

Respiration and ingestion rate of different sized *Daphnia pulex* fed on four algal species

Dihanje in prehranjevanje različno velikih osebkov vrste *Daphnia pulex* s štirimi vrstami alg

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Abstract: Respiration rate and ingestion rate for four different algal species (*Scenedesmus quadricauda*, *Asterionella formosa*, *Aphanizomenon flos-aquae* and *Planktotrix rubescens*) of different sized *Daphnia pulex* were measured in the laboratory. Population of *D. pulex* grew maximally when it fed *S. quadricauda*, but the presence of *P. rubescens* and *A. flos-aquae* caused negative population growth rate. Ingestion rates increased with increasing body size for all investigated algae; the lowest *b* value was obtained for *S. quadricauda* and the highest one for *P. rubescens*. The amount of ingested carbon exceeded the required amount for standard metabolism in both small and large sized individuals fed all four algal species. Relatively higher amount of ingested *A. flos-aquae* and *P. rubescens* in comparison with *A. formosa* and *S. quadricauda* and the results of the growth experiments indicate that the inhibitory effect of filamentous blue-green algae on *D. pulex* is more due to toxicity, low assimilation efficiency or/and inadequate composition than incapability of ingestion due to mechanical interference with filaments.

Key words: ingestion rate, respiration, *Daphnia pulex*, algae, growth scope

Izvleček: V laboratoriju smo pri različno velikih osebkih *Daphnia pulex* merili dihanje in stopnjo hranjenja s štirimi različnimi vrstami alg (*Scenedesmus quadricauda*, *Asterionella formosa*, *Aphanizomenon flos-aquae* and *Planktotrix rubescens*). Populacija *D. pulex* je najbolj uspevala pri hranjenju z algo *S. quadricauda*, v prisotnosti vrst *A. flos-aquae* in *P. rubescens* pa smo opazili negativno rast populacije. Stopnja hranjenja se je povečevala z naraščajočo telesno velikostjo pri vseh vrstah alg; najnižjo vrednost *b* smo dobili pri hranjenju s *S. quadricauda*, najvišjo pa s *P. rubescens*. Količina zaužitega ogljika je presegala porabo za standardni metabolizem pri hranjenju z vsemi štirimi vrstami alg. Večje količine zaužitih vrst *A. flos-aquae* in *P. rubescens* v primerjavi z vrstama *A. formosa* in *S. quadricauda* in rezultati rastnih poskusov kažejo, da je inhibitorni vpliv nitastih modro-zelenih alg na osebe vrste *D. pulex* bolj posledica strupenosti, nizke asimilacijske učinkovitosti ali/in neustrezne sestave kot pa nezmožnosti zaužitja zaradi težav, ki bi jih povzročala nitasta oblika alg.

Ključne besede: stopnja hranjenja, dihanje, *Daphnia pulex*, alge, obseg rasti

Introduction

Herbivorous zooplankton is functionally important in aquatic webs. They constitute a link between primary producers and higher

trophic levels. A number of studies have investigated the effect of food quality (e.g. Knisley and Geller 1986, Fulton III 1988, Butler et al. 1989, Hawkins and Lampert 1989, Gulati and DeMott 1997, Kilham et al. 1997, Wagner and

Kamjunke 2001) and food quantity (e.g. Porter et al. 1982, Urabe and Watanabe 1991) on feeding and/or on growth, survival and reproduction of *Daphnia*.

As eutrophication often results in a proliferation of blue-green algae (Arnold 1971), the blue-green algae had been studied as food for *Daphnia* in several studies (e.g. Arnold 1971, Gliwicz 1977, Richman and Dodson 1983, Fulton III 1988, Gilbert and Durand 1990, Gliwicz 1990, DeMott 1999, Trabeau et al. 2004). Blue-greens are usually found to be an inadequate food for *Daphnia* due to mechanical interference of colonies of filaments with food collection, low digestibility or poor nutritive quality. Many genera of blue-greens produce either hepatotoxic or neurotoxic secondary metabolites (Trabeau et al. 2004). In the recent years, food-quality research has increasingly focused on the biochemical nutrient requirements of *Daphnia*. It has been shown that fatty acid and phosphorous content of food affect the growth and reproduction of *Daphnia* (Sundbom and Vrede 1997, Park et al. 2002, Ferrão-Filho et al. 2003, Gladyshev et al. 2008, Martin-Creuzburg and Von Elert 2009).

Daphnia is filter feeders, having appendages specialized for respiration and food gathering. Food is rejected when the collected amount is greater than it can be ingested, when it is physically unacceptable (i.e., colonies or filaments too large) or if it is chemically unacceptable (see Lampert 1987). The dependence of filtering or ingestion rate (IR) on the body length (L) of *Daphnia* can be described by power equation of the form $IR = a L^b$ (Lampert 1987). One important factor influencing b is the size of the food. Although large particles can be better handled by large daphnids than by small ones (Lampert 1987), some studies showed that the feeding of larger *Daphnia* species and larger individuals of single species is more affected by the presence of filaments than the feeding of smaller ones (Hawkins and Lampert 1989, Gilbert and Durand 1990). As filamentous and colonial algae are differently consumed by different body sized *Daphnia* (Hawkins and Lampert 1989), different ingestion of food particles in juveniles and adults was expected. The effect of food quality on both feeding and respiration of *Daphnia* were investigated in few studies (Richman and Dod-

son 1983, Trabeau et al. 2004) where the effect of different blue-greens on respiration rate of adult stages of *Daphnia* in the presence of food was measured. However, information about the capability of different sized *Daphnia* to ingest enough food to meet their carbon demands, required for standard metabolism, is still lacking. Such studies are important to obtain the basic information on growth scope of different sized animals.

The aim of the present study was to determine an ingestion rate of different sized individuals of *D. pulex* that were fed on four different algal species, i.e. *Scenedesmus quadricauda*, *Asterionella formosa*, *Aphanizomenon flos-aquae* and *Planktotrix rubescens*. Respiration rates were measured in different sized developmental stages in order to estimate carbon demands for standard metabolism. It was hypothesized that ingestion rates of different algal species and respiration rates differ in different sized animals. Growth experiments were carried out to test nutritional value of a single alga and possible toxicity of blue-green algae used in the experiments.

Material and methods

Cultures

Daphnia pulex Leydig originated from a permanent laboratory culture in National Institute of Biology (Ljubljana, Slovenia). Animals were kept in 10 L aquaria and some hundred specimens were there all the time. The water temperature was 24.0 ± 1.5 °C. The animals were fed every second day with suspension of *Scenedesmus* sp. and yeast. For feeding experiments adult females without eggs were selected, but for growth experiments ovigerous females of similar size were selected. Single animal were transferred using a narrow glass pipette.

Algal cultures of *Scenedesmus quadricauda*, *Asterionella formosa*, *Aphanizomenon flos-aquae* and *Planktotrix rubescens* were obtained from the National Institute of Biology collection (Ljubljana, Slovenia). Algae were cultured in Jaworski medium. Algal cultures were maintained in log growth phase. Algal characteris-

Table 1: Morphological characteristics of algae used in experiments. Mean \pm SD (n - number measured).Tabela 1: Morfološke značilnosti alg, uporabljenih v poskusih. Povprečje \pm SD (n - število meritev).

	Width of particles (μm)	Length of particles (μm)	Max dimension of colony (μm)	Dry weight ($\mu\text{g cell}^{-1}$)
<i>Aphanizomenon flos-aquae</i>	3.54 ± 0.73 (25)	42.47 ± 25.90 (64)	-	$5.33 * 10^{-4}$
<i>Planktotrix rubescens</i>	4.96 ± 0.53 (31)	103.96 ± 52.75 (31)	-	$1.07 * 10^{-3}$
<i>Asterionella formosa</i>	3.98 ± 0.67 (37)	46.96 ± 14.4 (43)	88.45 ± 25.1 (20)	$2.36 * 10^{-4}$
<i>Scenedesmus quadricauda</i>	5.17 ± 0.59 (20)	8.70 ± 1.1 (20)	12.6 ± 3.51 (20)	$6.83 * 10^{-5}$

tics are given in Table 1. Cells were counted and measured by Soft Imaging System, GmbH, analySIS 3.0, Münster, Germany. Suspension of a single alga was filtered through pre-weighted filter (glass microfibrile filter Whatman GF/C) and dried for 24 h at 60°C. Filters were weighted on 10 μg electrobalance (Sartorius). Dry weight of single cell or filament was calculated from the concentration and volume of filtered suspension.

Population growth experiments

Fifteen ovigerous females of similar size (2.20 ± 0.23 mm; average eggs number per female was 2.2) were placed in bottles, each containing 600 mL of synthetic medium (ISO standard) with algal concentration of $1 * 10^4$ cells (or filaments in the case of blue-green algae) per mL. These animals were collected from the same container, in order to assure that they had similar age and number of eggs. Three replicate bottles for each alga as food were started at the same time to avoid other factors that might affect on experimental conditions. Experimental bottles were kept at 25°C. Before feeding half of water was changed every second day. Relatively constant food level was kept during the experiments. Population growth experiments lasted for 14 days. At the end, animals were killed in formalin solution. Body length was measured from the top of the helmet to the base of the spine using Soft Imaging System, GmbH, analySIS 3.0,

Münster, Germany. Population growth rates (r) were estimated as:

$$r = (\ln N_2 - \ln N_1) / (t_2 - t_1),$$

with N_1 and N_2 being the population sizes of sampling days t_1 and t_2 .

Feeding experiments

At the beginning of the experiments, animals were piped into tubes filled with 2 mL suspensions of algae. One animal was placed in each test tube. The initial algal cell concentration was $1 * 10^4$ cells mL^{-1} . Animals were fed for 3 hours. Animals and algae were then killed with formalin solution. In each tube, the ingestion rate (IR) were determined as

$$\text{IR} = (c_0 - c_1) * V / t$$

where c is the concentration of algae at the beginning (c_0) and the end (c_1) of the feeding time (t), and V is volume of suspension (2 mL). Animals were starved for 3 hours before being used in feeding experiments.

Respiration rate was estimated by the closed bottle method (Lampert 1984). 150 mL ground glass stoppered bottles were filled with synthetic medium and aerated water from the same, well-mixed, container. Ten bottles received animals (50 similar sized animals were placed in a single bottle), while three bottles served as final con-

Table 2: Population growth rates (d^{-1}) for population of *Daphnia pulex* fed different species of algae ($n = 3$).

Tabela 2: Stopnja rasti populacij (d^{-1}) pri vrsti *Daphnia pulex* pri hranjenju z različnimi vrstami alg ($n = 3$).

	Mean \pm SD
<i>Aphanizomenon flos aquae</i>	-0.481 ± 0.052
<i>Planktotrix rubescens</i>	-0.040 ± 0.021
<i>Asterionella formosa</i>	0.006 ± 0.001
<i>Scenedesmus quadricauda</i>	0.115 ± 0.010

trols. All bottles were kept at 25°C. After 24 h the concentration of dissolved oxygen in the experimental and control bottles was measured by polarographic oxygen electrode (OXI 96, WTW). The difference between the oxygen of each experimental as well as mean oxygen concentration of control bottles was taken as the amount of oxygen consumed by animals. The amount of oxygen consumed was then converted to respiration rate per individual ($\mu L O_2 / ind/h$). Respiratory carbon loss was calculated using the conversion factor $1 mL O_2 = 0.5 mg C_{org}$ (Lampert 1984). In con-

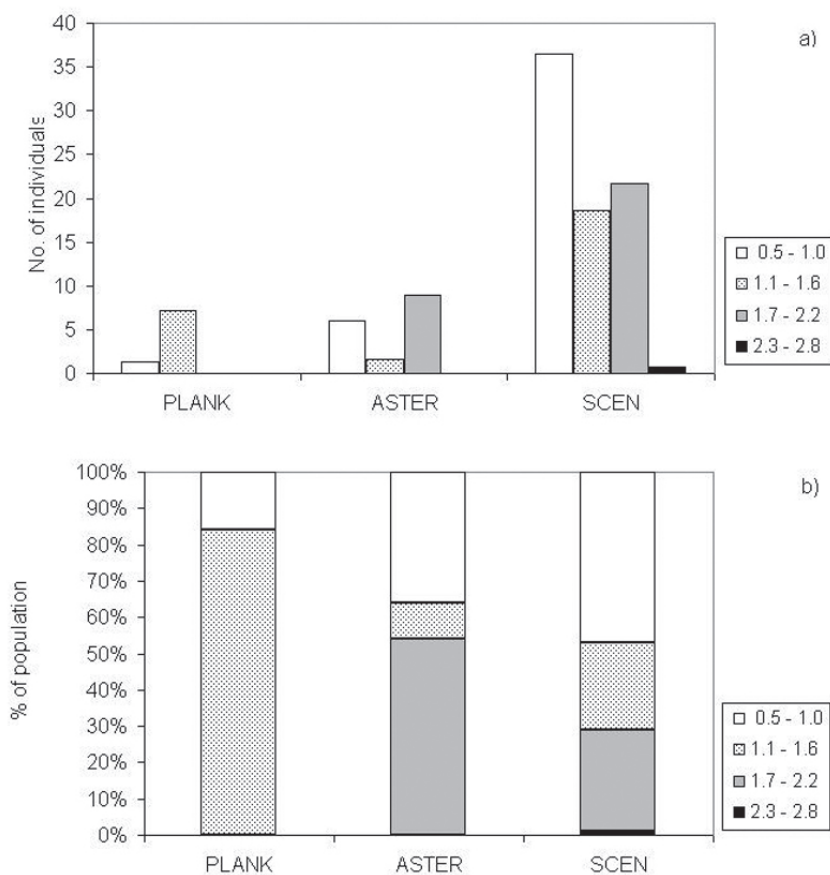


Figure 1: a) Number of individuals and b) percentage of populations for different size classes (mm) of *Daphnia pulex* fed *Planktotrix rubescens* (PLANK), *Asterionella formosa* (ASTER) and *Scenedesmus quadricauda* (SCEN).

Slika 1: a) Število osebkov in b) odstotki populacij po velikostnih razredih (mm) pri vrsti *Daphnia pulex*, ki se je prehranjevala s *Planktotrix rubescens* (PLANK), *Asterionella formosa* (ASTER) in *Scenedesmus quadricauda* (SCEN).

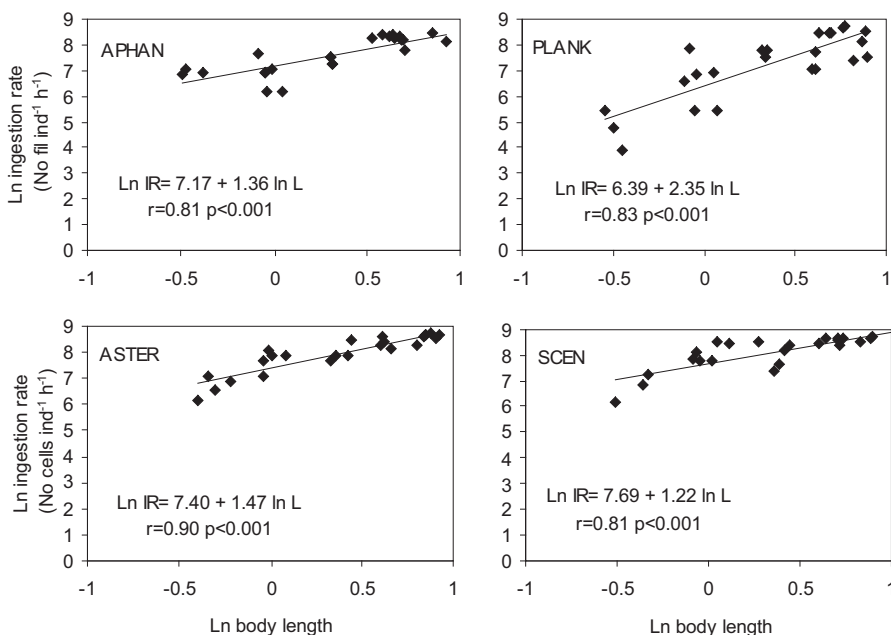


Figure 2: Relationships between ingestion rates and body length of *Daphnia pulex* fed *Aphanizomenon flos-aquae* (APHAN), *Planktotrix rubescens* (PLANK), *Asterionella formosa* (ASTER) and *Scenedesmus quadricauda* (SCEN).

Slika 2: Razmerje med stopnjo hranjenja in telesno velikostjo osebkov *Daphnia pulex* pri prehranjevanju s *Aphanizomenon flos-aquae* (APHAN), *Planktotrix rubescens* (PLANK), *Asterionella formosa* (ASTER) in *Scenedesmus quadricauda* (SCEN).

verting respiration to carbon units, a respiratory quotient (RQ) of 1.0 was assumed. Growth scope was calculated as a subtraction of respiratory carbon loss (C_{res}) from ingested carbon (C_{ing}).

Statistical analyses

One-way analysis of variance (ANOVA) on population growth rates was performed to test differences between different algae. Linear regressions between body length and ingestion rate, and between body length and respiration rate were calculated using Microsoft Excel.

Results and discussion

Growth experiments

Population growth experiments showed that population growth rates differed between food

sources (ANOVA, $p < 0.001$). Population of *D. pulex* grew maximally when it fed *S. quadricauda* (Table 2).

Populations that fed *A. formosa* had positive growth rates, but the presence of *P. rubescens* caused negative population growth rate. Structure of populations revealed that all individuals of populations that fed *P. rubescens* belonged to two the smallest size classes (Figure 1). Populations that fed *A. formosa* had larger individuals in comparison with *P. rubescens* as a food source, but the largest animals were observed in diet with *S. quadricauda*. Feeding on *A. flos-aquae* resulted in the collapse of populations during six days.

These results are in accord with those previous studies where blue-greens are considered as poor-quality food for *Daphnia*, due to the interference of the filaments with the collection of

available food, toxicity, and a low nutritional quality (Arnold 1971, Gliwicz 1977, Richman and Dodson 1983, Fulton III, 1988, Gilbert and Durand 1990, Gliwicz 1990, DeMott 1999, Tra-beau et al. 2004). Arnold (1971) reported that there were differences among the blue-greens in their effects on animals. In the present study *A. flos-aquae* showed toxicity towards *D. pulex*, but *P. rubescens* probably did not provide sufficient nutrition to maintain a population of *D. pulex* (Table 2). DeMott (1999) reported that *D. pulex* exhibited stronger inhibition than *D. magna*, *D. pulicaria*, and *D. galeata*, when it fed a mixture of *Scenedesmus acutus* and *Microcystis aeruginosa*. Sharp decline in gross growth efficiency showed on growth inhibition as a result of both feeding inhibition and direct toxicity (DeMott 1999). The results of the present study revealed that *S. quadricauda* was high quality food for *D. pulex* as the number and body size of animals exceeded those of animals fed *P. rubescens* or *A. formosa* (Figure 1). High quality of *Scenedesmus* sp. was also reported by Hawkins and Lampert (1989) and Vijverberg (1989). Size of particles of this species is convenient to be high quality food for all life stages of the crustaceans (Vijverberg 1989). As *Planktotrix* sp. has the lowest assimilation efficiency among

investigated algae and also, *Asterionella* sp. has lower assimilation efficiency than *Scenedesmus* sp. (cited in Lampert 1987), dissimilar growth of populations could be probably partly explained by differences in assimilation rates.

Feeding experiments

Ingestion rate increased with body size for all investigated algae (Figure 2). Increasing of ingestion rates with increasing body length of cladocerans was also observed in DeMott (1982) and Mourelatos and Lacroix (1990). Regression showed that larger individuals consumed significantly more food than smaller ones ($p < 0.001$). The b value ranged from 1.22 for *S. quadricauda* to 2.35 for *P. rubescens*. One important factor influencing b is the size of the food. Large particles can be better handled by large daphnids than small ones. On the other hand, small daphnids have finer filters and can retain smaller particles (Lampert 1987). Therefore, low b values which were obtained in the presence of small food particles and high b values for large particles (i.e. *P. rubescens*) are in accord with expectations.

Previous studies showed that ingestion rate depends also on food concentration (DeMott

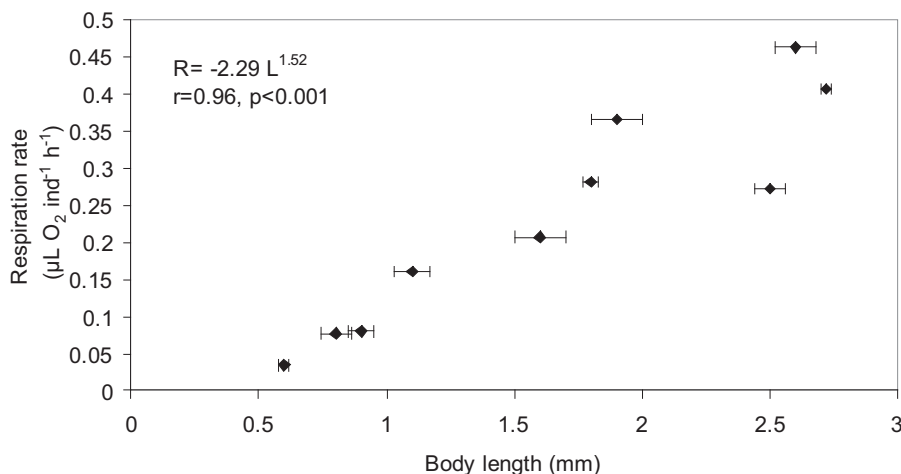


Figure 3: Relationship between respiration rate and mean body length of *Daphnia pulex* present in single experimental bottle. Bars represent \pm 1SD.

Slika 3: Razmerje med stopnjo dihanja in povprečno velikostjo osebkov *Daphnia pulex* v posamezni poskusni steklenici. Odkloni predstavljajo \pm 1SD.

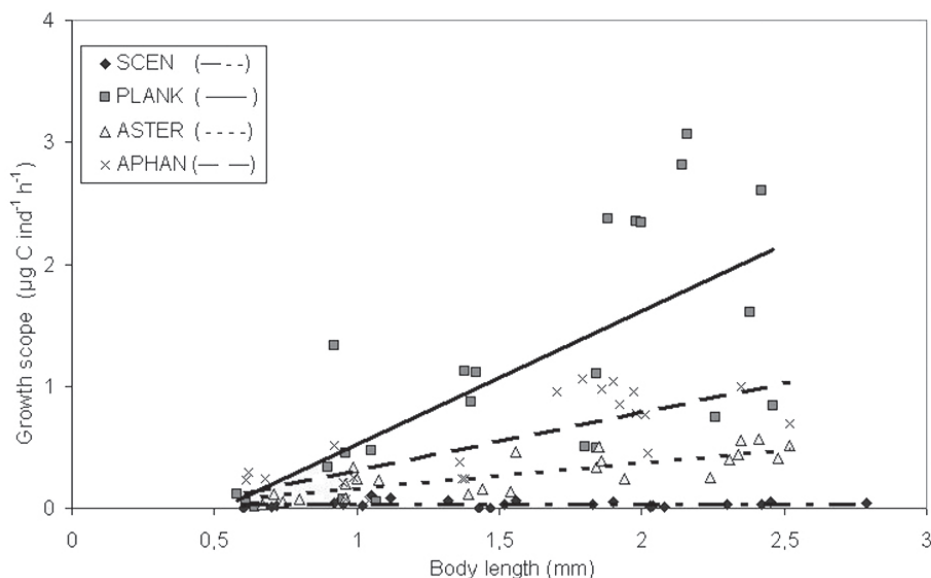


Figure 4: Relationship between the growth scope and body length of *Daphnia pulex* fed *Aphanizomenon flos-aquae* (APHAN), *Planktotrix rubescens* (PLANK), *Asterionella formosa* (ASTER) and *Scenedesmus quadricauda* (SCEN).

Slika 4: Razmerje med obsegom rasti in velikostjo osebkov *Daphnia pulex* pri prehranjevanju s *Aphanizomenon flos-aquae* (APHAN), *Planktotrix rubescens* (PLANK), *Asterionella formosa* (ASTER) in *Scenedesmus quadricauda* (SCEN).

1982, Porter et al. 1982, Gilbert and Durand 1990, Mourelatos and Lacroix 1990). In general, ingestion rates increased with increasing food concentration until incipient limiting level (ILL) was reached. Above the ILL the ingestion rate remains constant. Animals control the ingestion rate by rejecting of superfluous food from the food groove with abdominal claw. The rate of rejection remains constant below the ILL, but it increases at high concentration (Porter et al. 1982). In the present study, both growth and feeding experiments were performed at concentration that was considered as ILL (i.e., 1×10^4 cell mL⁻¹) (Porter et al. 1982). This food concentration should provide optimal feeding conditions for animals.

Respiration rate measurements

Respiration rates (R) increased with increasing body length (L) of *D. pulex* according regression equation: $\ln R = -2.28 + 1.52 \ln L$ ($r = 0.96$; $p < 0.001$) (Figure 3). In the present experi-

ments, the standard metabolism and expenditure on locomotion were measured. The expenditure on feeding and specific dynamic action (SDA) was minimal (Philippova and Postnov 1988) because the animals were not fed just prior to or during the experiments. Therefore, measured respiration rates represent minimal maintenance costs of metabolism in different sized animals. Feeding and processing of the food increase respiration rates (Philippova and Postnov 1988) so higher respiratory carbon demands can be expected in the presence of food.

Relation between respiratory carbon demands and ingested amount of food

The amount of ingested carbon exceeded the amount of that required for standard metabolism and locomotion in both small and large sized individuals for all four algal species (Figure 4). Therefore, animals of all sizes were capable of consumption sufficient amount of *S. quadricauda* and *A. formosa* as well as filamentous algae *A.*

flos-aquae and *P. rubescens* to meet needs related to minimal metabolic demands. The amount of ingested carbon was the lowest for *S. quadricauda*, while the highest values were observed for *P. rubescens*. The reason is probably different sized algal particles that were offered to animals, as a passive filtering of similar number of particles resulted in different amount of collected food.

The results of the present study indicate that although *P. rubescens* can be ingested by *D. pulex*, it cannot provide sufficient nutrition to support a population that does not have other food available. Arnold (1971) also found that some blue-green algae are inadequate food source for *D. pulex*. Animals can ingest food in large amounts but assimilate it poorly, or allocate most of the quantity assimilated to maintenance costs. Thus, those animals which fed on low quality food are unable to increase or even maintain the existent population.

Conclusions

It is concluded that both juvenile and adult *D. pulex* can ingest relatively large amount of blue-green algae as well as green algae and diatoms. Thus, these results indicate that the inhibitory effect of filamentous blue-green algae *A. flos-aquae* and *P. rubescens* is more due to toxicity, low assimilation efficiency or/and inadequate composition than incapability of ingestion due to mechanical interference with filaments. Also, relatively small amount of ingested *S. quadricauda* showed that this alga is high quality food for *D. pulex*. *A. formosa* probably should be considered as an adequate, but less qualitative food source in comparison with *S. quadricauda*.

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Povzetek

Rastlinojedi zooplankton ima v prehranjevalni mreži ključno vlogo, saj predstavlja povezavo med primarnimi producenti in višjimi trofičnimi nivoji. Številni raziskovalci, ki so preučevali vpliv količine in kvalitete hrane na prehranjevanje, rast, preživetje in razmnoževanje osebkov iz rodu *Daphnia*, poročajo, da so modro-zelene alge zaradi velikosti kolonij, slabe prebavljivosti, nizke hranilne vrednosti in celo strupenosti pogosto neustrezna hrana. V večini raziskav so preučevali vpliv hrane na odrasle osebkke, manj pa je znanega o prehranjevanju mladičev oz. različno velikih osebkov. Ker je količina zaužite hrane odvisna od velikosti osebkov in velikosti delcev hrane, smo ugotavljali, ali različno veliki osebki lahko zaužijejo zadostno količino hrane, ki je potrebna za vzdrževanje osnovnih fizioloških potreb. Tako smo ugotavljali stopnjo hranjenja pri različno velikih osebkkih *Daphnia pulex*, ki smo jih hranili s štirimi različnimi vrstami alg (*Scenedesmus quadricauda*, *Asterionella formosa*, *Aphanizomenon flos-aquae* in *Planktotrix rubescens*). Z merjenjem dihanja pri različno velikih osebkkih smo ocenili potrebo po energiji za standardni metabolizem. Hranilno vrednost in strupenost posamezne vrste alge smo ugotavljali z rastnimi poskusi. Največja je bila rast populacije *D. pulex* pri hranjenju s *S. quadricauda*, nato sledi *A. formosa*. V prisotnosti *P. rubescens* smo opazili negativno rast populacije, pri *A. flos-aquae* pa je prišlo do njenega propada že v nekaj dneh. Rezultati rastnih poskusov so pokazali strupenost vrste *A. flos-aquae*, nizko hranilno vrednost pri vrsti *P. rubescens* in najvišjo kvaliteto za vrsto *S. quadricauda*. V skladu s pričakovanji se je stopnja hranjenja povečevala z naraščajočo telesno velikostjo pri vseh vrstah alg. Najnižjo vrednost *b* smo dobili pri hranjenju vodnih bolh s *S. quadricauda*, najvišjo pa s *P. rubescens*. Količina zaužitega ogljika je presegala potrebe po energiji za standardni metabolizem pri hranjenju z vsemi štirimi vrstami alg. Raziskava je pokazala, da tako mladiči, kot tudi odrasli osebki *D. pulex* lahko zaužijejo dokaj veliko količino modrozelenih, zelenih in kremenastih alg. To pomeni, da je inhibitorni vpliv nitastih modro-

zelenih alg vrste *A. flos-aquae* in *P. rubescens* na *D. pulex* bolj posledica strupenosti, nizke asimilacijske učinkovitosti ali/in neustrezne sestave, kot pa nezmožnosti zaužitja zaradi težav, ki bi jih povzročala nitasta oblika alg. Vrsta *A. formosa* se je sicer izkazala kot zadosten vir hrane, a je bila v primerjavi z vrsto *S. quadricauda* manj hranilna.

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