kindtii* in the food web of a shallow, eutrophic lake in which 0+ age group fish were the main predators. The mean biomass of 0+ fish during three successive years varied from 0.39 g dry wt m⁻² in the first year to 0.05 g dry wt m⁻² in the second year to 2.49 g dry wt m⁻² in the third year. In the years with high fish biomass, densities of small-bodied (<1-mm) cladocerans (e.g., *Bosmina* spp., *Chydorus sphaericus*) were relatively high, whereas in the year with low fish biomass, densities of large-bodied *Daphnia galeata* were high, and densities of small-bodied cladocerans were lower. During the three study years, the predation pressure of juvenile fish and biomass and production of *Leptodora* were negatively correlated. Despite the low 0+ fish biomass in the second year, the *Leptodora* population densities were high only during the first part of the growing season. The elevated *Leptodora* mortality in July coincided with the lowest observed densities of small-bodied cladocerans, preferred prey items of *Leptodora*, and with an abundance of large-bodied *Daphnia*, the preferred food for 0+ fish. We conclude that the population dynamics of *Leptodora* during the growing season is predominantly regulated by direct predation effects.

The cladoceran *Leptodora kindtii* (Focke) is a common invertebrate predator in freshwater lakes and reservoirs of the Palearctic and Nearctic regions of the Northern hemisphere (Rivier 1998). It is one of the few larger invertebrates in the pelagial of lakes and reservoirs (size range, 1.4–14.0 mm). Although *Leptodora* is a common zooplankton of lakes, varying widely in productivity, it reaches its highest densities in eutrophic lakes and reservoirs.

Leptodora is a preferred prey item of many zooplanktivorous fish, despite the fact that it is extremely transparent (e.g., Van Densen 1985; Palmer et al. 2001; Uusitalo et al. 2003). Increasing selectivity by vertebrate predators with increasing prey size has been widely demonstrated and is predicted by optimal foraging theory, which assumes that foragers maximize net energy intake per unit time (Pyke 1984). However, positive size selection of prey by fish starts at a larger size for *Leptodora* than for less transparent prey species. *Leptodora* is selected from 4.0 mm onward, whereas *Diaphanosoma* and *Daphnia* are generally selected from 1.0

mm onward (Liu and Herzig 1996; Branstrator and Holl 2000). Thus, *Leptodora* juveniles are less visually perceptible to fish compared with other large-bodied zooplankters.

Leptodora feeds mainly on smaller cladocerans and avoids copepodite stages of copepods (e.g., Karabin 1974; Lunte and Luecke 1990; Herzig 1994). Although relatively large, *Diaphanosoma* and *Daphnia* spp. are eaten in a size range varying from that of a newborn (ca. 0.5 mm) to up to 1.0 mm (Browman et al. 1989; Branstrator and Lehman 1991; Herzig 1995). *Leptodora* only scarcely consume *Daphnia* of >1.0 mm (Branstrator and Lehman 1991). Small, juvenile *Leptodora* (i.e., <5 mm) eat both copepod nauplii and rotifers (Herzig and Auer 1990; Kulikov et al. 1991); in terms of biomass, however, these last two contribute little to the *Leptodora* diet as a whole (Arndt et al. 1993).

Numerous studies have suggested that *Leptodora* can significantly contribute to the regulation of herbivorous zooplankton communities, especially when it occurs in densities higher than 0.5 ind L⁻¹ (e.g., Hall 1964; Branstrator and Lehman 1991; Herzig 1995). However, this suggestion is based on either a simple correlation between *Leptodora* densities and prey densities or death rates or on predation rates measured in the laboratory (e.g., Gliwicz et al. 1978; Herzig 1994; Uusitalo et al. 2003). Such observations only roughly indicate the significance of *Leptodora* as predator on the herbivorous zooplankton. The outcome of these correlations may be particularly misleading because *Leptodora* will not be the only factor determining the abundance of herbivorous cladocerans.

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Acknowledgments

This is publication 3471 of The Netherlands Institute of Ecology (NIOO-KNAW). We thank Michaela Brehm and Guus Postema for technical assistance and Ramesh D. Gulati, Leonard V. Polishchuk, Matthijs Vos, and two anonymous reviewers for comments on the manuscript.

The relative importance of top-down and bottom-up control on *Leptodora* remains unclear. The abundance of *Leptodora* preferred prey is a measure of food availability for this predator. The abundance of such prey can be influenced by fish predation. A high fish predation pressure on the zooplankton community may result in a shift in the zooplankton size distribution toward small-bodied species, whereas a low fish predation pressure may lead to a dominance of large-bodied *Daphnia* (Size Efficiency Hypothesis: Hall et al. 1976).

Consumption rates of *Leptodora* are usually based on predation rates measured in the laboratory. These rates are highly variable (e.g., Browman et al. 1989; Herzig and Auer 1990; Pichlova and Vijverberg 2001) and, therefore, they form a poor basis for predicting the elimination rates of prey populations in the field. Therefore, instead of measuring consumption rates, we have chosen an alternative, one based on population dynamics and production. We measured growth and development rates of *Leptodora* in relation to temperature in the laboratory and densities, size distributions, and fecundities in the field. To our best knowledge, only Cummins et al. (1969) have previously employed this approach to quantifying the role of *Leptodora* in a food web.

Here we describe a 3-yr study of population dynamics and life history of *Leptodora* and its main prey and predators in Lake Tjeukemeer (The Netherlands), a shallow eutrophic lake. Our main objectives were to assess the effects on the population dynamics and production of *Leptodora* of (1) predation by 0+ fish and (2) the varying amounts of its potential prey (i.e., small-bodied herbivorous zooplankton).

Material and methods

Study area—Lake Tjeukemeer is a shallow (mean depth, 1.5 m), eutrophic, freshwater body with a surface area of 21.5 km² in the north of The Netherlands. It is much exposed to the wind and is well-mixed and thus thermally homogeneous. The lake is very turbid, and Secchi-disc depth usually varies between 25 and 35 cm. The littoral zone of the lake is poorly developed and represents only about 1% of the lake's surface area. The lake is part of an interconnected system of water bodies, which acts as a water reservoir for the surrounding polders (i.e., reclaimed land situated below sea level; for details see De Nie et al. 1980; Boersma et al. 1996). Water temperatures measured daily showed a pronounced seasonality: the highest annual temperatures (23–24°C) were recorded in July and August.

Leptodora is the most common invertebrate predator on small-bodied cladocerans in the lake. *Chaoborus* is absent, and predacious water mites are only occasionally observed (Vijverberg pers. obs.). The other common invertebrate predators in the lake are the advanced instars of medium-sized (max. length 1.1 mm) cyclopoid copepods (*Acanthocyclops robustus* and *Mesocyclops leuckartii*), at densities of about 25 ind L⁻¹ (Vijverberg 1977). Both of these copepods are assumed to feed mainly on noncladoceran prey items that are smaller than 0.1 mm (Hansen et al. 1994).

The fish community of the open water is characterized by age group >1+ bream (*Abramis brama*), >1+ pikeperch

(*Stizostedion lucioperca*), and 0+ fish. Both 1+ and older pikeperch are obligate piscivorous (i.e., feed on fish only), whereas the >1+ bream feed both on zooplankton and benthic invertebrates but rarely on *Leptodora* (Lammens et al. 1985). The 0+ fish in the open water zone consisted of smelt (*Osmerus eperlanus*), perch (*Perca fluviatilis*), and pikeperch and from July onward consisted also of a relatively small proportion of bream. This species showed a strong negative electivity for *Leptodora* (Van Densen 1985). In most years, smelt dominates the population of 0+ fish, comprising 80–90% of the population biomass (Vijverberg et al. 1990). From July onward, the young visually predating 0+ fish, comprising smelt, perch, and pikeperch, selectively feed on larger zooplankton species such as *Daphnia* spp. and *Leptodora* (Van Densen 1985). *Daphnia* density and body size are negatively correlated with the biomass of 0+ fish (Vijverberg and Van Densen 1984).

Leptodora sampling and sample analyses—Samples were collected in the morning between 1000 and 1200 h with two identical hoop nets each mounted on a pole. The nets were 100 cm long and had a mouth opening of 40 cm in diameter and a bar mesh size of 500 μm (cod end). At each sampling station the two nets were operated on both sides of the boat to sample simultaneously the near-surface and near-bottom waters. During each horizontal net haul, which took 30 s at a boat speed of 1 m s⁻¹, ca. 3.75 m³ was filtered. Samples were taken at 10 fixed stations in 1979 but at five stations in 1978 and 1980 in the lake's open water (see De Nie et al. 1980). For counting, samples containing more than 1,000 individuals were subsampled using the whirling vessel of Kott (Kott 1953). We distinguished between juveniles, females, and males based on morphological characteristics and size. Females have a well-pronounced brood pouch, which is lacking in juveniles and males. Also, males can be distinguished by their much longer first antenna. For length frequency distributions, samples from all stations for each date were pooled, and 100–200 individuals were measured in subsamples. Body length was measured to the nearest 0.5 mm from the top of the head to the base of the tail-fork using a stereo dissecting microscope.

Since females lose most of their eggs in formalin- or ethanol-preserved samples, only freshly caught live specimens were used for determining the clutch size. About 20 individuals at one time were lightly narcotized with CO₂-saturated water. The number of eggs or embryos per female was counted and the length of the female measured. Parthenogenetic eggs and resting eggs were distinguished, and the proportion of adult females with an empty brood pouch was noted. Resting eggs look similar to parthenogenetic eggs (Herzig 1985) but are much larger (more than 50% by volume) (Moshiri and Cummins 1969). Between 200 and 300 egg-bearing females were examined per sampling date.

Sampling potential prey items—Since *Leptodora* of >11.0 mm were very scarce, we defined the potential prey items as cladocerans of <1.0 mm. Cladocerans were sampled with a 5-liter trap-type sampler between 1000 and 1200 h and at the same depths and stations as for *Leptodora*. For each cladoceran species, the population density and size distri-

Table 1. Mean density ($n\ m^{-2}$), mean biomass ($mg\ dry\ wt\ m^{-2}$), and mean production ($mg\ dry\ wt\ m^{-2}\ yr^{-1}$) of *Leptodora* and mean biomass ($mg\ dry\ wt\ m^{-2}$) and mean production ($mg\ dry\ wt\ m^{-2}\ yr^{-1}$) of 0+ fish over the growing season (June–September) in the open water of Tjeukemeer, 1978–1980. Number of sampling dates in parentheses.

Year	<i>Leptodora</i> mean density	<i>Leptodora</i> mean biomass	<i>Leptodora</i> production	0+ fish mean biomass	0+ fish production
1978	1,344 (11)	53.7 (11)	792 (11)	389 (9)	1,479 (9)
1979	1,252 (14)	96.2 (14)	1,163 (14)	54 (9)	102 (9)
1980	476 (8)	28.5 (8)	438 (8)	2,491 (9)	7,235 (9)

bution were measured, and mean monthly biomass was calculated using the appropriate length–weight regression relationships (Vijverberg et al. 1990; Table 1). Monthly production was calculated using production (P) per unit biomass (B)(P/B) ratios, derived earlier under experimental conditions (Vijverberg 1980; Vijverberg and Richter 1982).

Sampling 0+ fish—The planktivorous 0+ fish in the large open water zone of the lake were sampled with larvae nets during the first half of June, with a 3-m beam trawl in the second half of June, and with a 5-m beam trawl from July onward (Lammens et al. 1985; Vijverberg et al. 1990). The trawls sampled the entire water column down to the bottom. The 3-m trawl had a head rope of 4.5 m, a foot rope of 6 m, and the length of the side panels was 0.9 m. The bar mesh of the netting material varied from 12 mm in the mouth of the trawl to 4 mm at the cod end. The 5-m trawl had a head rope of 8.5 m, a foot rope of 9.5 m, and a side panel height of 1 m. Two larvae nets were used to sample simultaneously the near-surface and the near-bottom water layers at the same sampling stations as for the *Leptodora* sampling. The larvae nets had a bar mesh of 1,000 μm .

Data analyses and calculations—In cladocerans, the number of eggs or embryos per female is generally considered to be a reliable indicator of the prevalent food conditions (Vijverberg 1989). This fecundity parameter, however, is also influenced by the size of the female. On each sampling date, the relationship between the number of eggs per ovigerous female (F) and the length (L, mm) of the female were determined from the regression relationship

$$F = aL^b \quad (1)$$

where a and b are constants.

In order to eliminate the effect of size on fecundity and to facilitate comparison of fecundity for different sampling dates, the mean egg number per ovigerous female was calculated for females of standard length ($L = 8.0\ mm$) using Eq. 1. This value is the standard egg number (SEN) according to Hebert (1977).

We converted numbers per size class to biomass using the relationship determined by us between the length (L, mm) and ash-free dry weight per individual (W, μg) of freshly caught *Leptodora*:

$$W = 0.79 L^{2.38} \text{ (log-log regression, } r^2 = 0.95) \quad (2)$$

The egg weight is considered to be equal to the weight of the resulting newborn (Boersma 1995).

In a separate study we cultured *Leptodora* in the laboratory at four constant temperatures (15, 17.5, 20, and 25°C) (Vijverberg and Koelewijn 2004). Growth in length, egg development times, and instar duration times were measured. These results were used, together with field data on density, size distribution, and fecundity, to estimate birth and mortality rates, production, and productivity of *Leptodora* in the lake. For these calculations the population dynamics model INSTAR (Hogeweg and Richter 1982; Vijverberg and Richter 1982) was used.

If we assume a 100% prey ingestion and an assimilation efficiency of 87%, as given in literature for feeding of *Leptodora* on zooplankton (Hillbricht-Ilkowska and Karabin 1970), the efficiency of assimilated energy utilized for growth and reproduction is 45%. This gives an overall conversion from prey biomass to *Leptodora* production of 39% ($0.87 \times 0.45 \times 100$). However, the assumption of 100% ingestion of all prey captured is a gross overestimate, because during prey capture by *Leptodora*, there is a considerable loss of the prey's body parts and body fluids because the prey is torn to pieces, and much debris, mainly exoskeletal refuse, is discarded (Browman et al. 1989). Thus, much of the prey biomass is lost before the food is eaten. Branstrator (1998) measured ingestion efficiencies ranging between 41% and 72% for *Leptodora* feeding on two species of small-bodied cladocerans. Lehman (1993) measured for *Bythotrephes cederstroemi*, a carnivorous cladoceran with a feeding behavior very similar to that of *Leptodora*, an ingestion efficiency of 58–59%. Therefore, for back-calculating the elimination rate (mortality) of cladoceran biomass by *Leptodora* from its production, we found a conversion efficiency of 23.4% (0.6×39) to be more realistic.

Population dynamics model INSTAR—The Individual Based Model INSTAR was used to simulate reproduction, individual growth per molt, and density changes per instar due to birth, death, or growth. The model is explained in detail by Hogeweg and Richter (1982), and this model has been earlier used in studies on population dynamics and production of cladoceran and copepod species (e.g., Vijverberg and Richter 1982; Hovenkamp 1990; Boersma et al. 1996). This model differs from the more commonly used continuous simulation models in that it is event-oriented. Because length growth by molting is a discontinuous process, event-orientated simulation is especially suited for simulating growth in copepods and cladocerans. This applies also for life-cycle phenomena such as egg production, egg development, and hatching of newborns, all of which are closely

related to molting in cladocerans. The model is based on the life-cycle events of an individual cladoceran. Output is organized per size class, but individuals in the model system keep acting as independent entities. We distinguished five size classes (mm): size class 1 = 1.4–3.9; size class 2 = 4.0–5.9; size class 3 = 6.0–7.9; size class 4 = 8.0–9.9; and size class 5 = 10.0–13.9. The duration of an instar in the field (D) is calculated stepwise as follows:

$$D = F_i \{D[T(t_1)] + D[T(t_2)]\} / 2 \quad (3)$$

$$t_2 = t_1 + F_i D[T(t_1)] \quad (4)$$

where F_i = juvenile instar-specific duration expressed as a fraction of the adult-instar duration at a constant temperature T ; i is the juvenile-instar number ($i = 1, 2, \dots, 7$); $D(T)$ = the adult-instar duration at a constant temperature T ; $T(t)$ is water temperature as a function of time t ; and t_1 is the time at which the present instar developed by molting from the preceding instar.

The model simulates the *Leptodora* population using field data on fecundity and length frequency distributions and estimates the number of individuals of different size classes that die in a certain period by comparing the computed numbers in the model system with those in the field. If the densities in the model system are higher than those observed in the field, this difference is set to zero and is attributed to animals that are assumed to have died. This provides an estimate of total mortality. In an opposite situation, (i.e., if the numbers in the model population are equal or lower than the observed densities in the field), the mortality is assumed to be zero. However, modeled numbers are almost never lower than those in the field. Field data were smoothed prior to application of INSTAR by using a three-point moving average.

The birth rate was estimated by keeping track of the number of newborn that hatched when adult females molted to a next instar. Both parthenogenetic and resting eggs are included in the model, but only the parthenogenetic eggs hatch. Each 24 h the number of new born per day relative to the total population (mean population over same time interval) was calculated.

In the model system, the length and age of each individual are known. The size of the newborn (L_{newborn}) can be predicted from the size of the mother (L_{ad}) using a linear regression model (Vijverberg and Koelewijn 2004):

$$L_{\text{newborn}} = 0.88 + 0.14L_{\text{ad}} \quad (5)$$

Somatic growth rate (length increase per molt) determines the transition speed from one length class to another. For estimating production and biomass, length is converted to biomass using Eq. 2.

Results

Abundance of zooplankton and fish—The densities of *Leptodora* in the lake changed both seasonally and annually (Fig. 1A; Table 1). Densities started increasing during the second half of May, and in all 3 yr, two population peaks could be distinguished: one in early summer, June–July, and the other in late summer, August–September. In 1978 the

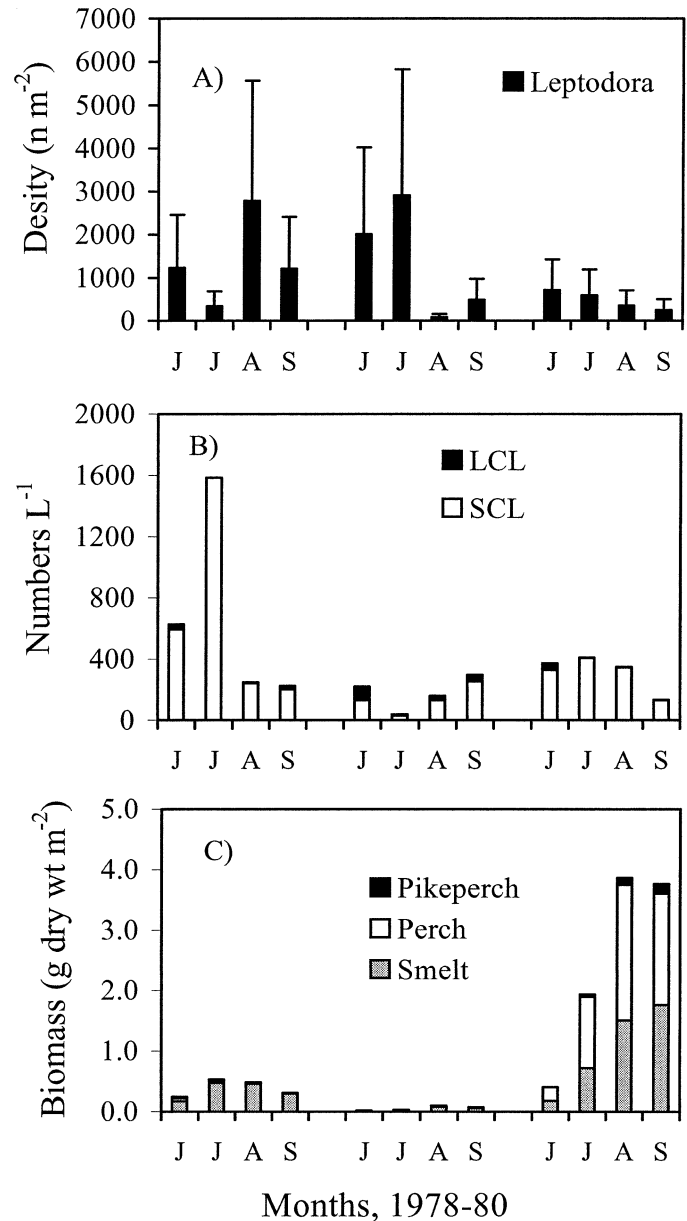


Fig. 1. Mean abundance per month of *Leptodora*, its food organisms (cladoceran zooplankton), and its predators (0+ fish) in the open water of Tjeukemeer during the growing season (June–September) in 1978, 1979, and 1980. (A) Densities ($n\ m^{-2}$) of *Leptodora*. Number of sampling dates: 1978, $n = 11$; 1979, $n = 14$; 1980, $n = 8$. Error bars represent $+1$ SD. (B) Densities (numbers per liter) of small-bodied cladocerans (<1.0 mm, SCL) and large-bodied cladocerans (≥ 1.0 mm, LCL). Number of sampling dates: 1978, $n = 8$; 1979, $n = 13$; 1980, $n = 9$. (C) Biomass (g dry wt m^{-2}) of 0+ fish. Number of sampling dates: 1978, $n = 9$; 1979, $n = 9$; and 1980, $n = 9$.

peak densities in late summer were the highest, but in 1979 and 1980, the early summer peak was higher than the one in late summer. In 1980 the densities were in general low, and the population maxima were less pronounced.

Cladoceran densities usually varied between 200 and 400 ind L^{-1} in the growing season (Table 2; Fig. 1B). The pro-

Table 2. Mean density per month (number per liter) of common cladoceran species in the open water of Tjeukemeer during the growing season (June–September) in 1978, 1979, and 1980. Number of sampling dates: 1978 ($n = 8$), 1979 ($n = 13$), and 1980 ($n = 9$).*

Species	1978				1979				1980			
	Jun	Jul	Aug	Sep	Jun	Jul	Aug	Sep	Jun	Jul	Aug	Sep
BC	333	563	62	61	17	9	18	48	44	68	92	43
BL	17	32	1	0	27	1	2	9	89	28	8	53
CH	189	981	169	113	1	17	101	162	149	306	225	17
DA	85	4	14	49	175	12	37	76	88	8	19	17

* BC, *Bosmina coregoni*; BL, *Bosmina longirostris*; CH, *Chydorus sphaericus*; DA, *Daphnia* spp.

portion of small-bodied cladoceran species (i.e., <1.0 mm) was generally high. Among these, *Chydorus sphaericus* was predominant, followed by *Bosmina coregoni* (Table 2). The large-bodied species *Daphnia galeata* was usually present in June and September and was especially common in 1979. Although *D. galeata* is considered as a large-bodied species, most juvenile daphnids (<1.0 mm) can be grouped with small-bodied cladocerans. Therefore, daphnids of this size were grouped with small-bodied cladocerans. Small-bodied cladocerans were observed in extreme high densities (ca. 1,600 L⁻¹) during July 1978, but their densities (ca. 30 L⁻¹) in the same month next year were the lowest during this study (Fig. 1B).

The biomass of 0+ fish varied both seasonally and from year to year (Table 1; Fig. 1C): in 1979 it was very low, in 1978 intermediate, and in 1980 it was high. It was highest during August or September, but in 1978 it was also relatively high in July. In 1978 and 1979, the 0+ fish age group was dominated by smelt, but in 1980 perch was also abundant.

Fecundity of Leptodora—For comparing seasonal and annual changes in *Leptodora* fecundity, we used Eq. 1; the SEN per sampling date was calculated for a female of standard length of 8.0 mm. The within-year variations in fecundity were relatively small (range, 13–18 eggs per female).

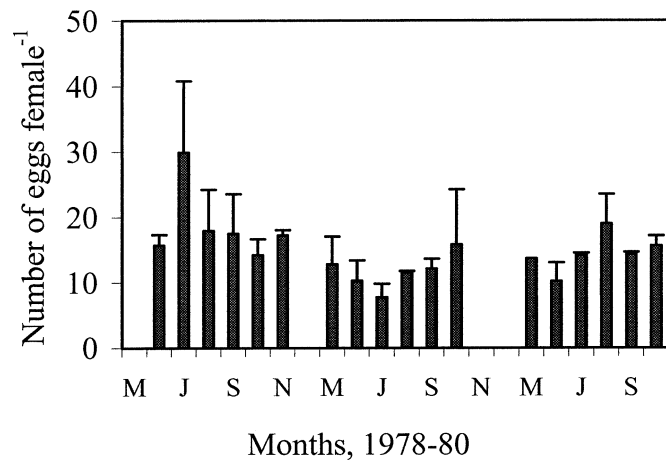


Fig. 2. Mean standard egg number of an ovigerous female of 8 mm (SEN, mean + 1 SD) per month of *Leptodora* in Tjeukemeer (1978–1980). Number of sampling dates: 1978, $n = 15$; 1979, $n = 13$; 1980, $n = 11$.

There were two exceptions: (1) in July 1978, when the females were very fecund (ca. 30 eggs per female) and (2) in July 1979, when the fecundity was exceptionally low (ca. 8 eggs per female) (Fig. 2).

Population dynamics—The seasonal pattern for birth rates was similar in all years: high to medium-high birth rates occurred during early summer, there was a peak in the second half of July or in the first half of August, and a progressive decrease in rates occurred thereafter (Fig. 3A). At the end of October and during November, the birth rates were either already zero or approached zero. This was not only the result of decreasing water temperatures, but was predominantly the effect of progressively increasing propor-

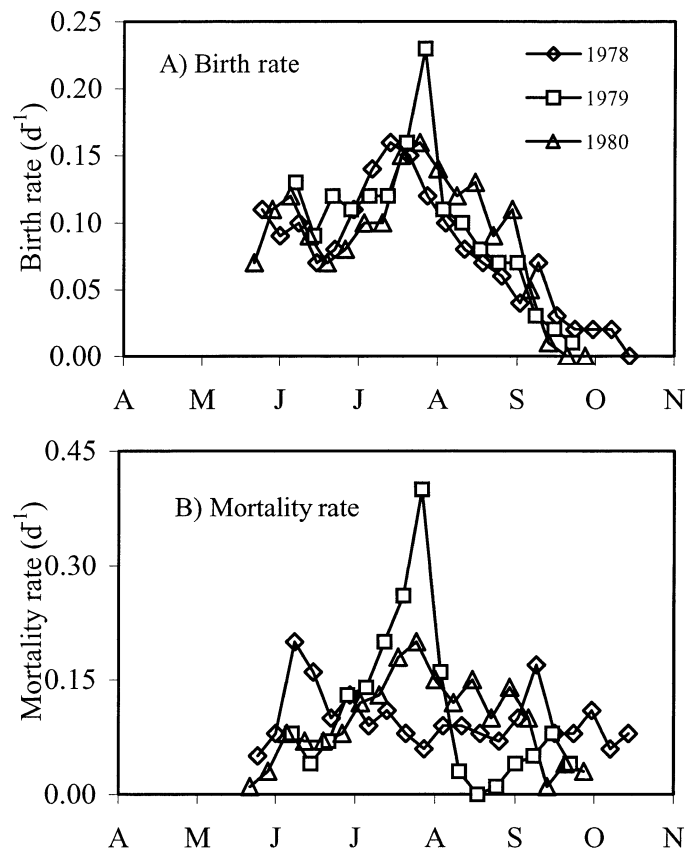


Fig. 3. Population dynamics of *Leptodora* in Tjeukemeer during three successive years: (A) mean birth rate (d⁻¹) and (B) mean mortality rate (d⁻¹) averaged over weekly intervals.

Table 3. Mean daily P/B ratios of *Leptodora* per month and per year in Tjeukemeer, 1978–1980. Also provided is the mean water temperature over the same period (°C). Annual values are given for (1) growing season June–September and (2) whole period that *Leptodora* was present. Mean + 1 SD in parentheses.

Months	1978		1979		1980	
	Daily P/B	Temperature	Daily P/B	Temperature	Daily P/B	Temperature
Jun	0.115 (0.0204)	17.2 (2.6)	0.102 (0.0046)	17.1 (0.9)	0.123 (0.0163)	16.1 (2.2)
Jul	0.126 (0.0307)	17.1 (3.0)	0.097 (0.0057)	17.0 (0.6)	0.119 (0.098)	17.9 (2.2)
Aug	0.139 (0.0121)	17.0 (1.3)	0.105 (0.0068)	18.0 (1.3)	0.136 (0.0106)	18.3 (2.4)
Sep	0.104 (0.0147)	15.0 (1.1)	0.092 (0.0167)	14.9 (1.9)	0.125 (0.0086)	16.0 (1.4)
Oct	0.065 (0.0143)	11.2 (1.2)	0.066 (0.0081)	12.3 (0.4)	0.103	12.5
Nov	0.071	9.6				
Mean (1)	0.121 (0.0148)	16.6 (1.0)	0.099 (0.0056)	16.8 (1.3)	0.126 (0.0034)	17.1 (1.2)
Mean (2)	0.103 (0.296)	14.5 (3.3)	0.092 (0.0158)	15.9 (2.3)	0.121 (0.0121)	16.1 (2.3)

tions of males and females with resting eggs in the population (not shown). In contrast with the birth rates, the patterns for mortality rates differed from year to year (Fig. 3B). In 1978 the mortality rates varied only between narrow limits (0.6–0.20 d⁻¹), with two minor peaks during the later part of June and in mid-September. In 1979, however, the mortality rates were quite high (0.2–0.4 d⁻¹) during the second half of July and early August but were much lower during the rest of the year. In 1980 mortality rates were rather low in early summer, exhibited a small peak in the second half of July and early August, and remained moderately high until early September, after which they dropped to low values.

Production and prey mortality—The productivity of *Leptodora* ranged from 438 mg dry wt m⁻² yr⁻¹ in 1980 to 1,163 mg dry wt m⁻² yr⁻¹ in 1979, with an intermediate value in

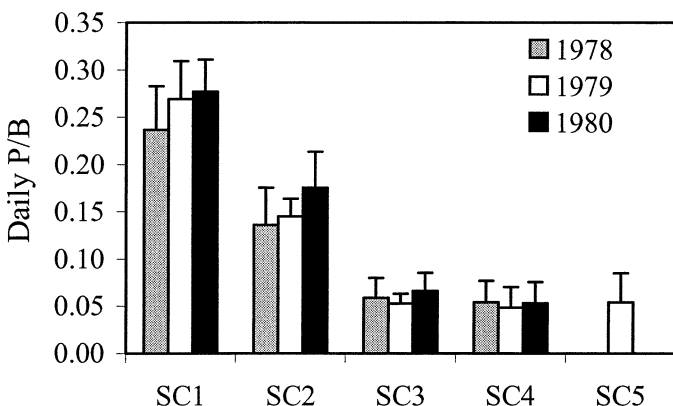


Fig. 4. Size-specific productivity of *Leptodora* in Tjeukemeer during three successive years (1978–1980). Mean daily P/B ratios per size class. Size classes: SC1 = 1.4–3.9, SC2 = 4.0–5.9, SC3 = 6.0–7.9, SC4 = 8.0–9.9, and SC5 = 10.0–13.9 mm. Error bars represent + 1 SD.

1978 (Table 1). The production P/B ratio of *Leptodora* did not change much during the growing season (June–September), but it was lower in October–November (Table 3). This ratio was similar during the growing seasons in 1978 and 1980 but somewhat lower in 1979. In addition to its dependence on temperature, the P/B ratio is also size dependent, especially for the individuals in the size range of 1.4–7.9 mm (Fig. 4). Because the water temperatures during these 3 yr were similar, the difference could only be attributed to the annual differences in the size composition of the populations: the 1979 population contained higher proportions of larger individuals than did the populations of 1978 and 1980.

0+ Fish predation—In all 3 yr, abundance of 0+ pike perch was low (Fig. 1C). Gut contents of pikeperch were analyzed in all 3 yr, but we analyzed gut contents of perch and smelt only in 1978 and 1979. The proportion of *Leptodora* biomass in the diets of 0+ perch and 0+ smelt was similar, but 0+ pikeperch generally consumed more *Leptodora* than perch and smelt (Fig. 5). Especially in August and September 1978, 0+ pikeperch had very large proportions of *Leptodora* in its diet.

Predation mortality of cladocerans—We back-calculated the elimination rate of small-bodied cladoceran biomass by *Leptodora* from the estimated *Leptodora* production, assuming a conversion efficiency of prey biomass to *Leptodora* production of 23.4%. We compared the monthly mortality of the small-bodied prey by *Leptodora* with that of the monthly production of these prey. The production of prey items was usually found to be sufficient for *Leptodora* to meet its metabolic demands and to grow and reproduce (Fig. 6), except in July 1979, when the estimated prey biomass eliminated by *Leptodora* was ca. 12 times higher than the production of its small-bodied prey (i.e., prey production was insufficient for *Leptodora* to realize its own production). This was confirmed by low fecundity (Fig. 2), very high

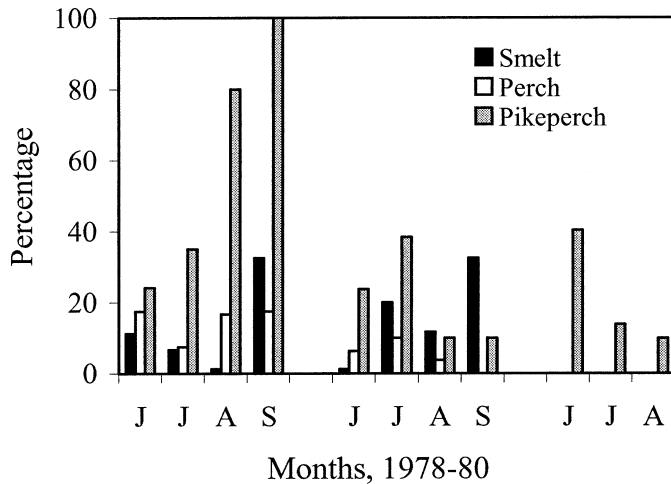


Fig. 5. Annual and monthly variation in the proportion of *Leptodora* (biomass, %) in the diets of 0+ smelt, 0+ perch, and 0+ pikeperch in the open water of Tjeukemeer. Number of sampling dates: 1978, $n = 8$; 1979, $n = 8$; 1980, $n = 8$. In 1980, only pikeperch gut contents were analyzed.

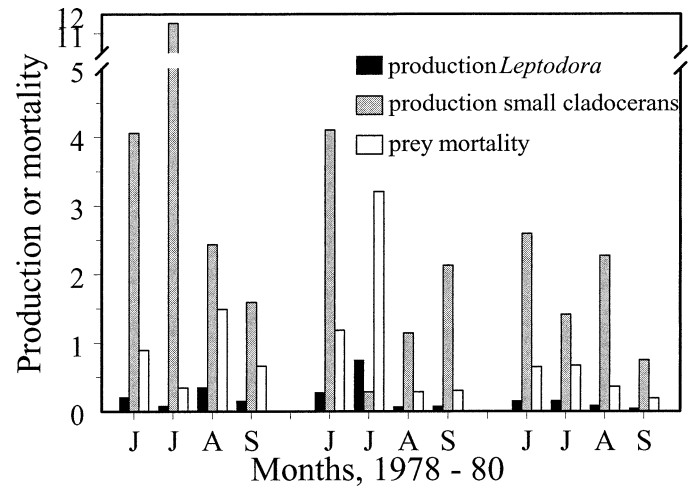


Fig. 6. Production per month (g dry wt m^{-2} month $^{-1}$) of *Leptodora* and small-bodied cladocerans (individuals <1.0 mm) and the estimated mortality per month of small-bodied cladocerans (g dry wt m^{-2} month $^{-1}$) attributed to *Leptodora* in Tjeukemeer during the growing season (June–September) in 1978, 1979, and 1980. For calculation of prey mortality, see text. Number of sampling dates for *Leptodora*: 1978, $n = 11$; 1979, $n = 14$; 1980, $n = 7$; number of sampling dates for cladocerans: 1978, $n = 8$; 1979, $n = 13$; and 1980, $n = 9$.

mortality rate (Fig. 3B), and densities of *Leptodora* that plummeted to very low values in early August 1979 (Fig. 1A).

Discussion

We used a population dynamics and production approach to assess the trophic status of *Leptodora* in the food web of Lake Tjeukemeer, a typical example of a shallow, eutrophic lake in The Netherlands. In this lake, 0+ fish, predominantly smelt and perch, are the main predators. The abundance of *Leptodora*'s predators (0+ fish) and prey (small-bodied cladocerans) varied annually (Tables 1, 2). This offered, therefore, a unique opportunity to investigate in the field the relative importance in different seasons of top-down and bottom-up control of *Leptodora*.

Leptodora–prey interactions—By removing juvenile prey (i.e., *Daphnia* and *Diaphanosoma* spp. <1.0 mm) *Leptodora* can alter the age structure of the prey population such that the proportion of adults in the population will increase. Therefore, this invertebrate predator may contribute to enhancement of the per capita birth rate of large-bodied cladocerans. Such an increase can act as a stabilizing mechanism, modulating the downward oscillation of the prey population and damping the amplitude of the predator cycle (Polishchuk 1995). Vertebrate predators, such as fish, do not possess such a mechanism to stabilize prey because they often feed selectively on egg-bearing adults with larger clutches and reduce the per capita birth rate of prey (Gliwicz and Pijanowska 1989).

The degree of prey selection by *Leptodora* depends both on its own size and behavior and on the size, behavior, and morphology of the prey species (Pichlova and Vijverberg 2001). *Leptodora* tears the cladocerans apart; the wider the ventral carapace gape of the prey, the easier it is for *Leptodora* to feed upon it (Browman et al. 1989). The size of

the 'feeding basket,' a structure formed by thoracic appendages enabling *Leptodora* to catch and handle prey for ingestion, determines the success with which a prey is captured (Herzig and Auer 1990; Manca and Comoli 1995; Branstrator 1998). Of the three prey taxa in our study, both juvenile daphnids and *Bosmina* spp. are most likely highly vulnerable to predation by *Leptodora*, because both of these prey possess a wide, ventral carapace gape and a soft carapace. Several experimental feeding studies have confirmed the suitability of these prey species for *Leptodora* (e.g., Branstrator 1998; Pichlova and Vijverberg 2001). Although it has a suitable small size, *Chydorus sphaericus* is probably the least vulnerable to predation by *Leptodora* because of its hard carapace and distinctly rounded valves and small gape width (Jamieson 1980).

Fecundity of *Leptodora* in Tjeukemeer was generally high and rather constant, implying favorable food conditions (i.e., constant availability of suitable prey organisms for *Leptodora* to grow and to reproduce). Food effects on *Leptodora* were the strongest in July 1978, when fecundity was the highest (SEN ca. 30 eggs \cdot female $^{-1}$) (Fig. 2), and in July 1979, when fecundity was, relatively, the lowest (SEN ca. 8 eggs \cdot female $^{-1}$). There is no doubt that the high fecundity was caused by the favorable food conditions in July 1978, when we observed the highest densities of small-bodied cladocerans, both *C. sphaericus* and *Bosmina* spp. (together ca. 1,600 ind L^{-1}) (Table 2). In contrast, as expected, the lowest fecundity of *Leptodora* in July 1979 coincided with the lowest densities of small-bodied cladocerans observed during the study period (ca. 30 ind L^{-1}). In this month, the estimated required prey production for *Leptodora* growth and reproduction was ca. 12 times higher than the actual measured production of small-bodied cladocerans. This means that the

amount of available food was insufficient to meet the metabolic demands of *Leptodora*. This is corroborated by the high mortality rates of 0.2–0.4 per day during the second half of July and early August, the highest mortality rates of that year, which caused a steep decrease in the population densities of *Leptodora*.

Effect of 0+ fish on Leptodora—The proportion of *Leptodora* biomass in the diet of 0+ pikeperch was higher than that in the diets of 0+ perch and 0+ smelt. Because juvenile pikeperch was not abundant in the lake, smelt (1978, 1979, 1980) and perch (1980) were mainly responsible for the predation mortality of *Leptodora*. Gut contents of smelt and perch were only analyzed in 1978 and 1979, but pikeperch diet was also examined in 1980. Since the diet of 0+ pikeperch contained similar proportions of *Leptodora* during 1979 and 1980, we assume that 0+ perch and 0+ smelt diets also contained similar proportions of *Leptodora* in 1979 and 1980. However, since the biomass of 0+ fish was much higher in 1980 than in 1979 and 1978, the amount of *Leptodora* ingested by 0+ fish must have been much larger in 1980 than in the previous 2 yr.

The seasonal mortality rates in 1980 that were the highest in July, August, and September agreed with the seasonal trend in biomass of 0+ fish. Such a correspondence was not observed in 1978 and 1979. In 1978, small mortality peaks were observed during the second half of June and in mid September, while the highest biomass of 0+ fish occurred during July–August. Because the seasonal variation in 0+ fish biomass was relatively minor, small differences in selective feeding behavior of the fish may explain this discrepancy. In 1979, the seasonal mortality pattern of *Leptodora* and the variation in 0+ fish biomass did not correspond with one another. High mortality rates observed during the second half of July and early August could not be ascribed to predation by 0+ fish, because biomass of this fish was very low. This mortality was most likely caused by food limitation (see *Leptodora*–prey interactions).

In Tjeukemeer, the main 0+ fish, smelt and perch, eat ca. 55% of the large-bodied zooplankton production in the open water, and 15% is eaten by 0+ and older bream (Vijverberg et al. 1990). Since 0+ and older bream are feeding both on zooplankton and benthic invertebrates, but rarely on *Leptodora* (Lammens et al. 1985), 0+ smelt, perch, and pikeperch are probably responsible for more than 95% of the *Leptodora* mortality due to fish predation.

In 1979, when 0+ fish biomass was eight times lower than in 1978, *Leptodora* biomass increased by ca. 80% and its production by about 50%. In contrast, in 1980, when 0+ fish biomass was six times higher than in 1978, both the biomass and production of *Leptodora* were 50% lower. Similar reciprocal effects were observed for *Daphnia*: its mean densities during July–September 1979 increased by ca. 100% compared with those in 1978, and its densities were ca. 15% lower in 1980 relative to 1978 (Table 2). The results of a regression analysis based on a larger data set (7 yr: 1976–1982) corroborate the results that *Daphnia* densities and size were negatively correlated with 0+ fish biomass (Vijverberg and Van Densen 1984).

In the present study we found only a weak effect of fish

predation on *Leptodora* size: *Leptodora* were relatively larger in size in 1979, when 0+ fish biomass was very low, but were of similar size in the two other years. The effect of fish predation on the size of *Leptodora* and other large-bodied cladocerans was also documented by Xie et al. (2000) in Lake Donghu (China) in a very long-term study (1957–1996). The effects of the increased fish predation, mainly after 1984, due to a progressive increase in fish stocks as the lake became more eutrophic, was significantly related to marked decline in body length of *Leptodora* as well as of other large-bodied cladocerans (e.g., *D. galeata*, *D. carinata*, and *Diaphanosoma brachyurum*.)

Although *Leptodora* is much larger in size than *D. galeata*, it shows a remarkably greater ability to survive size-selective predation by fish. This can be attributed to its low visibility to predators, as a result of its extremely transparent body. Adult females are more visible than juveniles because of their eggs and embryos and their relatively large black compound eye, the size of which is positively related to its body size (Branstrator and Holl 2000). However, during periods of heavy fish predation, *Leptodora* adults, like many daphnids, perform diel vertical migration (i.e., descend to deeper water layers during the day to avoid fish predation [Vijverberg 1991; Branstrator and Holl 2000]).

Direct and indirect effects of fish predation—Vertebrate predators such as juvenile fish often have high feeding rates and can remove substantial portions of prey populations (Vijverberg et al. 1990; Duncan 1997). In addition, young planktivorous fish often selectively feed on large, egg-bearing adults with larger clutches and hence not only increase the death rate but also suppress the per capita birth rate of zooplankton prey populations (Gliwicz and Pijanowska 1989). Therefore, juvenile fish are potentially very important in regulating prey size distribution and species composition in zooplankton communities.

In this study we found a direct relation between predation pressure of juvenile fish and the biomass and production of *Leptodora* in Tjeukemeer. A similar relationship was previously found between juvenile fish and *Daphnia* in the same lake (Vijverberg and Van Densen 1984). There were also indications for a possible indirect effect of fish predation on the densities of small-bodied cladocerans. In 1979, when fish predation was very low, *D. galeata* was abundant and was of a relatively large size: this also coincided with low densities of small-bodied cladocerans, such as *Chydorus sphaericus* and *Bosmina* spp. This shift in the zooplankton community agrees with the prediction that a competitively superior large-bodied species can outcompete smaller zooplankton species when positive size-selective predators are rare (Size Efficiency Hypothesis: Hall et al. 1976). However, our observations and model results clearly show that the population dynamics of *Leptodora* are predominantly regulated by direct predation effects.

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Received: 14 April 2004

Accepted: 15 September 2004

Amended: 1 October 2004