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Maarten Boersma

Competition in natural populations of *Daphnia*

Abstract I investigated the competitive relationships between two species of *Daphnia*, *D. galeata* and *D. cucullata*, and their interspecific hybrid. The term hemispecific competition was introduced to describe competition between parental species and hybrids. In eutrophic Tjeukemeer both parental species were found to compete with the hybrid, whereas competition between *D. galeata* and *D. cucullata* seemed limited. Although the effect of competition on life history traits of daphnids may be profound, the influence of the competitors on the seasonal dynamics of the *Daphnia* species seems limited.

Key words Coexistence · Hybrid · Competition · *Daphnia* · Hemispecific

Introduction

In the debates on competition and coexistence of species two different viewpoints can be distinguished (Bengtsson et al. 1994). The researchers advocating the 'equilibrium' viewpoint (e.g. Tilman 1982) assume that species can coexist through the avoidance of competition by niche segregation, or in 'Lotka-Volterra' terms by higher intraspecific than interspecific competition rates. The other view on coexistence of species emphasises the role of disturbance in the maintenance of the species diversity in a system (e.g. Paine 1966; Levin and Paine 1974). Although some species might be mutually exclusive under stable environmental circumstances, the speed of the process of exclusion may be so slow that the environment changes during the exclusion process, resulting in different competitive relationships and in other superior

M. Boersma[1]
Netherlands Institute of Ecology, Centre for Limnology, Rijksstraatweg 6, 3631 AC Nieuwersluis, The Netherlands

Present address:
[1] Max-Planck-Institut für Limnologie, Postfach 165, D-24302 Plön, Germany
Fax:+49 4522 763310
e-mail: boersma@mpil-ploen.mpg.d400.de

species. The process of exclusion may also be disturbed by some event, which 'resets' the system to an earlier successional stage, a phenomenon regularly observed in the succession of forest systems (e.g. Doyle 1981; Boersma et al. 1991).

Although competition between species has been the subject of research ever since the publications of the Lotka-Volterra models in the beginning of this century, competitive interactions between species and hybrids have been largely overlooked until now. This gap in our current knowledge is illustrated by the fact that no proper word exists to describe the competition between parentals and hybrids. In this paper, I will use the term hemispecific competition to describe the competition between the hybrids and the parent species, as distinct from intra- and interspecific competition.

Despite the wealth of information on genetic processes of hybridization and on the geographic distributions of hybrid and parental taxa, few experimental data exist on the relative fitness of hybrid offspring among environmental conditions (see Barton and Hewitt 1989; Harrison 1993). The zoological 'hybrid' literature is especially characterized by a lack of ecological data on hybrids. On the one hand this might be caused by the relative difficulties in recognising hybrids using traditional taxonomical methods, and on the other hand by the fact that, in a number of models on hybrid maintenance, endogenous factors, such as incompatibilities of parental genomes and resulting lower fitness of hybrids, are used to explain hybrid zone maintenance (Schwenk and Spaak 1995).

In facultatively parthenogenetic species genomic problems are probably of lesser importance, as parthenogenesis often occurs without meiosis. Therefore, the significance of competition between hybrids and parentals for hybrid maintenance is likely to be higher in animals which reproduce parthenogenetically. A large number of cladoceran zooplankton species have a cyclic parthenogenetic mode of reproduction. Hence, cladoceran zooplankton is well suited to study competitive relationships between hybrids and parental species, especially so since

in a large number of habitats parental species co-occur with their interspecific hybrids (Schwenk and Spaak 1995).

Competition and coexistence between species have been extensively studied in zooplankton communities (Mort and Jacobs 1981; Hebert 1982; Tillmann and Lampert 1984; Kerfoot et al. 1985; Romanovsky and Feniova 1985; Matveev 1986; Vanni 1986; Bengtsson 1987, 1993; Hanazato and Yasuno 1987; DeMott 1989; MacIsaac and Gilbert 1989; Schwartz and Hebert 1989; Rothhaupt 1990; Kirk 1991; Milbrink and Bengtsson 1991; Weider 1992). Different workers have, however, expressed different views on the coexistence of species. The equilibrium view, with niche segregation, was advocated by, for example, Hutchinson (1951), Makarewicz and Likens (1975) and DeMott and Kerfoot (1982), whereas the importance of changing environments and disturbances has been emphasized by such authors as Hebert and Crease (1980), Bengtsson (1986, 1987, 1993), Sommer et al. (1986), Weider (1992) and Spaak (1994). Although the existence of interspecific hybrids in cladoceran zooplankton has been widely recognised by now, the main body of the studies cited above only considered interactions between species and largely ignored the competitive relationships between species and hybrids.

In this paper I set out to investigate the competitive relationships between two species of the *Daphnia longispina* complex, *D. galeata* (Sars) and *D. cucullata* (Sars), and their interspecific hybrid in Tjeukemeer, a shallow eutrophic lake in the Netherlands. Although there is evidence that hybridization is an ongoing process (Schwenk 1993), I will treat this hybrid as a distinct taxonomical unit here. The emergence of animals from resting eggs, and hence the introduction of new hybrids only occurs in the beginning of the season (Wolf and Carvalho 1989), hence within a growing season hybrid *Daphnia* can be considered a separate group, with their own parthenogenetic reproduction. Food conditions for the three *Daphnia* taxa are known to be sub-optimal during large parts of the year (Boersma and Vijverberg 1994b). Moreover, the mesh sizes of the filtering apparatus may overlap considerably (Geller and Müller 1981). Therefore, competition for resources is likely to be important for these species. In order to clarify the importance of competition for *Daphnia* species in Tjeukemeer I pursued two lines of research. Firstly, I reduced the effect of competition by collecting animals from the field and culturing these animals on natural seston in the laboratory, using animal densities lower than the concurrent densities in the field. If competition for resources plays a role in the field, feeding conditions in the laboratory will be better than the feeding conditions in the field, resulting in higher growth rates, a larger size at maturity and higher fecundity of the animals in the laboratory. These laboratory conditions may, however, not reflect the natural conditions in the field. Therefore I also analysed field data on the densities and fecundities of *Daphnia* species in Tjeukemeer in order to assess the importance of com-

petition for resources between the sibling species under natural conditions.

In short, in this paper I addressed the following questions: do the three *Daphnia* taxa compete for resources, and is competition important in the seasonal succession?

Materials and methods

Comparison between laboratory and field data

Daphnia galeata, D. cucullata, and *D. galeata × cucullata* were collected from Tjeukemeer, using a 350 µm tow net. The animals were placed individually into 100 ml test tubes, and fed with lake seston which was filtered over a 35 µm filter to exclude other crustacean zooplankton. Three different temperatures of 12.5°C, 17.5°C and 22.5°C were used in the experiments. The medium was changed every other day in the cultures at 17.5°C and 22.5°C, and every 3 days in the 12.5°C cultures. The grandchildren of the animals collected from the field were used for the experiments. The animals were kept at a light-dark rhythm of 16:8 h. Once the animals reached maturity the number of eggs and the length were recorded for every adult instar. The animals were measured from the upper edge of the eye to the base of the tail spine to the nearest 0.01 mm. The number of neonates produced were recorded, and these neonates were removed from the tubes. Judging from the length frequency distributions in field samples, animals rarely survive beyond the fourth adult instar stage. Therefore, the daphnids in the cultures were discarded when they reached this instar.

To test for seasonal differences in growth conditions for *Daphnia* species the experiment was carried out three times, that is: in spring (18 April–31 May), summer (18 July–31 August) and in the autumn (9 October–25 November) of 1990. A number of clones (seasonal clones) were taken randomly from the field for every seasonal period. These were then evenly distributed over the different culture temperatures. In addition, one standard clone was cultured for each taxon in each seasonal period in order to evaluate the importance of temporal differences in clonal composition as a factor influencing the growth rates in the different periods. This standard clone was randomly selected from the spring populations of *D. galeata* and *D. galeata × cucullata*. As *D. cucullata* was not present in high enough numbers at the time the spring cultures were started, this species was cultured only in the summer and autumn periods of 1990. The standard clone of *D. cucullata* was also collected in the summer period. Growth conditions were established using two traits of the animals, which are known to vary greatly as a result of differences in food conditions, namely: size at maturity (SAM), and fecundity.

In the years 1989–1991 quantitative samples were taken weekly in the growing season (April-October) and fortnightly in the rest of the year, using a 5-l Friedinger sampler on five different stations in the lake, at two different depths. These samples were pooled, concentrated by filtration through a 120 µm filter and preserved in a 4% formaldehyde solution. The total number of animals were counted, and length-frequency distributions were established in a one-tenth subsample. An additional sample, which was preserved in 95% ethanol, was taken to establish length-fecundity relationships. Using the smallest gravid female found in the field as an estimate of size at maturity would lead to an underestimation of the average value of SAM in the field. Therefore, I used a logit regression technique with length as the independent variable and the presence/absence of eggs as the dependent variable. The length at which 50% of the females had eggs was taken as the average size at maturity in the field (see also Stibor and Lampert 1993).

In order to compare the fecundity of the animals in the field with the laboratory populations it was necessary to correct for length differences between the animals in the laboratory and in the field. The most straightforward way of doing this would be to perform an analysis of covariance with the length of the animals as a covariable. However, as the slope of the regression lines between

length and egg number is not constant between species and between sampling dates it is not possible to perform this kind of analysis. As a result, the standard egg production (SEP), that is the number of eggs carried by a female of a certain length, derived from the linear regressions between length and egg number was chosen instead (Hebert 1974). In order to make the comparisons between field and laboratory valid I assumed that both traits (SAM and SEP) were influenced by the feeding conditions only, and possibly also by the presence of kairomones produced by predators (e.g. Larsson and Dodson 1993). Since predators were excluded from the laboratory experiments the concentration of the cues influencing the life history traits will obviously have decreased. However, Loose et al. (1993) showed that even after 24 h at 25°C without predators, more than half of the kairomone activity was produced by fish still present in their cultures. Since the speed of the breakdown is temperature dependent (Loose et al. 1993), and my experiments were carried out at lower temperatures, the effect of fish cues in the laboratory was probably still strong. The computations for SAM and SEP in the field were made on pooled data of daphnids collected in the same periods as animals cultured in the laboratory, that is in spring, summer and autumn of 1990.

Field analysis

As a measure of potential competitive relationships I calculated the degree of niche overlap between the species. Niche segregation between species can be effectuated along spatial, temporal or resource axes. Tjeukemeer is very shallow, and hence vertical distributions of most cladoceran zooplankters are homogenous. Although some non-random horizontal distributions of zooplankton species were found, the horizontal differences between the species were small (de Nie et al. 1980). Since the exact food sources for daphnids under natural conditions are unknown, measurements of resource overlap were not possible in this study. Hence, the only axis along which niche segregation could be examined here was the time axis. As a quantitative determination of seasonal overlap between pairs of species, I calculated Schoener's (1968) index

$$D_{ij} = 1 - 0.5 \sum_{k=1}^{n} \left| P_{jk} - P_{ik} \right|$$

in which P_{ik} and P_{jk} are the proportions of populations i and j, respectively, sampled at date k. D_{ij} varies between 0 and 1, where 1 is total overlap and 0 is total separation. The significance of D_{ij} was calculated by making random pairs of the P_i and P_j values of the different species. This procedure was repeated 5000 times, and the average and standard deviation of these randomized D values were computed. The probability of the actual D_{ij} values coming from these distributions was then calculated.

The intra-, hemi- and interspecific competitive relationships were assessed by computing partial correlation coefficients of the average clutch size with the different species densities, while controlling for the densities of the other species. Since it can be expected that the density at time t will affect the fecundity at a later time t plus τ, a time-lag between the clutch size and density measurements was incorporated. Densities were interpolated between sampling dates using exponential interpolation. In order to estimate the magnitude of the time-lag, I computed Spearman Rank Order correlations between the average number of eggs in adult daphnids and total daphnid densities in the field. Time-lags from 0 to 12 days (in 1 day steps) were incorporated and the time-lag which resulted in the most negative correlation between densities and fecundity was established.

As neither number of eggs nor population densities were normally distributed, both were square root transformed. The analysis of the partial correlation coefficients was carried out using the data set from the years 1989–1991. Average clutch size was chosen instead of SEP values, since SEP values can only be accurately estimated when a large number of animals, covering a wide range of lengths, is counted. Since low densities of animals were important for this analysis, the average clutch size was chosen. However, in

order to avoid too big an influence of the sampling dates with only a few animals counted, I weighed the data from the different sampling dates with the natural logarithm of the number of animals used for the determination of the average number of eggs. The possible effect of temperature on the outcome of the correlation analyses was minimised by limiting the study period to those days in the 3 years when the average temperature of the water in Tjeukemeer exceeded 15°C, that is, in the periods from May to September.

In order to assess the effect of competition on the population dynamics of the species I also computed partial correlation coefficients between the square root transformed densities of the different species and the intrinsic rates of increase, r, of the different populations (Milbrink and Bengtsson 1991). This method will only detect competitive relationships, i.e. yield negative correlations, if competition actually affects population developments.

Results

The population densities of *D. galeata*, *D. galeata* × *cucullata* and *D. cucullata* varied greatly in 1990 (Fig. 1). In spring *D. galeata* × *cucullata* and *D. galeata* dominated, whereas the daphnid peak in autumn could be attributed to high densities of the hybrid and of *D. cucullata*. Densities of the smaller cladocerans *Bosmina coregoni*, *B. longirostris* and *Chydorus sphaericus* showed a similar seasonal pattern to that of the daphnids.
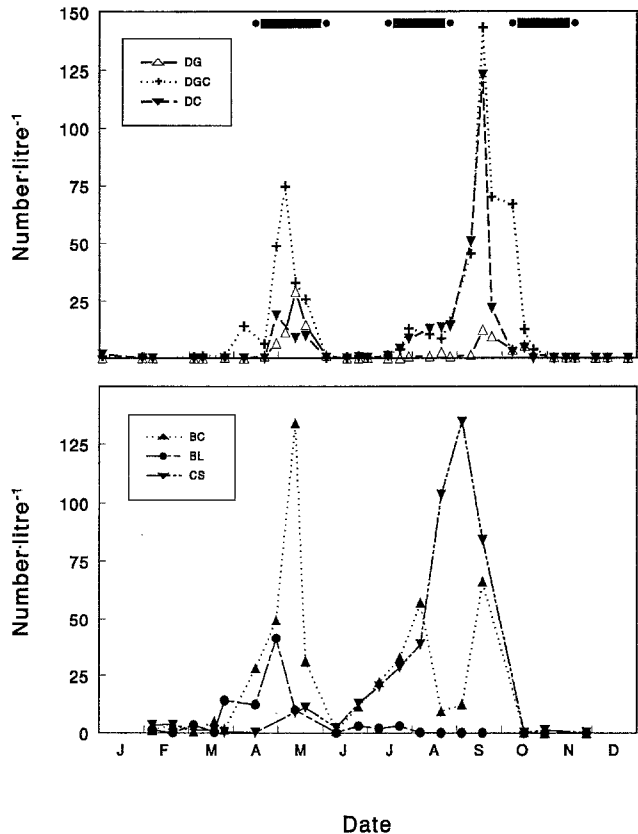

Fig. 1 Densities in Tjeukemeer in 1990 of *Daphnia galeata* (*DG*), *D. galeata* × *cucullata* (*DGC*), *D.cucullata* (*DC*), *Bosmina coregoni* (*BC*), *Bosmina longirostris* (*BL*), and *Chydorus sphaericus* (*CS*). The *horizontal bars* indicate the culture periods in the laboratory
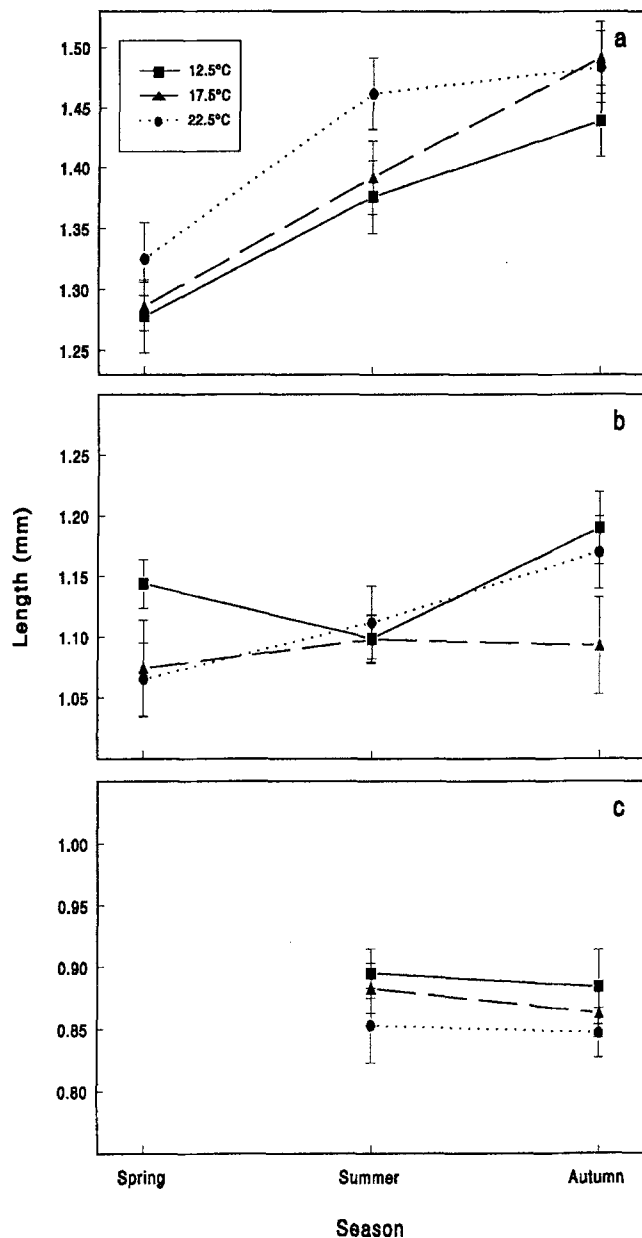
Fig. 2 Size at maturity (mm) for **a** *Daphnia galeata*, **b** *D. galeata* × *cucullata* and **c** *D. cucullata* cultured in different seasons at 12.5°C (*solid lines, squares*), 17.5°C (*dashed lines triangles*), and 22.5°C (*dotted lines, circles*). Error bars indicate 95% confidence intervals of the mean

Table 1 Summary table of the ANOVAs carried out on the log transformed values of the size at maturity with temperature (*Te*), Season (*Se*), and Clone (*Cl*) as independent variables. The analyses were done with *Daphnia galeata* × *cucullata*, *D. cucullata* (only two seasons, and *D. galeata*, respectively

Effect	MS	df	F	P
D. galeata × *cucullata*				
Cl	0.0619	1	12.10	<0.001
Se	0.0390	2	7.61	<0.001
Te	0.0548	2	10.70	<0.001
Cl × Se	0.0038	2	0.74	0.480
Cl × Te	0.0026	2	0.51	0.602
Se × Te	0.0179	4	3.49	0.008
Cl × Se × Te	0.0067	4	1.31	0.264
Error	0.0051	335		
D. cucullata				
Cl	0.0026	1	0.97	0.325
Se	0.0023	1	0.84	0.362
Te	0.0048	2	1.75	0.176
Cl × Se	0.0001	1	0.01	0.978
Cl × Te	0.0166	2	6.14	0.003
Se × Te	0.0003	2	0.10	0.905
Cl × Se × Te	0.0001	2	0.01	0.999
Error	0.0027	151		
D. galeata				
Cl	0.0354	1	9.82	<0.001
Se	0.3372	2	93.45	<0.001
Te	0.0265	2	7.34	<0.001
Cl × Se	0.0488	2	13.53	<0.001
Cl × Te	0.0856	2	23.72	<0.001
Se × Te	0.0155	4	4.30	0.002
Cl × Se × Te	0.0140	4	3.88	0.004
Error	0.0036	201		

Comparison between laboratory and field data

Growth in the laboratory varied considerably between the different seasons, as is illustrated by the differences in size at maturity (Fig. 2). In order to distinguish between the effect of the seasonal clonal composition of the *Daphnia* taxa and the feeding conditions, the taxa were analysed separately. For each taxon I tested the standard clone against the combination of the seasonal clones. For *D. galeata* × *cucullata* size at maturity was significantly affected by the season and the temperature. Moreover, the standard clone was smaller than the seasonal clones (Table 1). The standard clone and the sea-

sonal clones reacted in a similar manner to differences in temperature and season, as no significant interactions were found between the clonal effects and the other factors. For *D. cucullata* no significant seasonal, temperature or clone effects were found. However, at 12.5°C the SAM of the standard clone was smaller than the SAM of the seasonal clones, whereas at the higher temperatures the SAM values were similar, resulting in a significant interaction between temperature and clone (Table 1). No significant interaction effect was, however, found between season and clone, indicating that for *D. cucullata* the standard and seasonal clones also reacted in a similar way to the different seasons. For *D. galeata* the situation was different. Not only were the main effects significant, but also all of the interaction effects differed significantly from zero (Table 1). Thus, the standard clone reacted in a different manner to the lake seston in the various seasons when compared with the seasonal clones.

SEP values of the cultured daphnids (Fig. 3) also differed considerably between the different seasons and at the different temperatures. As it was not possible to analyse the different length-egg number regressions in one analysis of variance due to the differences in slopes between the different temperatures, seasons and species ($F_{17,1519} = 2.6$, $P < 0.001$), only pair-wise comparisons were possible. For *D. galeata* SEP values were significantly higher in summer than in spring, whereas summer and autumn values did not differ significantly. Average
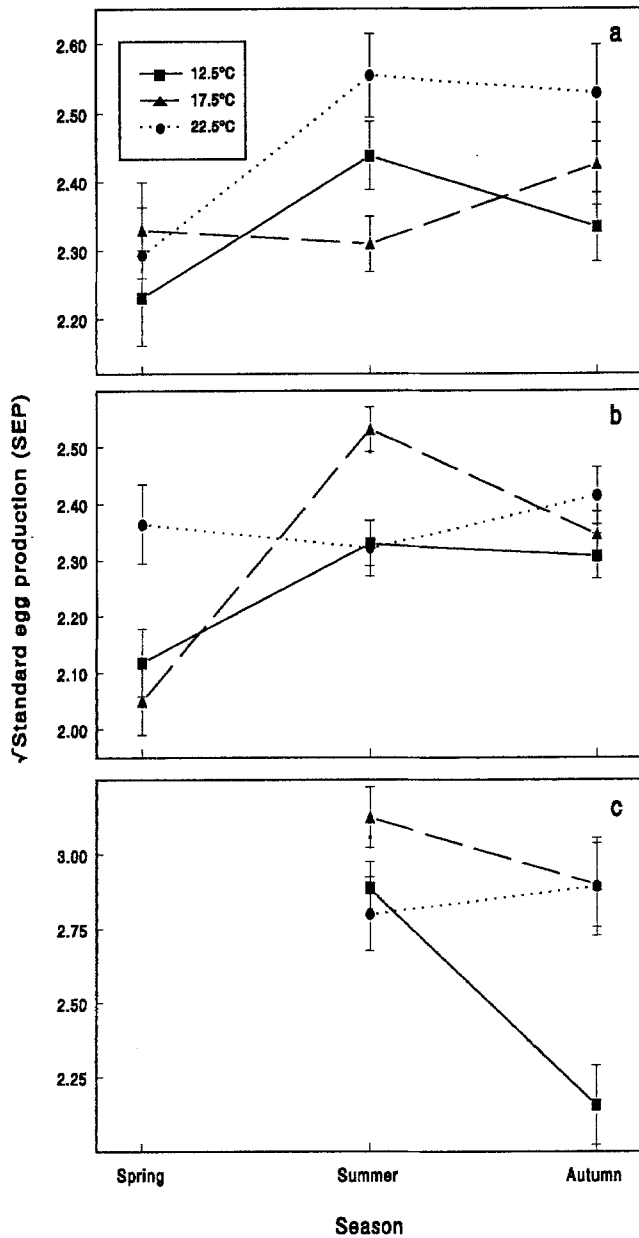
Fig. 3 Square root of standard egg production (SEP) values for **a** *Daphnia galeata* (length is 1.5 mm), **b** *D. galeata* × *cucullata* (length is 1.25 mm) and **c** *D. cucullata* (length is 1.25 mm) cultured in different seasons at 12.5°C (*solid lines, squares*), 17.5°C (*dashed lines, triangles*), and 22.5°C (*dotted lines, circles*). Error bars indicate standard errors

spring SEP values of the hybrid were also the lowest, differing significantly from both the summer and autumn values. *D. cucullata* showed significantly higher values in egg production in summer.

In only 3 out of the total of 24 cases (three temperatures × three seasons × three species minus *D. cucullata* in spring) did the SEP values differ significantly between the standard clones and the seasonal clones. This was once for each species. This finding indicates that if it had it been possible to do an analysis of variance it is unlikely that clone-season interactions would have been found. Hence the conclusions from the analysis of the SEP values were comparable with those from the analysis of SAM values, although the variation in SEP values was larger.

Since temperature affected both growth and reproduction in the laboratory, the values found in the field were compared with the animals cultured on roughly the same temperature as the ambient temperature in the lake at the time. The average temperature was 13.8°C in the spring period, 19.3°C in summer, and temperature averaged 9.2°C in autumn. Hence, data from the lake in spring and autumn were compared with the animals cultured at 12.5°C, whereas the data collected in the summer were compared with the animals cultured at 17.5 °C. From a comparison of the values for SAM (Table 2) and for SEP (Table 3) it becomes clear that the values found in the laboratory cultures were almost always significantly higher than the values found in the field. It can therefore be concluded that the feeding conditions in the laboratory cultures were better than the feeding conditions in the field at the same time. As the differences between laboratory and field data should be mostly caused by different levels of competition this was tested by correlating the differences between the values found for SEP and SAM in laboratory and field with the densities of the competitors at that time in the field. Unexpectedly, the differences between the field and laboratory measurements were smallest in the spring period, when the daphnid densities were highest in the field.

Field analysis

Seasonal overlap between *D. galeata* and *D. cucullata* was small compared with the overlap both species had with the hybrid. The average overlap of the random pairs was around 0.3 for all three combinations (Table 4). This

Table 2 Size at maturity (*SAM* mm) of daphnids in the field in different seasons of 1990, and SAM of the same species in the laboratory cultures under the appropriate temperature conditions (*SE.* standard error, *n* number of observations, t_s values were computed following Sokal and Rohlf [1981])

Species	Season	Field SAM	Laboratory SAM	SE	n	t_s	P
Daphnia galeata	Spring	1.136	1.278	0.014	41	1.554	NS
	Summer	1.003	1.392	0.016	34	4.065	<0.001
	Autumn	1.174	1.439	0.017	23	3.198	<0.01
D. galeata × *cucullata*	Spring	1.048	1.144	0.009	48	1.478	NS
	Summer	0.801	1.098	0.009	36	5.551	<0.001
	Autumn	0.974	1.190	0.016	19	3.102	<0.01
D. cucullata	Spring	1.053					
	Summer	0.760	0.883	0.010	26	2.697	<0.05
	Autumn	1.039	0.884	0.015	16	-2.492	<0.05

Table 3 Standard egg production (SEP) of the daphnids in the field in the different seasons of 1990 and SEP values of the same species in the laboratory cultures under the appropriate temperature conditions. The values were compared pair-wise, using the T'-method. All values of SEP are square root transformed values, *SE* standard errors, *n* number of observations, *Length* (mm) lengths which were used to compute the SEP values.

Species	Season	Length	Field			Laboratory			*P*
			SEP	SE	*n*	SEP	SE	*n*	
Daphnia galeata	Spring	1.500	2.084	0.049	253	2.230	0.068	67	NS
	Summer	1.500	2.059	0.056	127	2.310	0.041	103	<0.01
	Autumn	1.500	2.188	0.040	146	2.334	0.050	103	<0.05
D. galeata × cucullata	Spring	1.250	1.991	0.038	297	2.118	0.064	69	NS
	Summer	1.250	1.952	0.029	315	2.532	0.039	113	<0.01
	Autumn	1.250	1.708	0.034	239	2.307	0.042	94	<0.01
D. cucullata	Spring	1.250	1.591	0.069	41				
	Summer	1.250	2.174	0.056	269	3.124	0.102	87	<0.01
	Autumn	1.250	1.620	0.040	88	2.156	0.134	53	<0.01

Table 4 Schoener's index, D_{ij}, as calculated from 5000 runs of random pairing of seasonal observations with the standard deviation (*below diagonal*), and D_{ij} for the actual observed pairs, with the probability that these values were taken from the random distributions (*above diagonal*). The species represented are *Daphnia galeata* (*DG*), *D. cuculata* (*DC*), and their hybrid (*DGC*)

Species	DG	DGC	DC
DG		0.31 (0.756)	0.15 (0.034)
DGC	0.33 (0.06)		0.57 (<0.001)
DC	0.29 (0.07)	0.33 (0.06)	

resulted in a significantly lower than random value of D_{ij} for the combination of *D. galeata* and *D. cucullata*, and a significantly higher value of Schoener's index for the hybrid- *D. cucullata* combination.

It was found that the time-lag yielding the most negative correlations between clutch size and densities was around 6 days for all species. Hence this time-lag was used to compute the partial correlation coefficients between the average clutch size of the *Daphnia* species and the densities. Table 5 shows the results of this analysis. Most partial correlation coefficients were significantly smaller than zero, with the clear exception of two cases. The partial correlation coefficient of average clutch size of *D. galeata* with

the population abundance of *D. cucullata*, and the partial correlation coefficient of average clutch size of *D. cucullata* with the density of *D. galeata* were non-significant. This suggests that the competitive interaction between *D. galeata* and *D. cucullata* in Tjeukemeer was limited.

Once the competitive relationships were established it was possible to investigate the influence of competition on the different populations. The square root of the average clutch size versus the density of the competitors for the three taxa (*D. galeata* plus the hybrid for *D. galeata*, *D. cucullata* plus hybrid densities for *D. cucullata* and total daphnid counts for the hybrid) were plotted against one another. As could be expected from its size, in the absence of competitors *D. galeata* produced the largest clutches (Fig. 4), while *D. cucullata* clutches were the smallest. Judging from the three regression lines which were not significantly non-parallel ($F_{2,87} = 0.20$; $P = 0.8$) the reaction of the three species to an increase in densities of the competitors was similar. *D. galeata* always produced the largest clutches regardless of the density of the competitors present. This suggests that competitive relations do not change over the daphnid density axis, and that *D. galeata* is likely to be the more successful competitor. This result is not dependent by the choice of the competitors; taking total daphnid densities for all taxa yielded similar results.

Table 6 shows the results of the correlation analysis of the population growth rates, with the square root trans-

Table 5 Partial correlation coefficients (r_{part}) of the square root transformed values of average clutch size with the square root transformed values of *Daphnia* species abundances, weighted with the natural logarithm of the number of animals counted for the average clutch size. The given values indicate the partial correlation coefficients while controlling for the other two species abundances

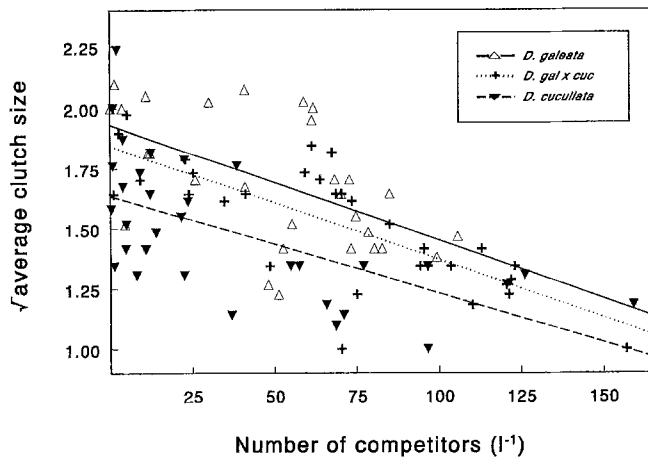| Clutch size	Abundances					
	D. galeata		*D. galeata × cucullata*		*D. cucullata*	
	r_{part}	*P*	r_{part}	*P*	r_{part}	*P*
D. galeata	−0.19	0.055	−0.22	0.029	−0.06	0.561
D. galeata × cucullata	−0.34	<0.001	−0.40	<0.001	−0.46	<0.001
D. cucullata	−0.05	0.628	−0.44	<0.001	−0.57	<0.001

Fig. 4 Responses of the average number of eggs per adult female of the *Daphnia* species to changes in the densities of the competitors. Regression lines are highly significant, but not significantly non-parallel. Post-hoc comparisons showed that *D. galeata* is significantly different from the other two (*D. galeata* - *D. galeata* × *cucullata*: $P = 0.004$; *D. galeata* - *D. cucullata*: $P = 0.001$). *D. cucullata* is not significantly different from the hybrid ($P = 0.83$)

formed values of the different densities. Only two partial correlation coefficients were significantly different from zero, although most of them were negative. Moreover, all correlation coefficients of *r*-values with total daphnid densities were negative, although only in the case of the hybrid the correlation coefficient different significantly from zero. Thus, although competition seems to affect clutch sizes of the daphnids, population growth rates appear to be more independent of the number of competitors present.

Discussion

Comparison between laboratory and field data

For *D. cucullata* and *D. galeata* × *cucullata* no significant differences in growth and reproduction between the standard clones and the seasonal clones were found. This indicates that the changes in maturity and fecundity were caused by changes in the feeding conditions in Tjeukemeer, and not by changes in the clonal composi-

tion. The pattern was different for *D. galeata*, with a significant interaction between the clone effect and the season effect. This was caused by the relatively large size of the standard clone in the summer cultures, whereas in the other seasons the differences between the standard clone and the seasonal clones were much smaller. This may lead to the conclusion that the apparent differences between the seasons were caused by differences in clonal structure. However, the seasonal differences in size at maturity were also highly significant for the standard clone ($F_{2,29} = 51.8$; $P < 0.001$). Hence, it can be concluded that the conditions for growth and reproduction of *Daphnia* species changed during a year in the highly eutrophic Tjeukemeer.

Resource competition may play an important role in the regulation of seasonal succession of *Daphnia* species in eutrophic lakes. In almost all cases the size at maturity and the SEP values were higher in the animals raised under laboratory conditions, indicating that the food quantity and/or quality was/were higher for the animals cultured in the laboratory. Only in the case of *D. cucullata* in the autumn period of 1990, was a larger size at maturity observed in the field than in the laboratory. However, since the SEP values in this period were higher under laboratory conditions this relatively large size at maturity in the field is very likely to be an artefact, possibly caused by the relatively low densities in the field, combined with the fact that a very high percentage of the *D. cucullata* individuals were adult, leading to difficulties with the estimation of the size at maturity. Moreover, it should be noted that taking the length when 50% of the individuals carry eggs will lead to an overestimation of the size at maturity under low food conditions, as under these conditions not all adult females carry eggs (Stibor and Lampert 1993). Hence the difference between field and laboratory conditions would be even larger than we estimated.

Although chemical cues of predators were probably still present in the culture vessels in the laboratory (Loose et al. 1993), the concentration will have been lower than in the field. Daphnids in the field are expected to remain smaller than the animals in the laboratory, as cues of juvenile fish, the main zooplanktivore, are known to cause a decrease in the size at maturity (e.g. Stibor and Lüning 1994). These authors, however, reported a decrease in size at maturity under the influence

Table 6 Partial correlation coefficients of the population growth rates, *r*, with the square root transformed values of *Daphnia* species abundances. The given values indicate the partial correlation coefficients while controlling for the other two species abundances

r	Abundances					
	D. galeata		*D. galeata* × *cucullata*		*D. cucullata*	
	r_{part}	*P*	r_{part}	*P*	r_{part}	*P*
D. galeata	−0.09	0.585	−0.04	0.810	−0.04	0.792
D. galeata × *cucullata*	0.06	0.714	−0.53	0.001	0.31	0.043
D. cucullata	−0.27	0.088	0.14	0.365	−0.26	0.103

of fish cues of 6%, at fish densities a factor 30 higher than the ones in Tjeukemeer. The differences in size at maturity observed in this study (averaging 18%) were higher than the ones reported by Stibor and Lüning (1994), and hence cues by these predators are not likely to have caused the differences between laboratory and field animals found in this study. It is more likely that by placing the animals individually into 100 ml tubes, the resources which normally would be consumed by all animals in the field were now exclusively available for the single animals. It could be argued that competition is not absolutely ruled out by this culturing method, since fresh water from Tjeukemeer is added to the animals at regular intervals, the composition of which is a result of all animals competing in the field situation. The exact nature of the food source of daphnids in highly eutrophic lakes like Tjeukemeer is still unclear. I hypothesize that the preferred food for daphnids is a small, highly productive pool of good quality food, such as bacteria (Brendelberger 1991), flagellates (Kerfoot et al. 1985), ciliates (Wickham and Gilbert 1993) or some algal species. This could explain the observed differences between the laboratory and field populations. My observation that the differences between field and laboratory results were smallest in the spring period could be caused by the fact that the period of pooling in spring was too long, since this period comprised the whole period of rise and fall of the daphnid densities. When only the second half of the spring period was used in the calculations, the differences between laboratory- and field-derived data were indeed much larger than the differences found for the other periods.

Field correlations

Most of the significant time-lags between animal densities and clutch sizes were found to be around 5–6 days. This is similar to the ones reported by Matveev (1983), but longer than the duration of egg development, which ranged around 3 days in summer (Boersma and Vijverberg 1994a). This is in contrast to the findings of Seitz (1980), who found time-lags very similar to the egg development time. Matveev (1983) argued that the time-lag is larger than the egg development time, because daphnids are known to store lipids when food conditions are good. As these can be metabolized later in time (Goulden and Hornig 1980) the length of the time-lag increases. However, since the average size of adult females in the field was relatively constant over a short period, and the growth in daphnids continued when the animals were adult, it can be concluded that there was mortality of the larger adults on the one hand, and input of new females on the other hand. Consequently, a large proportion of the animals affected by the high densities will have been juvenile at the time, and the average clutch size probably was predominantly determined by the first adult instars. It is well known that the effect of low food conditions will be most severe when the animals are

young (Threlkeld 1976), thus leading to a time-lag longer than the egg development time, similar to the time span between birth and maturation. This is similar to the second time-lag reported by Seitz (1980).

Competition

Only a few reports have been published on the competition between D. galeata and D. cucullata. Seitz (1980) reported coexistence between D. galeata and D. cucullata in the Klostersee (Germany), with D. cucullata densities having a negative correlation with the clutch size in D. galeata, but not the other way around. Recently, Gliwicz and Lampert (1993) carried out enclosure experiments with a larger range of Daphnia species, and observed that D. cucullata was the first species to disappear from the enclosures, followed by D. galeata. Only the larger Daphnia species survived. However, from this experiment, it is not possible to judge whether D. galeata and D. cucullata directly competed for resources or whether both species were outcompeted by the larger daphnids.

Data on competition between Daphnia species and their interspecific hybrids are almost non-existent. Only Mort (1990) investigated competition between D.galeata, D. hyalina and their interspecific hybrid, but it is difficult to draw general conclusions from her study.

My finding of the large differences in growth and reproduction between field and laboratory animals combined with the negative partial correlation coefficients between average clutch size and density suggests that the two Daphnia species and their hybrid competed for resources. D. galeata × cucullata seemed to compete with both D.galeata and D. cucullata. Both parental species competed with the hybrid, but the densities of D. cucullata were not negatively correlated with the clutch size of D. galeata, and vice versa (Table 5). It is difficult to envisage, however, that these two closely related congeners do not compete for resources (see also Bengtsson 1987). However, as was shown by Brendelberger and Geller (1985), under some circumstances the mesh size of the filtering apparatuses of D. galeata and D. cucullata can differ. They reported a range of 0.76–1.07 μm for the mesh size of D. cucullata and 0.30–0.74 μm for D. galeata. Although mesh size essentially determines the smallest particle to be retained, it is likely that differences in mesh size will lead to some differences in the food spectrum, and a possible reduction of the competition for resources. Alternatively, the apparent absence of competition between the two parental species could have been caused by the temporal segregation of D. galeata and D. cucullata. As was shown in Table 4 temporal overlap of the parental species was smaller than the temporal overlap of any of the parental species with the hybrid. (see also Müller and Seitz 1993). It is therefore likely that the outcome of the competition analysis depends on this temporal segregation between D. galeata and D. cucullata. If the temporal segregation between

these species would have been complete the correlation analysis performed here would have failed to show any competitive interactions, whereas individual daphnids co-occurring might have competed. Laboratory experiments on the competitive relationships in this species complex are needed to establish whether the apparent low competition between the two species was caused by temporal segregation, or that resource segregation is more important.

Although the species under consideration seem to compete for resources, limiting resources are not likely to be the only factor of importance in the seasonal dynamics of the species. As was shown in many studies different predation regimes may have large impacts on zooplankton communities (e.g. Milbrink and Bengtsson 1991). In fact, using the method of Milbrink and Bengtsson (1991), i.e. correlating population densities with population growth rates (Table 6) yielded much less significantly negative results than the correlations of clutch sizes with population densities. This indicates that although population densities seem to affect fecundity, they appear to have much lower effects on population growth. Most likely, predation or other external mortality factors, such as physical processes (e.g. Fryer 1991) must be held responsible for this apparent discrepancy.

In the analysis thus far I implicitly assumed that Daphnia species were the only herbivorous zooplankton species in Tjeukemeer, which is obviously not true. Smaller zooplankton species may also affect the feeding conditions for daphnids. However, the densities of the smaller species were strongly positively correlated with the densities of the daphnids (D_{ij} values larger than the random Ds). Hence, the computation of partial correlation coefficients, while also correcting for the densities of the smaller zooplankton, yielded mostly non-significant results for the effects of daphnid densities. However, as the likelihood of intrageneric competition is larger than the likelihood of intergeneric competition, and it has been shown that Daphnia species are the superior competitors over the smaller cladocerans (DeMott and Kerfoot 1982; Kerfoot et al. 1985; Vanni 1986), emphasis is put here on the competition within the genus Daphnia. The only means of assessing the effect of competition of small cladocerans would be to extend the data set, making sure that densities of the different species were not correlated.

It is tempting to speculate on the mechanisms behind the co-occurrence of hybrids and parental species in temperate lakes. The relative magnitude of the correlation coefficients between the two parentals gives the impression that the competition between the parentals is lower than the competition between the parentals and the hybrids. It is, however, difficult to assess the long term effects of the competition between the three taxa, because the correlation analysis was carried out only for a limited part of the year, and competitive relationships may change over time (Neill 1975). Moreover, one should recall that competition is only of importance when food is scarce. Although daphnids seem to be food limited during large parts of the year (Boersma and Vijverberg 1994b), periods of surplus food do occur, resulting in the absence of resource competition. In these periods the Daphnia species might co-occur, even if competition is severe under conditions of food scarcity.

In conclusion, in the two species of the D. longispina complex, D. galeata and D. cucullata interspecific competition seems limited, whereas hemispecific competition is found to be more severe: both parental species compete for resources with their interspecific hybrid. Further research is needed to establish whether the intensity of the different competitive interactions is such that the two species can coexist with their hybrid through niche segregation, or that non-equilibrium circumstances are needed to explain the coexistence of the species from this complex.

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