

Food web properties of the recently constructed, deep subtropical Fei-Tsui Reservoir in comparison with the ancient Lake Biwa

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Abstract Using carbon and nitrogen stable isotope analysis, we characterised food web properties of the deep subtropical Fei-Tsui Reservoir (FTR), which was recently altered from a lotic to a lentic system after dam construction. In the littoral zone, zoobenthos showed strong reliance (83.9%) on benthic algal production. Zoobenthos were never found in the profundal zone because of anoxia. Zooplankton depleted ^{13}C more than that of particulate organic matter as their putative food source, suggesting a

contribution of methane-derived carbon to pelagic food webs. Excluding juveniles, non-native and fluvial species, adult fish showed strong reliance (on average 80.9%) on benthic production, weakly coupled with pelagic food webs. These results contrast low benthic production reliance (on average 27.4%) for a fish community in Lake Biwa, which is also classified as a subtropical lake. Both lakes are characterised by deep pelagic waters but quite different in their geological ages, suggesting that the aquatic communities in the FTR have fluvial origins, and their lacustrine history was too short for them to adapt to newly emerged deep pelagic habitat. Our isotope data are useful as a reference of newly established lentic food webs to monitor ongoing ecological and evolutionary dynamics as a result of anthropogenic disturbances.

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Introduction

Dams and reservoirs have been constructed to meet accelerated demands for water and energy resources as populations experience explosive growth and climate change worldwide (Nilsson et al., 2005). While dams provide high public utility, they can negatively impact river ecosystems by drastically changing waterway

from lotic to lentic systems (McAllister et al., 2001). In dammed rivers, some taxa can modify and adapt their life histories to sustain their populations; however, others that cannot adapt may go into local extinction due to loss of original habitats. At present, dam construction is considered as one of the major drivers of biodiversity loss in the freshwater ecosystems through the alteration and homogenisation of natural hydrological regimes (Poff et al., 2007), the creation of physical barriers to migratory species (Liermann et al., 2012), the dispersal and colonisation of non-native lentic species (Havel et al., 2005), and the pollution and eutrophication at dam sites (Dudgeon, 2000). Therefore, it is important to perform ecosystem assessments after dam construction for water quality management and biodiversity conservation.

Stable isotope analysis (SIA) is a powerful tool to assess ecosystems, especially food web properties characterised by trophic interactions within a biological community. Food web characterisation is of ecological and social significance because trophic interactions can drive nutrient cycling and energy flows, which in turn affect ecosystem services (e.g. water quality, food supply for humanity). At present, the stable isotopic approach is the preferred method for studying aquatic food webs, in which carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios, for aquatic species, are used to distinguish primary trophic pathways, for example, pelagic versus littoral pathways (France, 1995a, b) or aquatic versus terrestrial pathways (Peterson & Fry, 1987; Finlay, 2001). Especially for fish, their isotopic signatures provide useful information in estimating the relative importance of trophic energy flows in lake ecosystems. Fish predators integrate a variety of trophic pathways as they couple pelagic and littoral food webs due to their high mobility and omnivory (Vander Zanden & Vadeboncoeur, 2002; Vander Zanden et al., 2011). The stable isotopic approach can also be applied to assess food web alterations in aquatic ecosystems under human disturbances (Vander Zanden et al., 1999; Layman et al., 2007; Anderson & Cabana, 2009; Hamaoka et al., 2010). In most cases, however, stable isotopic studies are conducted after ecosystem alterations were perceived. As such, limited information is available on original conditions before the disturbance (but see Okuda et al., 2012; Vander Zanden et al., 2003).

Newly constructed dams and reservoirs provide a good possibility to understand ecological processes of food web alterations if initial conditions of the lentic system are assessed soon after dam or reservoir construction. In this study, we conducted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis to characterise food web properties of the Fei-Tsui Reservoir (hereafter, FTR; Fig. 1; Table 1), which was established in 1987 to supply drinking water for more than 5 million people in metropolitan Taipei. Since its construction, the local government has been responsible for ecosystem management of the reservoir, focusing mainly on water quality. In contrast to physical and chemical characteristics, biological information was monitored less with the exception of phytoplankton data that were monitored as an indicator of water quality (Wu et al., 2007). Recently, Chang et al. (2014a, b) reported community dynamics and size-based food webs in the FTR, focusing on plankton communities in pelagic waters. A holistic approach that encompasses benthos and fish as higher consumers in coastal and pelagic waters is needed to view the overall trophic energy flows in lentic food webs of the FTR before future anthropogenic disturbances occur. This study can, therefore, be regarded as a reference for ongoing ecosystem monitoring.

In this study, we also intend to compare food web properties of FTR with those of Lake Biwa, in which a holistic approach towards food web analysis was performed in a similar way to the present study (Okuda et al., 2012). According to Yoshimura (1937)'s lake classification, both lakes were classified as subtropical, monomictic lakes in Monsoon Asia. During the quaternary glaciation, terrestrial and aquatic species migrated between southern Japan and Taiwan through a land bridge, often forming sister species (Chiang & Schaal, 2006; Ho et al., 2016). Such a biogeographical history has enabled the same species and congeners to exist in both lakes. These lakes are also similar in terms of depth and trophic state (Table 1). Considering their biogeographical and limnological backgrounds, they are comparable in relation to trophic positions of some common taxa. However, they are quite different temporally as the lentic waters emerged at different times. We will discuss how the historical difference in the lentic community colonisation affects trophic energy flows in these deep lakes.

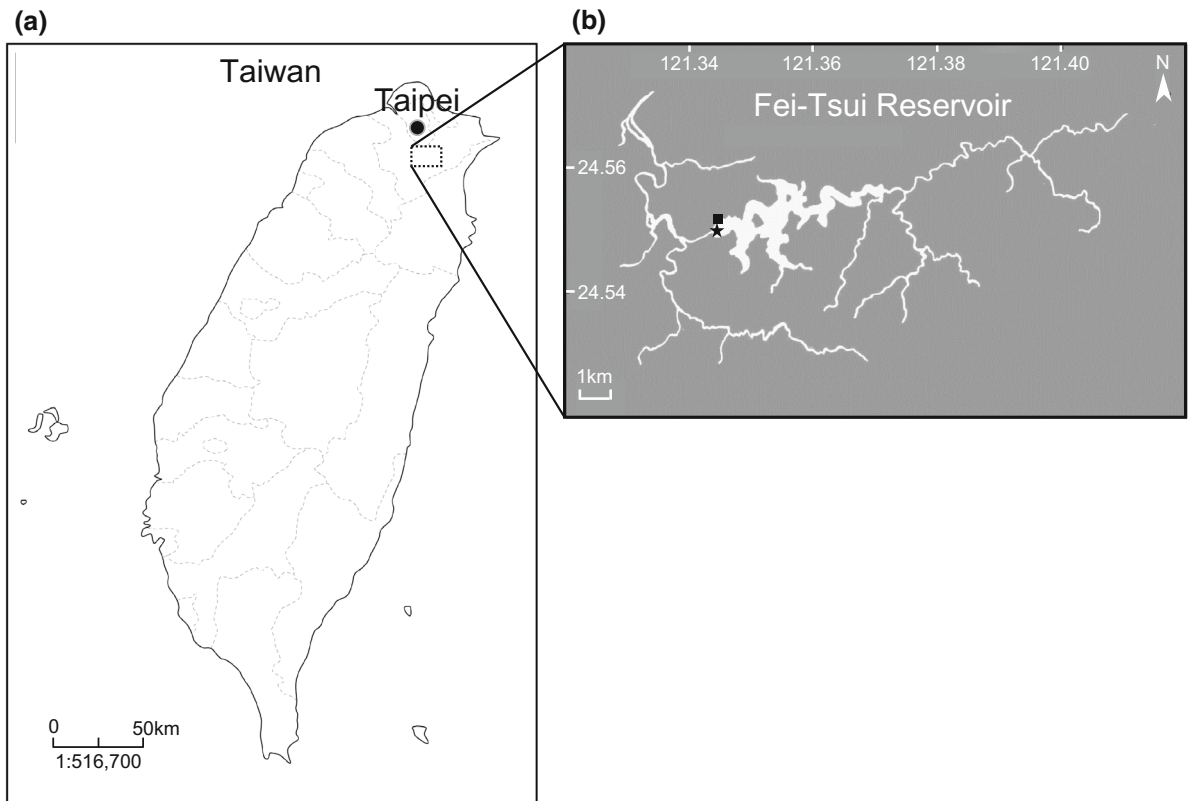


Fig. 1 The map of Fei-Tsui Reservoir (b) in Taipei, Taiwan (a). *Star* and *square* symbols represent the pelagic and littoral sampling sites, respectively

Table 1 Comparison of limnological and bathymetric characteristics between Fei-Tsui Reservoir and Lake Biwa

	Fei-Tsui Reservoir	Lake Biwa
History	Established in 1987	ca. 0.4-4 mya ago ^a
Lake surface area (km ²)	10.2	670.3
Maximum depth (m)	120.0	103.6
Mean depth (m)	39.7	41.2
Water volume (km ³)	0.4×10^9	27.5×10^9
Supply population (million)	More than 5	14.5
Trophic state	Mesotrophy—Eutrophy	Mesotrophy—Eutrophy
No. of existing species	Unknown	1769
No. of endemic species	Unknown	61

^a Paleo-Lake Biwa appeared ca. 4 mya ago, while the current lake basin was characterized by deep pelagic waters through faulting ca. 0.4 mya ago

Materials and methods

Study site and environmental issues

FTR, one of the largest reservoirs in Taiwan, is located downstream of Peishih Creek, residing in a watershed of 303 km² in northern Taiwan (121°34'E, 24°54'N; Fig. 1a). Its limnological and bathymetric

characteristics are shown in Table 1. Although the FTR was classified as an oligotrophic lake for several years after dam construction (Chang & Wen, 1997), its trophic state currently ranges between mesotrophic and eutrophic according to Carlson's trophic state index (Chou et al., 2007). Dominance in phytoplankton flora has shifted from dinoflagellates to cyanobacteria and green algae, suggesting a long-term trend

towards eutrophication (Wu & Chou, 1998; Wu et al., 2007).

In the reservoir, seasonal and vertical profiles of dissolved oxygen are affected by weather- and climate-driven hydrodynamics (Fan & Kao, 2008). A recent concern is the frequent release of typhoon-induced suspension interflows from the main tributary, increasing phosphorous loading and affecting water quality (Chen et al., 2006). Moreover, strong summer stratification and incomplete winter mixing due to warming have often caused hypoxia in profundal waters (Itoh et al., 2015), which may have non-linear and lethal effects on profundal communities. Considering such emerging environmental issues, long-term ecosystem monitoring was launched in 2004. The physical and chemical environmental data we obtained have been published (Itoh et al., 2015; Chow et al., 2016).

Field sampling

Prior to food web analysis, we conducted field sampling of fish, zooplankton, zoobenthos, and their basal food sources. We collected zooplankton and their putative food sources from pelagic waters at the monitoring station near the dam (113.5 m at depth; Fig. 1b). On 17 November 2009, meso- and macro-zooplankton were collected with a 100- μm -mesh plankton net towed vertically in the epilimnion (0–18 m at depth). For sampling of particulate organic matter (POM) as basal food for pelagic consumers, lake waters were collected at the depth of 2 m with a 5-L Go-Flo bottle (General Oceanics, Miami, FL) on 13 and 27 October and 10 November 2009. Water samples were screened with a 10- μm -mesh and then filtrated with glass fibre filter (GF/F, 0.7 μm , Whatman) pre-combusted at 450°C for 2 h. Particle sizes of 0.7–10 μm cover the size range of meso- and macro-zooplankton prey in the FTR (Chang et al., 2014b). These time-series POM samples were mixed in equal quantities to integrate temporal variations in their isotopic signatures, reflecting a high turnover rate for small-sized plankton. This procedure is reasonable because large-sized zooplankton biomass integrates temporal variation in their dietary isotopic signatures for a few months (Ho et al., 2016). In FTR, seasonal pattern of surface POM isotopic signatures is predictable (See Fig S1 in Ho et al., 2016), so that our mixing model with pooled POM data is robust to temporal variation in its isotopic signatures.

While monitoring the station near the dam, we collected surface sediment from the deep lake bottom as the putative food source for profundal consumers, using an Ekman-Berge grab sampler. The sediment samples were sorted for zoobenthos, but no individuals were found in profundal habitats.

We also collected zoobenthos and fish juveniles at a littoral site (Fig. 1b) using a Sarvar net. As a basal food source for littoral consumers, we collected epilithic organic matter (EOM) from the littoral habitat, scraping it off from each of four boulders with a brush. After removing zoobenthos from these suspended samples with a 150- μm -mesh net, they were mixed and filtered through pre-combusted GF/F filters. Leaf litter was also collected as allochthonous terrigenous organic matter (TOM).

Adult fish specimens were obtained from an aboriginal tribe, with government-authorised licenses to catch the fish in the FTR, during our sampling period. Except for the aboriginal fishing, fish sampling using fishing gears and boat in the FTR is strictly prohibited by Taipei Feitsui Reservoir Administration even if it is the academic purpose. Such an administrative constraint restricted our sampling design to small sample size and narrow sampling area.

These samples were chilled and transferred to the laboratory. Dominant zooplankton species were sorted and identified under a microscope. Due to their little mass, small-sized animal samples were prepared in bulk for SIA. For adult fish specimens, we measured their total length or standard length in millimetres and then excised their muscle tissues from the dorsal part of the lateral body. For zoobenthos and juvenile fish samples, their entire mass was prepared for SIA. All samples were dried at 60°C for 24 h.

Stable isotope analysis

Dry samples were ground into fine powder. For animals, the ground samples were immersed in chloroform:methanol (2:1) solution for 24 h to remove lipids according to Kling et al. (1992). Each sample was weighed and wrapped in a tin capsule for combustion. We determined carbon and nitrogen stable isotope ratios for each sample using a mass spectrometer (CF/IRMS; Conflo II and Delta S, Finnigan MAT, Germany), and carbon and nitrogen contents were measured using elemental analyzers (EA1108, Fisons, Italy). Ratios (R) of the heavy

isotope to the light isotope ($^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$) were expressed in parts per thousand, relative to the standards in delta notation following the formula:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000(\text{‰}).$$

Vienna Pee Dee belemnite and atmospheric nitrogen were used as standards for carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios, respectively. The analytical precision based on working standard was $\pm 0.1\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Estimation of trophic position

We estimated trophic position of consumers in the lentic food web of the FTR based on the following stable isotope mixing model (see also Okuda et al., 2012).

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

where f_1 and f_2 represent the proportion of reliance of the two major primary producers in the lentic food web, that is, phytoplankton (POM) and benthic microalgae (EOM), respectively. δR_1 , δR_2 , and δR_{cons} ($R = ^{13}\text{C}$ or ^{15}N) are stable isotope ratios of phytoplankton, benthic microalgae, and each focal consumer, respectively. TP is trophic position. $\Delta \delta^{13}\text{C}_{ef}$ and $\Delta \delta^{15}\text{N}_{ef}$ are trophic enrichment factors, assuming that consumer's $\delta^{15}\text{N}$ is enriched by 3.4‰ relative to its diets (Minagawa & Wada, 1984) and its $\delta^{13}\text{C}$ by 0.8‰ (DeNiro & Epstein, 1978). The above mixing model enables us to estimate TP and production reliance (i.e. f_n) for each consumer. If consumer's production reliance on either of the two basal foods slightly exceeds one, we regarded it as exclusive reliance (i.e. 100%). In the case in which fluvial fish migrate between coastal and stream habitats (see Results), we also used the EOM and TOM as basal food sources in the isotope mixing model.

Results

We measured a total of 45 samples, including 10 fish, 2 macrozoobenthos and 4 zooplankton taxa, together

with their basal food resources from littoral and pelagic waters in the FTR (Table 2). One littoral zoobenthos taxon (Chironomidae) was excluded from our isotopic data because its carbon and nitrogen contents were less than the lower detection limit. Its lentic food web was delineated on $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ bi-plot space (Fig. 2).

In pelagic habitats, trophic position cannot be estimated for meso- and macro-zooplankton because they depleted ^{13}C substantially more than POM, which is their putative food source (Fig. 2; Table 2). Amongst the zooplankton samples, two copepods and the bulk zooplankton community, which was also dominated by copepods, enriched ^{15}N by 3.5‰, on average, more than two cladocerans. This suggests that the former TLs were higher than the latter by around one although their absolute values could not be calculated because of large deviations from the isotopic range of their putative food sources, POM and EOM. In littoral habitats, by contrast, shrimp enriched their ^{13}C , showing strong reliance on EOM (83.9%; Table 2).

Fish occupied broad trophic niche spaces in the lentic food web of the FTR (Fig. 2; Table 1). A catfish *Silurus asotus* Linnaeus, 1758, a top predator, had the highest TP (3.84 TP), showing its strong reliance on benthic algal production (87.7%). Three fish species (i.e. juvenile *Rhinogobius* sp., *Carassius cuvieri* Temminck & Schlegel, 1846 and *Oxyeotris marmorata* (Bleeker, 1852)) had relatively low $\delta^{13}\text{C}$. SIA of a landlocked goby, *Rhinogobius* sp., in Lake Biwa revealed that adult fish are benthic feeders in littoral habitats, while 0^+ aged fish have a planktonic life stage before their settlement (Maruyama et al., 2001). Amongst juveniles of *Rhinogobius* sp. in the FTR, the highest reliance on phytoplankton production was 74.0% although adult fish showed strong reliance on benthic algal production (79.9%). *C. cuvieri*, a pelagic species endemic to Lake Biwa, was possibly introduced into the FTR after dam construction since it cannot sustain populations in lotic environment. *O. marmorata* is a fluvial benthic predator whose basal food may be derived from allochthonous terrigenous organic matter (TOM) in river habitats but not from pelagic POM since it migrates between littoral and river habitats. Assuming that this fish relies on allochthonous TOM (i.e. leaf litter) and autochthonous EOM, we estimated its production reliance on the TOM as 88.7% and its TP as 3.97. Excluding

Table 2 Stable isotope signatures of biological community and its basal food sources in FTR

Taxonomic group	Species	Origine	Trophic guild ^a	n	Body length (mm)		$\delta^{13}\text{C}$ (‰)		$\delta^{15}\text{N}$ (‰)		C/N (mol)	Trophic position	Benthic production	Taxon code
					Mean	Min.–Max.	Mean	SD	Mean	SD				
Fish	<i>Chanodichthys erythropterus</i>	Native	P	1	515.0 ^b	–	–16.53	–	8.44	–	3.64	3.37	100.0	1
	<i>Cyprinus carpio carpio</i>	Native	B	1	370.0 ^b	–	–22.29	–	5.65	–	3.61	2.14	60.9	3
	<i>Carassius auratus auratus</i>	Native	B	2	282.5 ^c	267.0–298.0	–25.91	0.52	7.79	0.63	3.73	2.32	18.1	5
	<i>Silurus asotus</i>	Native	P	1	294.5 ^b	284.0–305.0	–22.51	0.47	7.19	0.19	3.68	2.53	54.9	7
	<i>Oxyeleotris marmorata</i>	Native	P	1	61.6 ^b	–	–19.58	–	9.40	–	3.58	3.44	79.9	9
Zoobenthos	<i>Macrobrychium</i> sp.	Native	B	5	–	–20.26	1.02	4.87	0.61	3.93	2.15	83.9	11	
														12
Zooplankton	<i>Diaphanosoma dubium</i>	Native	B	1	–	–31.01	–	1.81	–	4.30	–	–	13	
														14
	<i>Daphnia cucullata</i>	Native	B	1	–	–29.99	–	5.36	–	4.62	–	–	15	
														16
	Bulk sample (>100 μm)													

Table 2 continued

Taxonomic group	Species	Origine	Trophic guild ^a	n	Body length (mm)		$\delta^{13}\text{C}$ (‰)		$\delta^{15}\text{N}$ (‰)		C/N (mol)	Trophic position	Benthic production	Taxon code
					Mean	Min.–Max.	Mean	SD	Mean	SD				
Basal food	POM			1			–28.56	–	3.95	–	7.31			17
	EOM			8 (4 for δN)			–19.76	1.51	0.39	0.79	9.69			18
	Leaf litter			1			–29.31	–	–1.88	–	45.66			19
	Sediment			2			–27.04	0.22	1.94	0.62	6.62			20

^a Trophic guilds are classified into B (Benthivore) and P (Piscivore), according to the website (<http://taibif.tw>)

^b Total length

^c Standard length

^d Parentheses represent values where allochthonous TOM but not pelagic POM is assumed to be the basal food source (see text for details)

juveniles, non-native and fluvial species, adult native lacustrine fish showed on average 80.9% benthic production reliance.

Discussion

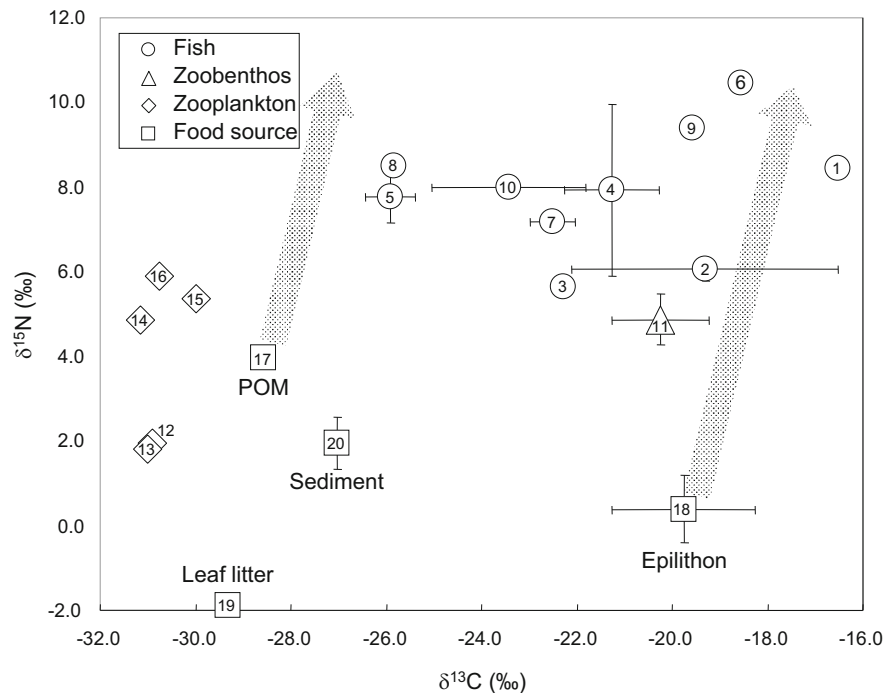
Pelagic and profundal food webs

In pelagic food webs of the FTR, TPs of zooplankton taxa could not be estimated appropriately because their isotopic signatures deviated from the isotopic range of putative food sources. Based on their low $\delta^{15}\text{N}$ values relative to POM, one may infer that pelagic food webs are subsidised by allochthonous TOM with a low $\delta^{15}\text{N}$ value as is often the case for small lakes (Pace et al., 2004; Cole et al., 2006, 2011). Cole et al. (2006) demonstrated that TOM is primarily passed to pelagic food webs as a part of POM. In the FTR, however, TOM contributes little to zooplankton production, rejecting the possibility of terrestrial subsidies (Ho et al., 2016).

Apart from their food sources, when focusing on the locations of copepods and cladocerans on the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ bi-plot space, their relative trophic positions were markedly different between the two dominant taxa. Assuming that cladocerans are grazers and also that the trophic enrichment factor is 3.4‰ for $\delta^{15}\text{N}$, copepods are considered carnivores. Such trophic niche segregation has hitherto been reported for these two taxa in many lakes (Yamada et al., 1998; Grey et al., 2001; Matthews & Mazumder, 2003; Karlsson et al., 2004). Since copepods are raptorial feeders, it is likely that they feed on small-sized grazers, such as protozoa, rotifers, nauplii, and cladoceran larvae. For plankton communities, intra-guild predation (i.e. predation on small-sized zooplankton by large-sized zooplankton) is often prevalent in lakes dominated by microbial loops (Grey et al., 2001; Karlsson et al., 2004).

In the FTR, it is also interesting that the zooplankton community had a much lower carbon isotope ratio than POM as its putative food source. As pointed out by Jones & Grey (2011), such an isotopic mismatch between POM and zooplankton could be ascribed to zooplankton consumption of ^{13}C -depleted phytoplankton, which assimilate ^{13}C -depleted CO_2 derived from bacterial respiration of terrigenous DOC in humic lakes. In the FTR, in contrast, bacterial

Fig. 2 Trophic positions of each taxon in the lentic food web of Fei-Tsui Reservoir. *Thick arrows* represent the hypothetical trophic pathways starting from phytoplankton and benthic microalgae using assumptions from our mixing model. Each *plot* and *bar* are averaged and presented with the standard deviation of isotopic signatures for each taxon. *Plot numbers* correspond to taxon codes in Table 2



decomposition of DOC is facilitated only when phosphorous is loaded from the catchment after strong typhoons (Tseng et al., 2010) and heterotrophically respired ^{13}C -depleted CO_2 is not so much reflected in the carbon isotope ratio of dissolved CO_2 in surface waters (-12 to -17‰ ; Itoh et al. unpublished data), suggesting another carbon source for zooplankton. In eutrophic and/or humic lakes, dissolved methane generated from the anoxic lake bottom and characterised by an extremely low carbon isotope ratio is one of the major carbon sources for zooplankton (Bastviken et al., 2003; Taipale et al., 2008; Kankaala et al., 2010). This trophic pathway from dissolved methane to zooplankton is mediated by methane-oxidising bacteria (MOBs), defined as methanotrophic food webs. Long-term monitoring of methanotrophic food webs is of ecological importance in understanding how carbon cycling is altered in lakes affected by anthropogenic activities.

In the FTR, it has been reported that MOBs dominate profundal bacterial communities, showing remarkable vertical and seasonal variations in community compositions (Kojima et al., 2014; Kobayashi et al., 2016). Itoh et al. (2015) experimentally demonstrated that the methane oxidation activity is highest in deep sub-oxic layers, in which both

dissolved methane and oxygen are available to MOBs. In the deep FTR, methanotrophic food webs can be mediated through zooplankton vertical migration to feed on profundal MOBs, leading to the coupling of pelagic and profundal food webs. Using isotopic and theoretical models, Ho et al. (2016) revealed that the relative contribution of MOBs to zooplankton production seasonally varied from 0.6 to 14.6% in the FTR, depending on hydrodynamic changes in dissolved methane and oxygen concentrations. In the FTR, methanotrophic contributions are not as great as the contributions in boreal lakes (up to 50%; Kankaala et al., 2010), which generate allochthonous carbon subsidies for pelagic food webs during less productive seasons. Using meta-analysis for lakes worldwide, Bastviken et al. (2004) predicted that methane production would increase with increasing total phosphorous and dissolved organic carbon concentrations. Considering the trend towards eutrophication after dam construction, it is reasonable to expect long-term changes in methanotrophic contributions to pelagic food webs in the FTR. As reported by Ho et al. (2016), the results from this study allow for long-term monitoring of plankton isotope signatures to assess alterations in trophic carbon flows in pelagic food webs due to climate and land use changes.

In deep lakes, the oxic–anoxic conditions of the lake bottom habitat also affect infaunal zoobenthos communities and their trophic carbon flows in profundal food webs. In Lake Biwa, many benthic species have adapted to profundal habitats since deepening of the lake basin ca. 0.4 million BC (Kawanabe et al., 2012). Some hypoxia-tolerant burrowing chironomids are characterised by extreme isotopic depletion of ^{13}C , suggesting the existence of methanotrophic food webs in the sub-surface of lake sediments where an oxidation–reduction boundary layer has developed (Kiyashko et al., 2001). In the FTR, by contrast, there exist no zoobenthos in the profundal habitat that is anoxic. Since original zoobenthos faunas were living in shallow and lotic environments before the construction of this reservoir, they may not be tolerant to deep anoxic conditions. The long-term monitoring revealed that the profundal habitat interannually alternates between anoxic and hypoxic conditions, depending on the intensity of winter vertical mixing under changing climates (Itoh et al., 2015). If there are some scopes for hypoxia-tolerant species to colonise populations from adjacent lakes, trophic carbon flows in profundal food webs may be modified over time.

Trophic energy flows to higher consumers

In the FTR, a lacustrine fish community, except for juvenile, fluvial and non-native fish, showed 80.9% of benthic production reliance. It contrasts with Lake Biwa in which the benthic production reliance is 27.4% for the whole fish community (Okuda et al., 2012). The food chain length, defined as the TP of top predators, was not so different between the FTR (3.84 TP for a catfish *Silurus asotus*) and Lake Biwa (3.75 TP for a giant catfish *Silurus biwaensis* Tomoda, 1961; Okuda et al., 2012), whereas their benthic production reliance was much higher for the former (87.7%) than for the latter (25.6%). Vander Zanden et al. (2011) estimated benthic production reliance as on average 57% for fish communities in 75 lakes worldwide, in which carbon isotope data are available for food web analysis. The relative contributions of benthic algae to whole-lake primary production can be affected by bathymetry (Vadeboncoeur et al., 2008). Amongst temperate lakes of North America, for instance, a lake trout, a top predator, shifts its production reliance from benthic to pelagic drastically when the lake's surface area is more than 10 km^2 (Vander Zanden &

Vadeboncoeur, 2002). Large lakes tend to have a lower perimeter-to-area ratio, and they also tend to be deeper than small lakes, thus reducing the relative contribution of benthic algae to the whole-lake production and subsequently to trophic carbon flows in zoobenthos and fish (Vadeboncoeur et al., 2002). Considering the limited area of shallow coastal habitats in dams and reservoirs with steep slopes, it is likely that benthic algae contribute little to the whole-lake primary production in the FTR.

In this study, because the sample size and sampling area were limited under the administrative constraints, our results may be less conclusive in relation to intraspecific and spatial variations in the fish trophic position and production reliance within the reservoir. Considering a general rule that large body-sized fish have high mobility and low turnover rate (McCann et al., 2005), however, our adult fish specimens should have time- and space-integrated isotopic information on food webs, ensuring that our estimation of their trophic position and production reliance is reliable. Since commercial and recreational fishing, except for small-scale aboriginal fishing, is prohibited by the Administration of Taipei FTR, the possibility of overexploitation of pelagic fish, which would bias fish community compositions to littoral species relying on benthic production, can be ruled out. Rather, strong benthic production reliance can be ascribed to the fact that the native fish have fluvial origins, associated with habits for feeding on benthos in river habitats before the reservoir was constructed.

In the FTR, interestingly, a non-native fish introduced from Lake Biwa showed the highest reliance (81.9%) on pelagic production. In Lake Biwa, many endemic fish species evolved from their fluvial ancestors to adapt to the pelagic environment after the lake deepened through faulting ca. 0.4 million years ago (Okuda et al., 2013). In the FTR, by contrast, its lentic history may be too short for the native fish to adapt well to the pelagic habitat. However, evolutionary biologists have recently reported numerous cases studying rapid evolution, which occurs on an ecological time scale much shorter than expected from conventional evolutionary process (Stockwell et al., 2003; Hairston Jr. et al., 2005). For instance, the bluegill sunfish *Lepomis macrochirus* Rafinesque, 1810 was introduced into Lake Biwa from the United States in the 1960s. Its colonised populations showed benthic morphs feeding on littoral zoobenthos during

the early phases of colonisation in the 1970s (Terashima, 1980). More than half a century after the introduction, however, some of the bluegill sunfish shifted to pelagic morphs with specialised feeding habits for plankton preys (Yonekura et al., 2002). Such trophic polymorphism was also detected by SIA (Uchii et al., 2007). For native fish species in the FTR, on one hand, it is interesting to correlate long-term changes in their isotopic signatures with the shift from benthic to pelagic habitats over time from now on. As in the case of the FTR, on the other hand, we have to warn against human introduction of non-native pelagic fish in term of biodiversity conservation because they easily occupy vacant niches after reservoir construction (Liew et al., 2016), decreasing opportunities for ecological adaptations of the native fish to the pelagic habitat.

At present, the trophic state of FTR has become mesotrophic and sometimes even eutrophic, a gross difference from its original state as oligotrophy immediately after reservoir construction. The dams and reservoirs are destined to become eutrophic, sooner or later, given nutrient loading from the catchment. The relative importance of whole-lake primary production will shift from benthic algal to phytoplankton production through eutrophication (Vadeboncoeur et al., 2001). Such a change in primary production can also alter trophic carbon flows to aquatic consumers, which can be detected by carbon isotope analysis (Vadeboncoeur et al., 2003). Our study is currently descriptive, but it can be a milestone for future ecosystem assessments and evolutionary research for the FTR. As reported for Lake Biwa (Okuda et al., 2012), long-term isotopic monitoring in the FTR will provide more insights into the dynamic nature of lentic food webs due to ongoing anthropogenic activities.

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