

Life History Response of *Daphnia magna* to a Mixotrophic Golden Alga, *Poterioochromonas* sp., at Different Food Levels

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Received: 31 August 2010 / Accepted: 1 June 2011 / Published online: 11 June 2011
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Abstract The toxicity of *Poterioochromonas* to *Daphnia magna* was investigated at different food (*Scenedesmus acutus*) levels. *Poterioochromonas* alone of 0.4–20 mg C L⁻¹ was not acutely toxic to *D. magna*, but did not support *D. magna* growth, either. When fed mixed diets (2 mg C L⁻¹ in total), *D. magna*'s survival and reproduction were significantly depressed when *Poterioochromonas* comprised above 50%, likely due to the inhibition of food ingestion. Large juveniles were less sensitive to poor quality food than neonates. Therefore, *Poterioochromonas* may affect *D. magna* living to various extents depending on its concentration, age structure of *D. magna* populations and availability of other food.

Keywords *Daphnia magna* · Food level · Life history response · *Poterioochromonas*

Mixotrophic golden algae, which are able to combine phototrophy with heterotrophic feeding methods (osmotrophy and phagotrophy), are common and abundant in

freshwater planktonic communities (Sanders et al. 1989). They may periodically be the most abundant flagellates in some eutrophic and oligo-mesotrophic lakes (Bennett et al. 1991) and can reach several thousand individuals per mL (Boenigk and Stadler 2004). Some mixotrophic golden algae (e.g. *Poterioochromonas*, *Ochromonas*) are recognized as important grazers on bacteria, cyanobacteria and various algae (Sanders et al. 1989; Zhang et al. 1996). Under certain conditions, they are able to control bacterial biomass, and their grazing may contribute up to 80% of bacteria loss (Sanders et al. 1989). Specially, certain strains of *Poterioochromonas* and *Ochromonas* are able to grow on toxic *Microcystis aeruginosa* (one of the most common cyanobacteria) (Zhang et al. 1996, 2008; Van Donk et al. 2009). Meanwhile, as important food sources for macrozooplankton (Hessen et al. 1989), the mixotrophic golden algae may function as a link between the microbial community and higher trophic levels. Therefore, the toxicity of the mixotrophic golden alga is important for evaluating their ecological roles in the aquatic system.

It was reported that some toxic substances extracted from *Ochromonas* or *Poterioochromonas* are toxic to fish or have antibiotic effects (Reich and Spiegelstein 1964; Blom and Pernthaler 2010), but these effects have not been fully characterized. On the other hand, a few studies have demonstrated that different strains of *Ochromonas* and *Poterioochromonas*, as well as the related 'Spumella-like' flagellates, had toxic effects on their grazers (e.g. *Daphnia*, rotifers) (Leeper and Porter 1995; Boxhorn et al. 1998). However, some strains of the mixotrophic golden algae demonstrated no acute toxicity to *Daphnia*, since those fed on the flagellates survived significantly longer than the starved ones (Boenigk and Stadler 2004). Large and neonate *Daphnia* have different sensitivities in toxicity tests, although neonates of *Daphnia* are most often used in

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standard toxicity tests. It is helpful in giving a full view of the toxicity by testing both large juvenile and neonate *Daphnia* under the same conditions.

In our former studies, neonates of *Daphnia magna* fed *Poteroiochromonas* sp. (strain ZX1) (5 mg C L^{-1}) had starvation-like performance in the life history experiments (Zhang et al. 2009). It seems that *Poteroiochromonas* is not acutely toxic to *D. magna*, but not a suitable food either, probably due to poor nutrition value. Based on these results, we hypothesized that the negative effects of *Poteroiochromonas* on *D. magna* would differ depending on *Poteroiochromonas* concentration, and the negative effects would be reduced or perhaps even eliminated when high-quality food was supplied. To test this hypothesis, life history experiments were designed to investigate the effects of different concentrations of *Poteroiochromonas* on survival, growth and reproduction of *D. magna*. To overcome nutritional insufficiency, high-quality food (i.e., *Scenedesmus acutus*) was added in different mixtures with *Poteroiochromonas*. Furthermore, life history responses of both neonates and 5-day old *D. magna* were tested and compared. Based on these results, the toxicity of *Poteroiochromonas* to *D. magna*, as well as the possible mechanisms, is discussed.

Materials and Methods

The green alga *Scenedesmus acutus* Meyen (originally obtained from the Max Planck Institute for Limnology, Plön, Germany) was cultured in sterilized Z8 medium (Kotai 1972) and maintained in a culture room with continuous light from white fluorescent lamps at $25 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (measured outside the culture vessels) and $20 \pm 1^\circ\text{C}$. *S. acutus* were harvested during the exponential growth phase by centrifugation for 10 min at 3,100 rpm. The concentrations of *S. acutus* were estimated according to previously established relations between algal biovolume and light absorbance at 800 nm (Rohrlack et al. 2001).

The golden alga *Poteroiochromonas* sp. (strain ZX1) was isolated by Zhang et al. (2008). It was grown on a sterilized organic medium consisting of 1.0 g L^{-1} each of glucose, tryptone and yeast extract, and cultured in the culture room as above. *Poteroiochromonas* was harvested by centrifugation for 10 min at 3,100 rpm when it reached the log growth phase after 4 days. The cell density of *Poteroiochromonas* was determined using a hemocytometer and light microscopy (OLYMPUS™, BH-2, magnification: $\times 400$). Dry weight of *Poteroiochromonas* was $8 \times 10^{-8} \text{ mg C cell}^{-1}$ and carbon content was calculated using a conversion factor of 0.5. All harvested algal cells (*S. acutus* and *Poteroiochromonas*) were resuspended in synthetic plankton medium ADaM (ADaM medium)

(Klüttgen et al. 1994) before being fed to the *Daphnia* cultures.

The cladoceran species *Daphnia magna* Straus was originally isolated from Langedam Denmark in 1978, and was kindly supplied by O. Kusk (Technical University of Denmark, Lyngby, Copenhagen). The culture has been maintained at the Freshwater Biological Laboratory for several years. The *D. magna* animals were cultured in ADaM medium with *S. acutus* as sole food source. Prior to the experiments 20 neonates were harvested from well-fed stock cultures, and transferred into 750 mL glass jars containing 500 mL suspension of 2 mg C L^{-1} *S. acutus*. The cultures were kept in a temperature controlled room at $20 \pm 1^\circ\text{C}$, in continuous darkness. The food suspension was renewed daily and any offspring were removed from the stock culture. The animals were maintained under these conditions for at least 2 weeks and then served afterward as mothers for the animals used in the experiments. All neonates for a given experiment were taken from a single brood and within 24 h after birth. Both neonates and 5-day old juveniles were used. To prepare large juveniles of 5-day old, 40 neonates within 24 h after birth were transferred into a 750 mL jar with 500 mL suspension of *S. acutus* (2 mg C L^{-1}) and maintained under the conditions as above. The *S. acutus* suspension was renewed daily for 5 days. These 5-day old *D. magna* (length of $2 \pm 0.1 \text{ mm}$) were used in one experiment.

Three sets of experiments, each including a starvation control, a control with good food (*S. acutus* alone), and treatments with the golden algae *Poteroiochromonas* alone or various mixtures of *Poteroiochromonas* and *S. acutus*, were carried out. Experiment 1 and 2 started with neonates of *D. magna*, whereas Experiment 3 started with 5-day old juveniles. In Experiment 1, *D. magna* were cultured on *Poteroiochromonas* alone of three different concentrations (0.4 , 4 and 20 mg C L^{-1}), and on mixtures of *S. acutus* (1 mg C L^{-1}) with *Poteroiochromonas* (0.4 , 4 and 20 mg C L^{-1}). In Experiments 2 and 3, we kept the total algal concentration high and constant (2 mg C L^{-1}) and varied the ratios of *Poteroiochromonas* (25%, 50% and 75%). The algal suspensions were renewed daily for 21 days or until all *D. magna* were dead.

All experiments were conducted in 25 mL glass vials, containing 20 mL algal suspension in ADaM medium or pure ADaM medium in the case of the starvation (non-food) control. One neonate was sampled randomly from the stock cultures and transferred into a glass vial using a plastic pipette. Ten replicates were prepared for each group. The experimental cultures were maintained under the same conditions as the stock cultures of *D. magna* (i.e., at $20 \pm 1^\circ\text{C}$ and dim light), but placed on a shaking table (50 rpm) to keep the algae in suspension. The production of neonates and mortality were monitored daily for 21

days, and the age at first reproduction, number of clutches, total number of juveniles as well as mean clutch size were noted. *Daphnia* was considered dead if it did not show any movement during 30 s of intensive disturbance (Rohrlack et al. 2001). The length defined as the distance from the centre of the eye to the base of the tail spine of all neonates was measured using a stereo microscope (Kyowa SD/2PL) every third day. The pH values and the concentrations of dissolved oxygen in suspensions before and after 1 day culture were measured with a pH meter (PHM85, PRECISION) and an oxygen sensor (PA2000, Unisense Picoammeter). In all algal suspensions, pH ranged 6.9–8.2 and the concentrations of dissolved oxygen were $8.5 \pm 0.5 \text{ mg L}^{-1}$ (above 95% saturation) before and after 1 day of incubation.

In life history experiments, the median survival time of *Daphnia* was calculated by probit analysis method using Biostat (AnalystSoft, version 2008). The statistical significance of possible differences between survival functions for the two treatments was determined with log-rank tests, using GraphPad Prism 5.01 (GraphPad software Inc.). Tukey's test after one-way analysis of variance (ANOVA) (for multiple comparisons) or student *t* test (for paired comparison) was used to compare median survival time, length and reproduction parameters (i.e., mean clutch size, number of clutches, total number of live juveniles and age at first reproduction) of *Daphnia* in different treatments.

Results and Discussion

In Experiment 1, *Poterioochromonas* was supplied at different concentrations ($0.4\text{--}20 \text{ mg C L}^{-1}$) with or without *S. acutus*. During 21-day culture, all *D. magna* fed *S. acutus* alone survived and 70% *D. magna* survived in the mixture of *Poterioochromonas* (0.4 mg C L^{-1}) and *S. acutus* (1 mg C L^{-1}) (Fig. 1). However, *D. magna* in the other groups all died within 10 days and the median survival times of *D. magna* were calculated in Table 1. Within the three groups with *Poterioochromonas* alone, the median survival time of *Daphnia* fed *Poterioochromonas* of 0.4 mg C L^{-1} was significantly longer than those in the other two groups (4 and 20 mg C L^{-1} *Poterioochromonas*) ($p < 0.05$, *t* test), which all shared the same lifespan as the starved ones ($p > 0.05$, ANOVA). That is, *D. magna* fed only *Poterioochromonas* ($0.4\text{--}20 \text{ mg C L}^{-1}$) survived longer than or at least as long as those in the starvation control (depending on algae concentration). This was quite unlike the toxicity of some well-known toxic cyanobacteria (such as *Microcystis*). *Daphnia* cultured with *Microcystis* of relatively small concentrations had significant shorter life spans than the starved ones, with median survival time of around 2 days (Nizan et al. 1986; Zhang et al. 2009). Therefore, it is possible to

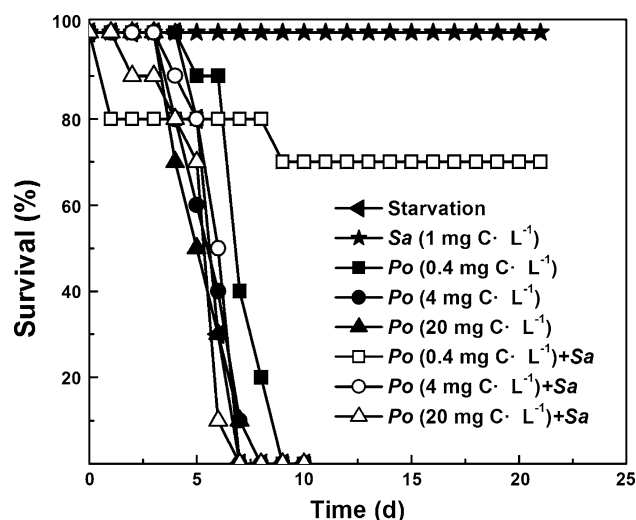


Fig. 1 Survival (percent of initial number) of *D. magna* neonates in different concentrations of *Poterioochromonas* without and with *S. acutus* (*Sa* represents *S. acutus*, *Po* represents *Poterioochromonas*)

Table 1 Median survival time (MST) of *D. magna* in Experiment 1

Algal suspension	Concentrations (mg C L^{-1})	MST (day) $\pm$ SE
Starvation	0	5.5 ± 0.5
<i>S. acutus</i>	1	$>21^*$
<i>Poterioochromonas</i>	0.4	$6.8 \pm 0.4^*$
<i>Poterioochromonas</i>	4	5.3 ± 0.4
<i>Poterioochromonas</i>	20	5.0 ± 0.4
<i>Poterioochromonas</i> + <i>S. acutus</i>	0.4 + 1	$>21^*$
<i>Poterioochromonas</i> + <i>S. acutus</i>	4 + 1	5.9 ± 0.5
<i>Poterioochromonas</i> + <i>S. acutus</i>	20 + 1	4.9 ± 0.3

* Significantly different (at the 95% confidence level) from starvation control

conclude that *Poterioochromonas* is not acutely toxic to *D. magna*. However, *Poterioochromonas* is of poor quality and cannot support the growth of *D. magna*, which may be due to the nutritional insufficiency.

To overcome nutritional insufficiency, high-quality food *S. acutus* (1 mg C L^{-1}) was added to *Poterioochromonas* of three different concentrations ($0.4\text{--}20 \text{ mg C L}^{-1}$). Most (70%) *D. magna* fed the lowest concentration of *Poterioochromonas* (0.4 mg C L^{-1}) mixed with *S. acutus* survived and released as many offspring as those fed solely *S. acutus* (Table 2), although the first reproduction was significantly delayed ($p < 0.05$, *t* test). This indicates that the nutritional insufficiency of *Poterioochromonas* was overcome when enough high-quality food was supplied, and *S. acutus* of 1 mg C L^{-1} should be enough to support the growth of *D. magna*. However, no obvious improvements were observed in other two groups with denser

Table 2 Reproduction parameters of *D. magna* in Experiment 1

Algal suspension (mg C L ⁻¹)	Age at first reproduction (day)	Number of clutches	Total number of offspring	Mean clutch size (number daphnid ⁻¹)
<i>S. acutus</i> (1)	8.5 ± 0.7	4.4 ± 0.7	19.0 ± 3.1	4.4 ± 0.7
<i>S. acutus</i> (1) and <i>Poterioochromonas</i> (0.4)	10.7 ± 1.1*	3.7 ± 1.0	16.6 ± 2.6	4.6 ± 0.8

* Significantly different (at the 95% confidence level) from control fed *S. acutus*

Poterioochromonas (4 and 20 mg C L⁻¹) after adding *S. acutus* ($p > 0.05$, Tukey's test after ANOVA), which also showed starvation-like effects with no significant differences relative to the starved control ($p > 0.05$, ANOVA). The differences among these three groups indicated that other factors (such as the relative concentration of *Poterioochromonas* and *S. acutus* in the algal suspensions) were responsible, rather than nutritional insufficiency.

In Experiment 2, *D. magna* were fed various mixtures of *S. acutus* and *Poterioochromonas* with the total algal concentration constant (2 mg C L⁻¹). The composition of food had a significant influence on the survival and life history response of *D. magna* (Fig. 2). During the 21-day incubation, all *D. magna* survived in the two groups with 100% and 75% *S. acutus*, while only 30% *D. magna* survived in the suspensions with 50% *S. acutus*. However, all *D. magna* died in the other groups within 12 days. The median survival time of *D. magna* increased with the increase of *S. acutus* in the algal suspensions (Table 3). *D. magna* fed algal suspensions of *S. acutus* or mixed with *S. acutus* all had significantly longer life-spans than those in the starvation control ($p < 0.05$, log-rank test), while *D. magna* fed only *Poterioochromonas* shared the same life-span as the starvation control ($p > 0.05$, log-rank test). *D. magna* fed 100% and 75% *S. acutus* grew significantly faster than those in other groups ($p < 0.05$, Tukey's test after ANOVA), while no obvious growth was found in the groups with 100% and 75% *Poterioochromonas*. Reproduction was found in three groups of 100%, 75% and 50% *S. acutus* (Table 4). No significant differences in reproduction parameters were observed between the two groups with 100% and 75% *S. acutus* ($p > 0.05$, t test), although slightly more juveniles were produced by *D. magna* fed 100% *S. acutus* than those fed 75% *S. acutus*. However, obvious delayed reproduction and fewer offspring were found in the group with 50% *S. acutus* ($p < 0.05$, t test).

Here, we found that the survival, growth and reproduction of *D. magna* were significantly depressed when *Poterioochromonas* comprised more than 50% of the food mixture. The negative effects may have been caused by feeding inhibition when the ratio of less suitable food (*Poterioochromonas*) was too high. Such feeding inhibition has previously been reported by Christoffersen and

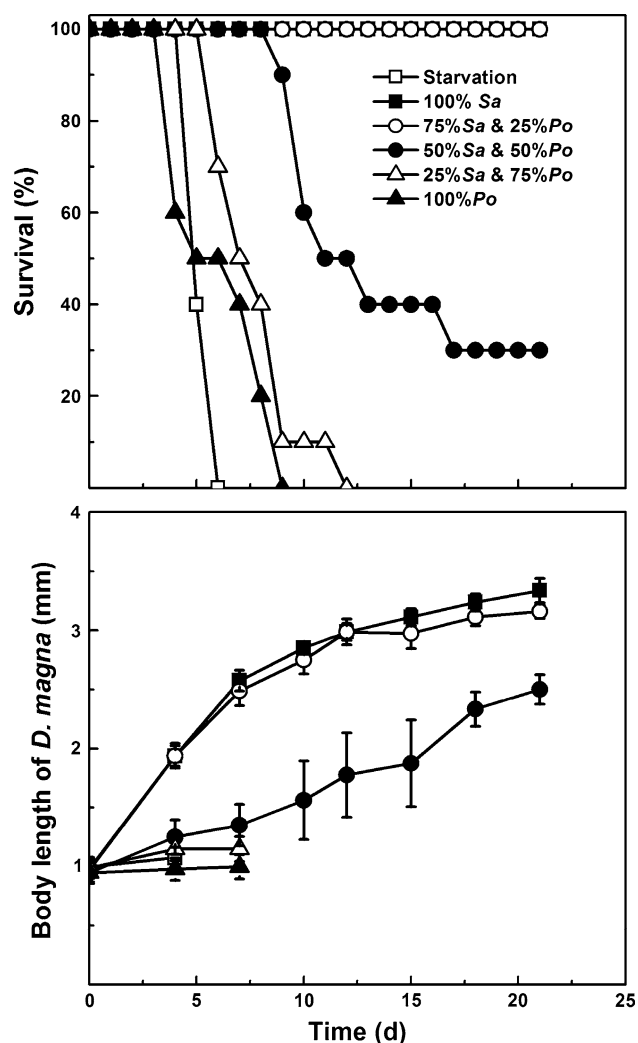


Fig. 2 Survival (percent of initial number) and body length of *D. magna* neonates in different concentrations of *S. acutus* and *Poterioochromonas* (Sa represents *S. acutus*, Po represents *Poterioochromonas*)

Bosselmann (1997), who found that the gut fullness of *Daphnia pulicaria* decreased with an increasing proportion of cyanobacteria in a food mixture of inedible cyanobacteria (filamentous *Cylindrospermopsis*) and edible chlorophyte (*Scenedesmus*). Thus, *Poterioochromonas* may perform negative effects by inhibiting the food ingestion, even though the food has no acutely toxic effect on

Table 3 Median survival time of *D. magna* in Experiments 2 and 3 (n = 10)

Algal suspension	MST (day) $\pm$ SE for Experiment 2	MST (day) $\pm$ SE for Experiment 3
Starvation	4.7 $\pm$ 0.6	5.9 $\pm$ 0.6
100% <i>S. acutus</i>	>21*	>21*
75% <i>S. acutus</i> and 25% <i>Poterioochromonas</i>	>21*	
50% <i>S. acutus</i> and 50% <i>Poterioochromonas</i>	14.2 $\pm$ 0.8*	>21*
25% <i>S. acutus</i> and 75% <i>Poterioochromonas</i>	7.2 $\pm$ 0.4*	
100% <i>Poterioochromonas</i>	5.7 $\pm$ 0.5	10.5 $\pm$ 0.7*

* Significantly different (at the 95% confidence level) from starvation control

Table 4 Reproduction parameters of *D. magna* in Experiment 2

Algal suspension	Age at first reproduction (day)	Number of clutches	Total number of offspring	Mean clutch size (number daphnid ⁻¹)
100% <i>S. acutus</i>	8.2 $\pm$ 0.5	5.0 $\pm$ 0	57.6 $\pm$ 8.8	11.5 $\pm$ 1.8
75% <i>S. acutus</i> and 25% <i>Poterioochromonas</i>	7.8 $\pm$ 0.4	4.9 $\pm$ 0.3	49.6 $\pm$ 6.1	10.2 $\pm$ 1.3
50% <i>S. acutus</i> and 50% <i>Poterioochromonas</i>	16.0 $\pm$ 2.8*	2.0 $\pm$ 0*	7.0 $\pm$ 4.2*	3.5 $\pm$ 2.1*

* Significantly different (at the 95% confidence level) from control fed 100% *S. acutus*

D. magna. Considering that in situ abundances of mixotrophic golden alga are often lower than several thousand individuals mL⁻¹ (<0.4 mg C L⁻¹) (Boenigk and Stadler 2004), such negative effects would hardly be detectable under natural conditions when sufficient food is available.

In Experiment 3, large juveniles *D. magna* (5-day old) were used for the toxicity evaluation of *Poterioochromonas*. All *D. magna* fed 100% *S. acutus* survived to the end of the 21 days incubation, while only 60% *D. magna* fed 50% *S. acutus* survived. However, in the other two groups all *D. magna* died within 17 days (Fig. 3). The median survival time of *D. magna* increased significantly with the increase of *S. acutus* in the algal suspensions (Table 3) ($p < 0.05$, t test), and all *D. magna* fed algal suspensions (mixture or only *Poterioochromonas*) had significantly longer life-spans than those in the starvation control ($p < 0.05$, log-rank test). The somatic growth of *D. magna* increased positively with increasing concentration of *S. acutus* in the food suspensions ($p < 0.05$, t test), and no growth was detected in *D. magna* fed only *Poterioochromonas*. Reproduction was found in the two groups of 100% and 50% *S. acutus* (Table 5). Delayed reproduction and fewer offspring were observed in the group with 50% *S. acutus* than those with 100% *S. acutus* ($p < 0.05$, t test). These results indicated that the growth and reproduction of *D. magna* were significantly suppressed when *Poterioochromonas* comprised more than 50% in the food, which were similar to those observed with neonates.

Similar results on larger *D. magna* have been reported before from studies by Boenigk and Stadler (2004). They found that 5- to 6-day-old *D. magna* fed two stains of

mixotrophic *Poterioochromonas malhamensis*, which were grown on heat-killed bacteria (*Gamaproteobacterium L. pelagia* CB5), survived significantly longer than those in the starvation control. Contrastingly, Leeper and Porter (1995) reported that mixotrophic *P. malhamensis* was toxic to *D. ambigua* when grown heterotrophically on an organic medium, but it provided sufficient nutrition for *D. ambigua* when cultured autotrophically in an inorganic medium. The differences among these results are likely due to differences in the strains of *Poterioochromonas* and *Daphnia* and differences in the culture conditions. In particular, the toxicity of *Poterioochromonas* to *Daphnia* is likely due to changes in biochemical pathways leading to increased toxin production when cells are growing heterotrophically versus autotrophically (Leeper and Porter 1995).

Comparing the results from Experiments 2 and 3, we found that neonates and 5-day old *D. magna* reacted differently when they were fed with the same food mixtures. Significantly longer life-spans and more offspring were found in 5-day old *D. magna* compared with neonates, indicating that larger animals are less sensitive to *Poterioochromonas* compared with neonates. This result agrees with previous reports that neonates are generally more sensitive than adult *Daphnia* to food quality (Vanni and Lampert 1992; Naji et al. 2005).

In conclusion, the mixotrophic *Poterioochromonas* strain ZX1 grown in an organic medium exhibited no acute toxicity to *D. magna*, although some species of golden algae (e.g., *Ochromonas*, *Poterioochromonas*) have been found to be toxic to fish, bacteria and/or some zooplanktons (i.e., *Daphnia* and rotifer) in other studies (Leeper and Porter

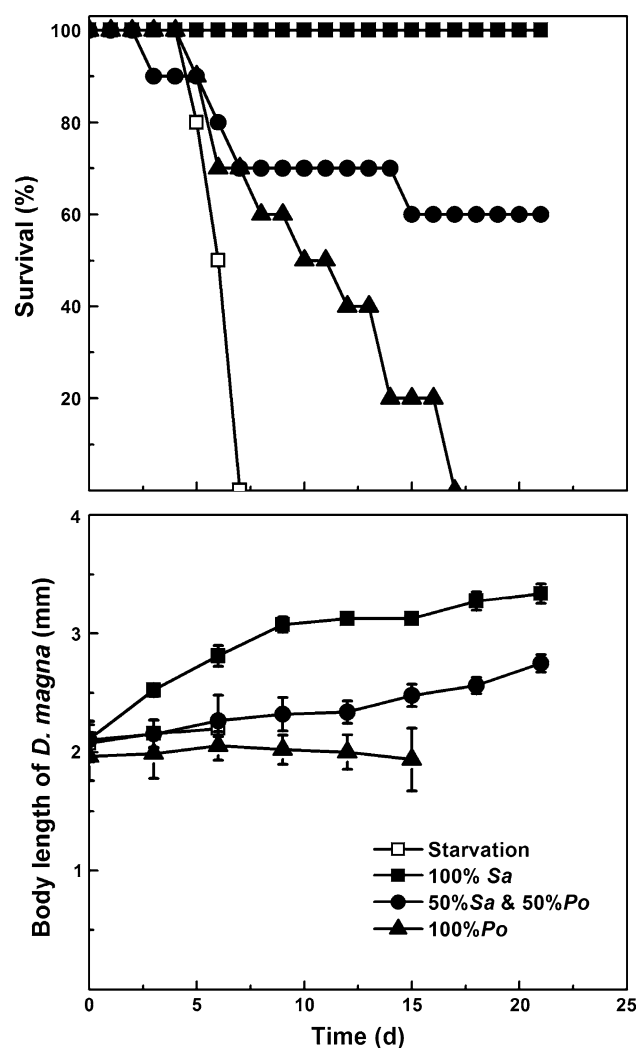


Fig. 3 Survival (percent of initial number) and body length of 5-day old *D. magna* in different concentrations of *S. acutus* and *Poterioochromonas* (*Sa* represents *S. acutus*, *Po* represents *Poterioochromonas*)

Table 5 Reproduction parameters of *D. magna* in Experiment 3

Algal suspension	Age at first reproduction (day)	Number of clutches	Total number of offspring	Mean clutch size (number daphnid ⁻¹)
100% <i>S. acutus</i>	5.9 ± 0.7	5.6 ± 0.7	53.1 ± 6.8	9.6 ± 1.4
50% <i>S. acutus</i> and 50% <i>Poterioochromonas</i>	11.6 ± 1.5*	2.9 ± 1.1*	10.6 ± 3.4*	3.9 ± 1.0*

* Significantly different (at the 95% confidence level) from control fed 100% *S. acutus*

1995; Boxhorn et al. 1998; Boenigk and Stadler 2004). However, *Poterioochromonas* is of poor nutrition, which cannot support the growth of *Daphnia*. The growth and reproduction of *D. magna* fed *Poterioochromonas* were

significantly improved after adding the good quality food *S. acutus*, and these improvements were in positive correlation with the relative concentration of *S. acutus*. The survival, growth and reproduction of *D. magna* (both neonates and large juveniles) were significantly depressed when *Poterioochromonas* comprised more than 50% of the food mixture, which may have been due to inhibitory effects on food ingestion. Large juveniles of *Daphnia* were less sensitive to poor quality food (*Poterioochromonas*) and survived longer than neonates under the same food conditions. Thus, the extent to which the negative effects of mixotrophic *Poterioochromonas* to *Daphnia* may actually occur under natural conditions depends on the concentrations of *Poterioochromonas*, the availability of high quality food (e.g., *Scenedesmus*), and the age structure of *Daphnia* populations.

Acknowledgments This study was funded by China National Science Fund for Distinguished Young Scholars (No. 50825801) and NSFC-JST joint-project (No. 50721140017). Additionally, we thank the China scholarship Council, as well as the Freshwater Biological Laboratory, University of Copenhagen, for financial and logistic support.

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