

# Seasonal patterns in the mortality of *Daphnia* species in a shallow lake

Maarten Boersma, Onno F.R. van Tongeren, and Wolf M. Mooij

**Abstract:** To assess the impact of predation by young-of-the-year (0+) fish on the population dynamics of *Daphnia* species, we made independent estimations of the mortality of *Daphnia* species during the year, and of the predation pressure exerted by the juvenile fish. Mortality of daphnids was computed using a model that allowed us to differentiate between different size-classes, while total fish consumption was estimated from the temperature-dependent daily weight increase and the population development of the 0+ fish. The predation pressure on the different size-classes of *Daphnia* species was estimated by combining the total fish consumption with estimates of the selective feeding behaviour of the fish. To make the estimates of fish consumption independent of our current (1989–1991) zooplankton data set, we estimated fish species-specific and fish length-dependent selectivity indices on zooplankton using a different data set (1976–1977). *Daphnia* population densities usually increased in spring and decreased rapidly in early summer. Predation by 0+ fish was not severe enough to explain the large mortality that caused the summer decline; later in the year most of the mortality in the larger size-classes of the daphnids (>1.0 mm) could be explained by fish predation.

**Resumé :** Pour mesurer l'impact de la prédation par les jeunes poissons de l'année (0+) sur la dynamique des populations des espèces de *Daphnia*, nous avons fait des estimations indépendantes de la mortalité des espèces de *Daphnia* pendant l'année, et de la pression de prédation exercée par les jeunes poissons. Nous avons calculé la mortalité des daphnies à l'aide d'un modèle qui nous permettait de différencier les classes de taille, tandis que la consommation totale des poissons était estimée à partir de l'augmentation de poids quotidienne dépendant de la température et du développement de la population de poissons 0+. Nous avons estimé la pression de prédation sur les différentes classes de taille de *Daphnia* en combinant la consommation totale des poissons à des estimations du comportement d'alimentation sélective des poissons. Pour rendre les estimations de la consommation des poissons indépendantes de notre série présente (1989–1991) de données sur le zooplancton, nous avons calculé les indices de sélectivité à l'égard du zooplancton qui sont propres à l'espèce de poisson et dépendants de la longueur des poissons, en nous servant d'une série différente de données (1976–1977). Les densités de la population de *Daphnia* augmentaient généralement au printemps et baissaient rapidement au début de l'été. La prédation par les poissons 0+ n'était pas assez forte pour expliquer l'importante mortalité qui causait le déclin estival; pendant le reste de l'année, la majeure partie de la mortalité chez les plus grandes classes de taille des daphnies (>1,0 mm) pouvait s'expliquer par la prédation des poissons.

[Traduit par la Rédaction]

## Introduction

Population densities of many zooplankton species usually show distinct seasonal patterns in temperate lakes. This seasonal behaviour has been well studied, particularly for daphnids (e.g., Luecke et al. 1990). Typically, the densities of *Daphnia* populations peak in late spring and then decline in early summer. This decline is often associated in time with a

distinct clear-water phase, with high water transparency, and with a low phytoplankton abundance. The clear-water phase is caused by the increased grazing pressure of the zooplankton as a result of the increase in densities (Lampert et al. 1986). This leads to a reduction in the phytoplankton densities, and often to a shift in the phytoplankton composition from small single-celled diatom species to larger cyanobacteria, resulting in deteriorating food conditions for the daphnids and consequently declining animal densities.

Not all lakes show a clear-water phase. Especially in eutrophic lakes no apparent changes occur in the phytoplankton composition, yet population numbers of *Daphnia* species still decline sharply in summer (Vijverberg and Richter 1982; Gulati 1990). Consequently, as food limitation is less obvious in eutrophic lakes an alternative hypothesis was formulated to explain the decrease in daphnid densities in the summer (Mills and Forney 1983; Hairston 1987): the temperature increase in spring leads to an increase in consumption of zooplankton by planktivorous fish. The rise in temperature also triggers the

Received February 8, 1995. Accepted July 20, 1995.  
J12768

M. Boersma,<sup>1</sup> O.F.R. van Tongeren,<sup>2</sup> and W.M. Mooij.  
Netherlands Institute of Ecology, Centre for Limnology,  
Rijksstraatweg 6, 3631 AC Nieuwersluis, The Netherlands.

<sup>1</sup> Present address: Max Planck Institut für Limnologie,  
Postfach 165, D-24302 Plön, Germany.

<sup>2</sup> Present address: Data Analyse Ecologie, Waemelslant 27,  
6931 HS Westervoort, The Netherlands.

spawning of fish (Mooij et al. 1994), followed by the recruitment of large numbers of fast-growing juvenile fish. Consequently, there is a sharp increase in the predation pressure on daphnids, which causes the population densities of these zooplankters to decrease.

In Tjeukemeer, a highly eutrophic lake, young-of-the-year (0+) fish constitute approximately 80% of the total fish production and are the main vertebrate zooplanktivores (Vijverberg et al. 1990). Hence, when investigating the effect of fish predation on the population dynamics of cladoceran zooplankton it suffices to evaluate the effects of 0+ fish, especially as older year-classes of most fish species often shift to other, more benthic, prey (Lammens et al. 1985).

We investigated the validity of the predation-induced decline hypothesis by estimating the impact of predation by juvenile fish on the population dynamics of daphnids. We compared two almost independent estimates of the mortality of daphnids. First, we estimated the total mortality of the daphnids using a method similar to the one derived by Paloheimo (1974). Secondly, we estimated the consumption of daphnids by 0+ fish, combining data on individual fish growth, selectivity, and fish densities. The comparison of these two estimates yielded information on the impact of juvenile fish on the population dynamics of *Daphnia* species.

Studies such as this one, integrating data on zooplankton production and fish consumption, are relatively rare (e.g., Luecke et al. 1990; Rudstam et al. 1992; Mehner et al. 1995), and might be subjected to criticism from two sides. On the one hand it might be argued that the assumptions and simplifications necessary for the computations completely underrepresent real systems, and combinations of different methods and sampling strategies will yield nontestable or irreproducible results, whereas on the other hand other workers might find the methods used in these computational exercises too elaborate. However, as the methods used in this study are a formalization of what is often done by rules of thumb we feel that an approach such as the one presented here is a useful tool to obtain more knowledge of aquatic systems as a whole, and results of studies like this one could direct further research.

## Materials and methods

### Study area

Tjeukemeer is a shallow (mean depth 1.5 m), wind-exposed, eutrophic lake, with a surface area of 21.5 km<sup>2</sup> and a poorly developed littoral zone. Phytoplankton biomass in the lake is high during summer, with chlorophyll *a* concentrations often exceeding 100 µg·L<sup>-1</sup>. Algal biomass is dominated by diatoms in February and March and by cyanobacteria, mainly *Oscillatoria* species, during the rest of the year. In general, no clear-water phase occurs; summer Secchi-disc depths vary between 25 and 35 cm.

The herbivorous zooplankton is dominated by cladocerans: *Bosmina coregoni*, *Bosmina longirostris*, *Chydorus sphaericus*, *Ceriodaphnia pulchella*, *Daphnia galeata*, *Daphnia cucullata*, and the hybrid between these two daphnid species. Invertebrate predators include *Leptodora kindtii*, different species of omnivorous cyclopoid copepods (*Cyclops vicinus*, *Acanthocyclops robustus*, and *Mesocyclops leuckarti*), and water mites. The opossum shrimp, *Neomysis integer*, is

usually present in low densities (Bremer and Vijverberg 1982), while larvae of the phantom midge, *Chaoborus* sp., are almost absent from Tjeukemeer.

The open-water fish community of the lake consists of eight species: bream (*Abramis brama*), white bream (*Blicca björkna*), roach (*Rutilus rutilus*), smelt (*Osmerus eperlanus*), pikeperch (*Stizostedion lucioperca*), perch (*Perca fluviatilis*), ruffe (*Gymnocephalus cernua*), and eel (*Anguilla anguilla*). Although adult bream has by far the largest standing stock of the fish species in Tjeukemeer, production is lower than the production of the 0+ fish (Vijverberg et al. 1990). As a result, young-of-the-year smelt, bream, perch, pikeperch, and roach are the main zooplanktivores in Tjeukemeer. In most years smelt constitute 70–80% of the 0+ fish biomass.

### Sampling

#### Zooplankton

During the years 1976–1977 and 1989–1991 zooplankton was sampled with a 5-L Friedinger sampler at five stations. At each station two samples were taken, one below the surface and the other just above the bottom of the lake. Sampling was done at weekly intervals during the growing season from April to October, and at fortnightly intervals during the rest of the year. The samples were concentrated by filtration through a 120-µm mesh sieve, pooled, and preserved in a 4% formaldehyde solution. The cladoceran zooplankters were identified to species, whereas the copepods were classified as cyclopoids and calanoids, and the densities were established. For the numerically important groups, length–frequency distributions were determined by measuring 100 individuals. Daphnids were measured from the top of the eye to the base of the tail spine. For the other cladocerans the total length minus the tail spine was measured. Because copepods usually have curved telsons in fish stomachs, or break in two, cephalothorax lengths were recorded for these groups. To compute birth and death rates the relationships between egg number and animal length were established for the *Daphnia* species on animals taken in additional samples that were stored in 95% ethanol.

#### Fish

Length–frequency distributions of the five major 0+ fish species were obtained from a routine sampling of fish in Tjeukemeer, which started in 1975 (Lammens et al. 1990). Trawling was done monthly at the same five stations in the open-water zone of the lake as the zooplankton samples were taken, with a 5-m small-mesh beam trawl (5-mm cod end, fishing speed 1 m·s<sup>-1</sup>, 10-min hauls). The 0+ fish were sorted, identified, and measured to the nearest 0.5 cm. Average numbers caught per sampling date were calculated using the geometric mean of the five stations (Buijse 1992). To estimate the absolute numbers of fish, the trawl catches were calibrated in 1976 using a purse seine (Coles et al. 1985) with an encircled area of 76.5 m<sup>2</sup>, assuming that with this type of netting 100% of the juvenile fish were caught. The calibrations were made in the growing season of the juvenile fish. No indications were found that the efficiency of the trawl net for juvenile fish changed during the course of the season.

In 1976, 0+ fish were caught at fortnightly intervals during the growing season and measured. The stomach contents of individual fish were analyzed, and the species and size

distributions of the prey in the stomach were established (van Densen 1985).

### *Daphnia* mortality

The mortality of the different *Daphnia* species was estimated using the discrete event model INSTAR (Hogeweg and Richter 1982; Vijverberg and Richter 1982; Hovenkamp 1990). The model simulates a population of zooplankton, 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 with the numbers observed in the field. If the numbers in the model are higher than the observed densities in the field, this difference in numbers is removed from the model population and these animals are assumed to have died. If the numbers in the model are lower, mortality is set to zero; no hatching from resting stages is included in the model. Modelled numbers are, however, only rarely lower than those in the field. Field data were smoothed prior to the application of INSTAR by applying a three-point moving average.

The model is essentially the same as the model to compute death rates described by Paloheimo (1974), which uses the equation  $r = b - d$ , in which  $r$  is the natural rate of increase,  $b$  is the birth rate, derived from the egg development time and the average number of eggs in the population, and  $d$  is the death rate. The difference is that with the help of INSTAR different size-classes can be considered, which can result in different death rates for these different size-classes. The somatic growth rates determine the transition speed from one size-class to the other, and hence the outcome of the analyses depends on the estimated growth rates. As a result of the continuous recruitment of the animals, it is not possible to measure growth of daphnids in the field. It is, however, possible to establish the size at maturity under field conditions. The size of the smallest individuals with eggs was taken as an estimate of the size at maturity in the field. By using laboratory-derived data on the relative growth of the juvenile instars (Boersma and Vijverberg 1994a) we computed the growth of the different juvenile instars. The ratio between the size at maturity and the maximal size an animal can reach was estimated using laboratory observations (Vijverberg 1976; Lei and Armitage 1980; Geller 1987; Urabe 1988; Boersma and Vijverberg 1994a) to be a value averaging 0.62. Assuming that the size at maturity is influenced only by the ambient conditions, we were able to estimate the maximum length of the animals in the field. Using a von Bertalanffy growth equation, the growth of the animals in the field was established. Hence, depending on the size at maturity of the animals in the field, different growth rates were used in the model, with small size at maturity reducing the somatic growth (see also Taylor and Slatkin 1981).

Mortality rates were estimated separately for *D. galeata*, *D. yugucullata*, and their hybrid. To compare the computed densities with the field densities, eight size-classes were arbitrarily chosen, with a size-class interval of 0.125 mm. In the generated output, length classes were merged to obtain four output classes: (i) <0.5 mm, (ii) 0.5–1.0 mm, (iii) 1.0–1.5 mm, and (iv) >1.5 mm. Because zooplankton was sampled every week, computing mortality on a daily basis suggests an accuracy that cannot be sustained by the original data. However, the period between the two dates at which mortality is computed should not be too long either, as this would cause an

overestimation of the mortality rates of the larger size-classes. Therefore, mortality was computed twice a week by comparing the computed densities with interpolated field data, and reports were generated on a weekly basis.

### Fish consumption

The consumption of different zooplankton species by juvenile fish was estimated using data on prey selectivity, fish growth, and densities of the different fish species.

### Selectivity

The preferences of the 0+ fish for different zooplankton species and size-classes were estimated using the data set collected by van Densen (1985) in the years 1976–1977, consisting of detailed analyses of the gut contents of 0+ fish in relation to their own length and to the zooplankton densities. Food preferences were established by computing the selectivity index ( $\alpha$ ) of Chesson (Chesson 1978, 1983) for every individual fish and every prey class. Chesson's  $\alpha$  is defined as the proportion of prey class  $i$  in the gut,  $r_i$ , divided by the proportion of prey class  $i$  in the environment,  $p_i$ , normalized in such a way that the sum of the  $\alpha$  values over all prey types equals 1, or

$$\alpha_i = \frac{(r_i/p_i)}{\sum (r_j/p_j)}$$

Smelt, perch, and pikeperch hardly forage at all on the smaller zooplankton species, such as *Ceriodaphnia pulchella*, *Bosmina coregoni*, *Bosmina longirostris*, and *Chydorus sphaericus* (van Densen 1985). If the smaller species are eaten at all, the numerical proportion of these species in the gut is usually low. This, combined with their small size and hence low individual biomass, results in a small proportion of the fish growth being attributable to the small cladocerans. Therefore, we omitted the smaller cladocerans from the analysis of the prey selectivity of smelt, pikeperch, and perch, and for these species we distinguished seven prey classes: copepods in two length classes (<0.5 mm, >0.5 mm), daphnids in four different length classes (<0.5 mm, 0.5–1.0 mm, 1.0–1.5 mm, >1.5 mm), and *L. kindtii* in one length class, as the densities of this latter species were too low to establish a length–frequency distribution.

0+ bream prefer smaller prey items (van Densen 1985), and hence the smaller cladocerans were incorporated in the analysis of the gut contents of 0+ bream. As data on stomach contents of 0+ bream were scarce, we were not able to discriminate between size-classes for the estimations of selectivity. Hence, only species-specific prey classes were used: copepods, daphnids, *Bosmina coregoni*, *Bosmina longirostris*, *Ceriodaphnia pulchella*, and *Chydorus sphaericus*. Stomach content data for roach were not available in adequate numbers to warrant proper analysis, and thus this species was omitted from the analyses.

The dependence of  $\alpha$  on fish length was estimated for the different fish species, using a logit regression technique (McCullagh and Nelder 1983). The length and square length of the fish were used as independent variables and Chesson's  $\alpha$  was used as the dependent variable. Thus,

$$\text{logit}(\alpha_i) = \log\left(\frac{\alpha_i}{1 - \alpha_i}\right) = k + l \cdot L + m \cdot L^2 + \varepsilon$$

in which  $k$ ,  $l$ , and  $m$  are the parameters to be estimated,  $L$  is the length of the fish, and  $\varepsilon$  is the error term. To obtain the best fit through the data we maximized the probability of finding the actually observed numbers of the different prey items in the guts given the estimated values of  $\alpha$ . This was accomplished by minimizing the  $-2\log(\text{likelihood})$  values of the observed numerical composition of the gut content in an iterative process, in two steps. First, the dependence of  $\alpha$  on fish length was estimated for each prey class separately. Subsequently, a multinomial fit was obtained by analyzing all prey classes per fish species together, constraining the sum of the Chesson's  $\alpha$  values at any fish length to be close (the difference being smaller than 0.001 for smelt and smaller than 0.0005 for the other species) to the expected value of the sum of  $\alpha$  over all prey classes, which is 1. To avoid weighting large fish (with many prey items in the gut) too heavily in the analysis compared with the smaller fish (with only a few prey items), we chose to weight the gut data with the reciprocal value of the total number of prey items in the gut, i.e., every individual fish had the same weight in the analysis. Constraining the sum of the  $\alpha$  values means that it is difficult to estimate the accuracy of the parameters  $k$ ,  $l$ , and  $m$ . Therefore, only the significance of the total regression model was computed by comparing the  $-2\log(\text{likelihood})$  estimates of the full model with the  $-2\log(\text{likelihood})$  estimates of the simpler models, that is, with the model with  $r_i$  constant, meaning that the proportion of all prey types in the gut is independent of the length of the fish and of the proportions of the prey types in the environment. Furthermore, the total regression model was compared with the model with  $\alpha_i$  constant, implying that the preference for certain prey types would not change during the ontogeny of the fish. As differences in  $-2\log(\text{likelihood})$  values are  $\chi^2$  distributed, the significance of the different models in relation to each other can be tested.

The  $\alpha$  functions derived from van Densen's (1985) data set were used to estimate the consumption of zooplankton by juvenile fish in the years 1989–1991.

### Fish growth

As we observed a significant effect of the length of the fish on their preferences for certain food types, estimates of the length of the different fish species were necessary for the estimation of the consumption rates in 1989–1991. Fish lengths were obtained by fitting the temperature-dependent growth model of Mooij and van Tongeren (1990) through the observed lengths of the juvenile fish as caught in the monthly field samples. The model of Mooij and van Tongeren has been shown to predict the field observations of 0+ fish length accurately (Mooij et al. 1994). Growth was computed as the resultant of feeding conditions, body weight ( $W$ ), and water temperature ( $T$ ):

$$\frac{dW}{dt} = a \cdot W^b \cdot (T - c)$$

The model has three parameters: a food ( $a$ ), weight ( $b$ ), and temperature ( $c$ ) parameter. It is not to be expected that the values of  $b$  and  $c$  will vary between years, as these parameters are intrinsic properties of the fish species. Hence, we used the

$b$  and  $c$  values for 0+ fish growth in Tjeukemeer in the years 1976–1988, which were estimated by Mooij et al. (1994) (Table 4), with  $b = 0.6$ . The food parameter,  $a$ , was estimated for each species for each year, to obtain an optimal fit of the growth model through the field data. We found that in 1989 the temperature- and weight-corrected growth rates of all species decreased sharply after 15 July. Therefore, we calculated two values for  $a$  for this year, one for the feeding conditions before, and the other after, 15 July.

### Fish densities

The changes in densities of 0+ smelt, pikeperch, and perch in the pelagic zone of Tjeukemeer were described using the familiar negative exponential equation:

$$N_t = N_0 \cdot e^{-zt}$$

The numbers per sampling date of the juvenile cyprinids, that is, bream and roach, usually increase during July and August, which can be explained by a migration of these species from the littoral zone to the pelagic zone in this period (Mooij 1992). The best fit through the data of the cyprinid abundances was given by the following equation:

$$N_t = N_0 \cdot e^{-(z+y)t}$$

The data on fish abundance were too sparse to estimate the mortality parameters  $z$  and  $y$  for each year separately. Therefore, 3-year averages of  $z$  and  $y$  were computed for every fish species. With the use of the parameters  $z$  and  $y$ , a standardized abundance for each species at 1 September in every separate year ( $N_0$ ) was calculated.

### Consumption

The growth model of Mooij and van Tongeren (1990) essentially computes daily weight increments. Using a conversion efficiency of 0.12 (O.F.R. van Tongeren, unpublished results) between the growth of the fish and the zooplankton consumption needed for this growth, we computed the daily zooplankton consumption per fish.

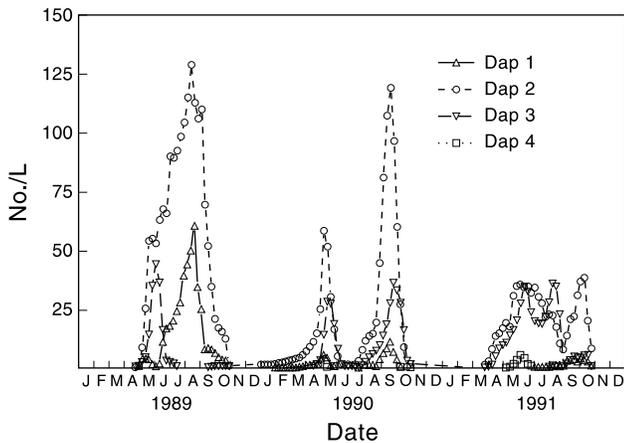
The combination of the computed lengths of the 0+ fish and the proportions of the different prey classes in the lake at the time with the relationships of  $\alpha$  values with fish length as computed from the 1976 data set yielded the proportions of the different prey classes in the guts of individual fish in 1989–1991. These expected proportions in the fish gut were expressed as numerical proportions, whereas total food uptake was expressed in mass units. The average weight of the zooplankters in the gut was estimated using the average mass of the different prey classes, weighted by their numerical proportions in the gut. Dividing the mass of the food consumed by each individual fish by the average prey mass gave the total number of consumed prey, which was then divided over the different prey classes using the expected numerical proportions.

Combining the densities of the juvenile fish with the consumption per fish yielded an estimate of the total mortality of the zooplankton caused by juvenile fish.

### Assumptions

Computational exercises, such as the one presented here, are based on several assumptions. In many cases, however, these assumptions are not mentioned, making results of the

**Fig. 1.** Seasonal variation in the densities of different size-classes of *Daphnia* species in 1989–1991 in Tjeukemeer (Dap 1, <0.5 mm; Dap 2, 0.5–1.0 mm; Dap 3, 1.0–1.5 mm; Dap 4, >1.5 mm).



computations difficult to interpret. To avoid such difficulties in interpretation we made the assumptions underlying our computations explicit.

(i) *Daphnia* species were lumped while considering predation by fish. Hence, we assume that 0+ fish feed aselectively on different species of *Daphnia* within a given size-class.

(ii) We were selective in the possible prey items for the 0+ fish species we included in our computations. For smelt, pikeperch, and perch the smaller zooplankton species were not considered as prey. Naturally this influenced the results, because by attributing all of the growth of the juvenile fish to daphnids, copepods, and *L. kindtii*, the predation pressure on the different size-classes of *Daphnia* species was most likely overestimated. However, as the biomass contribution in the fish gut of the smaller zooplankton species was small (<5%) (van Densen 1985), the size of this bias is likely to have been small.

(iii) No length measurements were available for the prey items of 0+ bream. Because of the high preference of 0+ bream for smaller (<1.0 mm) zooplankton species we assumed that the predation of 0+ bream on *Daphnia* species was limited to individuals of size-class 2 (0.5–1.0 mm).

(iv) By using the value of the selectivity indices of 1976–1977 for the years 1989–1991 we assumed that the fish length –  $\alpha$  relationships did not change between these years. During these 13 years the lake hardly changed: fish, zooplankton, and phytoplankton communities were stable, no new fish or zooplankton species were introduced, and no species disappeared. Therefore, there is no reason to expect changes in fish feeding preferences.

(v) Prey densities were not used as independent variables in the computations; only the proportions of the different prey items in the field were incorporated as independent variables in our analyses. This translates to the assumption that optimal foraging does not play a role in this predator–prey system. Although evidence exists that optimal foraging in fish may be of importance (e.g., Mittelbach 1981; Persson and Greenberg 1990), the impact of optimal foraging strategies on the diets of fish is as yet not clear (e.g., Mills et al. 1986).

(vi) We assumed that the conversion factor between fish growth and food uptake was equal for the different fish species, similar for all different prey types, and constant over the temperature range found in the lake in summer. A conversion efficiency of 0.12 between food uptake and growth of the fish was used (O.F.R. van Tongeren, unpublished results). The conversion efficiency may seem low when compared with the published values for well-fed carnivorous juvenile fish of 0.2–0.3 (Brett and Groves 1979). However, older planktivorous fish have a lower conversion efficiency (0.12; O’Grady and Spillet 1985). Moreover, Mills et al. (1989) reported conversion efficiencies for 0+ perch that were even lower (<0.10). All of the juvenile fish in this study are planktivorous, and we therefore feel that this low conversion efficiency is justified. By keeping the conversion factor at a fixed level over the temperature range some bias was probably introduced, because the conversion efficiency is known to decrease with increasing temperature. However, during the growing season of juvenile fish in Tjeukemeer the temperature of the lake is relatively constant (14–19°C). Moreover, as little is known about the exact relationships of the conversion efficiency of these different fish species with temperature, we chose to keep the values for the conversion efficiency constant. Had we included a change in conversion efficiencies with temperature, then the predicted predation rates in spring would have decreased, and the predicted predation rates in the summer months would have increased.

(vii) The data on fish abundance were too sparse to estimate the mortality parameters  $z$  and  $y$  for each year separately. Given the observation that the mortality of 0+ fish is mainly caused by predation (Mooij 1992), and that the densities of the main piscivorous fish, pikeperch, were similar in the years 1989–1991, we presumed that the shapes of the mortality curves were similar between the years, and hence 3-year averages of  $z$  and  $y$  were computed, meaning that the years 1989–1991 only differed in initial fish densities.

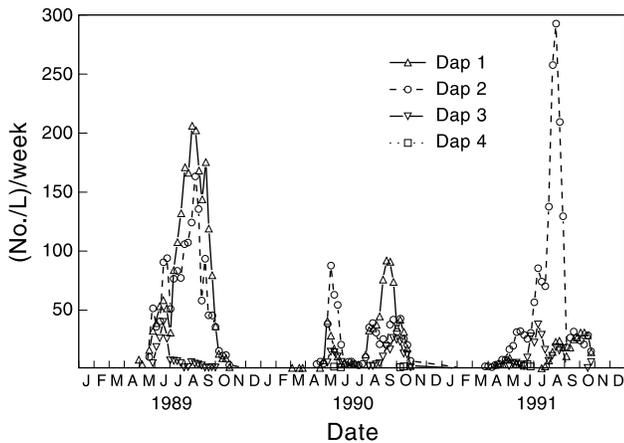
(viii) To be able to make the comparison between the absolute estimates of predation by fish and of mortality we had to compute the absolute densities of juvenile fish in the lake. This was done using trawl data and the net efficiency established for juvenile fish during the course of the year. As this calibration set was only small, it could be argued that using one net efficiency for all fish species, length classes, dates, and weather types is not appropriate. However, as we did not find a change in net efficiency, and temporal reproducibility of yields in trawl catches is high (Mooij 1992), differences in net efficiency are not likely to have been large.

## Results

### *Daphnia*

*Daphnia* size-class 2 (0.5–1.0 mm) dominated the size spectrum in 1989 and 1990, whereas size-class 3 (1.0–1.5 mm) contributed substantially to the total densities in 1991 (Fig. 1). These interannual differences were mainly the result of the varying densities of the different *Daphnia* species. In 1989 we observed a succession of *D. galeata* by the smaller hybrid, *D. galeata* × *cucullata*, which was again succeeded by the still smaller *D. cucullata*, responsible for the peak in densities of the smallest size-class in the summer of 1989. In 1990 the

**Fig. 2.** Mortality of the different size-classes of *Daphnia* species in Tjeukemeer, expressed as the number of daphnids that died per litre per week.



**Table 1.** Correlation coefficients ( $r$ ) and their significance ( $P$ ) between the per capita rates ( $d^{-1}$ ) of the different size-classes of the daphnids.

Size-class	Dap 1		Dap 2		Dap 3	
	$r$	$P$	$r$	$P$	$r$	$P$
Dap 2	0.37	0.001				
Dap 3	-0.13	0.195	-0.08	0.410		
Dap 4	-0.01	0.992	-0.08	0.527	0.27	0.030

**Note:** For definitions of the size-classes see the caption of Fig. 1.

**Table 2.** Correlation coefficients ( $r$ ) between the per capita death rates ( $d^{-1}$ ) of the different size-classes of the *Daphnia* species with the rate of increase of the populations at the time.

Size-class	<i>D. galeata</i> × <i>D. cucullata</i>								
	<i>D. galeata</i>			<i>D. galeata</i> × <i>D. cucullata</i>			<i>D. cucullata</i>		
	$r$	$P$	$N$	$r$	$P$	$N$	$r$	$P$	$N$
Dap 1	-0.17	0.542	15	-0.30	0.003	98	-0.10	0.387	85
Dap 2	-0.35	0.001	84	0.11	0.266	101	0.02	0.882	86
Dap 3	-0.14	0.188	84	0.09	0.938	84	0.12	0.418	48
Dap 4	-0.10	0.477	57	-0.41	0.011	38			

**Note:** For definitions of the size-classes see the caption of Fig. 1.

spring peak was dominated by *D. galeata* and the hybrid, whereas the autumn peak mainly consisted of *D. cucullata* and the hybrid. *Daphnia galeata* dominated the whole year of 1991, except for the small peak of size-class 2 late in the year, which was mainly the hybrid (see also Spaak 1994).

Mortality, expressed as the number of animals that died per litre in each week, differed greatly between the size-classes, and was not correlated to the densities in the field (Fig. 2). Animals in the smallest size-class showed a high mortality, whereas mortality in the largest size-class was much lower. A substantial difference in mortality patterns was found between years. To make the mortality figures between size-classes

**Table 3.** Year-specific log-transformed densities per litre on 1 September ( $\ln(N_0)$ ) and average rates of change in the population ( $z$  ( $d^{-1}$ ) and  $y$  ( $d^{-2}$ ) in the equation  $N_t = N_0 e^{-(z+y)t}$ ) of the five major 0+ fish species in Tjeukemeer during 1989–1991.

	Smelt	Pikeperch	Perch	Bream	Roach
$\ln(N_0)$					
1989	-7.71	-10.55	-7.07	-6.94	-9.15
1990	-7.59	-12.76	-13.45	-8.81	-10.51
1991	-6.16	-12.15	-12.13	-7.61	-10.29
$z$	0.0157	0.0374	0.0060	-0.0177	0.0018
$y$	0	0	0	0.00080	0.00076

**Table 4.** Year-specific food parameters,  $a$  ( $\times 10^{-3} g^{0.4} \cdot C^{-1} \cdot d^{-1}$ ), of the five major 0+ fish species in Tjeukemeer during 1989–1991.

	Smelt	Pikeperch	Perch	Bream	Roach
$a_{89a}$	1.34	5.26	6.15	8.84	5.88
$a_{89b}$	1.11	2.17	1.86	6.31	3.35
$a_{90}$	1.26	3.25	4.68	6.45	3.99
$a_{91}$	1.13	4.20	4.55	6.21	3.84
$a_{76-88}$	1.10	4.07	4.40	5.62	3.60
$c$	-3.6	9.8	9.8	12.8	10.2

**Note:** For 1989, two food parameters were estimated ( $a_{89a}$  and  $a_{89b}$ ), representing the feeding conditions before and after 15 July, respectively. Long-term values of  $a$  ( $a_{76-88}$ ,  $\times 10^{-3} g^{0.4} \cdot C^{-1} \cdot d^{-1}$ ) and of the temperature parameter,  $c$  ( $^{\circ}C$ ), are also presented. Parameter  $b$  was kept constant at 0.6 for all species and all years (Mooij et al. 1994).

more comparable, per capita death rates were computed by dividing the mortality by the densities of the different size-classes. Per capita death rates ( $d^{-1}$ ) for the smallest two size-classes were positively correlated, as were the rates for the largest two size-classes. The other correlations were not significantly different from zero, although all were negative (Table 1). Both *D. galeata* and *D. galeata* × *D. cucullata* showed significantly negative correlations between their respective population growth rates,  $r$ , and the per capita death rates in their smallest size-class (Table 2). Only a few of the juvenile *D. galeata* were smaller than 0.5 mm, so for this species the smallest size-class is class 2. No significant correlation was found between any of the per capita death rates of *D. cucullata* and the rate of population increase in this species. Only for *D. galeata* × *D. cucullata* was the per capita death rate of the largest size-class negatively correlated with  $r$ .

### 0+ fish

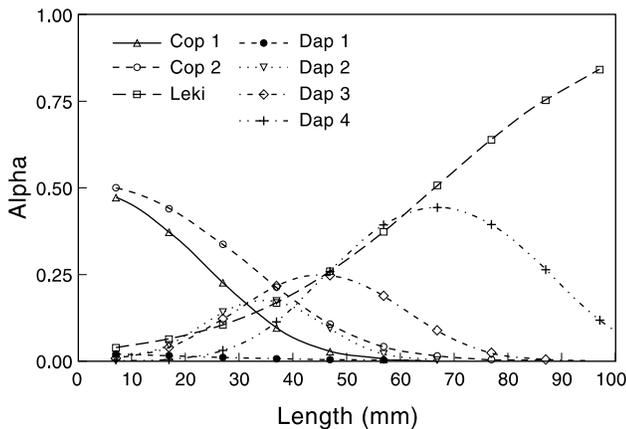
The total abundance of 0+ fish varied annually, and was four times higher in 1989 than in 1990 (Table 3). Fish densities in 1991 were intermediate between those in 1989 and 1990. In 1989 the 0+ fish community was dominated by smelt, perch, and bream in fairly equal numbers. In 1990 and 1991 smelt dominated the 0+ fish community; pikeperch and perch were almost absent in these years. Roach was present in low numbers in all 3 years, whereas the other fish species showed large interannual differences. It can be seen from Table 3 that the mortality of pikeperch was the highest of the species under consideration in 1989–1991, as the  $z$  value for pikeperch was

**Table 5.** Parameters of the length-logit transformed  $\alpha$  regressions for the different fish species.

Prey class	Parameter	Smelt	Pikeperch	Perch
Copepods <0.5 mm (Cop 1)	<i>k</i>	0.003 7	1.275 0	0.085 1
	<i>l</i>	-0.005 1	-0.168 2	-0.051 0
	<i>m</i>	-0.001 5	-0.001 0	-0.000 1
>0.5 mm (Cop 2)	<i>k</i>	0.054 9	-2.350 2	-1.189 1
	<i>l</i>	-0.000 95	0.137 8	0.010 1
	<i>m</i>	-0.000 97	-0.003 1	-0.000 01
Daphnids <0.5 mm (Dap 1)	<i>k</i>	-3.674 4	-1.729 4	-2.714 5
	<i>l</i>	-0.020 9	-0.189 7	-0.032 2
	<i>m</i>	-0.000 48	-0.001 0	-0.000 7
0.5–1.0 mm (Dap 2)	<i>k</i>	-7.184 1	-3.769 0	-2.669 4
	<i>l</i>	0.326 2	0.071 1	0.055 1
	<i>m</i>	-0.004 7	-0.001 2	-0.000 1
	<i>k</i>	-6.458 6	-3.739 9	-2.409 0
1.0–1.5 mm (Dap 3)	<i>l</i>	0.236 6	0.082 4	0.065 1
	<i>m</i>	-0.002 6	-0.001 4	-0.000 6
>1.5 mm (Dap 4)	<i>k</i>	-9.343 1	-3.955 0	-3.641 1
	<i>l</i>	0.271 4	0.088 7	0.043 4
	<i>m</i>	-0.002 0	-0.000 8	-0.000 01
<i>Leptodora kindtii</i> (Leki)	<i>k</i>	-3.043 9	-1.371 1	-3.255 8
	<i>l</i>	0.043 0	0.043 7	0.014 2
	<i>m</i>	0	0	0

**Note:** The parameters indicate the constant (*k*), and the regression coefficients for length (*l* (mm<sup>-1</sup>)) and square length (*m* (mm<sup>-2</sup>)).

**Fig. 3.** Feeding selectivity of smelt (*Osmerus eperlanus*) in relation to its own length (Cop 1, copepods <0.5 mm; Cop 2, copepods >0.5 mm; Dap 1, daphnids <0.5 mm; Dap 2, daphnids 0.5–1.0 mm; Dap 3, daphnids 1.0–1.5 mm; Dap 4, daphnids >1.5 mm; Leki, *Leptodora kindtii*).



the largest. The year-specific parameters of the fish-growth model are summarized in Table 4.

**Zooplankton and 0+ fish**

The parameters of the length-logit transformed  $\alpha$  regressions are given in Table 5 for smelt, pikeperch, and perch. Small fish

**Table 6.** Parameters of the length-logit transformed  $\alpha$  regressions for bream for different prey species.

Prey class	Parameter	Bream
Copepods	<i>k</i>	0.858 9
	<i>l</i>	-0.161 3
	<i>m</i>	0.001 0
Daphnids	<i>k</i>	-1.572 7
	<i>l</i>	0.017 2
	<i>m</i>	-0.000 01
<i>B. coregoni</i>	<i>k</i>	-1.887 3
	<i>l</i>	0.037 3
	<i>m</i>	-0.000 3
<i>B. longirostris</i>	<i>k</i>	-3.412 4
	<i>l</i>	0.015 3
	<i>m</i>	-0.000 01
<i>C. sphaericus</i>	<i>k</i>	-1.643 4
	<i>l</i>	-0.003 2
	<i>m</i>	-0.000 1
<i>C. pulchella</i>	<i>k</i>	-0.871 3
	<i>l</i>	0.014 3
	<i>m</i>	-0.000 7

**Note:** The parameters indicate the constant (*k*), and the regression coefficients for length (*l* (mm<sup>-1</sup>)) and square length (*m* (mm<sup>-2</sup>)).

**Table 7.** Number of fish (*N*) used for the gut analysis and  $-2\log(\text{likelihood})$  values of the models:  $r_i$  constant,  $\alpha_i$  constant, and  $\alpha_i$  dependent on the length of the fish.

	Smelt	Pikeperch	Perch	Bream
<i>N</i>	148	167	88	14
$r_i$ constant	2026	2286	1342	44
$\alpha_i$ constant	523	528	305	48
$\alpha_i$ length dependent	408	510	291	44

**Note:** The number of degrees of freedom in the comparisons of the different models,  $r_i$  constant versus  $\alpha_i$  constant, and  $\alpha_i$  constant versus  $\alpha_i$  length dependent, were 7 and 13, respectively.

of all three species showed the highest  $\alpha$  values for the two copepod classes (Fig. 3). With an increase in length,  $\alpha$  values for increasing size-classes of daphnids showed an optimal curve, although  $\alpha$  for the smallest daphnids was low over the whole length range. At around 65 mm in length, smelt started to prefer *L. kindtii* as prey (Fig. 3). The preference for the largest prey class began at smaller lengths for pikeperch. Perch showed high and constant  $\alpha$  values for the copepod 2 class. Juvenile bream showed a high preference for the smaller cladocerans (Table 6). In the case of smelt, pikeperch, and perch the  $-2\log(\text{likelihood})$  values of the length-dependent  $\alpha$  regressions were significantly lower than the  $-2\log(\text{likelihood})$  values of the constant  $r_i$  regressions (Table 7). In addition, the  $-2\log(\text{likelihood})$  values of the length-dependent  $\alpha$  regressions were also lower than the  $-2\log(\text{likelihood})$  values of the constant  $\alpha_i$  regressions. The difference, however, was only significant for smelt. It should be kept in mind, however, that the values for  $\chi^2$  (being the differences between the

$-2\log(\text{likelihood})$  values for the different models) are a severe underestimation, as a result of the weighting of the data, implicitly assuming that all fish only consumed one prey item. With two prey items consumed per fish the  $\chi^2$  values would already be doubled, yielding significant differences in all cases.

When the numbers of *Daphnia* spp. eaten by juvenile fish were compared with the total numbers of *Daphnia* spp. that died in the same period the different size-classes showed distinctly different patterns (Fig. 4). Animals in the smallest size-class (<0.5 mm) were not eaten by juvenile fish, yet they showed a high mortality. The mortality in the larger classes can be explained better by predation by fish; in the second half of 1990 and 1991 all of the mortality in the larger size-classes of the daphnids can be explained by predation by 0+ fish. If a peak in mortality in the larger classes occurs early in the year, as in 1990, juvenile fish predation cannot explain the mortality at that time.

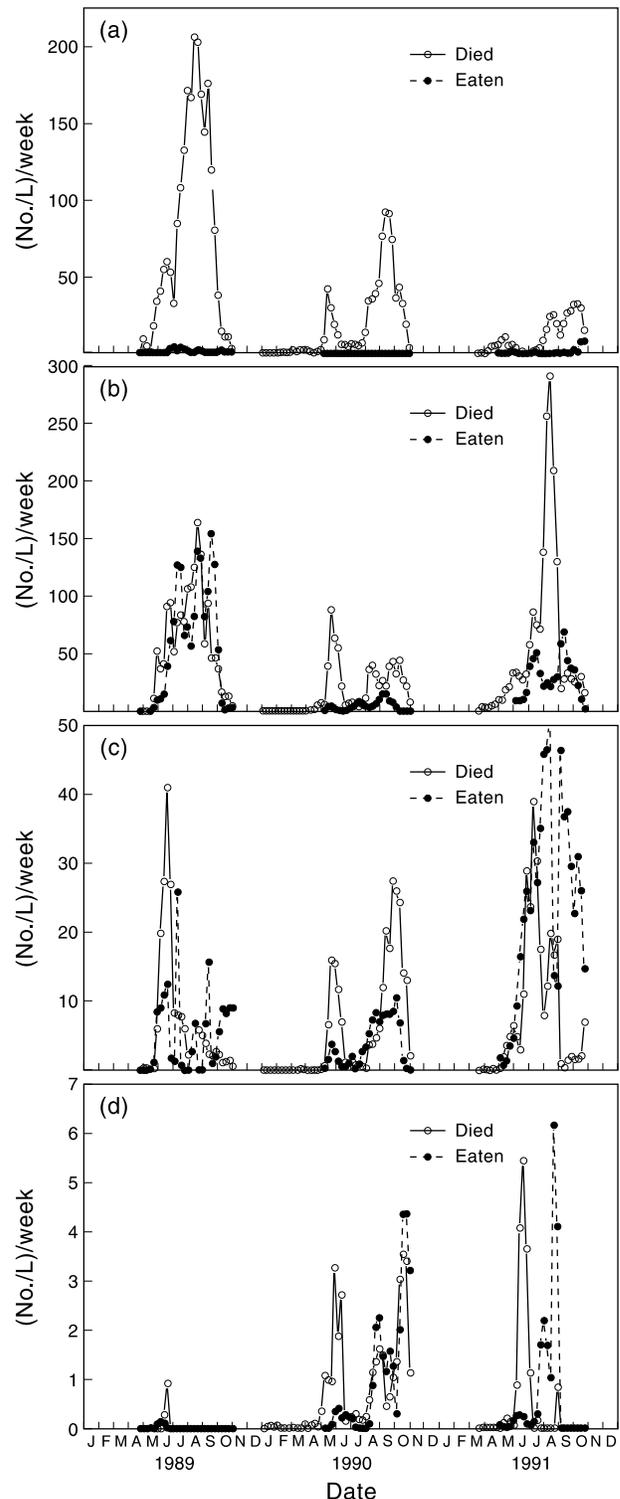
Although the number of daphnids eaten by fish in the larger size-classes was close to the number that died in the second part of the year, some differences were found mainly in the period from September to October in the 3 years. Age 0+ fish showed marked increases in preference for *L. kindtii* with length (Fig. 3), having the greatest preferences at the end of the year. However, because of the low densities of *L. kindtii* in the lake, numbers caught in the standard zooplankton sampling programme were small, and hence the determination of densities was inaccurate. Because of the high  $\alpha$  values for this prey item, the proportion of *L. kindtii* in the environment greatly influences the predicted predation rates on all alternative prey classes, and hence it is important to have a good estimate of its density. To assess the impact of inaccuracies on the estimates of *L. kindtii* densities, we reanalyzed the data with the observed densities of *L. kindtii* both plus and minus two standard deviations. Expected numbers in a sample are Poisson distributed, and hence the square root of the number of individuals counted is an estimate of the standard deviation. From the analysis it became clear that the density of *L. kindtii* as an alternative prey played an important role in the predicted predation rate on the larger size-classes of daphnids later in the year.

## Discussion

### Approach

The two ways of estimating mortality were almost completely independent. Consumption by fish was estimated using fish growth and fish densities obtained from the field, combined with a measure of prey selectivity, which was estimated using observations from 1976–1977, years with different fish densities and zooplankton numbers. *Daphnia* mortality was estimated using only the *Daphnia* densities and fecundities, in combination with some laboratory-derived parameters of the growth and temperature dependence of the growth and reproductive processes. The only data used for both the mortality and the consumption estimates were the densities of the different *Daphnia* size-classes. It is important to note, however, that in the estimates of consumption the densities were not used as such, but as proportions of the different prey classes in the environment, although these two were positively correlated ( $r^2$

**Fig. 4.** Total mortality of daphnids (number of individuals per litre per week) in size-classes 1 (a), 2 (b), 3 (c), and 4 (d), related to the predation mortality of 0+ fish. For definitions of the size-classes see the caption of Fig. 1.



values between densities and proportions of the different prey groups varied between 0.04 and 0.72).

Given the assumptions underlying the computations of the

mortality of the daphnids on the one hand and the consumption by the juvenile fish on the other hand it is remarkable that the results obtained from the two different ways of estimating the mortalities are of the same order of magnitude. However, it would be unwise to elaborate on the absolute magnitude of the predation and mortality rates reported here. It is difficult to assess the reliability of estimates in studies such as this one, which is illustrated by the fact that in similar studies no (Luecke et al. 1990) or very limited (Rudstam et al. 1992) attempts were made to estimate the reliability of the results. Sampling variation in the density determination of the different species is most probably driving the accuracy of the model output, with coefficients of variation estimated for zooplankton of approximately 15% (de Nie and Vijverberg 1985), a value lower than the ones reported for a large number of lakes by Pace et al. (1991). Sampling variation in the fish densities was higher, with a coefficient of variation of 60%. We have, however, most likely overestimated the predation by juvenile fish, as a result of the low conversion efficiency between food uptake and growth, as a result of the exclusion of some prey types, and as a result of the fact that the conversion efficiency was estimated in the laboratory at 20°C (O.F.R. van Tongeren, unpublished results). This means that in all periods in the 3 years with lower temperatures, predation will have been overestimated. Nevertheless, some general conclusions can be drawn from our results as these reflect differences in mortality rates and consumption rates of an order of magnitude.

#### Predation of 0+ fish

Given the limitations of the computations presented here, two main conclusions can be drawn from our results. Firstly, the smallest size-class of *Daphnia* (<0.5 mm) had a high mortality, but the consumption by 0+ fish of this size-class was almost zero. Thus, the cause of the mortality of this size-class cannot be explained by fish predation. Small *Daphnia* individuals have the lowest starvation resistance (Threlkeld 1976), and hence starvation could be responsible for the high juvenile mortality, especially because daphnids are food limited during most of the year (Boersma and Vijverberg 1994b). Moreover, smaller daphnids are more vulnerable to invertebrate predation than larger ones (e.g., Mordukhai-Boltovskaia 1958; Herzig and Auer 1990). Relatively little is known, however, about the selectivity and consumption rates of the invertebrate predators present in Tjeukemeer: *L. kindtii*, cyclopoid copepods, and water mites. Although Hovenkamp (1990) found that the mortality in the smallest size-classes of *Daphnia* species could be attributed to predation by *Chaoborus flavicans* and *L. kindtii* in mesotrophic Lake Vechten, and others have also reported large impacts of predation by invertebrates on the community structure of the herbivorous zooplankton (e.g., Kerfoot 1977), it is unlikely that the predation rates of the invertebrate predators in Tjeukemeer were high enough to explain the high mortality rates of the small daphnids. If we assume that each *L. kindtii* individual consumes 10 prey individuals per day (see Browman et al. 1989), and it does this aselectively, then it can be computed that predation by *L. kindtii* is too low to explain the high mortalities of daphnids (as was also concluded by Lunte and Luecke 1990): the densities of the smaller cladocerans are usually also high during the growing season of *L. kindtii*, which will most likely lead to a high predation

pressure of *L. kindtii* on the smaller species. The same is true for the predation by copepods, whereas the effect of the predation by water mites cannot be inferred, as no information is available on this group of predators in Tjeukemeer.

Our own observations showed that in cultures intrinsic mortality was highest when the animals were small; moreover, small daphnids seemed to be most vulnerable to physical disturbances. Herzig (1974) reported that death rates of *Diaphanosoma brachyurum* were strongly positively correlated with wind speed, whereas McNaught and Hasler (1961) reported large amounts of air-locked *Daphnia* species in the foam lines of Langmuir circulations (see also George and Edwards 1973). Fryer (1991) also reported patches of millions of doomed *Daphnia* individuals trapped in the surface film of the water. The fact that we do find a significantly negative correlation between the mortality of the smallest size-classes and the population growth rates in two of the three taxa (Table 2) does show that the mortality rate in this size-class is important for the population dynamics of the daphnids.

The second conclusion that can be drawn from this study is that the larger size-classes of the daphnids were hardly eaten at all in the first part of the year, although the mortality rate accompanying the end of the spring peaks was high in 1990. The utilization of the daphnids by 0+ fish early in the year is dependent on the timing of the population growth of the daphnids. If the growth starts early in the year, when the juvenile fish are not yet present, the zooplankters will overexploit their resources, and the population densities will decrease as a result of food limitation. Hence, it is not possible to explain the collapse of the spring densities by predation by juvenile fish. Irrespective of whether the 0+ fish are present or not, *Daphnia* populations will decline. The same observation was made by Luecke et al. (1990), who also found high mortality in spring, when fish predation is too low to explain this mortality.

It is important to note that even if all of the zooplankton mortality could be explained by fish predation, it would be incorrect to conclude that the population dynamics of the particular species under consideration is the only factor of importance. After all, in the computation of the population development of the zooplankton, field-derived length-fecundity relationships were used. These will greatly affect the computed birth rates, and hence the computed densities, implying that comparisons of mortality data for zooplankton will always underestimate the importance of the food conditions. In our case, the sharp decrease in fecundity at the time of the summer decline remained invisible; only the increased mortality at this time became apparent. Usually, the declines in birth rates are used to explain the decline in numbers in spring (e.g., Sommer et al. 1986). However, as we have shown here, even with the decrease in birth rates accounted for, mortality was also high at the time of the decline. This suggests that in this period the daphnids were so food limited that they died of starvation.

During the second half of the growing season, predation by juvenile fish may usually explain all of the mortality in the larger classes of the daphnids, resulting in the conclusion that *Daphnia* numbers may be regulated by 0+ fish later in the year. Thus, if juvenile fish biomass is as high as in 1989, the densities of the smaller size-classes of daphnids will be higher than the densities of the larger size-classes of *Daphnia* species. In contrast, when fish densities are lower (1990), larger

size-classes of daphnids will be more dominant. This type of seasonal regulation of *Daphnia* species by fish was also reported by Luecke et al. (1990) in Lake Mendota. The important difference between lakes Mendota and Tjeukemeer is that the main planktivores in Lake Mendota are older (>2+) year-classes of cisco (*Coregonus artedii*) and yellow perch (*Perca flavescens*); these fish were present throughout the year, in contrast to the case with 0+ fish in Tjeukemeer. Predation by cisco and yellow perch, however, also failed to explain the high mortality resulting in the end of the spring maximum densities of *Daphnia* species.

In their study on the annual variation of the food parameter of fish, *a*, Mooij et al. (1994) observed that the year-specific *a* values never differed by more than 20% from the grand mean of the years 1976–1988. The values of *a* calculated in this study (Table 4) for 1990 and 1991 were within this 20% range and hence there were no indications of food-limited growth of fish in these years. However, the values of *a* for the first part of 1989 (before 15 July) were all more than 20% higher than the species-specific grand means. For the second part of 1989 the values of *a* for pikeperch and perch were more than 20% lower than the average value. The *a* values of smelt, bream, and roach in the second half of 1989 were within the normal range. The low *a* values indicate apparent food limitation of the juvenile fish in 1989 after mid July, and could explain our observation that in 1989 more of the total mortality of the larger size-classes seems to be explained by fish predation than in the other years. The food limitation for pikeperch and perch could be explained by the observation that the densities of the preferred zooplankton (*L. kindtii* for pikeperch; copepods for perch) of these fish species were low after mid July compared with the other 2 years.

In conclusion, predation by 0+ fish usually affects population dynamics of *Daphnia* species in Tjeukemeer only in the second half of the year. The mortality that occurs when the population densities decrease in spring is too large to be explained by fish predation. Moreover, the smallest size-class of the daphnids is hardly eaten at all by 0+ fish.

## Acknowledgements

These investigations were supported by the Life Science Foundation, which is subsidized by the Netherlands Organization for Scientific Research. We thank Koos Swart and Steven Visser for their assistance in the field and Peter Mac Gillavry, Rob Hoekstra, Chris de Groot, and Guus Postema for their help in the laboratory. Ramesh Gulati, Riks Laanbroek, Rob Lingeman, Joop Ringelberg, Piet Spaak, Koos Vijverberg, and Karen Wiltshire are thanked for their comments on the manuscript.

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