Carbon as an indicator of *Daphnia* condition in an alpine lake

Monika Winder & Piet Spaak

Department of Limnology, EAWAG/ETH, Überlandstrasse 133, CH-8600 Dübendorf, Switzerland

Key words: Cladocera, zooplankton, phytoplankton, seasonal variation, nutritional status, food limitation, trade off, fecundity, chlorophyll *a*, vertical migration

Abstract

Carbon–length relationships can be used to indicate the condition of daphnids in natural situations. We examined the *Daphnia galeata* population of an alpine lake (Oberer, Arosasee, Switzerland), where most individuals display diel vertical migration behaviour (DVM). Normally, migrating daphnids face a trade-off between ‘predator safe areas’ in the hypolimnion and ‘food rich areas’ with high predation risk. However, in alpine lakes, with chlorophyll *a* and POC maxima typically in deeper layers and weak temperature gradients, migrating species are confronted less with this trade-off. We investigated the seasonal changes in carbon content of *D. galeata* in different depth strata in relation to environmental parameters of the lake. The carbon content of *D. galeata* was high in spring, but declined considerably in summer and increased slightly in autumn. The low values indicate that *D. galeata* are food limited for much of the year. The slopes of the regression lines between carbon content and body length varied seasonally, but were not significantly different among depths on a given date. In summer, *D. galeata* individuals residing in the deep layers during the day had a significantly higher carbon content than individuals in the surface layers. During the rest of the year, the carbon content of individuals was similar among all depth strata. We conclude that migrating *D. galeata* and individuals remaining in deep layer had better body conditions compared to non-migrating *D. galeata* in this alpine lake during summer, when migration amplitudes were highest.

Introduction

A number of studies have investigated the seasonal dynamics and production of zooplankton in temperate lakes (e.g. Sommer et al., 1986), and recognized that food limitation and predation are major factors influencing the size structure, reproduction and survival of zooplankton (Ghilarov, 1985; Lampert, 1988; Mitchell et al., 1992). In natural systems, however, it is difficult to disentangle the relative role of food and predation, because of the complexities in measuring the effects of food limitation and predation separately (Boersma & Vijverberg, 1994c). Moreover, it is difficult to establish the amount of accessible food for herbivores in a lake, as in most cases the exact food source is unknown. Studies on daphnids, for example, reported that their diet is a mixture of algae and cyanobacteria (Bloem & Vijverberg, 1984; Vijverberg et al., 1993), bacteria (Urabe & Watanabe, 1991) and detritus (Kerfoot & Kirk, 1991). Furthermore, the biochemical content of algae differs among species,

thus resulting in differences in food quality between them (Ahlgren et al., 1990; Groeger et al., 1991). Finally, other factors, such as selective feeding (DeMott, 1986), indigestibility of particles (Kirk, 1992; Van Donk & Hessen, 1993) and interference (Gliwicz & Siedlar, 1980), may result in only a small part of the available resources actually utilized by zooplankters. Thus, daphnids can be food limited even in eutrophic lakes (Boersma & Vijverberg, 1994b). In short, the actual measurement of food accessibility for herbivorous zooplankton is difficult. Hence, indirect measurements to assess the nutritional status of zooplankters have been proposed. For daphnids, laboratory experiments indicated that the number of eggs (Vijverberg, 1976), lipid content (Tessier & Goulden, 1982) and carbon content correlate positively with the quantity and quality of accessible food. As a result, parameters such as egg production (Hebert, 1977), number of eggs per female (Geller & Müller, 1985), lipid-ovary index (Tessier & Goulden, 1982), lipid content (Farkas, 1970) and carbon–length relation-

ships (Duncan, 1985) have been used to assess the condition status of daphnids in the field. Fecundity is used most frequently, but reflects body condition only in a limited way (Berberovic, 1990), because the number of eggs depends on the size of the animal, and lipid levels do not always correlate positively with animal growth rates (Sterner & Schulz, 1998).

The relationship between carbon content and body length of an organism seems most promising to evaluate a daphnid's condition. Duncan (1985, 1989) found that under controlled laboratory conditions the slopes of the carbon-length regression lines between length and weight were constant at different food levels, although the intercept, and hence the carbon content, significantly decreased as food levels became limiting. In contrast to animals reared in the laboratory, however, it is known from field populations that the slopes of the regression lines also vary during the year (Geller & Müller, 1985; Hessen, 1989; Boersma & Vijverberg, 1994b). Nevertheless, changes in the carbon-length relationships will reflect changes in the condition of the daphnids and hence yield information on their feeding environment. In addition, carbon-length (or dry weight) regressions are the most reliable method to estimate zooplankton biomass (Dumont et al., 1975; Bottrell et al., 1976; Persson & Gunnar, 1980).

In lakes with high fish densities, and hence a large risk of visual predation, zooplankton species typically exhibit diel vertical migration (DVM) (Ringelberg et al., 1991). Migration to deeper water layers during the day reduces the vulnerability to visual predation, although differences in food quality, quantity and temperature at different depths could result in metabolic costs for the migrating zooplankters (Orcutt & Porter Jr, 1983; Gabriel & Thomas, 1988), even though the energetic costs of migration are thought to be negligible (Loose & Dawidowicz, 1994). Metabolic costs can be expressed as a reduction in growth and reproduction (Ringelberg et al., 1991). The susceptibility of prey species to potential predators is usually associated with their physiological state, which is primarily determined by food and temperature (Gerritsen, 1982; Han & Straskraba, 1998). Zooplankton species migrate less or even stop migrating under food limitation (Johnsen & Jakobsen, 1987; Flik & Ringelberg, 1993).

Guisande et al. (1991) and Duncan et al. (1993) used the relationship between length and protein, or length and carbon content, as an index of daphnid condition at different lake depths, to distinguish subpopulations that differed in their migration strategy.

They showed that a trade-off exists between reduced mortality and poorer nutritive state at greater depths in lakes with food-rich surface waters and strong vertical temperature gradients. In lakes with high subsurface food abundance and weak temperature gradients, as is the case for many alpine lakes (Tilzer, 1973), however, migrating zooplankton may be confronted with this trade-off to a lesser extent. This should be reflected in a relatively good body condition of migrating daphnids.

The objective of this study was to evaluate the carbon content of a *Daphnia galeata* population across seasons, and the influence of seasonal biotic and abiotic fluctuations on the carbon-length regressions of the zooplankters in an alpine lake. In addition, carbon-length regressions were used to indicate the conditional status of *D. galeata* that undergo DVM. Hence, we compared the condition of *D. galeata* individuals caught at several depths. In addition, the carbon content of *D. galeata* was related to environmental parameters of the lake to test whether the seasonal variation in food availability was reflected in the condition of *D. galeata*. Furthermore, migrating *D. galeata* should have a better condition than individuals remaining in the surface water layers since migrating individuals can feed in the deep layers during their daytime refuge, whereas the individuals in the surface layers are confronted with low food conditions day and night.

Materials and methods

Study area

The study was conducted at the Oberer Arosasee, Switzerland), a dimictic lake (7.1 ha) situated 1734 m a. s. l. over slate rocks in the catchment of the River Rhine. Its maximum depth is 13 m and the lake is ice covered for about 6 months each year. During the open water period, a distinct thermocline is absent, and a weak but relatively continuous vertical temperature gradient develops. Spring turnover is incomplete and the hypolimnion becomes anoxic twice a year. During summer, dissolved oxygen concentrations become $<3 \text{ mg l}^{-1}$ at depths $>9 \text{ m}$.

Diatoms dominate the phytoplankton community in spring, whereas cyanobacteria and chlorophytes are abundant in summer, and cryptophytes in autumn. The zooplankton community consists of *Daphnia galeata*, *Cyclops abyssorum*, *Eudiaptomus gracilis* and *Bosmina longispina*. *Cyclops abyssorum* dominates in

spring, but *D. galeata* is the most abundant crustacean in the rest of the year. The fish community in the lake consists of introduced brown trout (*Salmo trutta*), which are most dominant, and rainbow trout (*Oncorhynchus mykiss*) as well as of native minnow (*Phoxinus phoxinus*) and charr (*Salvelinus alpinus*).

Field methods

Samples of zooplankton and water were taken on a weekly basis in 1998 and fortnightly in 1999 during the open water period, and twice in winter in both years. Zooplankton was sampled at mid-day from three stations around the deepest part of the lake at 2.5 m intervals from 0 to 12.5 m depth using a duo-closing net (95 μm mesh size) (Bürge, 1983). A total of 300 l per depth stratum was collected. Samples from each station were pooled, concentrated and preserved in 90% ethanol. In addition, *D. galeata* were sampled with the duo-closing net from each depth stratum at mid-day and midnight (in 1999) at one station and analysed for carbon content and egg number. In 1998/99, water samples from 6 depths (0, 2.5, 5, 7.5, 10 and 12.5 m) and in 1999/2000 from 12 depths (1 m interval: 0–12 m) were used to determine the concentration of particulate organic carbon (POC) and chlorophyll *a* in the lake. Chlorophyll *a* was measured after extraction in 90% ethanol using HPLC. Phytoplankton biomass was analysed every third week using the Utermöhl technique (Rott, 1981). Cell size and shape distinguished edible from inedible algal cells (Infante, 1973; Porter, 1973; Conover & Mayzaud, 1984).

Laboratory analyses

Directly after collection, animals were rinsed with distilled water, total length measured, number of eggs counted, and then individually transferred into clean (acetone washed and dried at 120 °C) tin capsules and frozen at –20 °C for transport to the laboratory. At the laboratory, the samples were stored at –80 °C until they were analysed. The carbon content of individual *D. galeata* was determined using a CHNS Analyser (Carlo Erba, ANA 1500). A *t*-test showed that there was no significant difference ($P < 0.05$) in carbon content between fresh and frozen animals (but see Boersma & Vijverberg, 1994a). For total length, measures were taken from the base of the spine to the top of the eye. At least 30 individuals from each stratum, or all individuals in small samples were measured.

Statistical analyses

Linear regressions were calculated from log transformed values using individual length (L in mm) as the independent variable and carbon content (C in μg) as the dependent variable. The relationship is expressed as:

$$C = a * L^b.$$

The intercept a represents the carbon content of a *D. galeata* of 1 mm body length. Since the length of all measured *D. galeata* was close to 1.5 mm in 1998, the regression equation was used to estimate the carbon content of an individual of 1.5 mm. This value is defined as the Standard Carbon Content (SCC) (sensu Boersma & Vijverberg, 1994c).

Regressions were tested for differences in intercept, slope and regression coefficients using regression analysis with dummy variables (Sokal & Rohlf, 1995). Significance between depths was tested using ANCOVA followed by Tukeys post hoc comparison test (Sokal & Rohlf, 1995). Correlations between SCC and environmental parameters were tested for significance by linear regressions.

Results

Chlorophyll *a* concentrations in the Oberer Arosasee reached a maximum in spring and early summer (Fig. 1). The concentration in the surface and middle layers decreased in July in 1998 and in August in 1999. During summer, chlorophyll *a* concentrations were low (0.5–7.0 $\mu\text{g l}^{-1}$) in the surface layer and middle layers, but higher in the deep layer in both years. After autumn turnover, chlorophyll *a* concentrations were low and uniformly distributed in the water column (0.5–1.0 $\mu\text{g l}^{-1}$). Pelagic POC concentrations ranged from 0.2 to 1.3 mg l^{-1} and phytoplankton biomass from 0.08 to 4.0 mg l^{-1} with a high proportion of edible algal biomass at all time. Both parameters showed high values in the spring of 1998 and in early summer in 1999 (Fig. 2a).

In 1998, the population density of *D. galeata* was low in spring and increased considerably in late June to its highest abundance of 46 ind. l^{-1} (Fig. 2b). The density of *D. galeata* was relatively high for the rest of the open-water period but declined considerably in winter. In 1999, density increased in late June and reached its highest value of 31 ind. l^{-1} in late August. Adult females were rare, even in summer, never exceeding 12 ind. l^{-1} in 1998 or 3.6 ind. l^{-1} in 1999.

Figure 1. Distribution of chlorophyll *a* concentration ($\mu\text{g l}^{-1}$) in the Oberer Arosasee from May 1998 to February 2000.

Figure 2. Seasonal variation in POC (line) and algal biomass (bars) (a); density of *D. galeata* (b); number of eggs, and carbon content (CC) of individuals for two size classes (1–1.5 mm and 1.5–2 mm) (c). Error bars equal ± 1 standard error.

The average number of eggs per female was highest in June 1998 and July 1999, declining in both summers with low values (Fig. 2c). After autumn turnover, average number of eggs increased in 1998. Egg-bearing animals were rare during periods of ice cover.

Carbon content

The mean actual carbon content of individual *D. galeata* for two size classes (1–1.5 mm; 1.5–2 mm) was high in spring and then declined in summer to the lowest values of $5.10 \mu\text{g C}$ for 1.5–2 mm and $3.04 \mu\text{g C}$ for 1–1.5 mm (Fig. 2c). In autumn, the carbon content increased slightly for both size classes. In the spring of 1999, the carbon content was very low, but increased in August and declined again in autumn. *Daphnia galeata* had relatively low carbon content under periods of ice cover.

Linear regressions between the natural logarithm of the carbon content and the natural logarithm of the length were calculated separately for every sampling date (Table 1). At some dates, results of regression analysis between carbon content and length showed poor coefficients of determination, which was caused by the small size range of available animals present at that moment. The SCC of *D. galeata* was analysed both for (1) different slopes derived from each date from linear regressions and (2) a fixed slope of 2.92 derived from linear regressions estimated for all seasonal data (38 dates). When the slope of the different regression lines was fixed to a common slope, the explained variance was 71%. SCC showed the same seasonal pattern as carbon content of the size classes and with values in the same range (Figs 2c and 3b). The intercepts and the slopes differed among dates ($F_{38,5210} = 138.6$; $P < 0.001$). Slopes declined toward early summer 1998, increased in July and August, and were more or less constant during the rest of the season. In 1999, slopes increased each month until September, and then declined (Fig. 3a, Table 1).

The SCCs of the *D. galeata* caught at different depths over each season were computed using carbon–length weight regressions (Fig. 3c). A test of parallelism showed that most slopes were not significantly different among the different depth strata for a given date (Table 1). After testing for significant differences among depths for each date, adjacent dates which did not significantly differ were pooled (Table 2). *Daphnia galeata* from the deep layer had a significantly higher SCC from July to September in 1998, as well as in September and October 1999, compared to the surface

layer (Table 2). From mid August to mid November 1998, as well as in August and late September 1999, the number of eggs per individual were significantly higher in mid and deep layers than in the surface layer (Table 2).

Comparing the SCC of the *D. galeata* population for different depth strata during day and night showed significantly higher SCC at night-time in the surface and middle layers in August, early September and October than at daytime (Fig. 4). In late September, there was no day-night difference in the SCC.

SCC values include all body tissue of the females including the eggs in the brood pouch. Hence, we found a significantly positive correlation coefficient between SCC and the number of eggs (Table 3). Moreover, there was also a significant positive relation with algal biomass, POC, chlorophyll *a* concentration and mean *D. galeata* length. Additionally, there was a significant negative correlation between SCC and slope, the density of *D. galeata* and water temperature.

Discussion

In this study, high intra- and interannual variability was found in the density, carbon content and number of eggs of the *D. galeata* population in the Oberer Arosasee (Fig. 2), comparable to the variation found in other studies of daphnids from lowland lakes (Geller & Müller, 1985; Berberovic, 1990; Boersma & Vijverberg, 1994b). Carbon content and number of eggs were high in the spring of 1998 when daphnids were rare and these parameters decreased toward summer as animal densities increased. Concomitantly, algal biomass and chlorophyll *a* also decreased. After autumn turnover in 1998 (mid September), the number of eggs of *D. galeata* and carbon content increased, whereas algal biomass remained low. A shift towards algae with better nutritional quality could be the reason for the relatively higher carbon content of *D. galeata* in autumn (Groeger et al., 1991). Carbon content increased only in August in 1999, and was constant after autumn turnover (end September). The maximal value in 1999 was about half the maximal carbon content in 1998. In comparison to other studies of more eutrophic lake (Geller & Müller, 1985; Hessen, 1989; Boersma & Vijverberg, 1994b), the mean carbon content values of *D. galeata* in this alpine lake were low. Under the assumption that the carbon content and number of eggs measured in spring 1998 and summer 1999 in-

Figure 3. Seasonal variation in slope (a), standard carbon content (SCC) of 1.5 mm *D. galeata* individuals calculated using a fixed slope (2.92) and different slopes (b), and the seasonal SCC at 5 depths (c) computed from the carbon-length regression equation ($\ln C = \ln a + b \ln L$) for each sampling date in the Oberer Arosasee. Error bars indicate ± 1 standard error.

Figure 4. SCC of 1 mm *D. galeata* at different depths at mid-day and mid-night (lines), and mean number of eggs per individual (bars) in 1999 in the Oberer Arosasee. Error bars equal ± 1 standard error.

Table 1. Carbon-length regressions for *D. galeata* populations in the Oberer Arosasee on each sample date for all depths combined. Equation: $\ln C = \ln a + b \ln L$ (C in μg , L in mm). The intercept a represents the SCC of an individual at 1.5 mm body length, and b the combined slopes with the size range (mm) of the measured individuals. And regression statistics (d. f., F , P) and correlation coefficients (r). Comparisons of the slopes in the 5 depth strata of each date for significant differences were made with a Test of parallelism (P_b). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; n. v. = no value, n. s. = not significant

Date	Size range	$a_{1.5}$	b	d. f.	F	P	r	P_b
26-May-98	0.76–1.71	17.50	2.24	1, 60	35.57	***	0.61	n. v.
02-Jun-98	0.90–1.86	15.31	1.15	1, 77	15.01	***	0.40	n. s.
09-Jun-98	1.00–1.82	9.14	3.02	1, 68	61.89	***	0.69	n. s.
16-Jun-98	1.20–1.74	7.45	2.70	1, 78	16.58	***	0.42	n. s.
23-Jun-98	0.95–1.77	9.28	2.59	1, 103	102.17	***	0.71	n. s.
01-Jul-98	1.22–2.09	9.68	1.97	1, 106	60.51	***	0.60	n. s.
07-Jul-98	1.12–1.73	7.98	1.86	1, 126	22.93	***	0.39	n. s.
14-Jul-98	1.12–1.73	6.81	2.05	1, 102	10.22	***	0.30	n. s.
21-Jul-98	1.33–1.71	4.59	2.43	1, 99	3.94	**	0.20	n. s.
03-Aug-98	1.33–1.81	4.74	3.34	1, 57	4.91	**	0.28	n. s.
11-Aug-98	1.30–1.90	4.22	6.43	1, 132	117.97	***	0.69	**
18-Aug-98	1.37–1.86	4.83	3.97	1, 156	33.32	***	0.42	n. s.
25-Aug-98	1.16–1.94	4.31	3.12	1, 134	68.42	***	0.58	*
31-Aug-98	1.31–1.96	4.00	2.79	1, 139	45.60	***	0.50	n. s.
08-Sep-98	1.27–1.88	3.56	3.74	1, 143	68.64	***	0.57	n. s.
14-Sep-98	1.37–1.92	3.78	2.79	1, 140	19.07	***	0.35	n. s.
22-Sep-98	1.31–1.82	5.74	2.50	1, 137	51.26	***	0.52	n. s.
29-Sep-98	1.25–1.98	6.19	1.94	1, 94	23.72	***	0.45	**
13-Oct-98	1.24–2.03	3.32	2.92	1, 125	64.06	***	0.58	n. s.
20-Oct-98	1.22–1.90	6.62	1.26	1, 130	6.75	**	0.22	n. s.
27-Oct-98	1.14–1.84	7.59	2.12	1, 144	44.69	***	0.49	n. s.
01-Nov-98	1.28–1.90	5.86	2.64	1, 146	20.11	***	0.35	n. s.
10-Nov-98	1.29–1.86	5.92	1.82	1, 126	18.48	***	0.36	*
05-Jan-99	1.14–1.79	1.47	2.89	1, 215	17.24	***	0.27	n. s.
16-Jan-99	0.95–1.90	3.43	2.17	1, 179	27.22	***	0.36	n. s.
30-Jun-99	1.31–1.69	1.78	1.67	1, 3	5.42	**	0.80	n. v.
16-Jul-99	1.14–1.84	8.30	1.54	1, 89	17.99	***	0.41	n. v.
03-Aug-99	0.57–1.90	8.17	2.35	1, 304	428.31	***	0.77	n. s.
23-Aug-99	0.76–1.75	6.59	4.13	1, 287	664.33	***	0.84	*
09-Sep-99	0.91–1.71	5.71	5.82	1, 228	201.41	***	0.69	n. s.
28-Sep-99	0.99–1.84	3.59	3.86	1, 279	267.68	***	0.70	n. s.
26-Okt-99	0.76–1.86	4.41	2.08	1, 289	84.83	***	0.48	*
15-Nov-99	1.10–1.94	4.64	2.18	1, 144	107.63	***	0.65	n. s.
05-Jan-00	1.25–1.20	3.65	2.57	1, 141	34.88	***	0.45	n. s.
15-Jan-00	1.22–1.84	4.64	1.96	1, 124	13.97	***	0.32	8

indicate a period of no food limitation, the low SCC and fecundity during the other parts of the year implies that the *D. galeata* population were food limited during most the year (Duncan, 1985; Berberovic, 1990).

Contrary to laboratory studies, regression lines varied for intercepts and slopes during the year, as was

shown before (Geller & Müller, 1985; Hessen & Van Donk, 1993; Boersma & Vijverberg, 1994b; Manca et al., 1994). However, the seasonal SCC patterns as well as the absolute values of the intercepts were similar irrespective of whether they were calculated with a fixed slope or with varying slopes (Fig. 3b). The

Table 2. SCC of *D. galeata* (1 mm body length) and egg number of measured individuals at different depths at mid-day calculated using a common slope of 2.92. Post hoc comparison was used to test for significant differences between the 0 and 2.5 m depth and the deeper strata following ANOVA (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)

Depth (m)	1998					1999					2000	
	15. Jun – 15. Jul	15. Jul – 15. Aug	15. Aug – 15. Sep	15. Sep – 15. Oct	15. Oct – 15. Nov	5. + 16. Jan	3. + 23. Aug	9. Sep	28. Sep	26. Oct	15. Nov	5. + 15. Jan
SCC												
0.0–2.5	2.45	1.31	1.08	2.14	1.79	1.34	2.31	1.01	0.99	0.94	1.68	1.27
2.5–5.0	3.03	1.38	1.12	1.93	1.91	1.40	2.13	0.58	1.19	1.52	1.44	1.29
5.0–7.5	3.07	1.52	1.12	1.73*	1.99	1.72	2.04	1.28	1.14	1.79**	1.52	1.28
7.5–10.0	3.37**	1.82**	1.39***	1.60**	1.62	0.79*	2.84	1.48***	1.52*	1.58	1.33	1.36
10.0–12.5	3.14	2.56***	1.72***	1.90	1.77	1.29	1.67	2.21***	0.78	1.75*	1.35	1.58
Egg number												
0.0–2.5	2.4	0.5	0.2	0.8	1.0	0.0	1.7	0.0	0.25	0.18	0.4	0.0
2.5–5.0	4.0	0.6	0.3	1.4*	1.7**	0.0	1.8	0.1	0.40	0.62	0.3	0.0
5.0–7.5	4.6*	0.6	0.6*	1.9***	2.0***	0.0	1.4	0.0	0.17	0.60	0.4	0.0
7.5–10.0	4.8**	0.7	0.8***	1.9***	2.3***	0.0	0.9**	0.0	1.31*	0.61	0.1	0.0
10.0–12.5	2.3	0.8	1.6***	1.9***	2.3***	0.0	0.1***	0.0	0.57	0.88	0.2	0.0

Table 3. Correlation coefficients (r) between SCC and several life history and abiotic field parameters ($P < 0.05$, Analysis of variance)

	r	P
Density	−0.430	0.046
Mean length	0.037	0.013
Egg number	0.715	0.000
Temperature	−0.210	0.021
Chlorophyll a	0.304	0.007
POC	0.384	0.008
Slope	−0.244	0.007

calculated slope for SCC using all seasonal data was close to 3, which is the exponent for isometric growth. As the slopes changed through the year (Table 1), we found that the condition of larger *D. galeata* was low relative to smaller *D. galeata* in spring and early summer. In summer, when chlorophyll a concentrations decreased in the surface and middle layers, the regression lines were steeper, indicating that large animals were in better condition relative to small individuals. After turnover, the condition of smaller individuals increased as indicated by the decrease in slopes, even the chlorophyll a concentration was low in the water column. Similar seasonal patterns in slopes are shown for other lakes (Geller & Müller, 1985; Boersma & Vijverberg, 1994b). In addition, the SCC and slopes

from the regression lines were negatively correlated (Table 3), suggesting that when food conditions were good smaller animals benefited more than larger ones (Persson & Gunnar, 1980; Geller & Müller, 1985; Boersma & Vijverberg, 1994b).

In lakes with high food concentrations in the epilimnion, non-migrating daphnids are higher in carbon (Duncan et al., 1993) and protein (Guisande et al., 1991) per unit length. In many alpine lakes, as in the Oberer Arosasee, however, chlorophyll a accumulates in the deep layers during summer (Tilzer, 1973). In the Oberer Arosasee, when food was highest in the deep layer and low in the surface and middle layer (mid July–mid September 1998, September–October 1999), the SCC of *D. galeata* in the deep layer was significantly higher compared to the surface layer (Table 2). During these months, migration amplitude also was highest (Winder unpubl.). After autumn turnover, the SCC of *D. galeata* was equal throughout the water column. Since the number of eggs per individual did not show the same pattern and average number of eggs was low, changes in SCC may be mainly caused by a change in somatic carbon (Boersma & Vijverberg, 1994b). Furthermore, after the autumn turnover, when the number of eggs per individual was significantly higher in the deep layer, SCC was not. Since the egg stage structure of measured *D. galeata* did not significantly vary between depths major differences of SCC are not expected to be associated with the egg stage structure (Tessier & Goulden, 1982).

These results indicate that migrating *D. galeata* and individuals that remain in the deep layer during night have an advantage over animals that stay in the upper layers in summer, since they can exploit the better food in the deep layer. The significantly higher carbon content in the surface and middle layers at night during this major migration period supports this. It seems that individuals with high body conditions migrate upwards at night, thus overcoming the costs associated with DVM (Loose & Dawidowicz, 1994). However, there was also a group of *D. galeata* in the deep layer during the night.

The density of *D. galeata* showed a negative relationship with SCC suggesting that competition may affect the condition of *D. galeata*. We found a significant positive correlation between SCC and egg number; *D. galeata* had more eggs when SCC was high. Food concentration, as chlorophyll *a*, POC, and algal biomass showed a significant positive relationship with SCC. The average length of *D. galeata* correlated closely with SCC on a given date, which suggests that the reduction in mean adult length was caused by food limitation rather than by other factors such as positive size-selective predation by fish (Tessier et al., 1992). Nutritional deficiency may be one of the main seasonal factors controlling *D. galeata* dynamics in the Oberer Arosasee, rather than predation.

In general, we found that changing environmental conditions were almost immediately reflected in carbon-length ratios. Therefore, the carbon content is a reliable parameter to measure the animal's condition since there is no time lag between environmental changes and response (Hessen, 1989). Geller & Müller (1985) found that thermal lake stratification combined with an increase of temperature, food supply and egg production were the major factors influencing the carbon-length regressions of daphnids. Also in the Oberer Arosasee lake, carbon-length regressions changed mainly with the stratification state of the lake. In this alpine lake, similar seasonal dynamics in density, number of eggs and carbon content of *D. galeata* were found compared to lowland lakes, although alpine lakes have a shorter growing season. In alpine lakes with chlorophyll *a* maxima in deeper layers, migrating daphnids and individuals remaining in deep layer have a better condition than daphnids from the surface layer. Hence, the main question arising from this study that needs to be answered is why daphnids migrate upwards in alpine lakes, since the food accessibility and condition are so good in the deeper water layers.

Acknowledgements

We thank Sandra Lass who helped collect the samples and Hans Rudolf Bürgi and Regula Illi for identifying and counting the algae. Thanks are due to Silke Meyns, Richard Illi and Bruno Ribí for analysing the chlorophyll and especially to Hermann Mönch for helping with the CHNS analyser. Support and comments by Maarten Boersma, Chris Robinson and three anonymous reviewers have improved the manuscript. This research was supported by a grant from the Swiss Federal Office for Education and Science (No. 97.0040).

References

- Ahlgren, G., L. Lundstedt, M. T. Brett & C. Forsberg, 1990. Lipid composition and food quality of some freshwater phytoplankton for cladoceran zooplankters. *J. Plankton Res.* 12: 809–818.
- Berberovic, R., 1990. Elemental composition of two coexisting *Daphnia* species during the seasonal course of population development in Lake Constance. *Oecologia* 84: 340–350.
- Bloem, J. & J. Vijverberg, 1984. Some observations on the diet and food selection of *Daphnia hyalina* (Cladocera) in an eutrophic lake. *Hydrobiol. Bull.* 18: 39–45.
- Boersma, M. & J. Vijverberg, 1994a. The effect of preservation methods on the carbon content of *Daphnia*. *Arch. Hydrobiol.* 130: 241–247.
- Boersma, M. & J. Vijverberg, 1994b. Seasonal variations in the condition of two *Daphnia* species and their hybrid in a eutrophic lake: Evidence for food limitation. *J. Plankton Res.* 16: 1793–1809.
- Boersma, M. & J. Vijverberg, 1994c. The use of carbon-to-length regressions as a tool to estimate the degree of food limitation in the field. *Verh. int. Ver. Limnol.* 25: 2392–2394.
- Bottrell, H. H., A. Duncan, Z. M. Gliwicz, E. Grygierek & A. Herzig, 1976. A review of some problems in zooplankton production studies. *Norw. J. Zool.* 24: 419–456.
- Bürgi, H. R., 1983. Eine neue Netzgarnitur mit Kipp-Schliessmechanismus für quantitative Zooplanktonfänge in Seen. *Schweiz. Z. Hydrol.* 45: 505–507.
- Conover, R. J. & P. Mayzaud, 1984. Utilization of phytoplankton by zooplankton during the spring boom in a Nova Scotia inlet. *Can. J. Fish. aquat. Sci.* 41: 232–244.
- DeMott, W. R., 1986. The role of taste in food selection by freshwater zooplankton. *Oecologia* 69: 334–340.
- Dumont, H. J., I. Van de Velde & S. Dumont, 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of Continental Waters. *Oecologia* 19: 75–97.
- Duncan, A., 1985. Body carbon in daphnids as an indicator of the food concentration available in the field. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 21: 81–90.
- Duncan, A., 1989. Food limitation and body size in the life cycles of planktonic rotifers and cladocerans. *Hydrobiologia* 186: 11–28.
- Duncan, A., C. Guisande & W. Lampert, 1993. Further trade-offs in *Daphnia* vertical migration strategies. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 39: 99–108.

- Farkas, T., 1970. Fats in fresh water crustaceans. I Fatty acid composition of lipids obtained from *Eudiaptomus gracilis* G. O. Sars (Copepoda) and *Daphnia cucullata* G. O. Sars (Cladocera). Acta Biol. Acad. Sci. Hung. 21: 225–233.
- Flik, B. J. G. & J. Ringelberg, 1993. Influence of food availability on the initiation of diel vertical migration (DVM) in Lake Maarsseveen. Arch. Hydrobiol. Beih. Ergebn. Limnol. 39: 57–65.
- Gabriel, W. & B. Thomas, 1988. Vertical migration of zooplankton as an evolutionarily stable strategy. Am. Nat. 132: 199–216.
- Geller, W. & H. Müller, 1985. Seasonal variability in the relationship between body length and individual dry weight as related to food abundance and clutch size in two coexisting *Daphnia* species. J. Plankton Res. 7: 1–18.
- Gerritsen, J., 1982. Behavioural response of *Daphnia* to rate of temperature change: possible enhancement of vertical migration. Limnol. Oceanogr. 27: 254–261.
- Ghilarov, A. M., 1985. Dynamics and structure of cladoceran populations under conditions of food limitation. Arch. Hydrobiol. Beih. Ergebn. Limnol. 21: 323–332.
- Gliwicz, Z. M. & E. Siedlar, 1980. Food size limitation and algae interfering with food collection in *Daphnia*. Arch. Hydrobiol. 88: 155–177.
- Groeger, A. W., M. D. Schramm & G. R. Marzolf, 1991. Influence of food quality on growth and reproduction in *Daphnia*. Freshwat. Biol. 26: 11–19.
- Guisande, C., A. Duncan & W. Lampert, 1991. Trade-offs in *Daphnia* vertical migration strategies. Oecologia 87: 357–359.
- Han, B. P. & M. Straskraba, 1998. Modelling patterns of zooplankton diel vertical migration. J. Plankton Res. 20: 1463–1487.
- Hebert, P. D. N., 1977. Niche overlap among species in the *Daphnia carinata* complex. J. anim. Ecol. 46: 399–409.
- Hessen, D. O., 1989. Factors determining the nutritive status and production of zooplankton in a humic lake. J. Plankton Res. 11: 649–664.
- Hessen, D. O. & E. Van Donk, 1993. Morphological changes in *Scenedesmus* induced by substances released from *Daphnia*. Arch. Hydrobiol. 127: 129–140.
- Infante, V. A., 1973. Untersuchungen über die Ausnutzbarkeit verschiedener Algen durch das Zooplankton. Arch. Hydrobiol./Suppl. 42: 340–405.
- Johnsen, G. H. & P. J. Jakobsen, 1987. The effect of food limitation on vertical migration in *Daphnia longispina*. Limnol. Oceanogr. 32: 873–880.
- Kerfoot, W. C. & K. L. Kirk, 1991. Degree of taste discrimination among suspension-feeding cladocerans and copepods. Limnol. Oceanogr. 36: 1107–1123.
- Kirk, K. L., 1992. Effects of suspended clay on *Daphnia* body growth and fitness. Freshwat. Biol. 28: 103–109.
- Lampert, W., 1988. The relative importance of food limitation and predation in the seasonal cycle of two *Daphnia* species. Verh. int. Ver. Limnol. 23: 713–718.
- Loose, C. J. & P. Dawidowicz, 1994. Trade-offs in diel vertical migration by zooplankton: the costs of predator avoidance. Ecology 75: 2255–2263.
- Manca, M., T. Spagnuolo & P. Comoli, 1994. Variations in carbon and nitrogen content with body length of *Daphnia hyalina-galeata* s. l. from laboratory and field observations. J. Plankton Res. 16: 1303–1314.
- Mitchell, S. F., F. R. Trainor, P. H. Rich & C. E. Goulden, 1992. Growth of *Daphnia magna* in the laboratory in relation to the nutritional state of its food species, *Chlamydomonas reinhardtii*. J. Plankton Res. 14: 379–391.
- Orcutt, J. D. & K. G. Porter Jr, 1983. Diel vertical migration by zooplankton: constant and fluctuating temperature effects on life history parameters of *Daphnia*. Limnol. Oceanogr. 28: 720–730.
- Persson, G. & E. Gunnar, 1980. Estimation of dry weight in zooplankton populations: methods applied to crustacean populations from lakes in the Kuokkel Area, Northern Sweden. Arch. Hydrobiol. 89: 225–246.
- Porter, K. G., 1973. Selective grazing and differential digestion of algae by zooplankton. Nature 244: 179–180.
- Ringelberg, J., B. G. J. Flik, D. Lindenaar & K. Royackers, 1991. Diel vertical migration of *Daphnia hyalina* (sensu lato) in Lake Maarsseveen: Part 1. Aspects of seasonal and daily timing. Arch. Hydrobiol. 121: 129–145.
- Rott, E., 1981. Some results from phytoplankton counting inter calibration. Schweiz. Z. Hydrol. 43: 34–62.
- Sokal, R. R. & F. J. Rohlf, 1995. Biometry. W. H. Freeman and Co, San Francisco U.S.A., 887 pp.
- Sommer, U., Z. M. Gliwicz, W. Lampert & A. Duncan, 1986. The PEG-model of seasonal succession of planktonic events in fresh waters. Arch. Hydrobiol. 106: 433–471.
- Sterner, R. W. & K. Schulz, 1998. Zooplankton nutrition: Recent progress and a reality check. Aquat. Ecol. 32: 261–279.
- Tessier, A. J. & C. E. Goulden, 1982. Estimating food limitation in cladoceran populations. Limnol. Oceanogr. 27: 707–717.
- Tilzer, M., 1973. Diurnal periodicity in the phytoplankton assemblage of a high mountain lake. Limnol. Oceanogr. 18: 15–30.
- Urabe, J. & Y. Watanabe, 1991. Effect of food conditions on the bacterial feeding of *Daphnia galeata*. Hydrobiologia 225: 121–128.
- Van Donk, E. & D. O. Hessen, 1993. Grazing resistance in nutrient-stressed phytoplankton. Oecologia 93: 508–511.
- Vijverberg, J., 1976. The effect of food quantity and quality on the growth, birth-rate and longevity of *Daphnia hyalina* Leydig. Hydrobiologia 51: 99–108.
- Vijverberg, J., R. D. Gulati & W. M. Mooij, 1993. Food-web studies in shallow eutrophic lakes by the Netherlands Institute of Ecology: main results, knowledge gaps and new perspectives. Neth. J. aquat. Ecol. 27: 35–49.