

3.2.4 A Food Web and its Long-term Dynamics in Lake Biwa: A Stable Isotope Approach

Noboru Okuda · Tomohiro Takeyama · Takefumi Komiya · Yoshikazu Kato
Yutaka Okuzaki · Jin'ichi Karube · Yoichiro Sakai · Michio Hori · Ichiro Tayasu
Toshi Nagata

Abstract We delineated the food web structure of the current ecosystem in Lake Biwa using stable isotope analysis (SIA) for a total of 1,163 specimens, including 29 fish species, 8 macrozoobenthos taxa and macrozooplankton (a mixture of copepods and cladocerans) with their basal foods. These animals occupied a variety of trophic positions and their trophic pathways were integrated by a top predator, the Biwa giant catfish (*Silurus biwaensis*), whose trophic level was estimated as 3.75. A food web of this lake highly relied on phytoplankton production, reflecting predominance of the pelagic habitat characteristic of deep lakes. We also measured the nitrogen isotope ratio for 1,177 archival specimens, including 45 aquatic species collected from the lake since 1914, to view the long-term trophic dynamics at the community level. As a whole, fish trophic levels rose in the 1970s when nutrient loadings began to occur, whereas they drastically decreased between

the 1980s and 1990s, during which eutrophication progressed, exotic fishes propagated, and littoral habitats were extensively modified. We stress that our stable isotopic approach is useful in assessing human impacts on lake ecosystems.

Keywords Archival specimens • Ecosystem assessment • Endemism • Production reliance • Trophic level

How to Assess Human Impacts on Food Webs?

All over the world, there are no longer lakes free from anthropogenic disturbances, including climatic changes. Especially local human activities, such as nutrient loadings, habitat destruction, overexploitation, and exotic species introduction, are considered strong drivers for ecosystem alteration of lakes. However, it is difficult, even for scientists, to answer exactly how and when they were altered, although it is easy to imagine. In order to manage lake ecosystems that provide public services, we have to quantitatively assess how each human activity can affect the properties of their ecosystems. Although traditional long-term studies on lake ecosystems are usually based on archival water chemistry data (Smith et al. 2006), such approaches only focus on a facet of the whole ecosystem. In contrast, archival biological specimens may provide us with a holistic view of long-term changes in their natal ecosystem because ecological and environmental information are recorded in their tissues in the form of stable isotope ratios.

SIA is a powerful tool to study food webs in lake ecosystems (Vander Zanden and Vadeboncoeur 2002; Vander Zanden and Fetzer 2007). The principle of this analysis is based on the general pattern that a consumer's carbon isotope ratio ($\delta^{13}\text{C}$) reflects its basal food source (DeNiro and Epstein 1978), while its nitrogen isotope ratio ($\delta^{15}\text{N}$) is

N. Okuda (✉) · J. Karube · Y. Sakai · I. Tayasu
Center for Ecological Research, Kyoto University,
2-509-3 Hirano, Otsu, Shiga 520-2113, Japan
e-mail: nokuda@ecology.kyoto-u.ac.jp

T. Takeyama
Department of Biology and Geosciences, Osaka City
University, 3-3-138 Sugimoto, Osaka 558-8585, Japan

T. Komiya · Y. Okuzaki · M. Hori
Department of Zoology, Kyoto University, Kitashirakawa
Oiwake-cho, Kyoto 606-8502, Japan

Y. Kato
Department of General Systems Studies, The University
of Tokyo, 3-8-1 Komaba, Meguro-ku, Tokyo 153-8902,
Japan

T. Nagata
Atmosphere and Ocean Research Institute,
The University of Tokyo, 5-1-5 Kashiwanoha,
Kashiwa, Chiba 277-8564, Japan

enriched by a given factor through trophic interactions (Minagawa and Wada 1984). It is also useful to perceive food web alterations under human disturbances (Vander Zanden et al. 1999; Layman et al. 2007; Anderson and Cabana 2009). A recent study has demonstrated that the technique is applicable to the $\delta^{15}\text{N}$ measurement for archival specimens preserved in organic solvents (Ogawa et al. 2001). Although it enables us to examine the long-term variation in the trophic level (hereafter *TL*) of a focal species (Nakazawa et al. 2010), the application to trophic dynamics at the community level remains limited and challenging (but see Vander Zanden et al. 2003).

In this section, we first delineate the food web structure of the current Lake Biwa ecosystem, which is characterized by the predominance of the pelagic habitat and endemism of pelagic species in association with its deep structure of lake morphology and long geological history (Sects. 1.2 and 2.5), using the SIA. Next, we examine the long-term food web alterations by measuring the $\delta^{15}\text{N}$ for archival specimens collected from this lake since 1914, and demonstrate that the lake food web was sensitive to a variety of human disturbances.

Current Food Web

To characterize the current food web based on the SIA, we collected a total of 1,159 specimens, including 29 fish species and 8 macrozoobenthos taxa (4 molluscs and 4 crustaceans) from Lake Biwa. We also collected four macrozooplankton samples (>300 μm), consisting of copepods and cladocerans, at a pelagic site Ie-1 (long-term monitoring site of CER: 35°12'58"N, 135°59'55"E). These animals were categorized by habitat type and functional feeding group (Appendix 1). As their basal foods, we regarded phytoplankton (particulate organic matter of 0.7–150 μm) in the pelagic habitat (Ie-1), periphyton (epilithic organic matter) in the littoral habitats, and terrestrial-derived organic matter from tributary rivers (riverine particulate organic matter; see Kohzu et al. 2009; Karube et al. 2010 for details).

After dry powder samples of their muscle tissues or whole body were immersed in a chloroform: methanol (2:1) solution for 24 h to remove lipids, following the methods of Focken and Becker (1998), we measured their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ using a mass spectrometer (Finnigan MAT Delta-S, Germany). We plotted their stable isotopic signatures on a $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ bi-plot (Fig. 1) and estimated their trophic position (Box 1). Almost all of these animals were located within the stable isotopic range between two

food chains starting from phytoplankton and periphyton. Zooplankton (hereafter referred to by its taxa code in Appendix 1, i.e., 38) was typical of primary consumers embedded in the pelagic food chain, showing a *TL* of 1.93 with its exclusive reliance on phytoplankton. Zoobenthos inhabiting the littoral zone showed strong reliance on either the pelagic or the littoral food chain, depending on their feeding habits: for example, for grazing snails (30) and a littoral grazing gammarid (35), their production reliance on periphyton was 85.0% on average, while filter-feeding bivalves (31, 32, and 33) relied on phytoplankton production for on average 86.2% of their biomass.

Fishes occupied a wide variety of trophic positions within the food web (Fig. 1). In relation to adult fish, pelagic species showed higher reliance (on average 81.8%) on pelagic production, compared to littoral species whose production reliance varied from 24.6% to 100% (on average 70.9%). Three piscivores (3, 6, and 21) had high *TL*s, with the highest (3.75 *TL*) for the Biwa giant catfish *S. biwaensis* (21), which is considered a top predator in Lake Biwa. Though they are all pelagic, their production reliance was intermediate between pelagic and littoral food chains, suggesting that they fed on both littoral and pelagic preys. Such cross-chain omnivory (*sensu* Polis and Winemiller 1996), that is, mixed feeding on preys derived from different food chains, can couple pelagic and littoral trophic pathways, resulting in integrated energy flows within the food web.

Among fishes, there existed a few exceptional cases in which their trophic position was outside of a continuum of pelagic–littoral food chains. For instance, juvenile crucian carps (16c) had more depleted $\delta^{15}\text{N}$ than that of phytoplankton and periphyton. In Lake Biwa, adult crucian carps usually migrate to littoral reeds, tributary attached lakes, paddy fields, and irrigation channels for spawning, while their hatchlings stay there, leaving for the main lake after growing (Sect. 7.2.1(2), (3)). In their natal habitats, terrestrial-derived organic matter, which shows relatively depleted stable isotope ratios, usually predominates as their potential food sources (Shibata et al. 2011). Therefore, the extraordinary isotopic signatures of the specimens studied suggest that these juveniles had recently migrated from their natal habitats to the main lake. In another case, *Odontobutis obscura* (24) was located on the pelagic food chain but its *TL* was estimated as 1.19, much lower than expected from its feeding habit as a benthic carnivore. Such discrepancy may be attributed to the fact that their main habitat is tributary rivers in which the primary food source is terrestrial-derived organic matter with depleted isotope ratios.

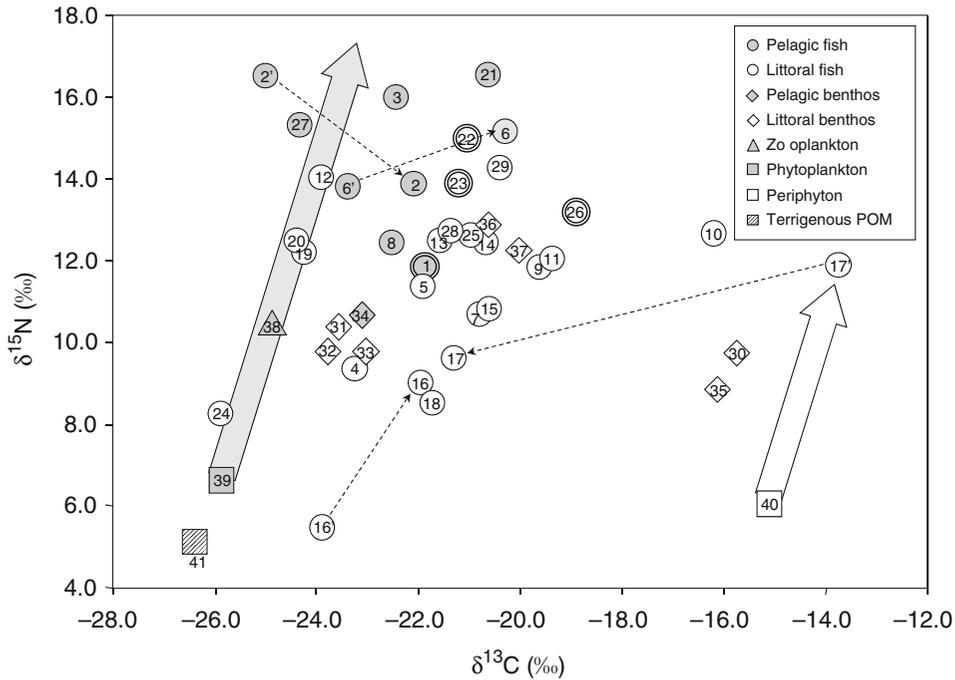


Fig. 1

The current food web of Lake Biwa in $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ bi-plot space. *Thick arrows* represent the hypothetical trophic pathway starting from each primary producer (*shaded*: phytoplankton; *open*: periphyton) with exclusive reliance on it. *Dotted arrows* represent life historical changes in stable isotopic signatures from juvenile or young to adult stages. *Double circles* are for exotic species. Plot numbers correspond to taxa code in Appendix 1.

Box 1 How to Estimate Trophic Position?

We can estimate trophic position of aquatic consumers embedded within the food web, based on their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and those of their basal foods, as follows:

$$\begin{cases} f_1 + f_2 = 1 \\ f_1 \delta^{13}\text{C}_1 + f_2 \delta^{13}\text{C}_2 + \Delta \delta^{13}\text{C}_{\text{ef}} * (TL - 1) = \delta^{13}\text{C}_{\text{cons}} \\ f_1 \delta^{15}\text{N}_1 + f_2 \delta^{15}\text{N}_2 + \Delta \delta^{15}\text{N}_{\text{ef}} * (TL - 1) = \delta^{15}\text{N}_{\text{cons}} \end{cases}$$

where f_1 and f_2 represent the proportion of reliance on two primary producers, phytoplankton and periphyton (hereafter production reliance), respectively. δR_1 , δR_2 , δR_{cons} ($R = {}^{13}\text{C}$ or ${}^{15}\text{N}$) are stable isotopic signatures of phytoplankton, periphyton, and each consumer, and TL trophic level. $\Delta \delta^{13}\text{C}_{\text{ef}}$ and $\Delta \delta^{15}\text{N}_{\text{ef}}$ are called trophic enrichment factors of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively, assuming that the consumer's $\delta^{15}\text{N}$ is enriched by 3.4‰ relative to its diets (Minagawa and Wada 1984) and its $\delta^{13}\text{C}$ by 0.8‰ (DeNiro and Epstein 1978). The two source mixing models mentioned above enable us to estimate the TL and the production reliance (f_n) for each consumer. If its production reliance on either of the two basal foods exceeds one only slightly, we regard it as exclusive reliance (i.e., 100%).

Except for such species relying on allochthonous (i.e., terrestrial-derived) resources, adult fish showed a high pelagic production reliance as a whole ($72.6\% \pm 16.6\text{SD}$, $n = 28$). Our finding is very interesting when compared to North American temperate lakes, in which fishes have been reported to strongly rely on benthic production (43–59%; Vander Zanden and Vadeboncoeur 2002). Vander Zanden and Vadeboncoeur (2002) pointed out that lake size is one of the important factors affecting their pelagic production reliance because perimeter-to-area ratios are lower for larger lakes, resulting in a higher contribution of pelagic habitats relative to benthic habitats. A deep structure, characteristic of tectonic lakes, will also diminish the relative contribution of benthic production because of substantial light attenuation at the lake bottom. In Lake Biwa, fishes, even littoral species, showed strong reliance on the pelagic production in spite of their benthivorous feeding habits, suggesting a direct trophic pathway via their feeding on plankton-derived detritus and/or an indirect pathway via their feeding on zoobenthos that rely on pelagic production. In this lake, in which the pelagic habitat is highly dominant, the food web structure seems to have a variety of trophic pathways linking with phytoplankton. Especially among endemic fishes, which have long evolved behavioral, morphological, and life historical traits adapted to pelagic environments (Sect. 2.5), their high pelagic production reliance was straightforward. In the tectonic Lake Biwa, the unique food web has been shaped by the lake's structure and longevity.

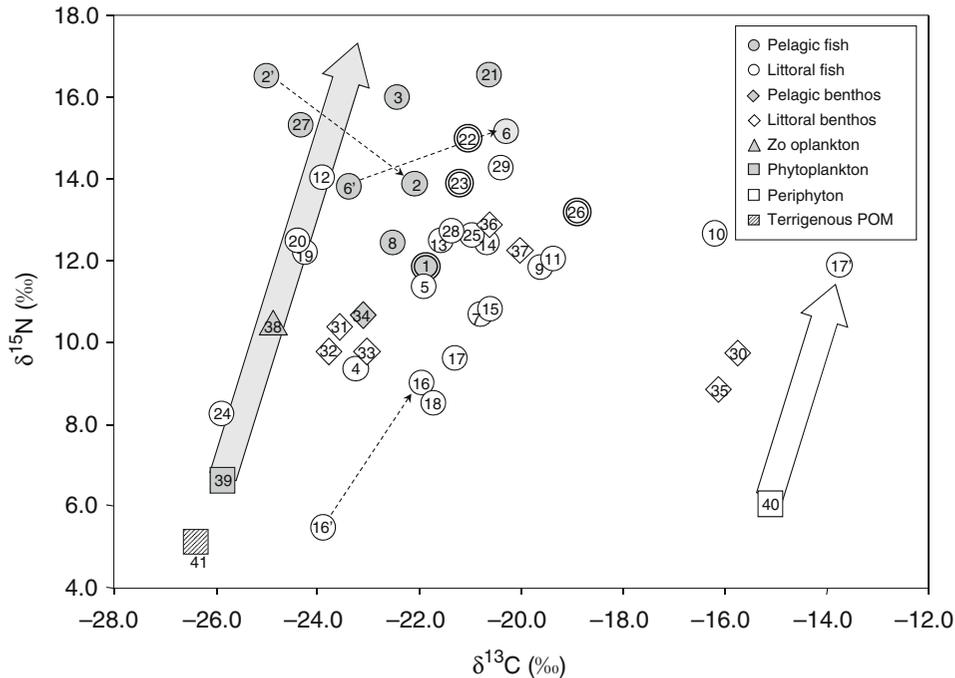
Long-Term Food Web Dynamics

Next, we examined the long-term dynamics of the past food web by measuring the $\delta^{15}\text{N}$ for archival specimens. We used a total of 1,177 preserved specimens, including 45 aquatic animal species (30 fishes, 8 molluscs, and 7 crustaceans) collected from Lake Biwa between 1914 and 2004. For the baseline adjustment to estimate their TL s, we used published data from Ogawa et al. (2001) who measured the $\delta^{15}\text{N}$ for chronological samples of a deep sediment core. Using the ^{210}Pb method, Ogawa et al. (2001) estimated that the measured sediment core samples were deposited from 1901 to 1995. We also measured the $\delta^{15}\text{N}$ of surface sediments in the deep zone of the lake to adjust for the last decade. In Lake Biwa, the deep sediment organic matter consists mainly of autochthonous (i.e., phytoplankton) products (Murase and Sakamoto 2000), so we considered it as an index of the food web base. There

was a strong positive correlation of the decadal average $\delta^{15}\text{N}$ between the chronological sediment samples and concurrent archival specimens of primary consumers (copepods and gammarids) ($r = 0.84$, $n = 8$, $P = 0.009$), with the mean difference of 3.4‰ (± 0.8 SD) which was equivalent to the literature average ($3.4\text{‰} \pm 1.1$ SD) from a variety of taxa in aquatic ecosystems (Minagawa and Wada 1984), confirming that the sediment $\delta^{15}\text{N}$ is appropriate for the baseline adjustment.

To view the long-term trophic dynamics of each species, we took its decadal averages and then calculated its TL , using a single source model of the $\delta^{15}\text{N}$. Grazing and filter-feeding macrozoobenthos showed TL s typical of primary consumers throughout all decades (gastropods: $2.07 TL \pm 0.47$ SD, bivalves: $1.48 TL \pm 0.41$ SD). By contrast, we found great temporal variation in the fish TL s (Fig. 2). For lack of systematic samplings, data were highly fragmented from the 1910s to the 1950s. When comparing variations in individual species' TL s among decades, there was no significant temporal trend in the first half of the twentieth century during which the lake ecosystem did not suffer from notable anthropogenic disturbances (Analysis of variance [ANOVA], $F_{4,45} = 0.31$, $P = 0.87$). In the latter half of the century, in contrast, their TL s showed significant decadal changes (ANOVA, $F_{4,82} = 8.77$, $P = 0.0001$). This trend remained highly significant after considering consecutive changes within the same species (repeated measure ANOVA, $F_{4,32} = 19.05$, $P = 0.0001$). In most fish species, their TL s reached a peak in the 1970s with an increase on average of 0.45 relative to that in the 1960s and was among the highest in any decades (repeated measure ANOVA, post hoc Scheffé's F-test, all $P < 0.05$). However, their TL s drastically decreased on average by 0.89 between the 1970s and 1990s. In 11 of 15 native species, whose data are available for systematic comparisons, the lowest TL was recorded in the 1990s. In shrimps, in contrast, such a temporal trend was not found in their TL s ($3.05 TL \pm 0.40$ SD, Fig. 2).

In Lake Biwa, which was originally oligotrophic, nutrient loadings have enhanced primary productivity since the late 1960s, consequently supporting a larger biomass of secondary and higher consumers. As reported by some ecologists (Thompson and Townsend 2005; Doi et al. 2009), resource availability might have a positive effect on the fish TL s, possibly through the increased availability of preys with higher TL s during the 1970s. Such a bottom-up effect can cascade to the top predators' TL s, resulting in an extended food chain length. After this time, however, the food web drastically shrank, reaching the bottom in the 1990s. This shrinkage cannot be attributed to temporal



■ Fig. 2

The long-term trophic dynamics of fishes and shrimps in Lake Biwa. Each plot represents the decadal averages of *TL* for each species (see Appendix 1 for functional feeding groups) and its consecutive decadal changes are linked by solid lines between neighboring two plots.

changes in *TL*s of primary consumers because macrozoobenthos showed relatively constant trophic dynamics, suggesting that the fish inclined toward single chain omnivory (*sensu* Pimm and Lawton 1977), that is, feeding shift to preys with lower *TL* within a food chain. During the period of the 1980s–1990s, this lake experienced a variety of severe human disturbances, such as eutrophication, littoral habitat modification, exotic species introduction, and global warming, leading to remarkable population declines in native species. In Lake Biwa, the food web shrinkage may be due to decreased availability of preys with high *TL*s for fishes and consequently to lack of intermediate trophic pathways, for which ultimate drivers must be human disturbances.

Stable Isotopes as Ecological Tools

Our stable isotopic approach provided a new insight for ecological and conservational studies as well as food web studies. In Lake Biwa, native fishes are well known to shift

their habitats and trophic niches through their life history. Such life historical patterns were reflected in their isotopic changes with their growth (► Fig. 1): for example, a crucian carp migrates from peripheral temporary waters (16′) to the main lake (16), some adults of a dwarf ayu change their pelagic migratory behavior (2′) into a sedentary lifestyle in the littoral zone (2), and a pelagic carnivorous three-lips shifts its feeding habit from zooplanktivory (6′) to piscivory (6) with the increasing reliance on the benthic food chain. In this lake, most of the native fishes utilize multiple habitats throughout their life history (Yuma et al. 1998). Although some ecologists point out the possibility that human disruption of habitat networks led to their recent population declines in this lake (Sect. 7.2.1(2)), our scientific knowledge is too limited to assess how it can affect their population dynamics and to what extent habitat restoration is effective in helping them recover from their population collapses. Considering marked isotopic variation across habitats in lakes (France 1995; Maruyama et al. 2001; Shibata et al. 2011), the SIA can be helpful to understand their unexplored migratory behavior and life history,

providing basic ecological information for biodiversity conservation.

Although the present study revealed that the Lake Biwa food web shrank due to a variety of human disturbances, we also found it has turned to recovery in the last decade (▶ *Fig. 1*). The reason for this remains unknown but the local government has just started to practice some environmental policies for biological conservation and ecosystem management (Sect. 7.2). We finally recommend not only ecologists, but also policy makers to adopt our isotopic approach for their assessment of ecosystem properties and their evaluation of the cost to benefit of conservation activities.

Acknowledgements

This research was supported by the 21st COE Program (A14), the Global COE Program (A06), and the JSPS Grant-in Aid for Young Scientists (B) (18770014). NO and YS were also supported by Japan-Taiwan Joint Research Program, Interchange Association, Japan. Archival specimens were used for the SIA with permission of Kyoto University Museum, Lake Biwa Museum, and Center for Ecological Research, Kyoto University. We deeply thank Dr. T. Nakabo and Dr. T. Nakajima for providing opportunities to use the specimens.