



# *Vallisneria natans* detritus supports *Daphnia magna* somatic growth and reproduction under addition of periphyton

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**Abstract** Submerged macrophytes are regarded as being hardly assimilated by zooplankton for their lack of essential nutrients such as polyunsaturated fatty acids (PUFAs) thus serve as poor quality food, contrary to field stable isotopic investigations with observed macrophyte carbon contributions to zooplankton. However, periphyton growing on them produces the PUFAs and is thus a nutrient supplement. We hypothesize that with this supplement, zooplankton can be supported by macrophyte carbon. To test this hypothesis, we fed zooplankton with (1)  $^{13}\text{C}$  enriched *Vallisneria natans* detritus, (2) periphyton and (3) a mix of the two. We compared growth and

reproduction of zooplankton under these three food treatments and calculated zooplankton assimilation of macrophyte carbon when fed a mixed diet, using a stable isotope-mixing model. The fatty acid profile of the two carbon resources was also analyzed. Our results demonstrate that *Daphnia magna* can grow and reproduce well, and use *V. natans* carbon when a supplement of periphyton is available.

**Keywords** Submerge macrophytes · Zooplankton · Periphyton · Stable isotope analysis

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## Introduction

Macrophytes play a crucial role in maintaining a clear water state in aquatic ecosystems (Scheffer and Jeppesen 1998). They can increase binding of phosphorus through oxidization of sediments, reduce re-suspension of sediments, and suppress algal growth through nutrient competition and allelopathy (Carpenter and Lodge 1986; Moss 1990; Jeppesen et al. 1998). Beside these well-known physical, chemical and physiological effects, they are also important benthic primary producers. They contribute significantly to total primary production of aquatic ecosystems, up to 99% in small lakes (Downing et al. 2006; Nõges et al. 2010; Brothers et al. 2013; Verpoorter et al. 2014).

However, their contributions to aquatic food webs have been poorly studied (Bakker et al. 2016) and their ability to serve as food sources has long been discussed (Lodge 1991; Bakker et al. 2016). In recent decades, increasing evidences stressed the contribution of benthic producers using stable isotopic techniques (Jaschinski et al. 2008; Zanden et al. 2011; Batt et al. 2012; De Kluijver et al. 2015; Wolters et al. 2018). Researches revealed that macrophyte-derived detritus can contribute to suspended particulate organic matter and ultimately subsidize invertebrates in aquatic ecosystems (Miller and Page 2012; Dalu et al. 2016; Palomar-Abesamis et al. 2018; Bearham et al. 2020).

Macrophytes are not the only benthic producer. Actually, together with rocky shores, they provide a substratum for the complex community of substratum-bound autotrophic and heterotrophic biota, known as the periphyton (Cattaneo and Kalff 1980). They both contribute to benthic primary production and often are difficult to distinguish in terms of natural abundance of carbon stable isotopic signatures (Connolly et al. 2005; Jaschinski et al. 2008; Cazzanelli et al. 2012; Paice et al. 2017). Zooplankton have a vital ecological role in aquatic ecosystem as consumers in aquatic foodweb (Gulati 1975). De Kluijver et al. (2015) reported 26–86% carbon contribution of macrophytes and their associated periphyton to zooplankton in a shallow lake with clear state. Some ecologists believe that periphyton, rather than macrophytes, make up the bulk of the benthic contribution to zooplankton (Cazzanelli et al. 2012; Pettit et al. 2017).

The main reason for this conception lies in the nutritional status of these two carbon sources. Zooplankton need protein, lipids and importantly, PUFA, for growth and reproduction (Müller-Navarra 1995). Normally, zooplankton cannot synthesize de novo some PUFA, e.g., DHA, EPA and ARA and needs to obtain them from food (Parrish 2009). These polyunsaturated fatty acids are crucial for somatic growth and reproduction of zooplankton, due to their role in maintaining membrane structure and being precursors of bioactive compounds in invertebrates (Heckman et al. 2008; Martin-Creuzburg et al. 2010). Vascular plant tissues possess relatively small amount of protein and lipids, and lack PUFA (Koussoroplis et al. 2010; Richoux et al. 2017). Thus, they can hardly support the growth and reproduction of zooplankton (Brett et al. 2009). In contrast, periphyton contains

high amount of PUFA (Hill et al. 2011). Lab experiments have shown that zooplankton grows and reproduces well on a periphyton diet (Siehoff et al. 2009; Hélène et al. 2012; Mahdy et al. 2014). Ingestion of periphyton by zooplankton in field conditions has been observed as well (Jones and Waldron 2003; Rautio and Vincent 2006).

We note that zooplankton needs for essential fatty acids are low, according to previous reports (Becker and Boersma 2003, 2005; Tang et al. 2019). Small amounts of these essential biochemicals significantly improve growth and reproduction of zooplankton (Becker and Boersma 2005; Ravet and Brett 2006). Taipale et al. (2016) showed that terrestrial carbon could not support the growth and reproduction of *Daphnia* alone, whereas it can with a supplement of algal food. Submerged macrophyte detritus, a component of suspended particulate organic matter, normally consists of a mixture of macrophyte tissues and periphyton and the latter one would probably serve as a nutritional complement. Therefore, we hypothesize that macrophytes with a supplement of periphyton suffice to support the growth and reproduction of zooplankton.

To test our hypothesis, we fed zooplankton (*Daphnia magna*) with differing diets, viz. macrophytes, periphyton and a mixture of both, and compared growth and reproduction of zooplankton with each diet. We also labeled *Vallisneria natans* and applied a stable isotopic probing analysis to confirm the assimilation of macrophyte carbon. This research will help us understand the entrance of macrophyte carbon to aquatic food webs and its possible pathway.

## Materials and methods

### Preparation of $^{13}\text{C}$ -labeled submerged macrophytes

Fifteen individuals of *V. natans* ( $17.8 \pm 0.77$  cm) were transplanted into 5 L beakers filled with distilled water, sealed with a transparent plastic film and incubated outdoors under natural sunlight for 96 h. Total 0.25 g of  $\text{NaH}^{13}\text{CO}_3$  (98 at. %  $^{13}\text{C}$ ) (ISOTECH, USA) was added twice a day evenly to the beaker. At the end of this treatment, we gathered all biomass (*V. natans* with periphyton scraped off). *V. natans* was then freeze-dried, ground using a high-speed grinder

and filtered with a 325-mesh sieve into small particles (< 45  $\mu\text{m}$ ).  $\delta^{13}\text{C}$  value of *V. natans* had increased to an average of  $\delta^{13}\text{C}$ : 1058.09‰ compared to an average natural level of  $\delta^{13}\text{C}$ :  $-20.35\text{‰}$  as a result of photosynthetic uptake of  $\text{H}^{13}\text{CO}_3^-$ .

#### Preparation of periphyton

Fifty individuals of *V. natans* ( $17.8 \pm 0.77$  cm) were transplanted into 10 beakers (5 L) filled with distilled water. A 6 cm  $\times$  9 cm polyethylene rigid plastic sheet was also placed into each beaker. We added 32.46 mg/L  $\text{KNO}_3$  and 0.84 mg/L  $\text{NaH}_2\text{PO}_3$  to each beaker every week to keep a nutrient load. After one month, periphyton was scraped from both macrophyte leaves and plastic sheet, washed, freeze-dried and also ground and filtered with a 325-mesh sieve into small particles (< 45  $\mu\text{m}$ ). Collected plant-based periphyton mainly consisted of *Fragilaria*, *Oedogonium*, *Aphanothece* and *Chroococcus*.

#### Fatty acids analysis of macrophyte and periphyton

Total lipids were extracted from approximately 20 mg dry biomass of periphyton and macrophyte *V. natans* respectively with dichloromethane/methanol (2:1, v/v) and reduced in volume by evaporation. The extracts were transesterified with 2 mL 3 mol/L methanolic HCl (60 °C, 15 min) for the analysis of fatty acids. Triplicate samples of transesterified or saponified lipid samples were mixed respectively and duplicate 1  $\mu\text{L}$  samples were injected into the device in splitless mode. Lipid types were analyzed using a Finnigan TRACE Gas Chromatography Mass Spectrometer equipped with a flame ionization detector and a DB-23 column (60 m  $\times$  0.32 mm) for FAME and identified by retention times and mass spectra. Fatty acid concentrations were quantified with both external standard Supelco 37 Component FAME mix and an internal standard (C12:0 methyl esters).

#### Growth experiment

Three diets including macrophyte detritus, periphyton and a mixture of the two for rearing *Daphnia magna* were prepared. All diets were delivered once a day at 2 mg C/L for 6 days and 3 mg C/L for following 15 days. Mixed diet consists of 1:1 (carbon content) of *V. natans* and periphyton. These food concentrations

were above the incipient limiting level for ingestion (Lampert 1987). Carbon contents of the macrophyte and periphyton were analyzed using an elemental analyzer (EA3000, EuroVector). The food concentrations were determined using known values for carbon concentration and OD (optical extinction) at 682 nm. The *D. magna* used in the experiment were provided by Jinan University, and raised at 25 °C under light intensity of 50  $\mu\text{mol m}^{-2} \text{s}^{-1}$  with a 12 L:12 D h light regime. In order to record *Daphnia* growth, in the same culture conditions, neonates (< 10 h old) were collected from third brood females and distributed randomly in 250-ml beakers (10 individuals per beaker). Body length, survival and number of offspring produced in each beaker were recorded daily. Experiments were performed at 25 °C with a 12:12 h dark: light cycle on three food sources with four replicates for each treatment. For the measurement of daphnid body length, 3–4 individuals were pipetted randomly from the vessels. Carapace length was measured using a Nikon microscope equipped with an ocular micrometer, and the sampled individuals were returned immediately to the culture vessel. Surviving *Daphnia* were counted daily and transferred to freshly prepared food suspensions. The offspring produced in each vessel were also counted daily and subsequently removed. The experiment lasted for 21 days. We also set a negative control of zooplankton with no food supplied.

The intrinsic rates of increase  $r$  ( $\text{d}^{-1}$ ) in population of *D. magna* were calculated using Euler's formula:

$$1 = \sum_{x=0}^n e^{-rx} \times l_x \times m_x$$

where  $x$  is the age or time interval (day),  $l_x$  is the proportion of individuals surviving to age  $x$ , and  $m_x$  represents the number of offspring produced per surviving female at age  $x$ .

#### Stable isotopic analysis and carbon contribution calculation

Zooplankton samples were collected after growth experiments and dried at 48 °C. Zooplankton, macrophyte and periphyton samples were subjected to carbon isotopic analysis carried in the Institute of Aquatic Biology in Jinan University, using a Hydra 20–20 mass spectrometer (SerCon, UK). Isotope

abundance was expressed using the conventional delta notation against the international standards (Pee Dee Belemnite for  $\delta^{13}\text{C}$ ).

$$\delta X(\text{‰}) = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$$

where  $X = {}^{13}\text{C}$  and  $R$  is ratio of  ${}^{13}\text{C}:{}^{12}\text{C}$ .

Carbon contribution of macrophyte to zooplankton was calculated using a stable isotope mixing model employing the *simmr* package (Parnell and Inger 2016) in R.3.4.3. Enrichment of  $\delta^{13}\text{C}$  by zooplankton was calculated respectively by  $\delta^{13}\text{C}$  values of each carbon resource and zooplankton fed solely with that carbon. The model was run using the *simmr\_mcmc* command with default parameters.

### Statistics

Body length and reproduction of *D. magna* reared on different diets were analyzed by repeated measures analyses of variance (RM-ANOVA), followed by LSD test. One-way ANOVA was performed to indicate differences in the intrinsic rates of increase in populations and stable isotopic values of different samples. Before statistical analyses, compliance with the ANOVA assumptions was checked with a normal probability plot of the residuals and a Levene's test of homogeneity of variances. All statistics was performed using SPSS 20.0.

## Results

### Fatty acid profiles of periphyton and *V. natans*

Fatty acids profiles of *V. natans* and periphyton are shown in Table 1 (average values). The constituent polyunsaturated fatty acid of *V. natans* includes mainly LIN (Linoleic acid, C18:2 $\omega$ 6) and ALA ( $\alpha$ -Linolenic acid, C18:3 $\omega$ 3), lack of long chain polyunsaturated fatty acids. Periphyton in our experiment possesses not only short chain polyunsaturated fatty acids, but also long chain polyunsaturated fatty acids including averagely 2.32  $\mu\text{g}/\text{mg}$  C EPA (Eicosapentaenoic acid, 20:5 $\omega$ 3), 0.53  $\mu\text{g}/\text{mg}$  C DHA (Docosahexaenoic acid, 22:6 $\omega$ 3) and 0.51  $\mu\text{g}/\text{mg}$  C ARA (Arachidonic acid, 20:4 $\omega$ 6).

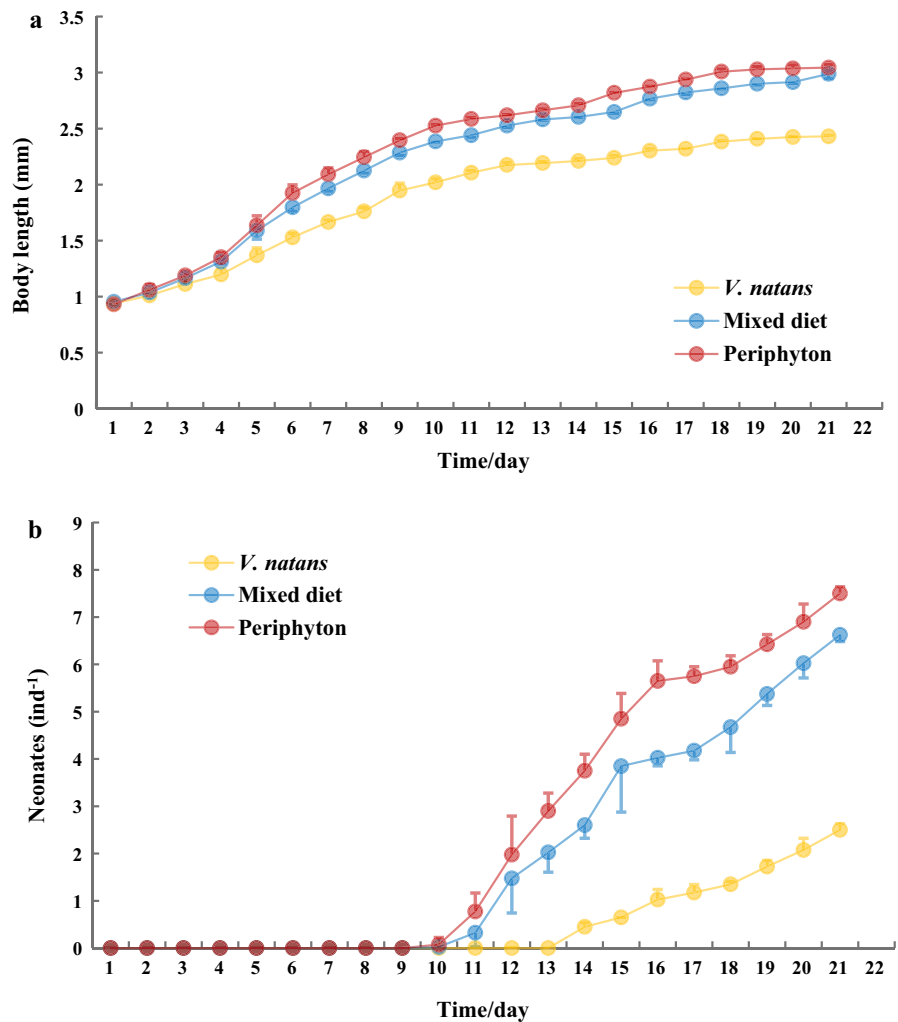
**Table 1** Mean fatty acid values of macrophyte *Vallisneria natans* and periphyton. – indicates a trace amounts < 0.01  $\mu\text{g}/\text{mg}$  C or not detected

	<i>Vallisneria natans</i>		Periphyton	
	$\mu\text{g}/\text{mg}$ C	%	$\mu\text{g}/\text{mg}$ C	%
<i>Saturated fatty acids (SAFA)</i>				
C14:0	0.31	1.03	1.60	3.07
C15:0	0.13	0.43	0.43	0.83
C16:0	11.73	38.99	22.54	43.26
C17:0	0.10	0.33	0.15	0.29
C18:0	1.89	6.28	2.14	4.11
C19:0	0.02	0.08	–	–
C20:0	0.15	0.50	0.11	0.21
C21:0	0.04	0.13	–	–
C22:0	0.20	0.66	0.64	1.23
C23:0	0.05	0.17	–	–
<i>Monounsaturated fatty acids (MUFA)</i>				
C16:1	0.54	1.80	7.73	14.84
C17:1	–	–	0.15	0.29
C18:1 $\omega$ 9	0.11	0.37	8.43	16.18
<i>Polyunsaturated fatty acids (PUFA)</i>				
C18:2 $\omega$ 6	6.96	23.14	2.06	3.95
C18:3 $\omega$ 3	7.69	25.56	1.71	3.28
C18:3 $\omega$ 6	0.16	0.53	–	–
C18:4 $\omega$ 3	–	–	1.05	2.02
C20:4 $\omega$ 6	–	–	0.51	0.98
C20:5 $\omega$ 3	–	–	2.32	4.45
C22:6 $\omega$ 3	–	–	0.53	1.02

### Growth of *D. magna*

*Daphnia* with diets all survived the full experimental period, while *Daphnia* with no food failed to survive for six days. *Daphnia* with differing diet grew and reproduced differently (Repeated measures ANOVA,  $F_{6,724, 30,256} = 64.244$ ,  $P < 0.001$  for growth;  $F_{2,418, 10,883} = 13.370$ ,  $P < 0.001$  for reproduction) with data shown in Fig. 1. Though highest body length and highest average accumulative reproduction rate was observed in *Daphnia* fed periphyton, the intrinsic rates of increase in populations showed no significant differences in *Daphnia* with mixed diet and periphyton diet (One-way ANOVA,  $F_{2, 9} = 32.427$ ,  $P > 0.05$ ). *Daphnia* with periphyton diet and mixed diet grew and reproduced significantly better than *Daphnia* with macrophyte detritus (Repeated

**Fig. 1** Individual growth and reproduction of *D. magna* with differing diet. **a** Body length, **b** cumulative reproduction. Mixed diet consists of 1:1 (carbon content) of *V. natans* and periphyton. Each data point shows average  $\pm$  SD ( $n = 4$ )



measures ANOVA followed by LSD pairwise test, all  $P < 0.001$ ), and showed much higher intrinsic rates of increase (one-way ANOVA, all  $P < 0.001$ ) (Fig. 2).

#### Carbon stable isotopic results and carbon contribution to zooplankton

Carbon stable isotopic signatures of all samples were shown in Fig. 3. The carbon stable isotopic signature of zooplankton fed with macrophyte detritus was similar to that of labelled *V. natans*. The carbon stable isotopic signature of zooplankton fed periphyton was also similar to that of periphyton. The carbon stable isotopic value of zooplankton with mixed diet showed an intermediate value between the former two carbon resources.

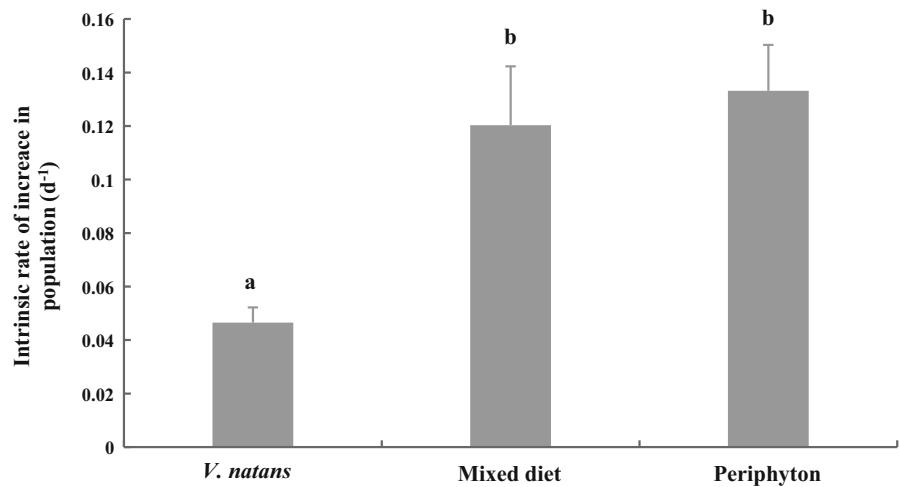
Based on a mixing model, *V. natans* contributes  $36.5\% \pm 2.3\%$  to zooplankton carbon when zooplankton were fed with a mixed diet. The comparison of zooplankton dietary proportions of different carbon sources is shown in Fig. 4.

#### Discussion

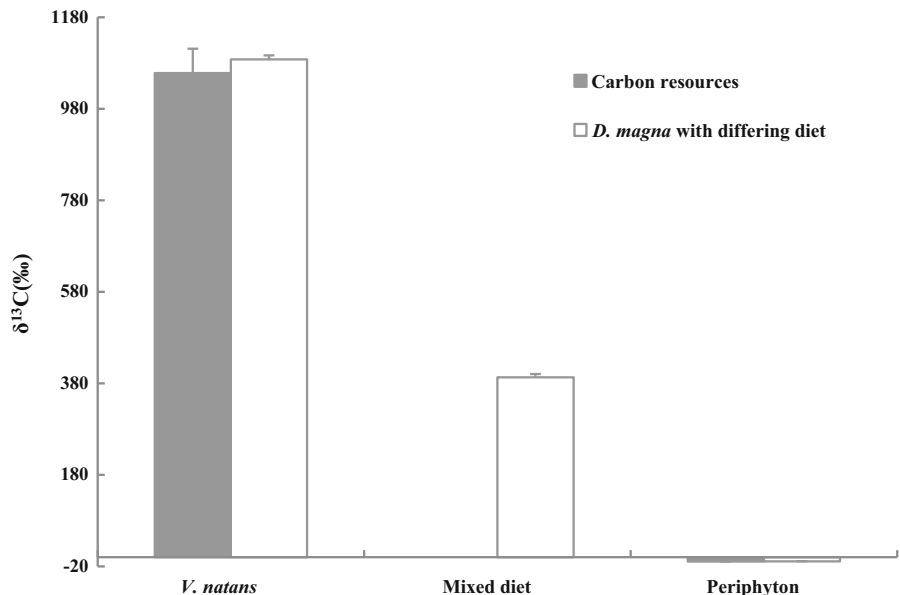
Using carbon stable isotope probing, we demonstrated that *D. magna* could assimilate *V. natans* carbon and grow and reproduce well on condition that *V. natans* was simultaneously supplied with periphyton.

*V. natans* in our experiment showed high concentration of LIN and ALA, but no EPA, DHA and ARA, probably because that higher plant lacks the essential

**Fig. 2** Population intrinsic rates of *D. magna* with different diet. Different letters above the column represents significant differences ( $P < 0.05$ ) using one-way ANOVA followed by LSD test. Mixed diet consists of 1:1 (carbon content) of *V. natans* and periphyton. Each data is average  $\pm$  SD ( $n = 4$ )

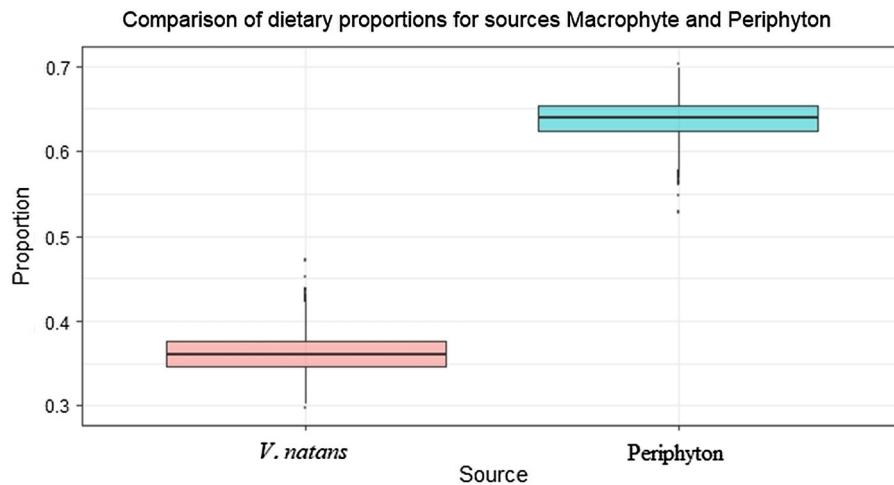


**Fig. 3** Carbon stable isotopic values of carbon resources and *D. magna* with differing diet. Each data is average  $\pm$  SD ( $n = 3$ )



enzymes to elongate these molecules (Sayanova and Napier 2004). In the growth experiment, *D. magna* survived in a *V. natans* diet with slow population increase, rather similar to when it was fed with vascular plants of terrestrial origin. Zooplankton with sole red alder or corn straw diet did not exceed the initial population size (Brett et al. 2009; Tang et al. 2019). That difference might reflect nutrient differences between submerged and terrestrial macrophytes. A higher N content (thus low C:N ratio) of freshwater submerged macrophytes than terrestrial plants has been recorded (Bakker et al. 2016) and a positive relationship between the nitrogen content in the

plant's tissue and its consumption by herbivores as well (Cebrian and Lartigue 2004). Even so, *D. magna* fed only *V. natans* detritus showed much smaller individual size and less reproduction compared to the other two diets. ARA and EPA are precursors of eicosanoids, which plays a pivotal role in the reproduction of *Daphnia* (Heckmann et al. 2008). *Daphnia* can convert LIN and ALA to growth-enhancing PUFAs ARA and EPA at a slow rate (Weers et al. 1997), which might explain a postponed reproduction in *Daphnia* fed only *V. natans*. All these results underscore the fact that *V. natans* detritus is a poor-quality food for *D. magna*.



**Fig. 4** Comparison of zooplankton dietary proportions for sources *V. natans* and periphyton when fed with 1:1 (carbon content) *V. natans* and periphyton mixed diet. The error bars indicate the uncertainty of the calculations

Gulati and Demott (1997) summarized that diatoms are good quality food for zooplankton, and chlorophytes are moderate quality food for zooplankton due to their different PUFA contents. The periphyton we used consisted of diatoms, chlorophytes and cyanobacteria, containing a relatively high EPA, DHA and ARA concentration, but probably also protists that could not be identified. *Daphnia* fed with periphyton, accordingly, grew and reproduced well with a much higher population intrinsic increase rate compared to those fed macrophytes.

The mixed diet consisting of only half of the periphyton carbon supported the population increase of *Daphnia* as well as total periphyton diet much better than the sole macrophyte diet. Taipale et al. (2016) found that *Daphnia* can grow and reproduce well with a reed (terrestrial plant) and *Cryptomonas*, and regarded that the most essential EPA need was satisfied by the algal food. Harfmann et al. (2019) also reported that a mixed diet of terrestrial plant tissues and algae can enhance the survival of copepod *E. affinis* over a diet of algae alone, indicating that terrestrial plant detritus can be a vital supplementary food source to zooplankton. Our work shows similar results, indicating that macrophyte carbon might be a supplementary food source to zooplankton also.

In field investigations, it happens that submerged macrophytes and periphyton share similar stable isotopic signatures, which makes it difficult to confirm the utilization of submerged macrophyte by zooplankton (Connolly et al. 2005; Jaschinski et al. 2008;

Cazzanelli et al. 2012; Paice et al. 2017). By using  $^{13}\text{C}$  enriched *V. natans*, our result clearly demonstrated that zooplankton assimilated submerged macrophyte carbon. Even though our mixed food was served as a 1:1 ratio, *Daphnia* showed a selective assimilation and assimilated more periphyton carbon. Taipale et al. (2016) speculated that *Daphnia* was able to use carbohydrate of vascular plant origin for energy and save algal proteins and lipids for structural components. That “sparing strategy” was fully reinforced by the current study, with *Daphnia*’s selective assimilation of algal food as strong evidence.

In conclusion, our results showed that when mixed with periphyton, *V. natans* supported the somatic growth and reproduction of zooplankton, and that macrophyte carbon was incorporated to zooplankton. These lab observations hint at the entrance of macrophyte carbon with that of associated periphyton to aquatic food webs. Zooplankton plays a key role in regulating the essential processes of aquatic ecosystem (Runge and Roff 2000) and high zooplankton/phytoplankton ratios are of high capacity of food webs controlling phytoplankton (Søndergaard et al. 2008; Jeppesen et al. 2012). Subsidy from submerged macrophyte carbon would possibly increase the zooplankton / phytoplankton ratios and may provide an enhanced ability of phytoplankton controlling, which gives implications for lake management.

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**Authors' contribution** YT made substantial contributions to design, interpret the data and draft the manuscript; DZ contributed to design, acquire and analyze the data; LS contributed to conception. ZL, XZ and HJD revised the manuscript critically.

**Data availability** The data that support this study are available from the corresponding author upon reasonable request.

## Declarations

**Conflict of interest** We declared no conflicts of interest/competing interests.

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