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# Diverse Dietary Strategy of Lake Anchovy *Coilia ectenes taihuensis* in Lakes with Different Trophic Status[1]

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**Abstract**—Omnivores always show flexible foraging habits and actively shift their diets responding to the varying local conditions as well as different ontogenetic trajectories. Littoral fish commonly exhibiting omnivorous diets across pelagic and benthic food webs has the potential effect on trophic dynamics and food web stability. Here, we studied dietary strategy of lake anchovy, a non-migratory omnivorous fish, in two freshwater lakes with distinctly different trophic states to reveal its trophic niche shifts and population-and individual- level feeding habits plasticity using stable isotope analysis. We found lake anchovy exhibited diverse dietary strategies at both population and individual levels according to habitat changes. In eutrophic Chaohu Lake, lake anchovy showed generalized niche but greater individual diet variation and fed primarily on zooplankton. Conversely, lake anchovy exhibited relatively specialized niche and lower individual variation, foraging mainly on shrimps and fishes in mesotrophic Dongting Lake. Hence, habitat trophic status can affect the diet composition of lake anchovy indirectly through complex prey responding, which constrains food web coupling and influence energy flux and trophic dynamics.

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*Keywords*: trophic niche, feeding habits, *Coilia ectenes taihuensis*, stable isotopes, habitat, Lake Chaohu, Lake Dongting

## INTRODUCTION

Omnivory defined as feeding on more than one trophic level (Pimm and Lawton, 1978), is widespread in nature and has the potential to produce complex population interactions through direct predation, trophic cascades, resource competition etc. (Polis et al., 1989; Diehl, 1993). It has been suggested to be a strongly stabilizing force in reticulate food webs (Fagan, 1997). Plastic feeding strategy is essential for species to adapt environmental changes due to anthropogenic perturbations such as eutrophication, habitat modification, and exotic species invasion. Generally, the littoral zone of lakes is more productive compared to the pelagic zone (Schindler and Scheuerell, 2002), thus littoral fish commonly exhibit more flexible foraging habits coupling pelagic and benthic food webs through inter-habitat omnivory (Schindler and Scheuerell, 2002; Eloranta et al., 2013).

Stable isotope ratios in organism tissues are tightly linked to those in their diet (Layman et al., 2007) and are widely used to trace resources within animals, plants and microbes (Newsome et al., 2012). The most commonly used naturally occurring stable isotope ratios are $^{15}N$: $^{14}N$ and $^{13}C$ : $^{12}C$ and $\delta^{13}C$ in consumers varies within 1‰ of their potential prey (DeNiro and Epstein, 1978) providing information on the carbon sources for consumers in lakes (France, 1995), while the trophic enrichment of nitrogen isotopes from food source to predator is around 3.4‰ serves as indicators of an organism's trophic position (Deniro and Epstein, 1981; Post, 2002). Meanwhile, variance of consumer values in δ-space can be a useful proxy for trophic niche width (Bearhop et al., 2004). Layman et al. (2007) proposed the convex hull methods to quantitatively characterize the community-wide aspects of trophic structure in $\delta^{13}C$–$\delta^{15}N$ niche space. Jackson et al. (2011) reformulated this method in a Bayesian framework to allow robust comparison among data sets consisting of variable sample sizes. In addition, it is essential to transform isotopic values into distinct source proportions via stable isotope mixing models in order to allow direct comparison with traditional types of ecological niche (Newsome et al., 2007).

Relatively few studies have investigated the trophic variation at both population and individual levels

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regarding littoral omnivorous fish species inhabiting freshwater lakes. Therefore, our study was conducted in two lakes (i.e. Lake Dongting and Lake Chaohu) with different trophic states located in the middle and downstream reaches of the Yangtze River, focusing on a widespread omnivorous fish called lake anchovy, *Coilia ectenes taihuensis*. The main purposes were to illustrate the spatial trophic niche width changes of lake anchovy at both population and individual levels using stable isotope analysis and also investigated dietary strategy shifts with Bayesian mixing model.

## MATERIALS AND METHODS

### *Study Area*

Lake Dongting (28°40′–29°25′ N, 112°00′–113°15′ E) and Lake Chaohu (31°25′–31°43′ N, 117°16′–117°51′ E), are the second and fifth largest freshwater lakes in China, respectively and take an important part in fishing, transporting, irrigating and local climate regulating. They also serve as an important nursery and feeding ground for numerous fish species such as *Acipenser sinensis, Tenualosa reevesii* (Zhang et al., 2013) and silver fish (*Hemisalanx prognathus Regan*), finless porpoise (*Neophocaena phocaenoides*) (Gao and Zhou, 1995) and many migrant birds (Fox et al., 2008). Due to rapid socioeconomic development and intensive anthropogenic disturbances, water quality of these lakes deteriorated with eutrophication and phytoplankton abundance increased significantly especially in Lake Chaohu. Table 1 has showed the overview of selected limnological characteristics of two studied lakes.

### *Sample Collection and Treatment*

Lake anchovy were collected from fishermen or by using nets during the major fishing season (September, 2013) from each lake. All samples were collected from the littoral zones (approximately 100 m from the shoreline, the average water depth = 1.5 m). We also collected potential food items of lake anchovy in the same areas, including zooplankton, shrimp and prey fishes, due to some previous works on gut content analysis (Diao and Wu, 1982; Guo, 2005; Xu et al., 2007). Zooplankton were collected using a 112-μm plankton net by repeat hauls until a sufficient material was obtained and then held in distilled water to enable gut evacuation. Two dominant shrimp species (*Macrobrachium nipponense* and *Exopalaemon modestus*) and four small-size fish species (*Neosalanx taihuensis, Hemiculter leucisculus, Ctenogobius giurinus* and *Saurogobio dabryi*) were also collected in the same time using a net (mesh size = 5 mm) named Yuduan (see numbers of shrimps and fishes in Table 3).

Each fish was identified, measured total length (*TL*, mm) and a small block of white dorsal muscle was dissected carefully for stable isotope analysis. The tail muscle tissues were anatomized from each shrimp and analyzed. All samples were oven-dried at 60°C for at least 48 h to a constant weight and ground to a fine powder using mortar and pestle (Wang et al., 2011; Xu et al., 2012).

**Table 1.** The average values of selected chemical characteristics of Lakes Dongting and Chaohu from 2008 to 2012*

| Parameters, mg/L | Lake Dongting | Lake Chaohu |
|---|---|---|
| $COD_{Mn}$ | 2.273 | 6.648 |
| $NH_4$-N | 0.292 | 1.988 |
| TN | 1.589 | 7.468 |
| TP | 0.108 | 0.898 |
| Chlorophyll *a* | 3.475 | 12.12 |

COD—chemical oxygen demand, $NH_4$-N—ammonia nitrogen, TN—total nitrogen, TP—total phosphorus; * data from: Yang et al., 2011; Jiang et al., 2014a, 2014b.

### *Stable Isotope Analysis*

The stable carbon and nitrogen isotope ratios of fish muscles and potential food source samples were measured with an EA1110 elemental analyzer (Carlo Erba, Italy) directly coupled to a Finnigan Delta Plus (Thermo Scientific, United States) continuous flow isotope ratio mass spectrometer at Institute of Hydrobiology, Chinese Academy of Sciences. The stable isotope ratios were expressed as δ values relative to the standard reference materials for carbon (Vienna Pee Dee Belemnite, VPDB) and nitrogen (atmospheric nitrogen, $N_2$) defined by: $\delta X (‰) = [(Rsample/Rstandard)-1] \times 1000$. Urea was used as an internal working standard with known isotopic composition and inserted in each run after every 5 to 10 measurements. The international reference materials used for $\delta^{13}C$ and $\delta^{15}N$ were carbonatite (IAEA-USGS24) and ammonium sulfate (IAEA-USGS26), respectively. The average replicated deviations were less than 0.2‰ and 0.3‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

### *Bayesian Mixing Model*

Three dominant food groups (i.e., zooplankton, shrimp and fish) were considered to calculate the feasible diet distribution using a Bayesian mixing model implemented in the SIAR package (Stable Isotope Analysis in R, v. 4.2) (Parnell et al., 2008) because it considered variability in the isotopic values of consumers, food sources, and trophic fractionation factors (Parnell et al., 2010). The trophic enrichment factors were 0.4 ± 1.3‰ for $\delta^{13}C$ and 3.4 ± 1.0‰ for $\delta^{15}N$ (Post, 2002), to account for trophic fractionation.

We used the SIBER (Stable Isotope Bayesian Ellipses in R, Jackson et al., 2011) method (measured as standard ellipse area (SEA) in $\delta^{13}C$–$\delta^{15}N$ space) running in R statistical program (v. 3.1.2) to study iso-

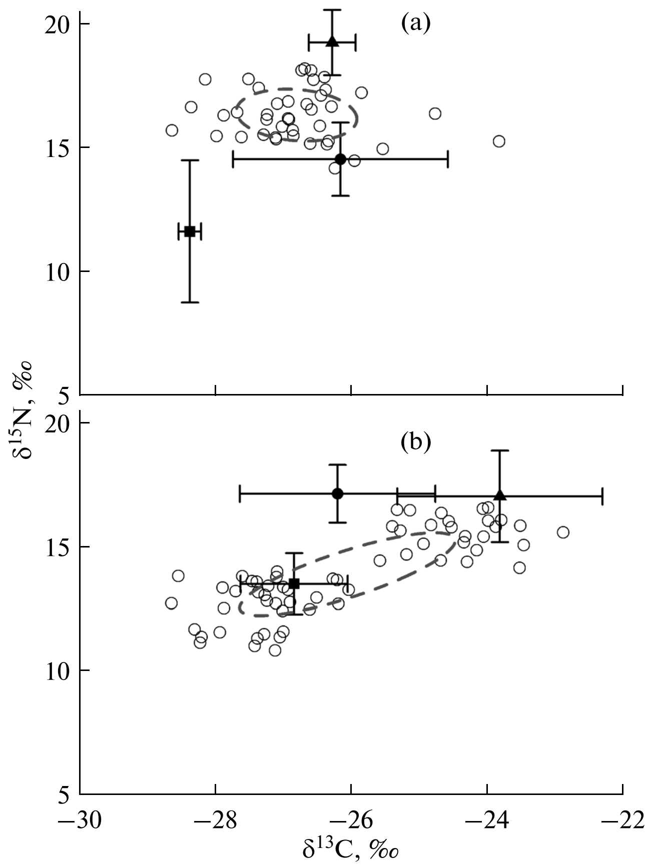


**Fig. 1.** Iso-space plots of all lake anchovy individuals and potential prey items showing the mean (±standard deviation) $\delta^{13}C$ and $\delta^{15}N$ values for fish muscle tissue (○), zooplankton (■), shrimp (▲) and prey fish (●) sampling from Lake Dongting (a) and Lake Chaohu (b). The estimated isotopic niches are depicted as standard ellipses (dashed lines). Source data have been adjusted by fractionation means and SDs. Error bars indicate ±1 SD.

tope niche width of different lake anchovy populations. The former metrics convex-hull methods presented by Layman (Layman et al., 2007) were sensitive to variable sample sizes and may provide an undesirable measure of niche area, whereas the new metric SEA was estimated incorporating uncertainties and other errors related to sampling process (Jackson et al., 2011). The original stable isotopic values were resampled 1000 times to generate 95% credible intervals of SEA.

In addition, we calculated the proportional similarity index $PS_i$ to quantify the degree of diet overlap between each individual and the population using the diet data estimated by SIAR. The population diet's proportion of a given resource category was calculated by adding up the feasible dietary proportions of all individuals for each resource and dividing it by the total use of prey for the population (Bolnick et al., 2002). The index was around 1 (no individual specialization) when all individuals consumed the full population diet and declined to zero (maximum individual specialization) when individuals used smaller subsets of the population diet. The population-wide prevalence of individual specialization (IS) could be calculated by the average of $PS_i$ values (Bolnick et al., 2002). We used the inverse of IS values (1-IS) to measure individual diet variation between different lake anchovy populations. A nonparametric Bootstrap Monte Carlo was operated by assigning each individual diet items drawn randomly from the population's resource distribution to test the null hypothesis that any observed diet variation arose from individuals sampling stochastically from a shared distribution (Bolnick et al., 2002).

### *Statistical Analysis*

We used the Shapiro-Wilk ($n < 50$) and Kolmogorov-Smirnov tests ($n > 50$) to check normality and the Levene's test for Homogenity of variances before statistical analysis. The non-parametric Kruskal–Wallis tests were used to compare differences in stable isotope ratios $\delta^{13}C$ (or $\delta^{15}N$) among three potential prey sources. Differences in $\delta^{13}C$ and $\delta^{15}N$ values, fish lengths and $PS_i$ values of all lake anchovy between Lake Dongting and Lake Chaohu were examined with Mann-Whitney U tests. Spearman's correlations were used to examine the correlation relationships between $PS_i$ values and *TL*. We chose a significance level as $\alpha = 0.05$. All statistical analyses were conducted using R 3.1.2 (R Development Core Team, 2014).

## RESULTS

A total of 102 lake anchovy of which 41 individuals in Lake Dongting and 61 individuals in Lake Chaohu and three dominant prey sources, including 11 zooplankton samples, 38 shrimps and 36 fishes were captured for stable isotope analysis (Fig. 1, Table 2, 3). The *TL* of lake anchovy ranged between 54–290 mm (Table 2) and lake anchovy caught from Lake Dongting were relatively large (Fig. 2). The largest and smallest lake anchovy fish catches were both appeared in Lake Chaohu, in addition, almost 60% individuals were less than 130 mm in Lake Chaohu (Fig. 2).

Three potential prey groups, zooplankton, shrimp and fish, had distinctly different $\delta^{13}C$ and $\delta^{15}N$ values within each lake (all $p < 0.05$, Fig. 1, Table 3) of which zooplankton caught from Lake Chaohu ($\delta^{13}C$: $-27.25 \pm 0.83$‰, $\delta^{15}N$: $10.08 \pm 0.72$‰) exhibited more enriched $\delta^{13}C$ and $\delta^{15}N$ than Lake Dongting ($\delta^{13}C$: $-28.8 \pm 0.3$‰, $\delta^{15}N$: $8.2 \pm 2.7$‰, Table 3). For shrimp and fish, multiple species have been combined because there was low variation in isotope values among species.

Lake anchovy showed significantly different $\delta^{13}C$ ($U = 1004$, $n = 102$, $p < 0.05$) and $\delta^{15}N$ ($U = 2191$, $n = 102$, $p < 0.001$) values between two study lakes which had significantly depleted $\delta^{13}C$ but significantly

**Table 2.** Summary of trophic niche metrics (mean±SD; SEA, average and 95% Bayesian credible intervals of standard ellipse area; 1-IS—mean specialization index), total length (*TL*, ranges in parentheses) and Mann–Whitney U test results between lakes of each parameter

| Lake | $\delta^{13}C$, ‰ | $\delta^{15}N$, ‰ | SEA | 1-IS | *TL*, mm |
|---|---|---|---|---|---|
| Dongting ($n = 41$) | –26.81 ± 0.88 | 16.28 ± 1.05 | 2.88 (2.10–3.97) | 0.0778 ± 0.0519 | 132.61 (75–215) |
| Chaohu ($n = 61$) | –26.07 ± 1.58 | 13.87 ± 1.67 | 4.87 (4.09–5.95) | 0.1921 ± 0.0886 | 126.73 (54–290) |
| Statistics: | | | | | |
| – *U* | 1004 | 2191 | 492 | 354 | 1439.5 |
| – *p* | 0.046 | 0.0001 | 0.0001 | 0.0001 | 0.099 |

Numbers of lake anchovy samples are given in parentheses following the lake names.

enriched $\delta^{15}N$ values in Lake Dongting compared to Lake Chaohu. The average $\delta^{15}N$ value in Lake Chaohu (13.87‰) was much lower than the minimum $\delta^{15}N$ value in Lake Dongting (14.14‰, Table 2). Besides, the muscle tissue of lake anchovy revealed broader ranges of $\delta^{13}C$ (–28.65 to –22.9‰) and $\delta^{15}N$ (10.81 to 16.55‰) in Lake Chaohu (Table 2).

Consequently, the results calculated from SIAR mixing model (Fig. 3) indicated a greater reliance on more enriched prey (e.g. shrimp and fish) of lake anchovy in Lake Dongting compared to Lake Chaohu. The total contributions of shrimp and fish to lake anchovy in Lake Dongting were 76%. Zooplankton was the most important food resource in Lake Chaohu (approximately 81%) and the contribution of fish was negligible (5%), which was consistent with the depleted $\delta^{15}N$ values.

The lake anchovy caught from Lake Chaohu showed larger isotopic niche and a higher degree of individual dietary variation compared to Lake Dongting population (Fig. 1, Table 2). The mean specialization index (1-IS) in Lake Dongting was significantly small (1-IS = 0.0778, $U = 354$, $n = 102$, $p < 0.001$), indicating individuals were more generalized in their diet. In addition, we found a significantly negative correlation relationship between $PS_i$ values and *TL* in Lake Dongting ($r = –0.4318$, $p < 0.01$) which also occurred in Lake Chaohu ($r = –0.1504$, $p = 1237$, non-significant).

## DISCUSSION

Stable isotope analysis revealed that diets of lake anchovy differed distinctly in Lakes Dongting and Chaohu. Meanwhile, lake anchovy exhibited significant spatial variation in isotopic composition and trophic niche width at both population and individual levels. These differences were partly reflecting the diverse feeding strategies of this fish in lakes with different trophic status (Table 1).

Generally, isotopic composition of a consumer reflects its assimilated diet over a period of time (Xu et al., 2008). As shown in our study, lake anchovy exhibit striking different preference for heavy isotopes between lakes with more enriched $\delta^{13}C$ but depleted $\delta^{15}N$ in Lake Chaohu and more depleted $\delta^{13}C$ but enriched $\delta^{15}N$ in Lake Dongting (Table 2). Differences in $\delta^{13}C$ and $\delta^{15}N$ values may therefore reflect diet shifts between habitats with differing trophic status. For example, we found that lake anchovy showed relatively enriched $\delta^{13}C$ in Lake Chaohu, but the contribution of zooplankton was exceeding 80%, whereas lake anchovy fed mostly on benthic prey but depleted in $\delta^{13}C$ in Lake Dongting. One explanation is that pri-

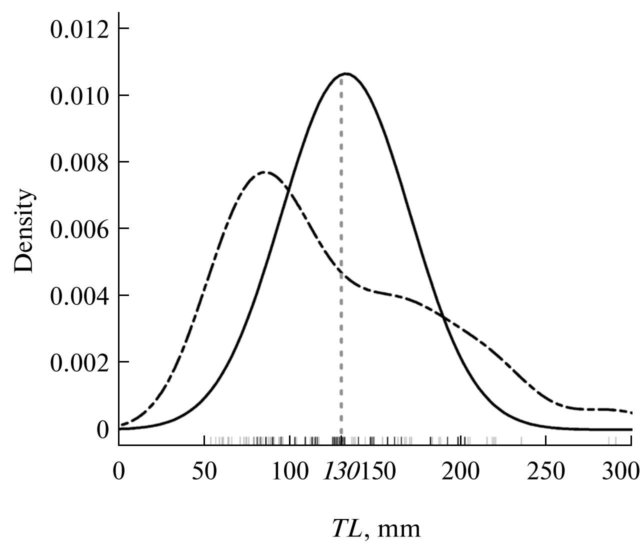


**Fig. 2.** The probability density distributions of lake anchovy total length (*TL*) in Lake Dongting (—) and Lake Chaohu (–––). The dotted line (---) represents the watershed between small and large lake anchovy (*TL* = 130 mm).

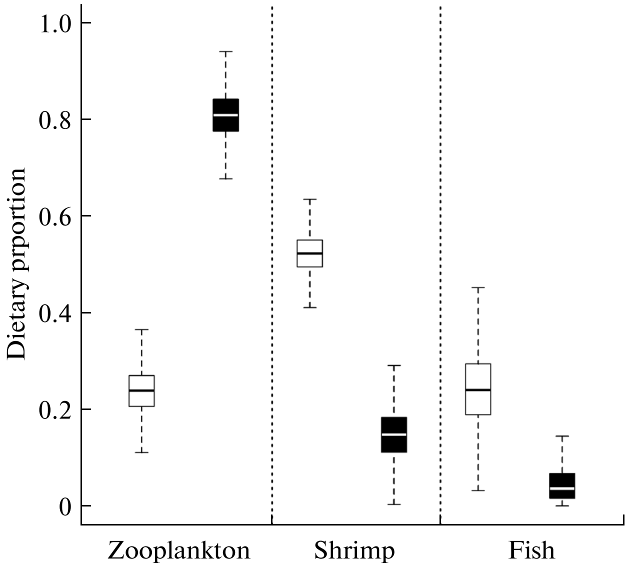


**Fig. 3.** Feasible dietary distributions of lake anchovy sampled from Lake Dongting (□) and Lake Chaohu (■). Boxes indicate 75% credible intervals and the position of the median; error bars show ranges of 95% confidence intervals. Source proportions were estimated with SIAR package implemented in R.

mary producers and zooplankton usually present enriched $\delta^{13}C$ and $\delta^{15}N$ in eutrophic lakes due to the enriched anthropogenic nutrients inflowing (Gu et al., 1996; Xu et al., 2005). This argument is in agreement with the results of previous studies that Xu et al. (2008) found shrimps from Lake Taihu showed relatively enriched $\delta^{13}C$ and $\delta^{15}N$ values than those in less eutrophic Lake Chaohu. A complementary transformation of δ-values also shows significantly different feeding habits between two lake anchovy populations of which rely mostly on high-quality prey, including shrimp and fish in Lake Dongting consistent with their enriched $\delta^{15}N$ values, although zooplankton also act as an important food source at a contribution of 24% (Fig. 3). On the contrary, lake anchovy show a great reliance on the pelagic food webs in Lake Chaohu (Fig. 3).

In aquatic ecosystem, fish predators always show considerable plastic feeding habits and sometimes undergo diet shifts that switch from small prey to fish during their first or second year of life (Persson and Greenberg, 1990). The increased proportion of larger prey in their diet probably reflects the enhanced effect of optimal foraging behavior in rapid growth (Wanink and Joordens, 2007). Lake anchovy, a non-migratory small-sized fish, fed on different resources during ontogeny referring to the previous studies (Diao and Wu, 1982; Xu et al., 2007). Small lake anchovy ($TL <$ 130 mm) fed primarily on zooplankton, including cladocerans and copepods, added benthic prey such as shrimps and chironomid larvae at > 130 mm and increased fish forage as *TL* was greater than 190 mm (Diao and Wu, 1982; Xu et al., 2007). With respect to lake anchovy in our study, it ranged from 54 to 290 mm in *TL* and a huge part of captures in Lake Chaohu (approximately 60%) was less than 130 mm. However, small individuals ($TL < 130$ mm) contributed only about 50% in Lake Dongting. The predominance of small lake anchovy may therefore give supports to the zooplankton-specialist diet in Lake Chaohu.

Fish predators often develop specific foraging strategies corresponding to the varying local conditions, including relative abundance of food sources, the distribution and quality of prey and predation risk, to maximize the net energy gains eliminating costs of handling and searching (Stephens and Krebs, 1986; Svanbäck and Bolnick, 2005). Accordingly, eutrophic lakes commonly have relatively lower abundance of prey resources and diversities due to intense anthropogenic disturbances. Moreover, trophic status is often

**Table 3.** Differences in stable isotope values of lake anchovy prey used in SIAR mixing model

| Lake | Food sources | $N$ | $\delta^{13}C$, ‰ | | | $\delta^{15}N$, ‰ | | |
|---|---|---|---|---|---|---|---|---|
| | | | mean | SD | $\chi^2$ ($p$) | mean | SD | $\chi^2$ ($p$) |
| Dongting | Zooplankton | 4 | –28.78 | 0.25 | 7.51 ($p < 0.05$) | 8.18 | 2.68 | 16.87 ($p < 0.001$) |
| | Shrimp | 6 | –26.69 | 0.44 | | 15.79 | 0.86 | |
| | Fish | 18 | –26.57 | 1.42 | | 11.07 | 1.09 | |
| Chaohu | Zooplankton | 7 | –27.25 | 0.83 | 30.66 ($p < 0.001$) | 10.08 | 0.72 | 17.21 ($p < 0.001$) |
| | Shrimp | 32 | –24.23 | 1.37 | | 13.6 | 1.55 | |
| | Fish | 18 | –26.61 | 1.32 | | 13.71 | 0.59 | |

Numbers of each prey category used for stable isotope analysis is visible in the column names *N*.

identified as the main factor that leads to differences in zooplankton abundance in freshwater lakes (Yang et al., 2012). In Lake Chaohu, zooplankton availability was high relative to that of shrimps and prey fishes and body size of lake anchovy was relatively small. These conditions would have forced the fish to choose zooplankton as the main food. Meanwhile, $\delta^{15}N$ values also provided specific evidence for the zooplankton specialist diet of the fish population. However, we found a wide isotopic niche breadth at the population level based on the muscle $\delta^{13}C$ and $\delta^{15}N$ values coinciding with the former opinion that under harsh conditions, species with wide resource niches could maintain a high level of fitness (Richmond et al., 2005). Besides, lake anchovy showed broader ranges of stable carbon and nitrogen signatures but less diet overlap between each individual and the population (Table 2). Therefore, we could conclude that the broad total niche breadth was induced by between individual variation, which was consistent with the niche variation hypothesis (NVH). Van Valen (1965) proposed that population would have broad niche width when variation among individuals in the population increased. However, relatively abundant prey shrimps and fishes along with larger body size would allow lake anchovy to shift to feed primarily on benthic food in Lake Dongting. Additionally, we also found the diet overlap between individuals and population was reduced gradually throughout growing up particularly in Lake Dongting. Optimal foraging theory predicts that fish predators will actively choose the more profitable and easier detectable preys to maximize energetic benefits when resources are abundant (MacArthur and Pianka, 1966). Therefore, large lake anchovy ($TL > 130$ mm) in Lake Dongting mostly switched to prey on shrimps and other fishes in order to require enough energy for growth and reproduction. Generally, as also found in our study, changes in local prey abundance and availability due to eutrophication as well as fish body size were both critical factors determining foraging habits (Briones et al., 2012).

Previous studies have revealed that omnivorous fish act as an important link between pelagic and benthic food webs of lake ecosystems (Vander Zanden and Vadeboncoeur, 2002; Wang et al., 2011; Xu et al., 2007). The main food sources of lake anchovy are zooplankton, shrimps and small fishes and its relative reliance varies according to prey abundances and ontogenetic development. In Lake Chaohu, anchovy exhibited relatively specialized diet in zooplankton and shrimp contributed only 16% in small groups ($TL < 130$ mm) (Fig. 3). Both intrapopulation diet differentiation and distinct growth phases in the use of resources may limit the fluxes of energy and nutrients across spatially separated pelagic and benthic food webs (Quevedo et al., 2009). In addition, lake anchovy show similar habitat and diet preferences with icefish (*Neosalanx taihuensis*) which is of value and commercial importance in Lake Chaohu (Yang et al., 2008). Unlike lake anchovy, icefishes showed relatively stable diet contents and the major diet components were zooplankton (Liu, 2001). The populations and commercial catches of icefish have declined sharply in recent years due to greatly environmental changes and intensively competitive pressures from sympatric species especially lake anchovy. Additionally, predation pressure by lake anchovy and other obligate zooplanktivorous fish in Lake Chaohu may change the zooplankton composition and abundance markedly leading to extensive algae bloom and aggravated eutrophication. Accordingly, it is essential to manipulate planktivorous fish stocks by intense fishing in order to reduce the abundance of planktonic algae which serve as food for the zooplankton. Meanwhile, an external nutrient loading reduction is also an indispensable part of shallow lakes restoration from eutrophication.

In conclusion, we found two distinctly different dietary strategies of lake anchovy in eutrophic Lake Chaohu and mesotrophic Lake Dongting based on stable isotope analysis. Environmental changes especially eutrophication, can affect the diet composition indirectly through complex prey response, causing alternative feeding habits to adapt varying local conditions. Ontogenetic dietary shifts are also an important adaptation to resource abundance and accessibility. Changes in dietary strategies of omnivorous fish, including individual diet divergence and ontogenetic dietary shifts, may restrict the efficiency of pelagic and benthic food web coupling and influence trophic dynamics and food web stability (Huxel and McCann, 1998). Therefore, shifts of dietary strategy due to anthropogenic disturbances and its impacts on community structures and trophic dynamics are essential to further studies.

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## REFERENCES

Bearhop, S., Adams, C.E., Waldron, S., Fuller, R.A., and MacLeod, H., Determining trophic niche width: a novel approach using stable isotope analysis, *J. Anim. Ecol.*, 2004, vol. 73, no. 5, pp. 1007–1012.

Bolnick, D.I., Yang, L.H., Fordyce, J.A., Davis, J.M., and Svanbäck, R., Measuring individual-level resource specialization, *Ecology*, 2002, vol. 83, no. 10, pp. 2936–2941.

Briones, J.C., Tsai, C.-H., Nakazawa, T., Sakai, Y., Papa, R.D.S., Hsieh, C.-H., and Okuda, N., Long-term changes in the diet of *Gymnogobius isaza* from Lake Biwa, Japan: effects of body size and environmental prey availability, *PloS One*, 2012, vol. 7, no. 12, p. e53167.

DeNiro, M.J. and Epstein, S., Influence of diet on the distribution of carbon isotopes in animals, *Geochim. Cosmochim. Acta*, 1978, vol. 42, no. 5, pp. 495–506.

DeNiro, M.J. and Epstein, S., Influence of diet on the distribution of nitrogen isotopes in animals, *Geochim. Cosmochim. Acta*, 1981, vol. 45, no. 3, pp. 341–351.

Development Core Team, *A Language and Environment for Statistical Computing*, Vienna: Found. Stat. Comput., 2014.

Diao, Z.S. and Wu, X.C., Dynamic of lake anchovy resource and suggestion of fishery utilization (in Chinese), in *Research Report on the Enhancement of Fisheries Resources in Lake Chaohu*, Chaohu: Fish. Manage. Comm. Lake Chaohu, 1982, vol. 1, pp. 62–73.

Diehl, S., Relative consumer sizes and the strengths of direct and indirect interactions in omnivorous feeding relationships, *Oikos,* 1993, vol. 68, no. 1, pp. 151–157.

Eloranta, A.P., Knudsen, R., and Amundsen, P.-A., Niche segregation of coexisting Arctic charr (Salvelinus alpinus) and brown trout (*Salmo trutta*) constrains food web coupling in subarctic lakes, *Freshwater Biol.,* 2013, vol. 58, no. 1, pp. 207–221.

Fagan, W.F., Omnivory as a stabilizing feature of natural communities, *Am. Nat.*, 1997, vol. 150, no. 5, pp. 554–567.

Fox, A.D., Cao, L., Barter, M., Rees, E.C., Hearn, R.D., Cong, P.H., Wang, X., Zhang, Y., Dou, S.T., and Shao, X.F., The functional use of East Dongting Lake, China, by wintering geese, *Wildfowl*, 2008, vol. 58, pp. 3–19.

France, R.L., Differentiation between littoral and pelagic food webs in lakes using stable carbon isotopes, *Limnol. Oceanogr.*, 1995, vol. 40, no. 7, pp. 1310-1313.

Gao, A. and Zhou, K., Geographical variations of external measurements and three subspecies of *Neophocaena phocaenoides* in Chinese waters, *Acta Theriol. Sin.,* 1995, vol. 15, no. 2, pp. 81–92.

Gu, B., Schelske, C., and Hoyer, M., Stable isotopes of carbon and nitrogen as indicators of diet and trophic structure of the fish community in a shallow hypereutrophic lake, *J. Fish Biol.*, 1996, vol. 49, no. 6, pp. 1233–1243.

Guo, L.G., Studies on fisheries ecology in a large euthrophic shallow lake, Lake Chaohu, *PhD Thesis*, China: Inst. Hydrobiol., Chin. Acad. Sci., 2005.

Huxel, G.R. and McCann, K., Food web stability: the influence of trophic flows across habitats, *Am. Nat.*, 1998, vol. 152, no. 3, pp. 460–469.

Jackson, A.L., Inger, R., Parnell, A.C., and Bearhop, S., Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R, *J. Anim. Ecol.*, 2011, vol. 80, no. 3, pp. 595–602.

Jiang, Y., Chen, L., Li, L.Q., Zou, Z.R., and Dai, W.N., Time series analysis of Dongting lake water quality, *Liaoning Chem. Ind.,* 2014a, vol. 43, no. 3, pp. 288–291.

Jiang, Y.J., He, W., Liu, W.X., Qin, N., Ouyang, H.L., Wang, Q.M., Kong, X.Z., He, Q.S., Yang, C., and Yang, B., The seasonal and spatial variations of phytoplankton community and their correlation with environmental factors in a large eutrophic chinese lake (Lake Chaohu), *Ecol. Indica*, 2014b, vol. 40, pp. 58–67.

Layman, C.A., Arrington, D.A., Montaña, C.G., and Post, D.M., Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology*, 2007, vol. 88, no. 1, pp. 42–48.

Liu, Z., Diet of the zooplanktivorous icefish *Neosalanx pseudotaihuensis* Zhang, *Hydrobiologia*, 2001, vol. 459, no. 1, pp. 51–56.

MacArthur, R.H. and Pianka, E.R., On optimal use of a patchy environment, Am. Nat., 1966, vol. 100, no. 916, pp. 603–609.

Newsome, S.D., del Rio, C.M., Bearhop, S., and Phillips, D.L., A niche for isotopic ecology, *Front. Ecol. Environ.*, 2007, vol. 5, no. 8, pp. 429–436.

Newsome, S.D., Yeakel, J.D., Wheatley, P.V., and Tinker, M.T., Tools for quantifying isotopic niche space and dietary variation at the individual and population level, *J. Mammal.*, 2012, vol. 93, no. 2, pp. 329–341.

Parnell, A., Inger, R., Bearhop, S., and Jackson, A.L., SIAR: stable isotope analysis in R, Comprehensive R archive network, 2008. http://cran.r-project.org/web/packages/siar/index.html

Parnell, A.C., Inger, R., Bearhop, S., and Jackson, A.L., Source partitioning using stable isotopes: coping with too much variation, *PLoS One*, 2010, vol. 5, no. 3, p. e9672.

Persson, L. and Greenberg, L.A., Juvenile competitive bottlenecks: the perch (*Perca fluviatilis*)–roach (*Rutilus rutilus*) interaction, *Ecology*, 1990, vol. 71, no.1, pp. 44–56.

Pimm, S. and Lawton, J., On feeding on more than one trophic level, *Nature*, 1978, vol. 275, no. 5680, pp. 542–544.

Polis, G.A., Myers, C.A., and Holt, R.D., The ecology and evolution of intraguild predation: potential competitors that eat each other, *Annu. Rev. Ecol. Syst.*, 1989, vol. 20, pp. 297–330.

Post, D.M., Using stable isotopes to estimate trophic position: models, methods, and assumptions, *Ecology*, 2002, vol. 83, no. 3, pp. 703–718.

Quevedo, M., Svanback, R., and Eklov, P., Intrapopulation niche partitioning in a generalist predator limits food web connectivity, *Ecology,* 2009, vol. 90, no. 8, pp. 2263–2274.

Richmond, C.E., Breitburg, D.L., and Rose, K.A., The role of environmental generalist species in ecosystem function, *Ecol. Model.,* 2005, vol. 188, no. 2, pp. 279–295.

Schindler, D.E. and Scheuerell, M.D., Habitat coupling in lake ecosystems, *Oikos,* 2002, vol. 98, no. 2, pp. 177–189.

Stephens, D.W. and Krebs, J.R., *Foraging Theory*, Princeton: Princeton Univ. Press, 1986.

Svanbäck, R. and Bolnick, D.I., Intraspecific competition affects the strength of individual specialization: an optimal diet theory method, *Evol. Ecol. Res.*, 2005, vol. 7, no. 7, pp. 993–1012.

Valen van, L., Morphological variation and width of ecological niche, *Am. Nat.*, 1965, vol. 99, no. 908, pp. 377–390.

Vander Zanden, M.J. and Vadeboncoeur, Y., Fishes as integrators of benthic and pelagic food webs in lakes, *Ecology*, 2002, vol. 83, no. 8, pp. 2152–2161.

Wang, Y., Yu, X., and Xu, J., Decreased trophic position as a function of increasing body size of a benthic omnivorous fish from the largest freshwater lake in China, *Environ. Biol. Fish.*, 2011, vol. 91, no.4, pp. 505–512.

Wanink, J.H. and Joordens, J.C.A., Dietary shifts in *Brycinus sadleri* (Pisces: Characidae) from southern Lake Victoria, *Aquat. Ecosyst. Health*, 2007, vol. 10, no. 4, pp. 392–397.

Xu, J., Wen, Z.R., Gong, Z.J., Zhang, M., Xie, P., and Hansson, L.-A., Seasonal trophic niche shift and cascading effect of a generalist predator fish, *PloS One*, 2012, vol. 7, no. 12, p. e49691.

Xu, J., Xie, P., Zhang, M., and Yang, H., Variation in stable isotope signatures of seston and a zooplanktivorous fish in a eutrophic Chinese lake, *Hydrobiologia*, 2005, vol. 541, no. 1, pp. 215–220.

Xu, J., Zhang, M., and Xie, P., Size-related shifts in reliance on benthic and pelagic food webs by lake anchovy, *Ecoscience*, 2007, vol. 14, no. 2, pp. 170–177.

Xu, J., Zhang, M., and Xie, P., Stable isotope changes in freshwater shrimps (*Exopalaemon modestus* and *Macrobrachium nipponensis*): trophic pattern implications, *Hydrobiologia*, 2008, vol. 605, no. 1, pp. 45–54.

Yang, L.B., Han, X.Y., Sun, P., Yan, W.J., and Li, Y.C., Canonical correspondence analysis of algae community and its environmental factors in the Lake Chaohu, China, *J. Agro-Environ. Sci.*, 2011, vol. 30, no. 5, pp. 952–958.

Yang, Q.C., Liu, E.S., Bao, C.H., Wu, C.J., Wang, S.R., Li, H.Y., and Song, X.M., Analysis of the component of the food for *Neosalanx tangkahkeii taihuensis* in Chaohu Lake, *J. Anhui Agric. Sci.*, 2008, vol. 36, no. 36, pp. 15922–15924.

Yang, G.J., Qin, B.Q., Tang, X.M., Gong, Z.J., Zhong, C.N., Zou, H., and Wang, X.D., Contrasting zooplankton communities of two bays of the large, shallow, eutrophic Lake Taihu, China: their relationship to environmental factors, *J. Great Lakes Res.*, 2012, vol. 38, no. 2, pp. 299–308.

Zhang, H., Wu, G.G., Zhang, H., Xie, P., Xu, J., and Zhou, Q., Role of body size and temporal hydrology in the dietary shifts of shortjaw tapertail anchovy *Coilia brachygnathus* (Actinopterygii, Engraulidae) in a large floodplain lake, *Hydrobiologia*, 2013, vol. 703, no. 1, pp. 247–256.