Food effects on life history traits and seasonal dynamics of *Ceriodaphnia pulchella*

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SUMMARY

1. This paper describes the effects of differences in food quantity and quality on selected life history traits of *Ceriodaphnia pulchella*. Animals were fed with four concentrations of two green algae, *Scenedesmus obliquus* and *Chlamydomonas globosa*, given separately as well as in a 1 : 1 mixture.
2. In most cases growth, reproduction and condition of the animals and consequently the rate of population increase, *r*, increased with food concentration. Life history parameters of animals raised on *S. obliquus* were lowest, whereas no significant differences were found between animals fed with *C. globosa* and with the mixture of the two algal species.
3. In contrast to the large effects of food quantity and quality found in the laboratory, an analysis of the population dynamics of *C. pulchella* in Lake Tjeukemeer showed that the effect of changes in food conditions during the growing season of this species was limited, although overall food levels seemed to be poor throughout the year.
4. Changes in the birth rate of the population are mainly governed by changes in temperature, and possibly by changes in the densities of the invertebrate predator *Leptodora kindtii*.

Introduction

Aquatic filter feeders are among the most non-selective consumers, often ingesting all particles within a given size range, including algae, bacteria, protozoa and detritus. This implies that these animals are faced with a large spectrum of resources of varying quality. Since the ability for food selection seems limited, differences in both food quantity and quality are likely to be of importance to these animals. While the effect of food quantity on life history characteristics of zooplankton has been addressed by many workers (e.g. Lampert, 1977; Duncan, Lampert & Rocha, 1985), influences of food quality have received considerably less attention. Only relatively recently have differences in quality among (e.g. Ahlgren *et al.*, 1990; Lundstedt & Brett, 1991) and within food species as a result of the culturing conditions of the algae (Müller-Navarra, 1993; Sterner, Hagemeier & Smith, 1993; van Donk & Hessen, 1993) become the subject of research.

Even though roughly half the studies reviewed by Vijverberg (1989) on growth and reproduction in zooplankton were carried out with a combination of food types, only a few papers deal with the effects of different food types fed to herbivorous zooplankton both in combination and alone (Jamieson, 1980; Lewis & Maki, 1981; Hanazato & Yasuno, 1984; Roman, 1984; Cowgill, Keating & Takahashi, 1985; Lundstedt & Brett, 1991; Vanni & Lampert, 1992; Boersma & Vijverberg, 1995). Although poorly studied in zooplankton the phenomenon of complementary resources seems to be important in a wide variety of consumers (see references in Pennings, Nadeau & Paul, 1993), with two or more food sources each providing different proportions of different essential elements (Tilman, 1982).

In this paper we present a study of the effects of feeding *Ceriodaphnia pulchella* Sars with different

concentrations of two green algae, *Scenedesmus obliquus* (Turp.) Kürtz. and *Chlamydomonas globosa* Snow, on selected life history traits. Both algal species have been used extensively as food for zooplankton, and are considered to be high quality food sources (Vijverberg, 1989).

As many zooplankton species appear to be food limited during large parts of the year (Tessier, 1986; Chapman & Burns, 1994; Manca, Spagnuolo & Comoli, 1994; Boersma & Vijverberg, 1994c) the effect of food on the seasonal dynamics of herbivorous zooplankton species has been a well-researched field. Most studies, however, have focused on *Daphnia* species, and only a small number of studies has appeared on the seasonal dynamics of smaller cladocerans (e.g. DeMott & Kerfoot, 1982; Balseiro, Modenutti & Queimalinos, 1992). Therefore, we assessed the importance of changing food conditions in the determination of the population dynamics of the smaller crustacean, *Ceriodaphnia pulchella*. As direct assessments of food level and food quality under field conditions are difficult, the analysis of the effect of food conditions was done indirectly. Carbon content and fecundity of the animals in the field were monitored, and the effects of different environmental factors on the birth rate were analysed.

Materials and methods

Laboratory

Chlamydomonas globosa and *Scenedesmus obliquus* were cultured axenically in 2-l flow-through systems (Boersma & Vijverberg, 1994b). The algae were harvested daily from the overflow bottles of these continuous cultures. The culture medium of the algae was removed by centrifuging twice for 20 min at 3000 r.p.m., and by subsequent washing of the algae with distilled water. The algae were resuspended in 0.45-μm-filtered Lake Tjeukemeer water. The algal density was measured using a haemacytometer, counting a minimum of 500 cells. The carbon content of *C. globosa* was 2.52×10^{-11} g C cell^{-1}, and that of *S. obliquus* was 2.30×10^{-11} g C cell^{-1}, resulting in carbon : dry weight ratios of 0.53 and 0.50, respectively. *Scenedesmus obliquus* was usually unicellular. Both algal species had a maximum length of around 15 μm.

Ceriodaphnia pulchella individuals were collected with a 120-μm tow net from Lake Tjeukemeer. The animals were placed individually in 100-ml test tubes

and fed on a 1 : 1 mixture of *C. globosa* and *S. obliquus*. The algal carbon content of this culture medium was 1 mg C l^{-1}. The incubation temperature used was 17.5 °C, and the light : dark regime was 16 : 8 h. As soon as the field-caught animals produced newborn the mothers were removed. The first generation animals were reared to maturity on the same medium as their mothers. The offspring produced by these animals were used for the experiments described below.

Different amounts of *C. globosa* and *S. obliquus* were added to 0.45-μm-filtered Tjeukemeer water to obtain four food levels, with carbon contents of 0.13, 0.25, 0.50 and 2.5 mg C l^{-1}, respectively. Three types of media were prepared: (i) a series of pure *C. globosa* media (CHLAM); (ii) a series of *S. obliquus* media (SCENE); and (iii) a series of *C. globosa* and *S. obliquus* in a 1 : 1 mixture (CH_SC). The temperature and photoperiod used in the experiments were the same as during the acclimatization period. For each series, forty neonates were collected within 12 h of birth, and placed individually in 100-ml test tubes. The animals were selected in such a way that the clonal composition of all series was the same. The animals were examined daily for moulting by inspection of the medium for exuviae, and transferred to clean tubes with fresh medium. The time needed to reach maturity, defined as the first appearance of eggs in the brood pouch, the size at maturity, and the number of juvenile instars of the animals were recorded. Once the animals reached maturity, the number of eggs was counted for each adult instar. Growth and reproduction were measured until the animals reached the fourth adult instar. The rate of increase (r) was estimated using the Euler equation, and standard errors for r were computed using a jackknifing method (Meyer *et al.*, 1986). As only one value of r was available per treatment it was impossible to compute the significance of the interaction between food type and the food concentration. In order to overcome this problem we split the animals per treatment randomly, and computed r for each of these two series per treatment, yielding two independent estimates of r.

Field

In 1991 quantitative zooplankton samples were taken weekly with a 5-l Friedinger volume sampler at five stations in Lake Tjeukemeer, a shallow, eutrophic,

polymictic lake in the northern part of the Netherlands (mean depth 1.5 m, surface area 21 km^2). Sampling was done at two depths, one below the surface and the other just above the bottom. These samples were pooled, concentrated by filtration through a 120-μm filter and preserved in a 4% formaldehyde solution. Total number of animals and length–frequency distributions were measured in a one-tenth subsample. Preserving animals in formaldehyde may cause egg loss from the brood chamber, hence an additional sample was taken and preserved in 95% ethanol. Length–fecundity relations were established using this sample.

A formal way to test influences of different factors on changes in the birth rate was proposed by Polishchuk (1994; 1995). The well-known formula of Paloheimo (1974):

$$b = \ln(1 + E)/D \qquad (1)$$

where b is the birth rate, D is the egg development time, and E is the average number of eggs in the population, is rewritten to yield the following equation:

$$b = V\ln(1 + FA) \qquad (2)$$

where $V = 1/D$, F is the fecundity (mean number of eggs per adult female) and A is the proportion of adults in the population. Polishchuk (1994; 1995) then computed the contribution (Con) of the different factors to changes in the birth rate using partial derivatives, resulting in the following expressions for these contributions:

$$\text{Con } V = \ln(1 + FA)(\mathrm{d}V/\mathrm{d}T) \qquad (3)$$

$$\text{Con } F = VA/(1 + FA)(\mathrm{d}F/\mathrm{d}T) \qquad (4)$$

$$\text{Con } A = VF/(1 + FA)(\mathrm{d}A/\mathrm{d}T) \qquad (5)$$

Polishchuk claimed that the causes behind changes in parameters V, F and A are more directly related to specific environmental conditions than are changes in the birth rate. V, the reciprocal of the egg development time, is almost uniquely influenced by the ambient temperatures. F, the fecundity, is mainly dependent on food conditions, but may also depend on the age structure of the population, while A, the proportion of adults, and hence the age structure of the population, is mostly linked to predation. Polishchuk proposed this method to detect quick changes in the impact of different steering factors on the birth rate of a population and hence on its dynamics.

Carbon content

Both cultured animals and individuals taken from the field at weekly intervals were washed in distilled water and analysed for carbon while alive (Boersma & Vijverberg, 1994a). Regression lines were computed with the log-transformed values of length (mm) as the independent variable and the log-transformed carbon content (μg) of the animals as the dependent variable.

Results

Laboratory

An effect of both food concentration and food type on the development, growth and reproduction of *C. pulchella* was found (Table 1). Higher food concentrations resulted in a shorter time to reach maturity (Fig. 1a). Size at maturity was only affected by food source and not by the concentration (Fig. 1b). Animals fed solely *Scenedesmus* were significantly smaller at maturity than the animals reared on the other two media (Table 2), and took longer to mature (Figs 1a and b). The number of eggs produced by the first adult instar increased with increasing food levels for the mixed food, decreased at the highest food level when the animals were fed with only *Chlamydomonas*, and was relatively constant for *Scenedesmus*-fed animals (Fig. 1c). This resulted in a significant food type, concentration and interaction effect (Table 1). Animals fed *Scenedesmus* produced significantly fewer eggs than the animals reared on the other two media (Table 2; Fig. 1c). Table 1 shows the results of two analyses of variance with r. The single measurements of r were analysed first, with the effects of the treatments tested using the interaction term as the error term. Only food type showed a significant effect on r. The analysis of split r values showed the existence of a marginally significant interaction, making the analysis of the single r values less interpretable. This split r analysis shows that the effect of food concentration is also significant (Table 1). Animals reared on the SCENE series showed the lowest values for r in all cases (Fig. 1d). As was the case with the single life history traits, the overall differences between the three food types were significant between the SCENE and the two other series only (Table 2).

Regression lines of the log-transformed values of length with the log-transformed carbon contents
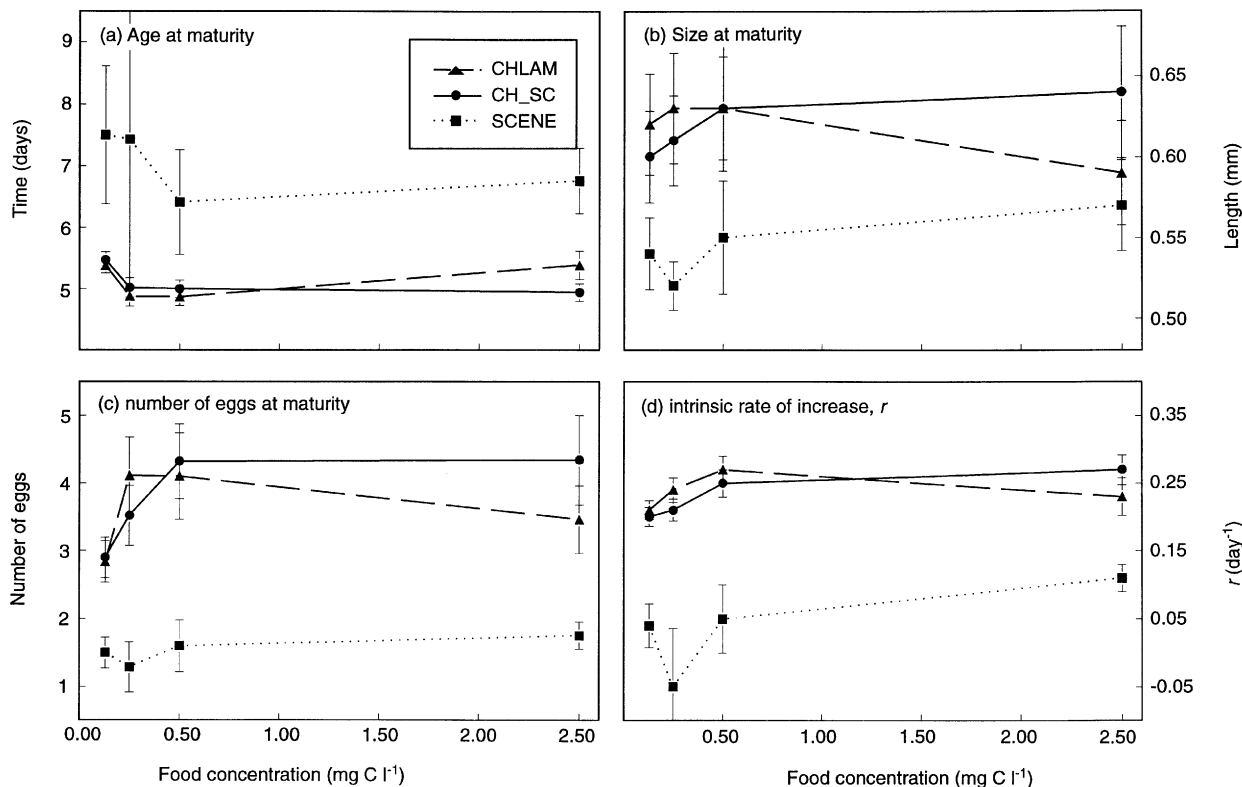
Fig. 1 The response of selected life history traits of *Ceriodaphnia pulchella* to the different experimental treatments. The food types used were *Chlamydomonas globosa* (CHLAM, dashed line, triangles), a 1 : 1 mixture of *C. globosa* and *Scenedesmus obliquus* (CH_SC, solid line, circles), and *S. obliquus* (SCENE, dotted line, squares). Error bars indicate 95% confidence limits of the means in all cases. (a) Time needed for neonates to reach maturity; (b) size at maturity (mm); (c) mean number of eggs per primiparous female; (d) rate of population increase, r (day^{-1}).

Table 1 F values of two-way ANOVAs for selected life history characteristics of *Ceriodaphnia pulchella*. The numbers of eggs per female were square-root transformed and carbon contents were log-transformed
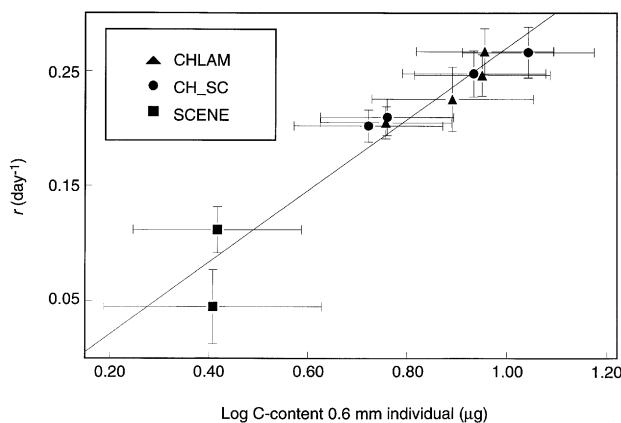
		Food type			Food concentration			Interaction		
Trait	Error df	d.f.	F	P	d.f.	F	P	d.f.	F	P
Time to maturity	326	2	75.6	< 0.001	3	5.7	< 0.001	6	1.6	0.160
Size at maturity	325	2	17.6	< 0.001	3	0.7	0.567	6	1.6	0.145
Egg number	295	2	83.8	< 0.001	3	6.7	< 0.001	6	2.4	0.028
r	6	2	36.9	< 0.001	3	2.3	0.177	—	—	—
Split r	12	2	143.3	< 0.001	3	6.0	0.010	6	2.5	0.086
Carbon content	267	2	17.5	< 0.001	3	1.7	0.160	6	1.6	0.143

differed significantly in slope between the different experimental treatments ($F_{11,256}$ = 3.05; P < 0.001). This was mainly caused by the regression lines of the animals reared on two of the SCENE media (0.25 and 0.50 mg C l^{-1}), although only four and five animals were analysed, respectively, as a result of poor growth. After deletion of these two series the regression coeffi-

cients were no longer significantly different, which allowed a length-independent estimation of the carbon content of the animals. Using the common slope and the different intercepts of the length–carbon regressions at the different food types and concentrations, the logarithm of the carbon content of 0.6 mm individuals, which is the long-term average size of adult *C. pulchella*

Table 2 Probabilities of Tukey HSD tests between the different food media for selected life history characteristics of *Ceriodaphnia pulchella*. The significance of the differences between different combinations of the three food media (CHLAM, pure *Chlamydomonas globosa*; SCENE, pure *Scenedesmus obliquus*; CH_SC, 1 : 1 mixture of *C. globosa* and *S. obliquus*) is shown

Trait	CH_SC–CHLAM	CH_SC–SCENE	SCENE–CHLAM
Time to maturity	0.981	< 0.001	< 0.001
Size at maturity	0.967	< 0.001	< 0.001
Egg number	0.576	< 0.001	< 0.001
r	—	—	—
Split *r*	0.846	< 0.001	< 0.001
Carbon content	0.427	< 0.001	< 0.001

Fig. 3 Seasonal dynamics of *Ceriodaphnia pulchella* in the year 1991, numbers l^{-1} (n) and rate of population increase, r (day^{-1}, smoothed using a three point running average).
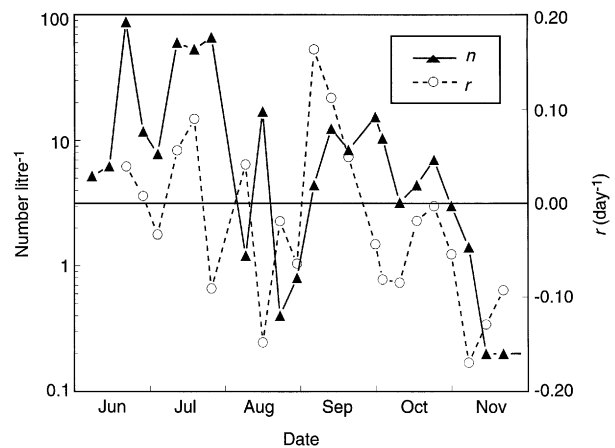

Fig. 2 Relation between the natural logarithm of the carbon content of hypothetical 0.6 mm individuals as calculated from the length–carbon regressions (μg) and r (day^{-1}). The correlation was significantly larger than zero ($r = 0.96$; $P < 0.001$; $n = 10$).

Fig. 4 Seasonal changes in birth and death rates of *Ceriodaphnia pulchella* (day^{-1}). Both rates were smoothed using a three point running average. The numbers indicate the different periods of monotonously increasing or decreasing birth rates (see text).
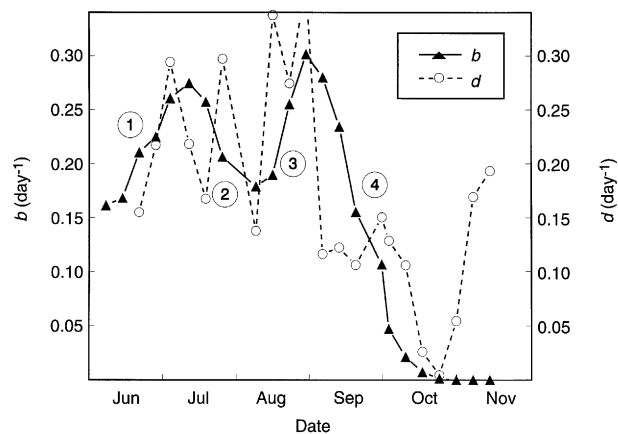
in Lake Tjeukemeer, was computed. These values correlated significantly with the computed values of r for the different series ($r = 0.96$; $P < 0.001$; $n = 10$) (Fig. 2).

Field

Fig. 3 shows the population dynamics of *C. pulchella* in 1991, and the values of the rate of population increase, r. *C. pulchella* was present only in the summer months, between June and the end of October. The seasonal changes in birth and death rates are shown in Fig. 4. A correlation coefficient significantly different from zero was found between r and b (0.47; $P = 0.036$; $n = 20$).

Length–carbon regression lines for animals collected in the field were not significantly different in slope between the different sampling dates ($F_{13,353} = 0.96$; $P = 0.491$) and, hence, an analysis of covariance was applied to compare the intercepts of the different sampling dates, which proved to be significantly different ($F_{13,366} = 18.8$; $P < 0.001$). Fig. 5 shows the exponential of the computed carbon content for 0.6 mm individuals. The length-specific carbon content is reported to be a measurement of the condition of the animals, as is the average number of eggs per adult female in a population. This latter quantity, however, showed very little variation during the period of parthenogenetic reproduction (Fig. 5).
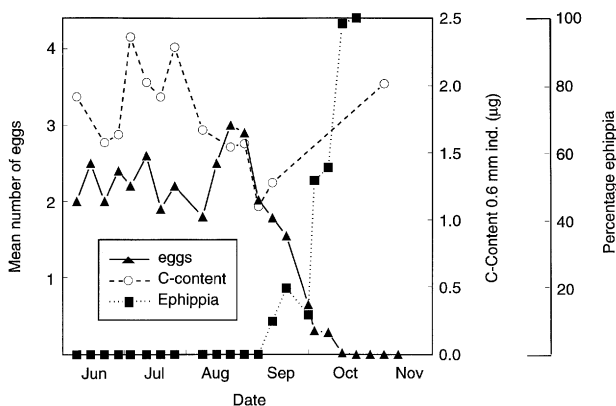
Fig. 5 Seasonal changes in the average number of eggs per adult female, the carbon content of 0.6 mm individuals (μg), and the percentage of reproductively active adult females carrying ephippial eggs.

Hence, these quantities were not correlated (-0.14; $P = 0.658$; $n = 13$). The values of r and length-specific carbon content were found to be significantly, but negatively correlated (-0.63; $P = 0.026$; $n = 12$).

Our observation that r is correlated positively with the average number of eggs per adult female (0.49; $P = 0.026$; $n = 20$) suggests that the feeding conditions of *C. pulchella* are of importance in the population dynamics of this species. Analysing the data using the more formal approach of Polishchuk (1994; 1995) yielded rather scattered results: the relative contribution of the different parameters changed rapidly. It is, however, difficult to imagine that when birth rates change monotonously over a longer period, different factors are causing this behaviour on adjacent sampling dates. Therefore, the data were smoothed with a three-point running average, and the analysis was repeated. In the seasonal pattern of the smoothed birth rates, four periods (Fig. 4) can be recognized, each being characterized by a monotonous increase or decrease in birth rate. The contributions of the three different factors (V, the reciprocal of the egg development time; F, the mean number of eggs per adult female; A, the proportion of adults) for these four periods were averaged per period, and expressed as a percentage of the total change in birth rate computed (Table 3). The different factors made different contributions to the birth rate in the four periods. In the first period, the steady increase in the birth rate could be attributed almost entirely to changes in egg development time resulting from an increase in the temperature of the lake. The second period was characterized by a decrease in the proportion of adults in the

population. This, accompanied by decreasing densities of animals in this period, points to a higher mortality for adults compared with the mortality rate of juveniles. In the third period the percentage adults increased again, causing an increase in the birth rates, suggesting that the higher mortality rates for the adults were relaxed, and the mean age of individuals in the population was increasing. In the fourth period decreasing fecundities and to a lesser extent increasing egg development times could be held responsible for the decrease in birth rates. The sharp decrease in the average number of eggs per adult female in this period suggests that food conditions deteriorated for *C. pulchella*, but was in fact mainly caused by a drastic increase of the proportion of the females carrying ephippial eggs, rather than by a decline in the number of eggs carried by parthenogenetic females (Fig. 5).

Discussion

Our laboratory results show that both growth and reproduction in *Ceriodaphnia pulchella* were influenced by the quantity and the quality of available food, with lower rates on the pure *Scenedesmus obliquus* media than on the pure *Chlamydomonas globosa* media, whereas mixed food treatments were never significantly different from the *C. globosa* treatments. Concentration effects were relatively small, which was caused by the very small differences in growth and reproduction of the animals cultured on the *Scenedesmus* media (Figs 1a–d), combined with the lower values in the life history parameters of animals cultured on the highest *Chlamydomonas* level. These results suggest that the incipient limiting level for *C. pulchella* is below 0.5 mg C l^{-1} (see also Lynch, 1992).

Both *Chlamydomonas* spp. and *Scenedesmus* spp. are widely used as food for cladocerans and are usually regarded as high quality food items (e.g. Lampert, 1977; Vijverberg, 1989; Ahlgren *et al.*, 1990), although both *Chlamydomonas* and *Scenedesmus* species have been reported to be inadequate food for zooplankton (Taub & Dollar, 1968; Hart & Santer, 1994; Boersma & Vijverberg, 1994b). It has become increasingly clear, however, that not only the algal taxonomical status determines food quality for zooplankton, but that also the culture conditions of the algae (Sterner *et al.*, 1993), or the fact that they have come into contact with zooplankton (van Donk & Hessen, 1993; Lampert,

Table 3 Average changes of the birth rate, and contributions to these changes of changes in egg development time (Con *V*), average number of eggs (Con *F*), and the proportion of adults in the population (Con *A*), plus the magnitudes of the three relative to the total change in birth rates

Period	db/dt	Con *V*	Con *F*	Con *A*	%*V*	%*F*	%*A*
Period 1	0.0034	0.0027	0.0001	0.0009	81	2	25
Period 2	−0.0039	0.0003	−0.0007	−0.0034	−9	17	86
Period 3	0.0036	−0.0007	0.0022	0.0028	−20	−1	132
Period 4	−0.0054	−0.0011	−0.0040	−0.0005	21	74	9

Rothhaupt & von Elert, 1994), are of importance for the quality as food for grazers.

This study indicates that under the culture conditions used in our experiments *Scenedesmus obliquus* is an inadequate food source for *C. pulchella*. This in contrast to our findings with *Daphnia galeata* Sars, which showed better growth on *Scenedesmus* than on *Chlamydomonas* (Boersma & Vijverberg, 1995). However, the quality of algae as food may change, even in continuous, axenic, cultures, as we showed in a previous paper (Boersma & Vijverberg, 1994b) where we observed that the quality of *S. obliquus* changed in such a way that it actually became toxic for daphnids, even though the culture conditions apparently did not change. For *C. pulchella* the combination of *Scenedesmus* with *Chlamydomonas* yielded growth and reproduction rates similar to the pure *Chlamydomonas* series indicating that, whatever the nutritional inadequacies of *Scenedesmus*, these were substituted completely by *Chlamydomonas* cells. This is in contrast to our results with *D. galeata* where we observed that the mixture of the food sources yielded higher growth and reproduction as compared to both mono-algal diets, and hence for *D. galeata* the two algal species seemed to be complementary resources (Boersma & Vijverberg, 1995).

The method proposed by Polishchuk (1994; 1995) is meant to detect rapid changes in important factors changing the birth rate. However, computing the importance of each factor per sampling date yielded results which were difficult to interpret, because the contribution of the different factors to the changes in birth rate varied greatly. Averaging the data over a period with similar qualitative changes in *b,* e.g. periods with increasing or decreasing *b* values, yielded more interpretable results. We conclude that, although *C. pulchella* is considered to be a typical summer species of temperate lakes and normally occurs in the months June–October only, temperature usually plays a key role in the determination of birth rate.
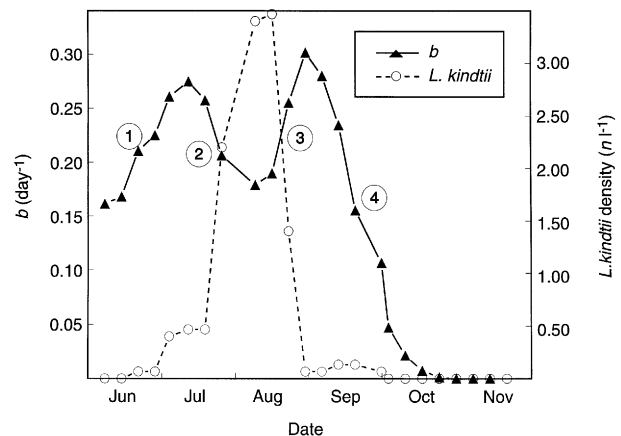
Fig. 6 Birth rates of *Ceriodaphnia pulchella* (day^{-1}) and densities of *Leptodora kindtii* during 1991 (no. l^{-1}).

In the period July–August, when changes in temperature were of lesser importance, changes in birth rates were mainly governed by changes in the proportion of adults in the population. A decrease of the proportion of adults in the population is usually explained by selective predation on the larger individuals by fish (e.g. Polishchuk, 1994). However, in this case it is difficult to attribute the disappearance of the adults to fish predation, because 0 + smelt (*Osmerus eperlanus* Linnaeus), the main planktivorous fish in Lake Tjeukemeer, prefers prey larger than 1.0 mm at this time of the year. The greatest preference for prey in the range of 0.5–1.0 mm is usually found in smaller fish and, hence, earlier in the season (Boersma, van Tongeren & Mooij, 1995). The invertebrate predator *Leptodora kindtii* Focke, however, showed its peak densities in the periods 2 and 3 (Fig. 6). In populations of *Daphnia* invertebrate predators, such as *L. kindtii*, are known to select the smaller animals (Lane, 1978; but see Lunte & Luecke, 1991). *Ceriodaphnia pulchella*, however, is much smaller than most *Daphnia* species, with sizes at maturity in the field around 0.5 mm. In prey selection experiments with *L. kindtii* as a predator and *Diaphanosoma brachyurum* Lieven as prey, Herzig & Auer (1990)
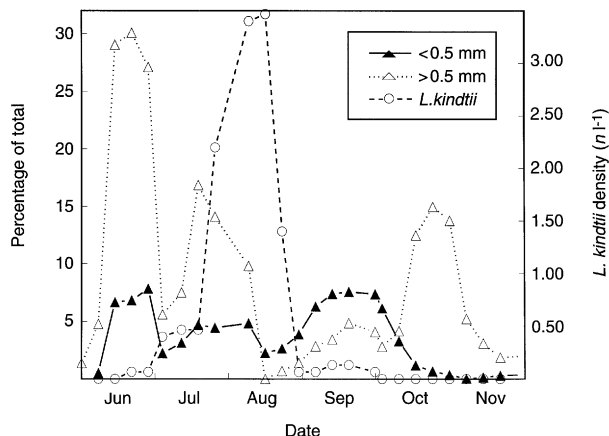
Fig. 7 Densities of *Leptodora kindtii* (no. l^{-1}) and the percentage of the two size classes of *Ceriodaphnia pulchella* (< 0.5 mm and 0.5–1.0 mm) each in relation to the total densities of cladoceran zooplankton in these size classes.

found that the main sizes of the prey items attacked were between 0.5 and 0.9 mm and, from their results, it can be concluded that *L. kindtii*, with lengths of 4–11 mm, hardly forages on prey smaller than 0.5 mm. Hence, in the case of *C. pulchella*, *Leptodora* is expected to show positive size-selective predation. This could explain the decreasing proportion of adult *Ceriodaphnia* with increasing densities of *L. kindtii*. Others, however, have claimed that *L. kindtii* also consumes large numbers of small cladocerans, such as bosminids and chydorids (e.g. Mordukhai-Boltovskaia, 1958; Lunte & Luecke, 1991). Browman, Kruse & O'Brien (1989) concluded that predation by *Leptodora* is passive, determined mainly by the vulnerability of the prey, as encounter rates are most likely similar. This implies that, assuming also that the prey vulnerability of equally sized cladocerans is similar (Branstrator, 1994), consumption of *Leptodora kindtii* will be determined strictly by the proportions of the different prey items in the field. Fig. 7 shows the percentages of two size classes of *C. pulchella* (< 0.5 mm, > 0.5 mm) each in relation to the total densities of cladoceran zooplankton of these size classes. From this graph it can be concluded that in the period of increasing densities of *L. kindtii* in Lake Tjeukemeer in 1991, the proportion of larger *Ceriodaphnia* relative to the total density of cladocerans of that size class was higher than the proportion of smaller *Ceriodaphnia* individuals. This means that, if prey choice is strictly determined by the relative densities of prey items in the field, the larger (adult) individuals of *C. pulchella* were more vulnerable to predation in this period, and hence the

proportion of adults in the population of *Ceriodaphnia* decreased. This decrease in the proportion of adults caused the observed decline in the birth rate. After the densities of *L. kindtii* decreased, predation rates on adult *C. pulchella* decreased, and hence the proportion of adults in the population could rise.

It is possible to estimate the death rates of *C. pulchella* as a result of predation by *L. kindtii*. When we assume that: (i) *L. kindtii* consumes 10 prey ind. day^{-1} (Browman *et al.*, 1989); (ii) this is independent of the prey densities, and hence the prey abundance is always in the saturated range of the predator's functional response (Herzig & Auer, 1990); (iii) only prey between 0.5 and 1.0 mm are eaten (Herzig & Auer, 1990); and (iv) no prey selection takes place, i.e. prey choice is determined solely by the relative densities in the field (Browman *et al.*, 1989), then the death rates for *C. pulchella* in the period of maximum *L. kindtii* abundance were around 0.3 day^{-1}, values in the same order of magnitude as the values computed for the animals in the field (Fig. 4). No correlation, however, was found between the *Leptodora* densities and the death rates of *C. pulchella*. This is most likely caused by the effect of sampling errors in b and r, accumulating in the estimates of the death rates (see also DeMott, 1980). The analysis of the more accurately estimated birth rates, however, shows that *L. kindtii*, although scarce, seems capable of affecting population dynamics of its prey species.

The length-corrected carbon contents of the animals in the field in 1991 were correlated negatively with r and not correlated with the average number of eggs in the population. A negative correlation between r and the condition of the animals in the field can be found if the population dynamics of the species are not governed by food conditions which, from the analysis of the changes in the birth rates, seemed to be the case. A non-significant correlation between egg number and carbon content of the animals is more difficult to explain, because most studies report a positive correlation between these two (Duncan *et al.*, 1985; Boersma & Vijverberg, 1994c; Manca *et al.*, 1994), and our laboratory results also showed a positive correlation between the length-specific carbon content and the average number of eggs. This lack of a significant correlation is probably caused by the relatively low number of observations, by the relatively constant egg numbers of *C. pulchella* adults early in

the growing season, and by the increasing proportion of females producing resting eggs later in the season.

It is important to note that, although changes in food quality or quantity do not seem to contribute very much to changes in the birth rate in the field, food conditions for *C. pulchella* are suboptimal through the whole growing season. This can be concluded from the comparison of the average number of eggs in the field with the average number of eggs produced by primiparous females in the laboratory, and from the higher carbon content of the hypothetical 0.6 mm animals in the laboratory at the higher food levels as compared with the carbon content of the animals in the field (Figs 2 and 5).

In conclusion, the population dynamics of *C. pulchella* in Lake Tjeukemeer seem to be governed mainly by temperature and by the positive size-selective predation by the invertebrate predator *L. kindtii* (see also Branstrator & Lehman, 1991). Although the condition of the animals changed during the season (Fig. 5), and food has a large impact on the animals under laboratory conditions, changes in food quantity or quality do not seem to play an important role in the seasonal dynamics of *C. pulchella*, even if the animals are food limited. This is in contrast to our findings with *Daphnia* species in the same lake (Boersma & Vijverberg, 1994c), which showed distinct periods where food limitation was important. Later in the year the change in fecundity of *C. pulchella* does have an impact on birth rates. This, however, is a result of the large proportion of animals producing resting eggs in this period, which is probably caused by physical factors, such as a decrease in day length or temperature. The findings reported in this paper indicate that the seasonal dynamics of species which are often lumped into one trophic group, i.e. herbivorous zooplankton, can be driven by different factors.

Acknowledgments

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