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Intra-lake stable isotope ratio variation in naked carp *Gymnocypris przewalskii* with different body size in Qinghai Lake, China

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ABSTRACT

Stable carbon and nitrogen isotopes were measured in biota collected from Qinghai Lake (China) to describe trophic relationships and diet of naked carp (Gymnocypris przewalskii). The results showed that naked carp were at the apex of the food web with dissolved organic matter (DOM) forming the food web base. $\delta^{13}C$ ranged from -26‰ (DOM) to -18‰ (submerged macrophytes) with invertebrates ranging between -23‰ (benthos) and -20‰ (zooplankton). $\delta^{13}C$ values of naked carp spanned the entire range of other taxa, from -25.7 ‰ to -18.1 ‰, with larger fish having higher $\delta^{13}C$ values. However, $\delta^{15}N$ values of naked carp showed relatively little variation, ranging from 11.3 ‰ to 14.4 ‰. Body size was correlated with $\delta^{13}C$ and $\delta^{15}N$ values, indicating naked carp elevate their trophic position as they mature. Naked carp in Qinghai Lake have a broad diet associated with opportunistic feeding, although larger individuals consume larger preys which have higher trophic positions, including its own young. Opportunistic feeding, including cannibalism, may reflect the response of this top predator to deteriorating ecological conditions in Qinghai Lake. This new knowledge of the feeding behavior and trophic ecology of naked carp can help us manage this potentially endangered species and provide insight into better management and improvement of the current fate of the species.

Keywords Stable isotope , Trophic level, Ontogeny , Cannibalism, Food web

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INTRODUCTION

Qinghai Lake is the largest inland lake in China. Situated 3200 m above sea level on the Qinghai-Tibet Plateau, this alkaline (pH 9.1-9.5) and saline (9-13 ppt) lake is typified by a cool semi-arid climate [1]. Endemic to the lake are naked carp *Gymnocypris przewalskii*, a moderate sized (< 2 kg) cyprinid that migrates between the saline lake and freshwater rivers to spawn during March-July [2]. For the remainder of the year, the fish reside in the lake where most feeding and growth occurs [3, 4]. *G. przewalskii* is the only fish species in the lake and has no competitors or predators [5]. High elevation and low temperature (mean annual air temperature -0.6ºC) limit lake productivity including availability of prey resources. As a result, naked carp grow slowly and have low reproductive output [2, 4]. Overfishing and destruction of spawning habitat through dam building for irrigation had reduced the abundance of naked carp to less than 10% of historic levels by the 1990s [6]. The commercial fishery was suspended in 1994 and some spawning habitat has been restored [7]. However, on-going diversion of water for agriculture, compounded by climate change, has resulted in tributaries drying up, lake levels decreasing, and salinity increasing [7]. The productivity of *G. przewalskii* declined sharply from 230,024 t in 1960 to 3,391 t in 1999 [5]. It has now become an endangered fish and been listed as a state-protected rare species [6]. Besides their economic importance [8], naked carp play a central role in many trophic relationships in the Qinghai Lake ecosystem [4, 9]. Their loss could have serious ecological consequences for the region and would severely degrade the ecological balance of the Qinghai Lake ecosystem [6]. Therefore, understanding the trophic status and feeding behavior of *G. przewalskii* is important for conservation of this species.

Wang [10] described naked carp as omnivorous, with diet changing seasonally in response to prey availability. While ontogenetic differences in diet were noted, no distinction was detected for fish > 45 mm (age 1+). Prey items included invertebrates (primarily copepod zooplankton and midge larvae), algae (mainly diatoms) and sediment [10]. However, in the more than three decades since that study, the lake has undergone considerable environmental changes that may have contributed to shifts in resource availability and feeding behavior. In addition, conventional gut content analyses only provide a snapshot of recent feeding events that might not be typical of the long-term trophic relationships. Stable isotope analyses provide a method to define the functional role of organisms [11-17]. The ratio of nitrogen isotopes ($\delta^{15}N$) can be used to estimate trophic position because $\delta^{15}N$ of a consumer is typically enriched 3-4‰ relative to its diet [18-20]. In contrast, the ratio of carbon isotopes changes very little as carbon moves through food webs [20, 21] and is therefore used to evaluate the carbon source for an organism. In aquatic systems, $\delta^{13}C$ has been used to differentiate littoral production (attached algae and detritus) from pelagic production (phytoplankton) because the $\delta^{13}C$ base of a littoral food web is enriched in ^{13}C relative to the base of the pelagic food web [21]. In this study, we used stable carbon and nitrogen isotopes to characterize the diet of naked carp in Qinghai Lake. An improved understanding of the feeding behavior and trophic position of naked carp will help managers better understand the recovery potential and ecological role of this endangered species.

MATERIALS AND METHODS

Study site

Qinghai Lake has a surface area of about 4,260 km^2 and is fed by a high alpine catchment of 29,660 km^2 on the Qinghai-Tibet Plateau. The climate is dominated by the Southeast monsoon and the high-pressure system of Siberia [22], with long, severe winters and short cool summers. Average monthly air temperature ranges between -14.7 and 15.2ºC (average -0.6ºC), while water temperature ranges between -0.6ºC (January) to 13.5ºC (August). The lake becomes thermally stratified in summer with water temperatures at or below 0ºC from November to March (100-129 ice-days each year). Mean annual precipitation is about 300-400 mm, 80% of which falls between July and September. Evaporation (800-1100 mm) exceeds the freshwater supply (precipitation plus river inflow) leading to declines in lake level and increasing salinity.

Analyses of stable carbon and nitrogen isotopes

Between July and August 2008, fifty naked carp (total length: 19-55 cm, weight: 0.03-1.60 kg) were captured at four sites with the permission of the Qinghai Lake National Nature Reserve. A sample of skinless, boneless, lateral white muscle was removed for stable isotope analyses. White muscle was chosen because it reaches isotopic equilibrium within a few months [23]. To establish trophic position of naked carp, we sampled other dominant food web components. Phytoplankton (mainly Pennatae) was represented by combining three surface tows with a 50 □m plankton nets at each site. Zooplankton were collected with triplicate vertical hauls (3m to surface) of a 250 m plankton net at each site, and separated into three categories: Rotifera, Cladocera and Copepod prior to analysis. Triplicate samples of particulate organic matter (POM) were collected 3m below the surface at each site using a Minitan tangential flow ultrafiltration apparatus fitted with multiple 0.2-μm Durapor (polyvinylidene fluoride) filter plates with three replicates. The concentrated POM was then collected on precombusted Anodisc inorganic filters and dried at 60°C. The ultrafiltrate was acidified and concentrated for dissolved organic matter (DOM) analysis by freeze drying. Five samples of the sediment organic matter (SOM) and benthos from the lake bottom were collected at each site using a petite Ponar. Benthic invertebrate groups consisted of ostracods, amphipods (*Gammarus* spp.), midge larvae (Tendipes) and oligochaetes. Macrophytes (*Potamogeton pectinatus* and *Zannichellia qinghaiensis*) and floating leaves (mainly terrestrial Cyperaceae) were collected with a fishing net.

All samples were oven dried at 70ºC for 48 h and ground finely. Isotope analyses were performed at Stable Isotope Lab for Ecological and Environmental Research, the Chinese Academy of Forestry (Beijing, China). Samples were placed in tin boats and analyzed with a continuous flow elemental analyzer (Flash EA 1112 HT, Thermo Fisher Scientific, USA) and mass spectrometer under the following operating conditions: oxidizing furnace temperature was 900ºC, reducing furnace was 680ºC, pillar temperature was 40ºC. CO_2 was separated in a GC column and injected into a Finnigan MAT Delta^{plus}XP mass spectrometer and collector system, respectively (Thermo Fisher Scientific, USA). CRM was Urea Standard (SIGMA) for QA/QC purposes, which was certificated by Mountain Mass Spec, Inc. (USA). $\delta^{13}C$ and $\delta^{15}N$ values of Urea Standard were -49.1 ‰ and -1.3‰ relative to the international standards (PDB and atmospheric nitrogen gas respectively).The results are expressed in $\delta^{13}C$ and $\delta^{15}N$ relative to the international standards in the conventional δ per mil notation. The interior precision (2δ mean) for $\delta^{13}C$ and $\delta^{15}N$ were 0.02 ‰ and 0.05 ‰ respectively.

Estimation of trophic relationships and gut content analyses

Mean isotopic ratios for juvenile and adult naked carp and their prey were used to establish trophic position ($\delta^{15}N$) and carbon source ($\delta^{13}C$) in Qinghai Lake. Contribution of prey items to the diet of large naked carp was based on the IsoSource software with an increment of 3 ‰ and tolerance of 5 %. Ten dietary sources were used in the model, i.e., naked carp fingerlings, benthos, Qinghai gammarids, zooplankton, SOM, submerged plants, phytoplankton, POM, DOM, and terrestrial floating leaves. The isotopic discrimination values of $\delta^{13}C$ and $\delta^{15}N$ were 1.09 ‰ and 3.41 ‰ respectively, based on artificial feeding experiments with naked carp (body length: 5 to 45 cm) in natural environments at the Qinghai Lake National Nature Reserve. We choose ten carp with body mass over 1200 g (from 55) for gut content analyses and all gut samples were put into sterilized saline water for separation and identification. Large and visible items were separated by naked eyes, while invisible items were separated with aid of microscopes. Percentages of each item were calculated based on dry weight. Occurrence rates of each item in gut contents were also recorded.

Data analysis

Naked carp mature at approximately 7 years of age, which corresponds to a body length of ~26 cm (Walker et al., 1996). We used this criterion to distinguish small (sub-adult) from large (adult) naked carp. Fishes with body length ranged from 29 cm to 55 cm were regarded as large naked carp, n = 31), while those with body length ranged from 19 cm to 26 cm represent small ones (n = 19). Statistical Package for the Social Sciences (SPSS 16.0) was used for data analysis. GLM analyses were used to test for differences in $\delta^{13}C$ or $\delta^{15}N$ for large vs small naked carp, due to inequality of sample size of large and small carp. The error distribution was specified using Levene's Test. If the error variance is equal, LSD Test was used; otherwise, Tamhane Test was used. ANOVA was used to evaluate the relationship between $\delta^{13}C$ and $\delta^{15}N$ values, and between $\delta^{13}C$ (and $\delta^{15}N$) and body size (length and weight) and of naked carp.

RESULTS

The overall shape of the Qinghai Lake food web is encompassed by a convex polygon, with larger naked carp at the apex (higher ^{15}N and ^{13}C signifying higher trophic position and greater reliance on pelagic carbon sources) and DOM at the base (Fig. 1). Floating leaf litter had an expected depleted $\delta^{13}C$ signature characteristic of terrestrial carbon, in comparison to phytoplankton (-21.9‰) and submerged macrophytes (-18.2‰). Taxonomic groups were fairly discrete when using both isotopes, with expected trophic position increasing from lower right to upper left. $\delta^{13}C$ values of naked carp spanned the entire range of other taxa, from -25.7‰ to -18.1‰, suggesting carbon is derived from multiple sources. $\delta^{15}N$ increased expectedly from 2-6‰ (primary producers) to 5-10‰ (consumers) and 11-14‰ (naked carp) (Fig. 1). GLM revealed significant differences in $\delta^{13}C$ (F = 34.391, df = 1, P < 0.0001) and $\delta^{15}N$ (F = 5.058, df = 1, P = 0.029) between small and large naked carp (Fig. 2). There was no significant relationship between $\delta^{13}C$ and $\delta^{15}N$ of naked carp (ANOVA regression, F = 0.140, df = 1, P = 0.710) (Fig. 2). Both $\delta^{13}C$ and $\delta^{15}N$ increased with standard length: (F_C = 41.738, df = 1, P < 0.0001; F_N = 11.324, df = 1, P = 0.002) and weight (F_C = 39.578, df = 1, P < 0.0001; F_N = 16.005, df = 1, P < 0.0001) (Fig. 3). $\delta^{13}C$ of small carp was correlated with their standard length (F = 4.351, df = 1, P = 0.05), however, $\delta^{13}C$ of large carp tended to be scatter response to body length (F = 3.181, df = 1, P = 0.085).

The mixing model analysis using IsoSource revealed the average diet of large naked carp to consist of: 38.9 % naked carp fingerlings, 15.9 % benthos, 10.7 % Qinghai gammarids, 6.7 % zooplankton, 6.6 % SOM, 6.4 % submerged plants, 5 % phytoplankton, 4.5 % POM, 2.2 % DOM, and 2.1 % floating (terrestrial) leaves, well supported by the results of gut content analyses that fingerlings contributed more to food source of naked carp in Qinghai lake (Table 1).

DISCUSSION

The discrete $\delta^{13}C$ signatures for terrestrial (floating) leaves, phytoplankton, and submerged macrophytes enabled us to quantify the relative importance of these carbon pathways to the Qinghai Lake food web. Submerged macrophytes were enriched and showed the highest $\delta^{13}C$ values, while the floating litter was depleted in ^{13}C. This difference was related to CO_2 availability in water and air. Aquatic plants mainly assimilate free CO_2 in water through C_3 photosysthetic pathway [24], while floating litter was often leaves and stems of terrestrial plants that assimilate free atmospheric CO_2 performing C_3 or C_4 photosysthetic pathway. Plants utilizing the Hatch-Slack (C_4) pathway have $\delta^{13}C$ values ($^{13}C/^{12}C$) in the range from -6‰ to -19‰, with an average of -12.5‰, while those utilizing the Calvin (C_3) pathway have $\delta^{13}C$ value between -22‰ to -34‰ [25]. Phytoplankton were not depleted in $\delta^{13}C$ as is often reported in other aquatic ecosystems [26-28]. This difference is likely due to the high pH of Qinghai Lake, prompting phytoplankton to rely on bicarbonate rather than atmospheric CO_2 for photosynthesis [29]. DOM was depleted in ^{13}C relative to POM suggesting significant terrestrial sources of carbon enter the lake ecosystem. SOM and benthos (other than amphipods) reflect a trophic pathway tied back to DOM (terrestrial carbon), while the amphipods and zooplankton rely more heavily on internal POM (phytoplankton) as their carbon source. Submerged macrophytes were highly enriched relative to other taxa suggesting grazer links are weak in the Qinghai Lake food web. This conclusion is supported by Wang [10] who concluded phytoplankton to be the principle primary producer in the system.

Naked carp in Qinghai Lake had $\delta^{13}C$ values that fall between -25.7 ‰ to -18.1 ‰, more negative than those of fishes collected from other freshwater lakes and marine ecosystems [28, 30-32], however, no great difference was found in $\delta^{15}N$ values (11.3 ‰ to 14.4 ‰) from others. The wide range of $\delta^{13}C$ values associated with naked carp individuals indicates they rely on multiple carbon sources for their food. The mixing model analyses reaffirmed this high degree of omnivory, as all possible prey sources were incorporated into the diet of naked carp. We did not find a significant correlation between $\delta^{13}C$ and $\delta^{15}N$ reported for other fish species [33], which can be explained by the fact that fishes are likely to feed on diet with high $\delta^{13}C$ but low $\delta^{15}N$ [34]. The wide variation in $\delta^{13}C$ relative to the small variation in $\delta^{15}N$ reduced the expected pattern of trophic enrichment to a non-significant effect. Large naked carp were enriched in both ^{13}C and ^{15}N relative to smaller individuals, indicating larger individuals consume higher trophic level prey. Such ontogenetic diet shifts have been reported for other species in other systems [12, 35]. A high degree of cannibalism was evident; a result confirmed by our gut content analyses and previous studies [4]. Cannibalism is often more prevalent in stressed or resource-poor systems [36-39]. These results indicated that, although invertebrates could be important part of the diet of large naked carp, carp fingerlings might be the opportunistic prey, as no other small fishes were found in Qinghai Lake [5]. This particular trend as seen in other stressed lakes [36-40] is associated with stressed or resource-poor systems.

$\delta^{13}C$ is an indicator of carbon source [21, 41], and larger naked carp exhibited a higher degree of scatter in $\delta^{13}C$ than small ones, suggesting a higher degree of omnivory which could be interpreted as more opportunistic feeding. This pattern is opposite to that reported by Campbell et al. [42] who suggest smaller-sized fish are more opportunistic in their feeding behavior. These results imply that naked carp might have undergone considerable shifts in feeding behavior in recent three decades, as Wang [10] state that fishes with body length more than 45 mm show no distinction in diet more than thirty years ago. Once again, increased omnivory/opportunism in larger individuals may suggest resource-limitation induced by environmental changes. Biomass and diversity of prey items has decreased in Qinghai Lake as a result of changes in lake chemistry and overfishing [43, 44], supporting our hypothesis that ecological stress has contributed to resource limitation, forcing naked carp to become more opportunistic in prey selection.

Traditional methods to unveil the trophic relationships involve direct observation, gut content analysis, antigen-antibody reaction measurement, and tracers involving radioisotopes and biological pigments [45-47]. This gives a picture of the last meal at a specific time, but might not be typical of the long-term trophic relationships. However, stable isotope techniques have proven to be powerful to reveal long-term feeding behavior and define the functional role of organisms in ecosystem. Naturally occurring stable light isotopes are usually more cost effective and give us a precise picture of whole feeding history [21, 48]. It was the first time that stable isotope technology was used to study diet and trophic relationship of naked carp in Qinghai Lake. The isotopic fingerprints successfully revealed ontogenetic differences in diet and feeding behavior of naked carp characterized by extreme low growth rate. Naked carp represent an economic and ecologically important top predator in Qinghai Lake whose feeding behavior and stable isotopic signatures are possibly associated with food availability and resource limitation. This approach can be adapted to understand other imperiled fishes to address a specific hypothesis or uncertainty about the species, or the ecosystem elsewhere in the world. It has been suggested that large Nile perch may be consuming young of the same species because of the decline in the availability of hapolochromine prey [36]. The difference in stable isotopic values of naked carp with large and small sizes in this study would seem to support the cannibalization hypothesis [35]. Changes in stable isotope values with fish growth may occur due to shifts in diet with increased fish size in naked carp. This new knowledge of the feeding behavior and trophic ecology of naked carp can help us manage this potentially endangered species and provide insight into better management and improvement of the current fate of the species. Restoration of naked carp will require improved access to spawning habitat in tributaries, but also enhanced prey resources in the lake proper. Both of these constraints are strongly influenced by water load, mainly precipitation feeding tributaries that not only provides spawning habitat but also delivers organic matter from the surrounding watershed that stimulates lake productivity. While climate change is affecting patterns of precipitation and evaporation in the region [49], management plans and restoration targets for naked carp need to be developed at the watershed scale.

Table 1 Gut content analyses large naked carp, shown are percentage and occurrence rates of each food item

Food items	Submerged plants	Zooplankton	Qinghai gammarid	Benthos	Phytoplankton	Floating leaves	Fingerling	Unidentified
Percentage (%)	2.18	4.21	7.63	12.48	0.76	1.46	54.73	16.55
Occurrence rate%)	100	100	90	100	100	80	100	100

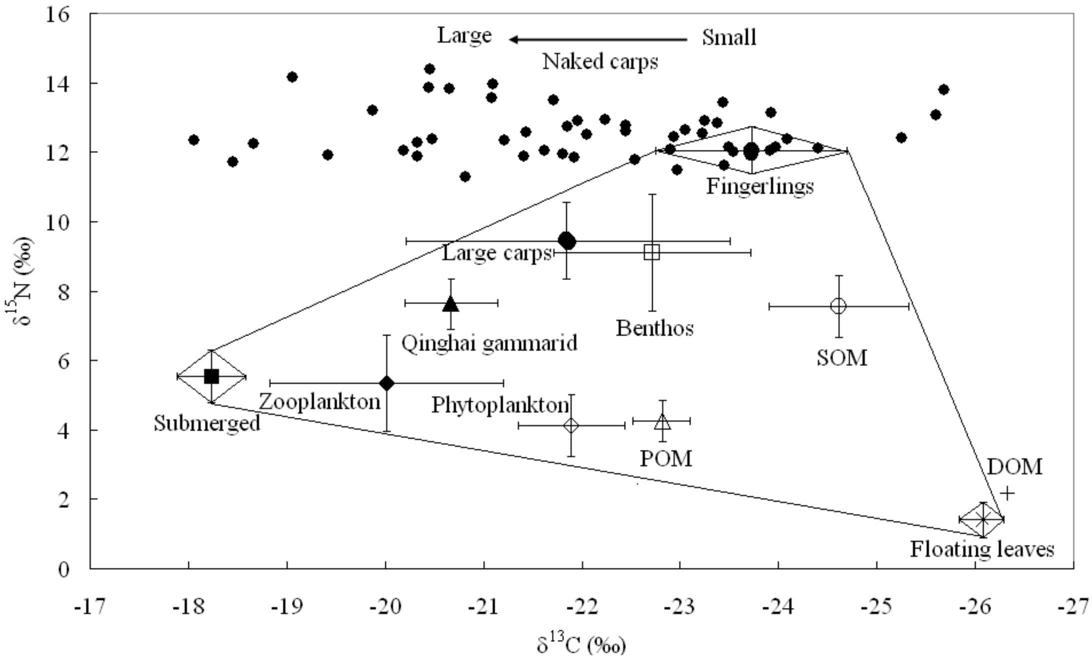

Fig. 1. Stable isotope food web plot for Qinghai Lake, China

δ^{13}C reflects potential carbon sources whereas δ^{15}N increases with increasing trophic level. Relative size of naked carp is indicated. A convex polygon was created by the dietary endpoints where δ^{13}C and δ^{15}N values of large naked carp have been adjusted with the appropriate diet-tissue discrimination factors (1.09 ‰ and 3.41 ‰)

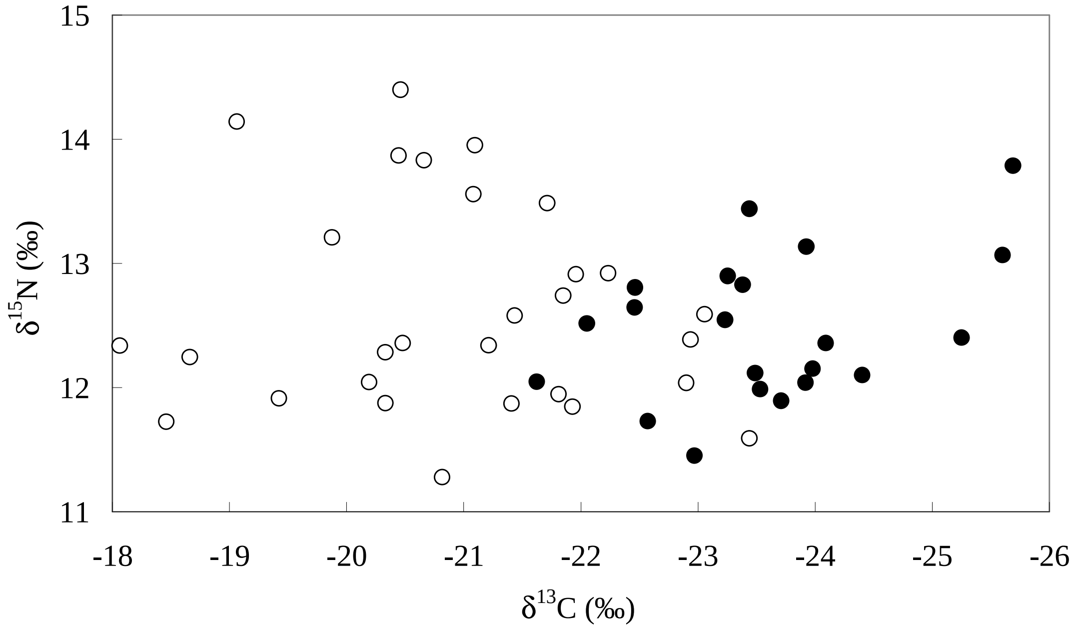

Fig. 2. Relationships between $\delta^{13}C$ and $\delta^{15}N$ for naked carp from Qinghai Lake, China

Fish ranged in size from 19 to 55 cm. Open circles represent large naked carp (body length 29-55 cm, n = 31), while solid circles represent small naked carp (body length 19-26 cm, n = 19)

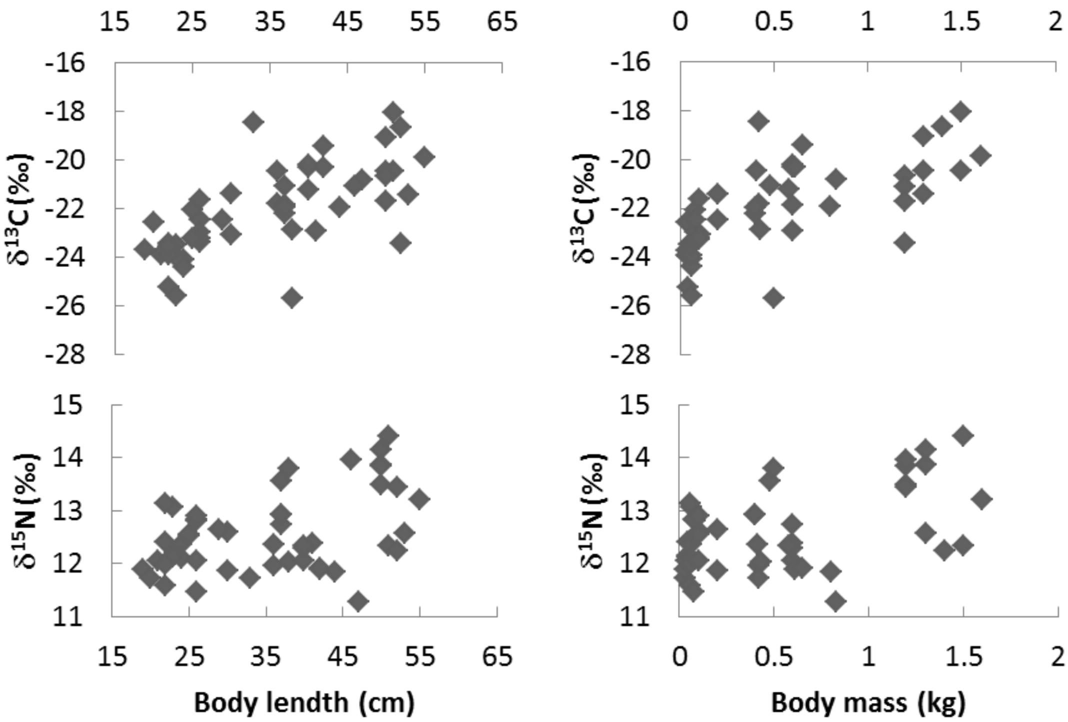

Fig. 3. The relationships between $\delta^{13}C$ and $\delta^{15}N$ and body length and weight for naked carp in Qinghai Lake, China

CONCLUSION

This integration demonstrates that naked carp in Qinghai Lake can serve as a model to understand ecological stress and response, such as exploitation, habitat alteration through modification of hydrologic regime, impacts of climate change on alpine systems [6, 8, 50, 51]. Observations and lessons can be learned from other large lake systems that have faced similar over fishing, loss of top predators, deleterious land use practices, and pollution from various sources, contributing to the mass extinction of indigenous fishes [52-59]. More efforts should be taken to characterize the restoration potential of indigenous fish communities, by considering present-day trophic relationship and diet composition revealed by stable isotope analyses. Consequently, this can provide a basis for establishing restoration targets and developing management actions that will favor successful restoration in fish population in these large lakes.

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