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Food quality dominates the impact of food quantity on *Daphnia* life history: possible implications for re-oligotrophication

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Abstract

The elemental composition of phytoplankton is highly variable compared to the relatively narrow stoichiometry of zooplankton grazers. Using a full factorial design, we tested the effects of alterations in algal elemental composition (i.e., food quality) combined with food quantity on the life history of a *Daphnia galeata* clone from Lake IJsselmeer. Lower food quality reduced survival, growth, and reproduction. Food quantity became important at high food quality only. The strong effect of food quality indicates the potential for a stoichiometric bottleneck in Lake IJsselmeer, resulting in less high quality food for higher trophic levels as a result of re-oligotrophication.

Key words: *Daphnia galeata*, food quality and quantity, life history, phosphorus, re-oligotrophication, stoichiometry

Introduction

Different trophic levels differ in their elemental chemical composition (stoichiometry) and flexibility therein. For example, where algae are known for their stoichiometric flexibility, zooplankton and higher trophic levels often have a lower carbon to phosphorus ratio (C:P) and display a much narrower range (DeMott et al., 1998; Sterner et al., 2008; van de Waal et al., 2010). This can create stoichiometric bottlenecks, where zooplankton production is not limited by energy (C) but by nutrients such as nitrogen (N) and especially P when they feed on algae of high C:P.

Increased P and N loading has caused major eutrophication of many lakes worldwide. Loss of macrophyte vegetation, nuisance cyanobacterial blooms, and impoverished invertebrate, fish, and waterfowl communities, are common characteristics of these eutrophic waters (Gulati and van Donk, 2002; Ibelings et al., 2007; Smith and Schindler, 2009). Since the 1970s, international efforts to reduce eutrophication have been partially successful, especially in controlling P. For instance, total phosphorus (TP) in the River Rhine has fallen from a peak value of 1 to present levels of 0.2 mg L⁻¹ (Noordhuis et al., 2010).

The effects of re-oligotrophication vary widely and are dependent on lake morphometry and depth (Jeppesen et al., 2005; van Donk et al., 2008). In general, chlorophyll concentration increases with increasing TP, but sestonic C:P ratio decreases (Hessen, 2006). Gulati and van Donk (2002) correlated increased seston C:P to reduced *Daphnia* numbers.

We hypothesised that the effect of food quantity on life history traits of *Daphnia galeata* is strongly modulated by food

quality, here defined as algal food grown in continuous cultures under different P concentrations. A *Daphnia galeata* clone, isolated from Lake IJsselmeer (The Netherlands), which is in a process of re-oligotrophication, was subjected to different regimes of food quality and quantity in a full factorial design. We tested if low food quality and quantity—both potentially induced by lower P availability—will interact to have a negative impact on *D. galeata* life history. We expected that food quantity would be the dominant parameter for survival, while somatic growth and especially fecundity would be mainly determined by food quality because basal maintenance metabolism requires mainly C, but growth and reproduction require a P-rich diet (Sterner, 1997; Anderson and Hessen, 2005).

Material and Methods

Isolation and rearing of *Daphnia*

Zooplankton samples were collected in November 2009 from Lake IJsselmeer (mean depth 4.5 m, surface area 1190 km²) at 5°29'0"E 52°33'24"N. After returning to the lab, monoclonal cultures grown from individual *D. galeata* were established in 100 mL tubes filled with membrane-filtered (0.2 µm) lake water from Lake Maarseveen, which typically has soluble reactive phosphorus levels below detection limit (Gsell et al., 2013). Filtered Lake Maarseveen water was used throughout the experiment. Clones were fed with the green alga *Scenedesmus obliquus* at the incipient limiting food level, which is the concentration above which ingestion by *D. galeata* will no longer increase (0.5 mg CL⁻¹; Müller-Navarra and Lampert 1996).

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Experimental design

Four levels of food quality were combined with 4 food concentrations in a fully crossed design (16 treatments) to assess the relative importance of food quality, food quantity, and possible interactions between these 2 factors on life history traits of *D. galeata*. Survival, reproduction, and somatic growth were measured in 48 animals (3 per treatment) over a period of 12 days.

To create algal food of different qualities, *S. obliquus* was cultured in four 2 L chemostats supplied with algae growth medium (van Liere and Mur 1978; Table 1) adjusted to achieve a gradient from severe P limitation to P-replete conditions. This process resulted in 4 levels of algal food quality: low phosphorus (LP), low intermediate phosphorus (LIP), high intermediate phosphorus (HIP), and high phosphorus (HP). Dilution rate was 0.4 d^{-1} . Incident irradiance was kept constant at an average intensity of $40 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$. The 4 levels of food quantity were created by adjusting the C concentrations in the experimental tubes to 0.10, 0.30, 0.43 and 0.50 mg C L^{-1} , with the highest level being at the incipient level. Using a Casy particle counter (Schärfe System, Germany) we established a relationship between C content and cell density to standardize the daily C content of the experimental food.

Shortly before the start of the experiment, samples were taken from the chemostats, filtered onto precombusted GF/F filters, and the dried seston retentate was analysed to establish chemical cellular composition (C:N:P; Table 1) of the food algae as described in Bukovinszky et al. (2012). Comparison between the P concentration in the growth medium and in the medium with the algae showed that all P was taken up by the algae. An exception to this was the HP algae, which contained only 28 % of the P concentration available in the medium, a value still at least 3 times more than in the HIP algae (Table 1). The LIP algae had relatively high C concentrations. Thus, the resulting C:P ratio of the LIP algae was higher than the C:P ratio of the LP algae (Table 1).

To remove possible toxic residuals we centrifuged samples from the chemostat (5 min at 4000 rpm) and discarded the supernatant. The pellet was then resuspended in filtered Lake Maarseveen water with the same mass. This procedure was repeated another time before the algae suspension was used as food.

Five descendants from one *D. galeata* clone of similar age (just before release of the third clutch) were pooled from individual tubes into a beaker containing filtered lake water. Within 24 h, 48 neonates of their clutches were placed individually into 100 mL tubes and subjected to the experimental treatments (3 replicates per factor level). The tubes were kept in a light–dark cycle of 16:8 h at 20°C . Additionally, we determined initial neonate dry mass based on 3 samples, each consisting of 4 individuals, taken from the neonate pool.

Each day, the animals were transferred manually into tubes with fresh, filtered lake water and their experimental diet to keep food conditions stable and avoid the build-up of *D. galeata* excretes. Daily presence of eggs and body length were recorded for each individual under a stereo microscope. If offspring were

present, they were counted and discarded. Because the mothers of the experimental animals were grown under optimal food conditions, there was the potential of nutrient transfer from the mothers to their offspring. To reduce the influence of stored nutrients, statistical analysis of reproduction was reduced to the numbers of offspring (n) hatched in the third clutch of the surviving experimental animals. Care was taken to keep the animals wet during measurements and to keep time of transfer as short as possible. After 12 days, when most of the surviving animals had hatched their third clutch, the experiment was stopped, and dry weight of the survivors was measured.

Data analysis

All data analyses were done in R (R Core Team, 2013). A Cox proportional hazard regression was used (Therneau, 2013) to test the effect of treatments on instantaneous mortality (hazard h). The model allows comparing the proportional change of the hazard per treatment level, without knowledge of the baseline function (h_0), by calculating the exponential of the summed predictors food quality ($\beta_1 \text{ quality}$) and food quantity ($\beta_2 C_{iq}$). The later predictor is allowed to vary per food quality level:

$$h_i(t | q, C) = h_0(t) e^{\beta_1 \text{ quality}_i + \beta_2 C_{iq}} \quad (1)$$

In our analysis, all treatments were compared relative to the LP treatment.

Results

In general, a positive effect of food quantity on life history traits of *D. galeata* (such as survival, growth, and reproduction) could be observed for high food quality treatments only. At low food quality, food quantity had little effect on life history.

Survival

Foremost, survival was much lower in low food quality treatments (LIP and LP) than in high food quality treatments (HIP and HP). From the 19 of 48 animals that survived until the end of the experiment, only 3 were from LIP and LP treatments (Figure 1). In the high food quality treatments, survival was significantly higher with increasing food quantity, while survival was low regardless of food quantity at lower food quality (overall likelihood ratio test 26.5 on 7 df, $p < 0.001$, $R^2 = 0.424$; details in Appendix I).

None of the animals died before day 2, and while death occurred during the remainder of the experiment for HP and HIP treatments, most of the animals from LIP and especially LP died around day 5, before reaching maturity.

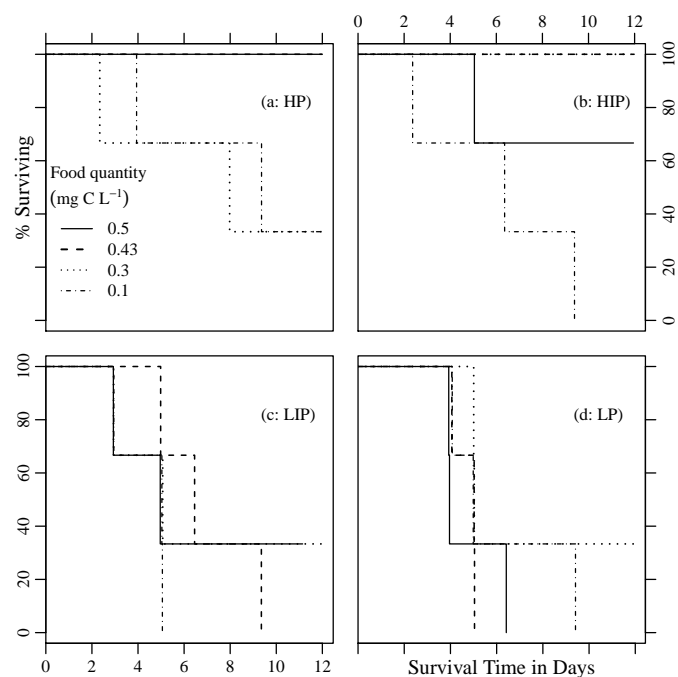
Somatic growth

The limited number of surviving *D. galeata* resulted in loss of replicates, especially in the low P treatments, and this imposed several limits to the statistical analysis of growth and reproduction. Therefore, regression analysis of daily specific growth rate,

$$\mu = (\ln(W_t) - \ln(W_0)) / \text{days}, \quad (2)$$

Table 1: P content of algal growth medium and stoichiometry of seston high phosphorus (HP), high intermediate phosphorus (HIP), low intermediate phosphorus (LIP) and low phosphorus (LP) chemostats used as food for *Daphnia* at different treatment levels: phosphorus (LIP) and low phosphorus (LP).

| Treatment | Medium P mg L ⁻¹ | Seston in Chemostat | | | | | |
|-----------|--------------------------------|----------------------|----------------------|----------------------|-----------|-----------|-----------|
| | | P mg L ⁻¹ | C mg L ⁻¹ | N mg L ⁻¹ | C:P molar | C:N molar | N:P molar |
| HP | 10.8 | 3.0 | 93.5 | 15.8 | 80 | 6.9 | 11.6 |
| HIP | 0.93 | 0.97 | 56.1 | 10.3 | 150 | 6.3 | 23.6 |
| LIP | 0.39 | 0.39 | 80.4 | 9.2 | 536 | 10.2 | 52.6 |
| LP | 0.14 | 0.14 | 21.0 | 2.5 | 397 | 9.6 | 41.4 |

Figure 1: Kaplan-Meier estimates of survival over food quality and food quantity. Lines indicate food concentrations (mg C L⁻¹). Panels indicate individual food qualities (abbreviations as in Table 1). Note that in panel (a: HP) the line for 0.5 mg C L⁻¹ masks the one for 0.43 mg C L⁻¹, and in panel (b: HIP) the line for 0.43 mg C L⁻¹ masks the one for 0.3 mg C L⁻¹.

based on initial neonate dry weight (W_0) and adult dry weight at the end of the experiment (W_t), was performed only for *D. galeata* individuals from HP and HIP treatments. The regression,

$$\mu_i = \beta_1 + \beta_2 C_i + \epsilon_i \text{ and } \epsilon_i \sim N(0, \sigma^2), \quad (3)$$

showed that individual (i) dry weight-based growth rate (μ) increased significantly with food concentration (Figure 2; $\beta_1 = 0.20$, $\beta_2 = 0.22$, $p < 0.001$, $R^2_{\text{adj.}} = 0.69$). An additional change in intercept or slope due to food quality did not significantly change the model ($p = 0.09$ and $p = 0.25$, respectively).

Fecundity

Food quality and quantity both had a strong effect on reproduction; with one exception, no offspring hatched in LP and LIP treatments, regardless of food quantity, whereas even for HP

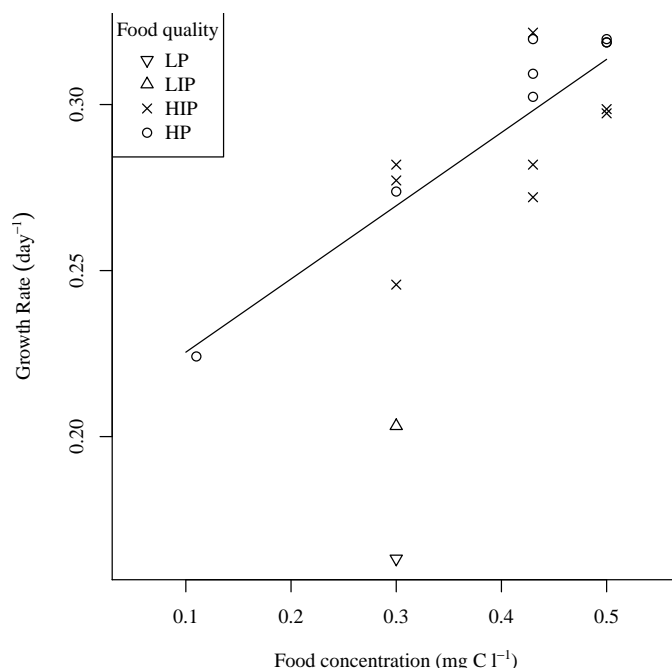


Figure 2: Average specific growth rate of survivors over 12 days. Regression line plotted only for HIP and HP treatments (abbreviations as in Table 1).

and HIP treatments, the food concentration in the lowest food quality treatment (0.1 mg C L⁻¹) was not sufficient to support the production of offspring.

Similar to the analysis of somatic growth, in the regression analysis of fecundity, only HP and HIP treatments were considered. Unlike somatic growth, however, the ANCOVA regression of reproduction,

$$No_{iq} = \beta_1 \text{quality} + \beta_2 C_{iq} + \epsilon_{iq} \text{ and } \epsilon_{iq} \sim N(0, \sigma^2), \quad (4)$$

showed a significant interaction between food quantity and food quality (Figure 3; $R^2 = 0.71$; regression parameters in Appendix II). With increasing food concentration, the number of third clutch offspring (No) increased in HP treatment. For the HIP treatment, however, the number of offspring remained the same regardless of food quantity (mean = 8.3, SE = 0.6).

Most individuals reached first maturity (i.e., bearing the first clutch) on the fifth to sixth day. The 2 individuals that reached maturity at the lowest food concentration (0.11 mg C L⁻¹), did

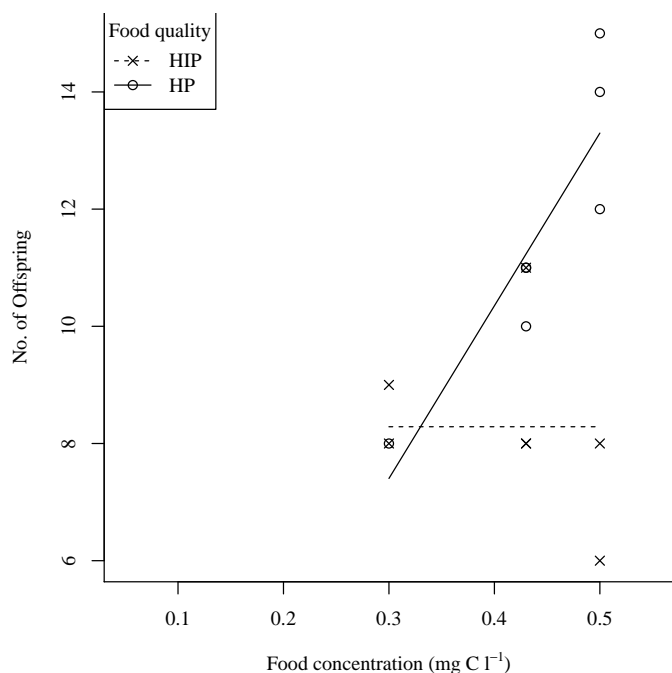


Figure 3: Number of offspring per individual in third clutch. Regression line plotted for HP treatment, mean for HIP treatment (abbreviations as in Table 1). Regression parameters in Appendix II.

so with a delay of several days and either lost their eggs or died before hatching any offspring (not entered in statistical analysis).

Discussion

Life history of *D. galeata* in our study was strongly influenced by the combination of food quality and food quantity. Only the combination of high food quality and quantity resulted in high survival, growth rates, and reproduction. The results of this study support published literature on effects of food quality and quantity on herbivorous zooplankton (Sterner and Hessen, 1994; Sterner, 1997; Sterner and Schulz, 1998; Anderson and Hessen, 2005). Sterner (1997) showed that food quality becomes an important factor at higher food quantity only. In our study, food quantity became an important factor at higher food quality (HP and HIP treatments) only; survival, and therefore also growth and reproduction, was low at low food quality (LIP and LP treatments), even for the highest food quantities.

The high mortality under low food quality conditions in our study was unlikely caused by handling alone because procedures were identical in all treatments; more likely it was caused by the combination of the stress induced by the experimental food treatments and handling. Although basal metabolism is considered to be mainly C driven, lowered survival at lower food quality is not uncommon (Sterner, 1993; Sundbom and Vrede, 1997; Urabe and Sterner, 2001). Urabe and Sterner (2001) offer one possible explanation for high mortality, especially in juvenile *Daphnia*, noting a high demand of P by juveniles, reflected in

low C:P ratios found in juvenile somatic tissue compared to 3–4 times higher ratios in eggs.

This relatively high C:P ratio of egg mass compared to the animal itself suggests that the P demand for egg production is relatively low. Nevertheless, although in our study the increase of growth rate with food quantity was independent of the quality of the food for higher food quality (HP or HIP), reproduction only increased with food quantity for HP, but not for HIP. Sterner and Schulz (1998) contend that reduced clutch size is induced by poor overall condition of the mother under P limitation. While in general C:P ratios >200 are reported to make *Daphnia* P limited (e.g., Sterner 1997; Urabe et al. 1997, DeMott et al. (1998) and our study show evidence for P limitation at lower C:P ratios (C:P 90–101 and <150, respectively). The intersect (at 0.33 mg C L⁻¹) of the 2 lines representing food quality (Fig. 3) can be seen as a switch from food quantity to food quality limitation. To the left of the intersect, food quantity is limiting; to the right, food quality is limiting. This finding was supported by the absence of hatched offspring at the lowest C concentration (0.11 mg C L⁻¹) for any food quality level.

The published literature and this study show the dependence of *D. galeata* on low C:P food. Re-oligotrophication of freshwaters can lead to increased C:P ratios. For example, the P loading of 3 hypereutrophic lakes was reduced by lake restoration measures, and the following increase in C:P ratio was strongly correlated with decreased *Daphnia* abundance (DeMott and Gulati, 1999). Also, in Lake IJsselmeer the decline in P is accompanied by increased total C:P ratios, reduction in biomass of smelt (the zooplankton-eating fish *Osmerus eperlanus*; Table 2) and a relative increase of smaller phytoplankton groups (Noordhuis et al., 2010). *Daphnia* are a preferred food of smelt (Salujõe et al., 2008), but analysis of recent smelt stomach contents from Lake IJsselmeer showed few *Daphnia* and mainly gammarids and copepods (de Graaf and Keller, 2010), which have higher C:P ratios than *Daphnia* (Sterner and Robinson, 1994; Fink et al., 2006). This diet indicates that access to high quality food, which itself depends on low C:P food, for smelt in Lake IJsselmeer may have been reduced.

Unfortunately we could not verify if *Daphnia* abundances changed during re-oligotrophication because zooplankton data from the period before the reduction in P concentration in the 1990s are anecdotal (Prins et al. 1994), and the shallow nature of the lake (mean depth 4.5 m) makes estimates from resting egg banks in the sediment problematic. Our results show a lower fecundity at a combination of high food concentrations and moderate C:P ratios (HIP: 150) compared to high food concentration and low C:P ratios (HP: 87; Figure 3). Hence, an increase to and beyond the moderate C:P ratios found in IJsselmeer from 1991 onward already has the potential to reduce the *Daphnia* biomass of the lake.

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Table 2: Median values of different measurements from Lake IJsselmeer. TP, C:P, and chlorophyll a (Chl-a) data from Monitoring Waterstaatkundige Toestand des Lands Milieumeetnet rijkswateren (2013, , station Vrouwezand) and smelt data from Noordhuis et al. (2010). Surface samples to determine TP, C:P, and Chl-a were sampled once or in some years, twice every month, while smelt was sampled once in autumn every year.

| | TP ($\mu\text{g L}^{-1}$) | C:P (molar) | Chl-a ($\mu\text{g L}^{-1}$) | (kg ha^{-1}) |
|--------------|-----------------------------|-------------|--------------------------------|-------------------------|
| 1975 to 1990 | 256 | 135 | 84.1 | 382 |
| 1991 to 2010 | 130 | 234 | 58.5 | 111 |

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Appendix 1: Proportional change in mortality due to food quantity and quality, based on Cox proportional hazards regression (Therneau, 2013). Overall likelihood ratio test: 26.5 on 7 df, $p < 0.001$, $R^2 = 0.424$.

| Parameter | Food quality | Coef | lower.95 | higher.95 | p |
|-----------|--------------|-------|----------|-----------|------|
| β_1 | LIP | 0.92 | -1.26 | 3.10 | 0.41 |
| β_1 | HIP | 0.97 | -1.38 | 3.32 | 0.42 |
| β_1 | HP | 0.64 | -1.62 | 2.90 | 0.58 |
| β_2 | LP | 1.78 | -2.44 | 6.01 | 0.41 |
| β_2 | LIP | -1.73 | -7.89 | 4.42 | 0.26 |
| β_2 | HIP | -7.79 | -16.41 | 0.82 | 0.03 |
| β_2 | HP | -6.49 | -14.49 | 1.50 | 0.04 |

Appendix 2: Regression parameters for fecundity. $R^2_{adj.} = 0.71$

| Parameter | Food quality | Coef | SE | p |
|-----------|--------------|------|------|-------|
| β_1 | HIP | 10.6 | 2.9 | 0.004 |
| β_2 | HIP | -5.7 | 6.8 | 0.42 |
| β_1 | HP | -1.5 | 4.5 | 0.024 |
| β_2 | HP | 29.4 | 10.4 | 0.007 |