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The importance of terrestrial carbon in supporting molluscs in the wetlands of Poyang Lake*

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Abstract Allochthonous organic matter plays an important role in nutrient cycling and energy mobilization in freshwater ecosystems. However, the subsidies of this carbon source in floodplain ecosystems have not yet well understood. We used a Bayesian mixing model and stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) of primary food resources and dominant molluscs species, to estimate the relative importance of allochthonous carbon sources for consumers in a representative sub-lake of Poyang Lake during a prolonged dry season. Our study inferred that terrestrial-derived carbon from *Carex* spp. could be the primary contributor to snails and mussels in Dahuchi Lake. The mean percentage of allochthonous food resources accounted for 35%–50% of the C incorporated by these consumers. Seston was another important energy sources for benthic consumers. However, during the winter and low water-level period, benthic algae and submerged vegetation contributed less carbon to benthic consumers. Our data highlighted the importance of terrestrial organic carbon to benthic consumers in the wetlands of Poyang Lake during the prolonged dry period. Further, our results provided a perspective that linkages between terrestrial and aquatic ecosystems might be facilitated by wintering geese via their droppings.

Keyword: allochthonous; *Carex* spp.; molluscs; floodplain wetland; stable isotope analysis; Poyang Lake

1 INTRODUCTION

Identifying the relative importance of multiple food resources in aquatic food webs is essential for understanding ecosystem functioning. Freshwater food webs should be supported by autochthonous organic carbon and allochthonous carbon inputs that could influence population dynamics and predator-prey interactions (Polis et al., 1997; Jefferies, 2000; Pace et al., 2004). In many lakes, food webs are heavily reliant on the input of large amounts of organic matter from the surrounding terrestrial environment (Carpenter et al., 2005; Solomon et al., 2011). Particularly in some floodplain ecosystems, a subsidy from terrestrial inputs is very common in aquatic food webs (Wantzen et al., 2002; Oliveira et al., 2006; Marchese et al., 2014). In contrast, Wang et al. (2011) found that seston was the most important carbon source for fish consumers in Poyang Lake during the dry season. Consequently, the relative importance of autochthonous and allochthonous organic carbon for aquatic consumers remains uncertain.

As a subtropical floodplain ecosystem, the wetlands of Poyang Lake consist of a mosaic of several isolated sub-lakes, a large mudflat and massive herbaceous vegetation in the dry season when water level falls to their lowest. Due to a high abundance of food resources and diverse habitats, this wetland provides important foraging and roosting grounds for numerous migratory waterbirds (Wu and Ji, 2002). In a recent

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decade, a prolonged drought period resulted in shrinkage of sub-lake surface area and the expansion of terrestrial vegetation, and the wetland of Poyang Lake formed a huge grassland. However, little is known on how these changes affect resource utilization and energy mobilization in the sub-lakes of Poyang Lake.

Stable isotope analysis has been proven to be a powerful approach for tracing energy flow from basal food sources to higher trophic level consumers in aquatic ecosystems. In contrast with gut content analysis, stable isotope analyses provide dietary information over a longer time period, and effectively reflect food assimilation rather than ingestion (Peterson and Fry, 1987). In recent decades, stable isotope analyses have been widely used to evaluate the contribution of multiple food resources to consumer biomass (Molina et al., 2011; Solomon et al., 2011; Scharnweber et al., 2014). For example, in a study in Lake Michigan, Turschak et al. (2014) suggested that lake consumers have switched the nutrient pathway from a pelagic to a littoral energy source, as revealed by significant shifts in δ^{13}C in fishes and benthic invertebrates.

In this study, we determined the δ^{13}C and δ^{15}N signatures for terrestrial vegetation (*Carex* spp.), benthic algae, seston, submerged macrophyte (*Vallisneria natans*) and five dominant molluscs species in a representative sub-lake of Poyang Lake during a prolonged dry season. As the high productivity of terrestrial vegetation may subsidize the aquatic consumers in the sub-lake, we hypothesized that terrestrial reliance by molluscs would be high in the dry season. The main objectives were to (1) evaluate whether allochthonous organic matter (particularly *Carex* spp.) was an important pathway for the benthic food web of Dahuchi Lake, and then (2) examine the proportional contributions of different basal carbon sources to benthic consumers in the dry season using a Bayesian mixing model.

2 MATERIAL AND METHOD

2.1 Study area

Dahuchi Lake (115°56′E, 29°7′N) is one of the most representative sub-lakes in the Poyang Lake National Nature Reserve (PLNNR) (115°55′–116°03′E, 29°05′–29°15′N), Jiangxi Province, China (Fig.1). The PLNNR is an important Ramsar Site, and located in the northwest basin of Poyang Lake. PLNNR receives over 400 000 migratory waterbirds each winter, which makes this site one of the most important wintering areas on the East Asian-Australasian Flyway (Wu and Ji, 2002).

During the period of water recession (from October to March), water level of Dahuchi Lake decreases rapidly to less than 1 m and the water area gradually shrinks. At that time, the sub-lake is disconnected from the open area of Poyang Lake and becomes isolated. The newly-emerged area is then extensively covered by riparian vegetation (You et al., 2015). *Carex* spp. dominate the community of riparian vegetation along the lakeshores. These vegetation are mainly preferred by wintering geese, such as White-fronted geese (*Anser albifrons*) and Bean geese (*Anser fablis serrirostris*) (Zhang and Lu, 1999; Wang et al., 2013). Although the submerged macrophyte community is comprised of multiple species, the dominant species in Dahuchi is *Vallisneria natans*.

From December 2013 to March 2014, water temperature ranged from 4.5 to 13.8°C, and dissolved oxygen ranged between 8.29 and 10.79 mg/L. Averaged total nitrogen and phosphorus concentrations were 151 µg/L and 41 µg/L, respectively. Meanwhile, Chlorophyll *a* varied between 22.08 and 50.48 µg/L, and the maximum concentration occurred in December 2013 (Zhang et al., unpublished data).

2.2 Sample collection

Considering the isotopic turnover rate, different energy sources and molluscs samples were collected from the waterbody and riparian zone in Dahuchi Lake in December 2013 and March 2014, respectively. During the sampling period, the mean water depth of the sub-lake was less than 0.5 m. Five dominant macroinvertebrate species (the surface-grazing snails (*Bellamya aeruginosa* and *Cipangopaludina cathayensis*) and the filter-feeding mussels (*Corbicula fluminea*, *Unio douglasiae* and *Sinanodonta woodiana*)), were sampled from the littoral zone with a hand-held invertebrate dip net. Although numerous macrozoobenthic taxa have been recorded in Poyang Lake, these five species dominate the community in terms of abundance (Liu et al., 2008). All snails and mussels were kept alive in tanks overnight to allow gut clearance. Individual samples of muscle tissue were then removed from their shells. We rinsed the muscle tissues with distilled water and froze them in the field.

Green leaves of *Carex* spp. were collected by hand from the riparian zone. Meanwhile, several fresh

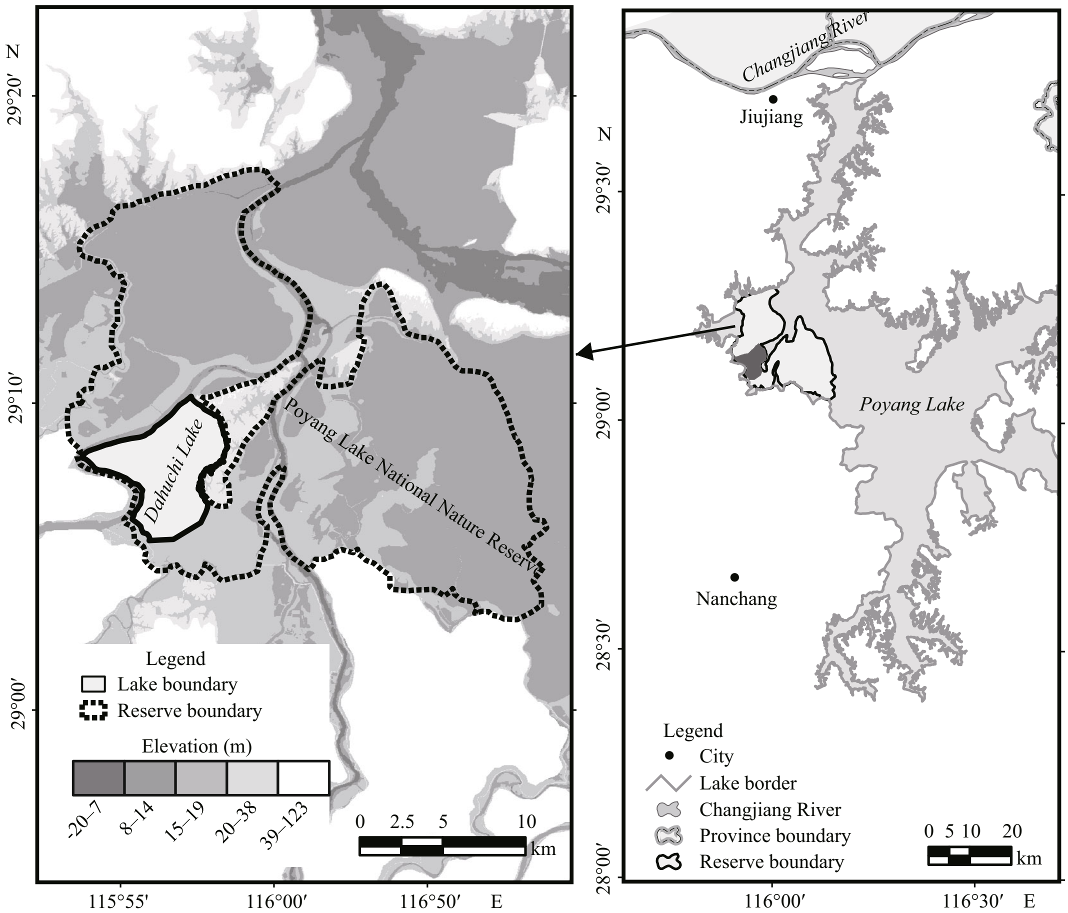

Fig.1 Map of Poyang Lake and the Poyang Lake National Nature Reserve (PLNNR) and our study area in Dahuchi Lake

goose dropping samples were also collected. The samples were immediately transferred to the laboratory and dried. *Vallisneria natans* was collected from the sub-lake. All the leaves were cleaned with distilled water before being dried. Filamentous algae was scraped from the substrates, and then rinsed with distilled water to remove sediment and large particles of detritus. As this collection was unlikely to yield pure samples, this basal production source, composed of attached filamentous algae and probably other materials is referred to as "benthic algae." Lake water was passed through a 64-μm mesh sieve to remove zooplankton, ensuring the sample contained both phytoplankton and suspended organic matter; this source is referred to as "seston" (following the methods of Zeug and Winemiller, 2008). Sieved samples were filtered onto precombusted glass fiber filters (Whatman GF/F) and frozen for later analysis. In the laboratory, all biological samples were dried at 60°C for 48 h, and then pulverized using a mortar and pestle.

2.3 Stable isotope analysis

Samples for $\delta^{13}C$ and $\delta^{15}N$ were analyzed at the Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, using a Flash Elemental Analyzer (Thermo Scientific, USA) coupled with an isotope ratio mass spectrometer (Finnigan MAT 253, Thermo Scientific, USA). Isotope ratios were calculated as per thousand (‰) according to the following equation:

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

where R=^{13}C or ^{15}N and X is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The international standards were Vienna Pee Dee Belemnite (PDB) for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$. The analytical precisions of repeated analysis of samples were 0.1‰ for $\delta^{13}C$ and 0.3‰ for $\delta^{15}N$.

2.4 Data analysis

To evaluate the proportional contribution of different basal food sources to benthic consumers, a

Table 1 Mean and standard deviation of stable isotope values of basal organic carbon sources collected in Dahuchi Lake

	n	Mean $\delta^{13}C$ (‰)	SD $\delta^{13}C$	Mean $\delta^{15}N$ (‰)	SD $\delta^{15}N$
Seston	8	-27.3	0.5	6.5	0.9
Benthic algae	6	-25.5	1.0	8.1	0.7
Vallisneria natans	8	-18.7	1.6	5.6	1.2
Carex spp.	14	-29.6	1.0	4.0	1.3

Bayesian mixing model with the package "stable isotope analysis in R" (SIAR; Parnell et al., 2010) in R software (version 3.2.1) was used in this study. We chose this model because it allowed us to account for variation in discrimination factors and to incorporate prior information. The mixing model analysis was based on the $\delta^{13}C$ and $\delta^{15}N$ values of seston, benthic algae, *V. natans* and *Carex* spp. collected in Dahuchi Lake, which represented different types of end-members for consumer taxa. Trophic fractionation of $\delta^{13}C$ values and $\delta^{15}N$ values were taken as 0.4‰±1.3‰ and 3.4‰±1.0‰, respectively (Post, 2002). We reported means, and low 95% and high 95% feasible percent contributions for each basal food source supporting molluscs as the ranges for each species.

To predict stable isotope mixing model bias, resource polygon geometry and uncertainty analysis were performed following the methods of Brett (2014).

3 RESULT

Isotopic signatures of the basal food resources were clearly distinct (F=168.928, P<0.001 for $\delta^{13}C$; F=19.280, P<0.001 for $\delta^{15}N$) except for the $\delta^{15}N$ values between seston and *V. natans* (Table 1, Fig.2). We observed depleted ^{13}C mean signatures for *Carex* spp. (-29.6‰) compared with other food sources ($\delta^{13}C_{seston}$=-27.3‰; $\delta^{13}C_{benthic\ algae}$=-25.5‰; $\delta^{13}C_{V.\ natans}$=-18.7‰). The $\delta^{15}N$ values of the basal carbon sources varied from 2.4‰ to 9.0‰, and *Carex* spp. was more depleted in ^{15}N than other sources. Additionally, mean $\delta^{13}C$ and $\delta^{15}N$ values of geese droppings in Dahuchi Lake were -26.0‰ and 5.9‰, respectively (Fig.2).

The $\delta^{13}C$ values of five molluscs species ranged from -29.8‰ to -24.5‰ in our study (Figs.2, 3). Species had similar mean $\delta^{13}C$ values, and no statistical difference was found among these benthic consumers (F=2.552, P=0.053). *Bellamya aeruginosa* exhibited a wider range of $\delta^{13}C$ values (-29.8‰ to -24.5‰) than other consumer species, reflecting the contribution of diverse food resources in their diet. The $\delta^{15}N$ values of benthic consumers ranged from 5.6‰ for *C. cahayensis* to 10.4‰ for *B. aeruginosa*, showing significant differences among groups (F=10.632, P<0.001) (Figs.2, 3). *Bellamya aeruginosa* had the highest $\delta^{15}N$ values of all five molluscs species. While, *C. cahayensis* exhibited a depletion in ^{15}N relative to the mean values of other consumers.

Resource polygon geometry in our study included four potential resources and a surface area of 20.04 SD^2. Results from SIAR indicated that *Carex* spp. could be a major basal food source for primary

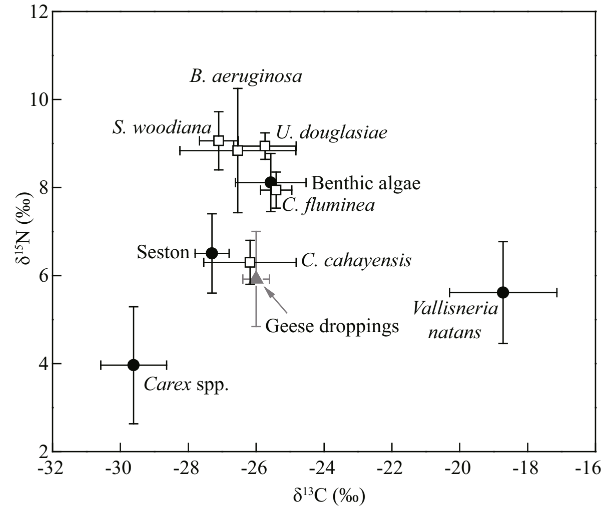

Fig.2 Biplots of $\delta^{13}C$ and $\delta^{15}N$ values of basal production sources (circle), geese droppings (triangle) and benthic consumers (square) collected from Dahuchi Lake during the dry season

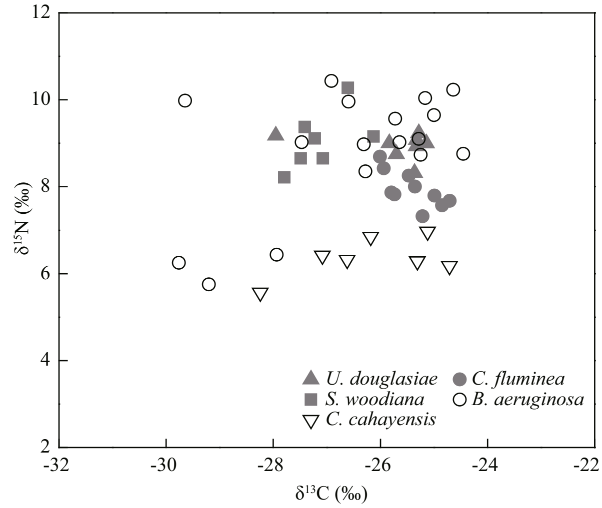

Fig.3 Carbon and nitrogen isotope ratio biplots of all individuals collected in Dahuchi Lake for *Unio douglasiae* (*n*=8), *Corbicula fluminea* (*n*=10), *Sinanodonta woodiana* (*n*=7), *Bellamya aeruginosa* (*n*=17) and *Cipangopaludina cahayensis* (*n*=6)

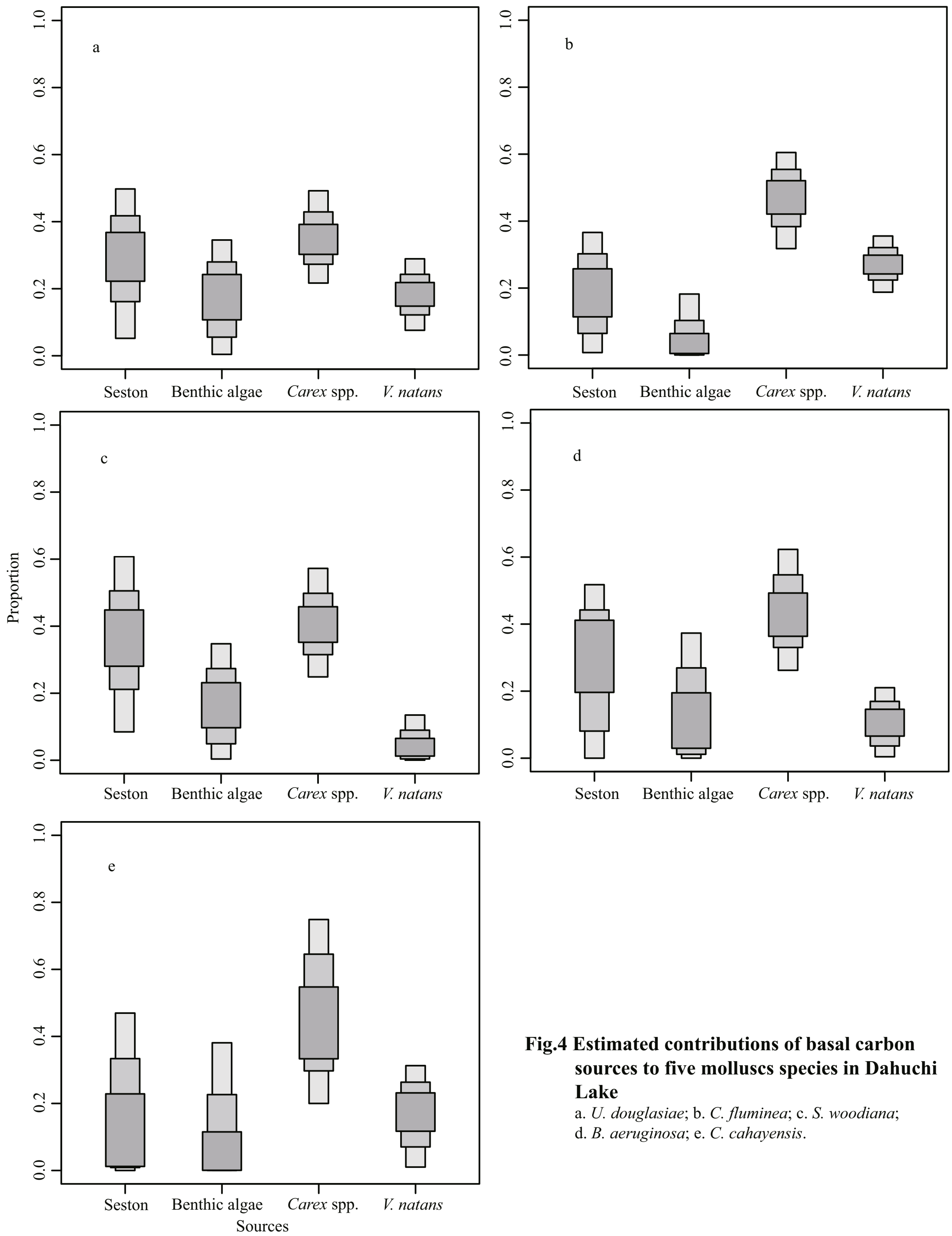

Fig.4 Estimated contributions of basal carbon sources to five molluscs species in Dahuchi Lake

a. *U. douglasiae*; b. *C. fluminea*; c. *S. woodiana*; d. *B. aeruginosa*; e. *C. cahayensis*.

consumers during the winter dry season in Dahuchi Lake, with relatively high contributions, mean ranging from 35% to 50% (Fig.4). Seston was another important source for benthic consumers, with feasible contributions of up to 35% for *S. woodiana* and 28% for *B. aeruginosa*. However, results from mixing models indicated that benthic algae and *V. natans* appeared less important for snails and mussels; on average, the proportional contributions to consumers were less than 20%.

4 DISCUSSION

In floodplain wetland ecosystems, basal food sources for benthic invertebrates are usually considered as limiting to algae and biofilm. For example, Cremona et al. (2014) found that the benthic food web of shallow turbid lakes mostly derived from phytoplanktonic carbon sources, rather than terrestrial materials. However, in this study we demonstrated that terrestrial carbon (*Carex* spp.) could be the primary food source supporting molluscs biomass in Dahuchi Lake during the low water period.

In accordance with our results, several studies have also demonstrated the importance of allochthonous organic carbon of terrestrial origin in underpinning lake food webs (Jones et al., 1998; Pace et al., 2004; Carpenter et al., 2005; Cole et al., 2006). For example, Jones et al. (1998) suggested that about 40% of the carbon resource supporting the pelagic food web in Loch Ness was terrestrial in origin. Additionally, results from whole lake ^{13}C-addition experiments have also provided strong evidence that carbon flows to lake consumers were highly dependent on organic carbon from the catchment (Pace et al., 2004; Carpenter et al., 2005). These findings suggested that terrestrial organic sources enter lake food webs in dissolved form. It appears that *Carex* spp. can be assimilated by benthic consumers via indirect use in the form of dissolved organic carbon (Bartels et al., 2012; Scharnweber et al., 2014). Moreover, evidences from the gut analysis showed that food composition of the mollusc species collected in this study was heavily depended on detritus and phytoplankton (Liu et al., 2006; Liu and Wang, 2007), which was consistent with our modeling results.

Some studies have demonstrated that allochthony of consumers is reduced if nutrients of lake water are enriched (Pace et al., 2004; Carpenter et al., 2005). Given the eutrophic status of Dahuchi Lake, our study still showed high terrestrial resource use for molluscs. In contrast to the study of Carpenter et al. (2005), our study was performed during the winter season, and low light and cold temperature could limit the production of phytoplankton (Schumann et al., 2005), affecting the relative availability of autochthonous carbon for benthic consumers. Compared with the significant terrestrial support, benthic algae and submerged macrophytes presented a lower contribution to benthic consumers in the present study. Meanwhile, molluscs of Dahuchi Lake were highly depleted in ^{13}C relative to *V. natans*, indicating that this carbon source had a lesser contribution to molluscs. It can thus be inferred that the relatively low importance of benthic algae and *V. natans* is related to the low production of these two food resources. Doi (2009) suggested that the inflow of terrestrial subsidies to lake consumers could be affected by resource availability. In the wetlands of Poyang Lake, the *Carex* community is considered as the most extensive, dominant species during the dry season, with more than 50% of the total landscape covered by the *Carex* community (Zhang et al., 2012). In contrast, production of benthic algae could be limited due to the low temperature and highly turbid water caused by the activities of waterbirds (Luo et al., 2010), although lake water depth is very low during the study period. The submerged macrophytes, *V. natans* also had low biomass, due to being extensively grazed by herbivorous waterbirds such as Little swans (*Cygnus columbianus*) and Swan geese (*Anser cygnoides*) (Fox et al., 2011). Due to the low availability of these two carbon sources, they were insufficient in sustaining molluscs biomass during the winter and low water period.

Previous studies have shown that migratory geese can bring a considerable amount of allochthonous nutrients to the waterbodies of wetlands, especially if the wetland is a favored roosting area (Kitchell et al., 1999; Sekercioglu, 2006; Sebastian-Gonzalez et al., 2012). In Dahuchi Lake, hundreds of thousands of wintering geese frequently foraged in *Carex* habitats but roosted nearby at the lake shore (Wu and Ji, 2002). Their excrements contained large amounts of undigested leaves or stems of *Carex* spp. and other vegetation species (Zhang and Lu, 1999; Wang et al., 2013). In this study, we found similar δ^{13}C ratios between geese droppings and molluscs, reflecting that these consumers may have used organic carbon from geese droppings. This finding provides a possible explanation for the use of terrestrial-derived carbon by benthic consumers during a long drought in Poyang Lake's sub-lake. Further research is needed to trace the fate of geese droppings entering lake food webs, and determine how wintering geese influence energy fluxes across ecosystem boundaries in the sub-lakes of Poyang Lake.

Our data suggested that *Carex* spp. contributed, on average, 35%–50% of energy to the benthic consumers in Dahuchi Lake. This is a little difference with the findings of Wang et al. (2011), who have studied the permanently open waters of Poyang Lake. In their study, the energy source of *C. fluminea* was highly depended on terrestrial plants in the dry season, although seston was suggested to be the most important carbon source during the same period (Wang et al., 2011). For *B. aeruginosa*, Wang et al.

(2011) found that the feasible contribution of seston was higher than terrestrial plants. In contrast, our study showed that *B*. *aeruginosa* relied more on *Carex* spp. The variation in the relative importance of terrestrial organic carbon to this snail species was probably associated with the difference between two study habitats during the dry season.

Little variation in $\delta^{13}C$ value among five molluscs species was observed in Dahuchi Lake, indicating that they probably fed on similar food resources. In agreement with this finding, Liu and Wang (2007) also found macroinvertebrate consumers in shallow lakes along the Changjiang (Yangtze) River mainly utilized detritus from adjacent riparian habitats, and the dietary overlap of benthic consumers was relatively high. On the other hand, it was depleted in $\delta^{15}N$ signatures of *C*. *cathayensis* which was largely associated with the low $\delta^{15}N$ values of its main food resources.

Bayesian mixing model analyses of resource and consumer stable isotope composition are biased towards prior or null generalist assumptions (Brett, 2014). In our study, the resource polygon geometry included four potential resources and a surface area of 20.04 SD^2, and the influence of the consumer scenario considered was estimated as ~25%. This indicates that any individual resource outcome below 25% is within the expected background error for this particular polygon resolved by the Bayesian mixing model. In our case, the terrestrial and seston resource that was being assessed contributed to consumer as the dominant resources typically higher than 30%. This indicated the results from our Bayesian mixing model supporting the dominance of terrestrial and seston resource to local food web, which confirmed our main conclusion.

5 CONCLUSION

Most studies have highlighted the importance of allochthonous organic carbon to consumers during the flood period. However, the contribution of this resource has been less concerned during the dry season. This study showed that during the dry season, the energy source for molluscs was largely derived from allochthonous carbon produced by terrestrial vegetation, which could partially explained by the high contribution of allochthonous carbon associated with the predominant biomass of *Carex* spp. Moreover, our results provided a perspective that subsidy of allochthonous carbon to benthic consumers might be facilitated by wintering geese moving between terrestrial areas and waterbody via their droppings.

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