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亞熱帶高山湖泊食物網結構的季節變化

Seasonal variation of food web structure in subtropical mountain lakes

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國立臺灣大學碩士學位論文
口試委員會審定書

亞熱帶高山湖泊食物網結構的季節變化

Seasonal variation of food web structure in subtropical mountain lakes

本論文係范芷瑄君（R03622008）在國立臺灣大學生物環境系統工程學研究所完成之碩士學位論文，於民國 105 年 6 月 24 日承下列考試委員審查通過及口試及格，特此證明

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摘要

高山湖泊是位在高海拔的自然的靜止水體，具有獨特的生態系結構，亦是對環境變化相當敏感的生態系。前人有關於高山湖泊生態系的研究主要集中在溫帶地區，在亞熱帶亞洲地區的高山湖泊生態系卻很少被探討，由於亞熱帶地區的高山湖泊生態系統常受到季節性的環境擾動影響，如夏季的強降雨事件而造成的水文擾動或是夏季強烈的太陽輻射所導致的能量源的變化，可能會影響其中食物網能量源變化。

本研究探討位在亞熱帶台灣北部的翠峰湖及鴛鴦湖，這兩個研究樣點海拔高度及氣候條件相近，然而，這兩個研究樣點的沿岸植被有明顯差異，翠峰湖是相對較為開闊的自源生態系統且只有稀疏的沿岸植被；但是鴛鴦湖則是部分水面受到陸域植物遮蔽且較為封閉的異源生態系統。在本研究期間，翠峰湖食物網中生物的穩定碳同位素數值整體來看是高於鴛鴦湖，同時，我們的結果也發現雖然鴛鴦湖周圍植生茂密，然而落葉並非最重要提供鴛鴦湖整個生態系的能量源，穩定同位素混合模型（SIAR）的結果證實，在異源的鴛鴦湖，細菌是食物網中最主要的能量源。然而，翠峰湖是一個典型的自源生態系統，其主要提供整個食物網的能量源是自源性的浮游藻類以及附生藻類。另外，我們的研究結果顯示鴛鴦湖食物網結構其複雜度高於翠峰湖，主要原因是鴛鴦湖周圍植生茂盛而湖中有繁茂的

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水生植物床與豐富的藻類物種，大大提升鴛鴦湖的棲地複雜度，為浮游動物及水生無脊椎動物等營造合適躲藏的棲地。至於在兩個高山湖泊食物網結構之季節變異，主因為隨著夏季到來而提高的水溫以及太陽輻射所導致自源能量源的光合作用率提升，進而增加整個生態系統的初級生產力。我們的研究結果顯示，異源性鴛鴦湖的水生生物主要的基礎能量源是細菌，而自源性的能量源(如: 浮游藻類及附生藻類)是自源性翠峰湖中水生生物的主要基礎能量源。

關鍵字：亞熱帶高山湖泊、營養傳輸、異源性、自源性、穩定碳氮同位素分析

Abstract

Mountain lakes are natural and remoted lentic water bodies with unique ecosystem structure housing high level of biological endemism. They are sensitive to environmental changes though most studies of the mountain lake ecosystems have been focused on the temperate region. Yet, only limited investigation has been undertaken in such ecologically important habitats in tropical/subtropical Asia. As the subtropical mountain lake ecosystems are strongly influenced by seasonal environmental perturbations, such as periodic and stochastic hydrological disturbances due to heavy rainfall events, and the intense solar radiation during summer. It could be the major factor characterizing the energy basis for the lake food webs.

In this study, the trophic structure and food utilization patterns of primary consumers, secondary consumers, and top predators in two subtropical mountain lakes in Taiwan, including Lake Tsuifeng (TFL) and Lake Yuanyang (YYL) were investigated using stable carbon and nitrogen isotope analyses. The two study lakes exhibited marked difference in riparian vegetation pattern, TFL was relatively unshaded with only sparsely distributed riparian vegetation whereas YYL was a densely shaded system with continuously distributed riparian forest. This resulted in distinct difference

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in the availability of different food sources to the food webs. During the study period, the variation of water temperature and precipitation pattern was similar between the two study lakes with most heavy rainfall events in summer. Our results showed that the food web components were more δ^{13}C-enriched in TFL than in YYL. Despite the high availability of the two most dominant allochthonous food sources including fine particulate organic matter (FPOM) and leaf litter in the densely shaded YYL, they were least utilized by aquatic consumers. Instead, results of the stable isotope mixing model (SIAR) indicated that the δ^{13}C-depleted bacteria represented the major energy basis in the allochthonous YYL. In contrast, TFL was a typical autochthonous ecosystem dependent on autochthonous food sources (periphyton and phytoplankton) which accounted for the major primary production supporting the food web. In addition, the increased complexity of food web structures in YYL as compared to TFL could be primarily due to higher habitat complexity in YYL where dense macrophyte bed and accumulation of leaf litter mass on the lake bottom. Moreover, the observed seasonal shift of food web structures in the two study lakes could be due to the enhanced primary production due to higher light intensity and water temperature in summer. Our study confirmed that the most important basal food sources for aquatic organisms in

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allochthonous YYL was bacteria, whereas autochthonous basal food sources (e.g. phytoplankton and periphyton) had the higher contribution to aquatic organisms in autochthonous TFL during the study periods.

Key words: subalpine lakes, trophic transfer, autochthonous, allochthonous, stable C and N isotope analysis, SIAR

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1. Introduction

Mountain lakes are natural and remoted lentic water bodies with unique ecosystem structure housing high level of biological endemism. Their water sources directly come from precipitation or ground water. Since the mountain lake ecosystems are generally oligotrophic or dystrophic with relatively scarce food sources, this would result in shorter food chain due to the weak energy bases in such systems. Previous studies in temperate region have confirmed that the food chain length was clearly short in the mountain lake ecosystems (Campbell et al. 2000, Rognerud et al. 2002). In mountain lake ecosystems, autochthonous carbons manly come from phytoplankton and periphyton whereas allochthonous carbons (e.g. leaf litter and FPOM) are organic input from the riparian vegetation and catchment (Pace et al. 2004, Weidel et al. 2008, Hessen & Tranvik 2013).

The availability and characteristics of energy sources in aquatic food webs are considered as integrated measure of ecological and environmental characteristics (such as water depth, nutrient, canopy cover, and lake size) of the lake ecosystem and its catchment (Doi 2009). The canopy cover represents its shading condition. Dense canopy cover from riparian vegetation could provide large amount of terrestrial input of organic matter (e.g. leaf litter) into the water body and reduce the light penetration to

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water surface (Lamberti & Steinman 1997, Hill et al. 2001, Doi et al. 2007), leading to the dominance allochthonous energy sources in the lake ecosystems. In contrast, a relatively open water body with low/no canopy cover could enable higher light penetration into water and promote photosynthesis of aquatic plant and algal producers resulting in increased autochthonous importance of the lake ecosystems (Hill et al. 1995, Lamberti & Steinman 1997, Hill et al. 2001). As nutrients are critical limiting factors for phytoplankton productivity, the decrease in aquatic nutrient concentration limit the biomass and productivity of phytoplankton. Thus, there were more autochthonous energy sources supported lake ecosystems in lakes with higher phosphorus concentration (Schindler 1978, Wetzel 2001, Genkai-Kato & Carpenter 2005). In addition, the lake ecosystem size (e.g. surface area) could affect the availability and characteristic of energy sources. The increase in the wetted area of a lake would reduce the lake edge-to-surface-area ratio, and this results in lowering the proportion of terrestrial organic matter inflow into the lake (Francis et al. 2007). Also, the larger surface area of a lake would also increase the solar radiation into lakes. Thus, the autochthonous energy sources would dominance the lake ecosystems with larger surface area (Vadeboncoeur et al. 2008, Doi 2009).

Seasonality showed strong influence of the relative importance of allochthonous and autochthonous of energy sources to mountain lake food webs. The increased abundance of fallen leaves of riparian vegetation in temperate lakes during autumn would increase the availability of allochthonous food sources to the aquatic consumers. Seasonal variation of temperature pattern could play important role on determining the availability and characteristics of energy sources of lake ecosystems (Grey et al. 2001, Pulido-Villena et al. 2005, Doi 2009). Previous studies showed that the seasonal shifting of dietary reliance on different energy sources of various consumers based on stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope analysis in the temperate oligotrophic lake ecosystems. Grey et al. (2001) revealed that zooplankton $\delta^{13}C$ rapidly became more $\delta^{13}C$-depleted due to increased assimilation of more phytoplankton during summer whereas the zooplankton $\delta^{13}C$ signature gradually became more $\delta^{13}C$-enriched resulting from higher utilization of the allochthonous FPOM in winter. Such seasonal change of food utilization pattern of zooplankton confirmed that their opportunistic feeding behavior was highly associated with the food availability in the oligotrophic or dystrophic mountain lakes. Other researches also showed that the oligotrophic mountain lake ecosystems resulted in the opportunistic feeding behavior of most consumers associated with the seasonal availability of food sources (Dawidowicz & Gliwicz 1983,

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Tiberti et al 2014). In temperate lake ecosystems, thermal stratification has been considered as the most important factors for the vertical environmental gradient and the seasonal vertical mixing represented the essential driver for nutrient and material cycling in the water column (Dake & Harleman 1969). However previous studies were documented in lakes in temperate zones (e.g. Grey et al. 2001, Bertolo et al. 2005, Pulido-Villena et al. 2005, Ask et al. 2009). Yet, little has been done to evaluate the seasonality effect on the food web structure in subtropical mountain lakes. For the subtropical mountain lakes, the strong seasonality of precipitation pattern, i.e. monsoon rainfall and typhoon events in summer, could cause severe disturbance to solute concentrations, primary productivity and associated fauna dependent on autochthonous energy. The dystrophic mountain lakes with shallow depth and low pH due to local geology and long term accumulation of organic debris are poor in nutrients and polymictic lentic water bodies where thermal stratification is uncommon (Lewis 1983). In fact, vertical mixing due to seasonal freezing and thawing events is unlikey to occur in subtropical/tropical lake ecosystems. However, the heavy rainfall events (e.g. typhoon) in summer would be the major seasonal disturbance to these lake water bodies resulting in mixing and nutrient upwelling in subtropical/tropical lakes (Von Westernhagen et al. 2010, Wang et al. 2012). Also, large quantities of plant materials

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and debris were washed into the lake by runoff during the rainy seasons (Yang et al. 2011). Such strong precipitation could not only influence the allochthonous food sources into mountain lakes, but also affect the community composition and succession of bacteria and phytoplankton in lakes (Shade et al. 2010).

Accumulated studies on temperate mountain lakes have revealed ecological importance of such ecosystems according to their biodiversity, food web structure and various aspect of lake ecology (Campbell et al. 2000, Vives et al. 2005, Matthews & Mazumder 2006, Catalan et al. 2009). Catalan et al. (2009) confirmed that these habitats were listed as the most sensitive ecosystems to environmental changes and given the highest priority for conservation. Despite the ecological importance of mountain lakes, only limited investigation has been under taken on these habitats in subtropical/tropical area. Therefore, it would be important to investigate the trophic dependence of consumers and predators from higher trophic levels upon different food sources to enhance the understanding of ecosystem processes and food web structures in subtropical/tropical mountain lakes. Despite the increasing of global awareness of the ecological impact of mountain lakes, most previous study about the mountain lakes mainly focused on the single components (e.g. monitoring physical and chemical characteristics, and the ecological investigation of aquatic fauna). Therefore, there were

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limited researches that connected the different ecological components above and then to discuss more comprehensive on the entire mountain lake ecosystems through understanding the environmental characteristics and establishing the food webs. Also, there were relatively limited studies focused on the mountain lake ecosystems in subtropical Taiwan. Previous studies investigating mountain lakes in Taiwan mainly focused on the relatively large scale of the geology of mountain lakes, such as the informative historical record of climate changes in lake ecosystems and their drainage basins (e.g. Wu et al. 1997, Chen & Wu 1999, Chen et al. 2009, Wang et al. 2013, Wang et al. 2014). These previous studies have provided detailed knowledge of historical geology events in mountain lakes in Taiwan, but there was no investigation on food web structure and trophic transfer patterns of mountain lake ecosystems that resulting in the limited understanding of environmental-biotic interactions and biodiversity-ecosystem processes the prestigious mountain lake ecosystem in Taiwan. In fact, ecology of most subtropical mountain lakes has not been detailed studied. Thus, it would be essential to study food web structures in mountain lakes in Taiwan to enhance our understanding of the influence of environmental conditions on aquatic biodiversity, trophic linkages and ecosystem structure.

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In this study, we investigated the seasonal variation of food web structure, food utilization pattern of various trophic consumers and predators in the subtropical mountain lakes from Taiwan using stable carbon and nitrogen isotope analysis with the importance of various basal food sources determined using the stable isotope mixing model SIAR v 4.0 (Stable Isotope Analysis in R) in our study. The gut content of the dominance predators was analyzed to provide as the supplementary information for their food utilization (intake) pattern. The zooplankton and fish biodiversity were also evaluated at the study sites during the study periods. Also, we studied the pattern of food resource partitioning between sexes and among different body sizes of the dominant fish predators were evaluated in the study dystrophic lake ecosystems. Our experiments were carried out in the two subtropical mountain lakes, lake Yuanyang (allochthonous lake) and lake Tsuifong (autochthonous lake), during 2014 to 2015 to investigate the inter-site and seasonal variation of the food web structures and relative importance of various energy basis. Results could provide important baseline information of food web structure and trophic ecology of the subtropical mountain lake ecosystems in Taiwan.

2. Materials and methods

2.1. Study sites

The two study sites, Lake Tsuifong (TFL) (24˚52’ N, 121˚60’E) and Lake Yuanyang (YYL) (24˚58’ N, 121˚40’E), are located in northern Taiwan (Figure 1). TFL locates at 1,840 m a.s.l. on Tai-ping Mountain National Park in Yilan County and it is the largest subalpine lake in northern Taiwan (wetted area ≈ 24 ha; mean depth = 3.4 m; maximum depth = 5.4 m) (Wang et al. 2013). YYL locates at 1,670 m a.s.l. on Chi-lan Mountain in Yuanyang Lake Nature Reserve in Hsinchu County (wetted area ≈ 3.6 ha; mean depth = 4.4 m; maximum depth = 5.7 m) (Wu et al. 2001). Both lakes are shallow, polymictic lakes without development of clear thermal stratification. As strongly influenced by the East Asia monsoon, the climate of both sites are characterized by subtropical monsoons with strong seasonal variation in rainfall pattern, such that heavy rainfall events in summer due to typhoons and continuous drizzling throughout winter. Since YYL and TFL were located at high altitudes in subtropical zones, that temperature was similar to the lakes in temperate zones but the rainfall patterns were influenced by subtropical monsoons and typhoons. In particular, the surface of the study lakes would be frozen and thawed within a few days during winter every year.

TFL was relatively unshaded autochthonous ecosystem with only sparsely distributed riparian vegetation, but the drainage basin was covered by yellow cypress forest composed of *Chamaecyparis formosensis* (Matsum 1901) and *C. obtusa* Siebold & Zucc. var. *formosana* (Hayata) (Rehder 1914). The drainage basin was undisturbed by human activity. The bottom of TFL was predominantly made up with metamorphic rock, in particular gray-black slate (Wang et al. 2013). YYL was frequently covered by heavy cloud layers and fog and the solar radiation to the lake was largely reduced (Liao et al. 2003). YYL was a densely shaded allochthonous system with continuous distribution of riparian vegetation composed of coniferous and hardwood forest dominated by *C. obtusa* Siebold & Zucc. var. *formosana* (Hayata) (Rehder 1914) and *Rhododendron formosanum* (Hemsl 1895), and pteridophytes, with densely coverage of epiphytic mosses and liverworts, aquatic plants dominated by *Miscanthus transmorrisonensis* (Andersson 1855), *Schoenoplectus mucronatus* (L.) Palla subsp. *robustus* (Miq.) (T. Koyama 1978) and *Sparganium fallax* (Graebn 1898) at the shore and shallow areas. Leaf litter was in the terrestrial runoff from the surrounding mountains to enter YYL, particularly during heavy rains (Wu et al. 2001). An earlier study showed high species richness of phytoplankton in YYL including 40 species of Bacillariophytes, 48 species of Chlorophytes, 16 species of Cyanophyte, 17 species of Chrysophytes, 3 species of Phyrrhophytes, 3 species of Euglenophytes, and 4 species of

Cryptophytes (Wu et al. 2000). Other algae species including filamentous algae (*Spirogyra*), *Oscillatoria*, *Chara*, and *Batrachospermum* were also observed in YYL (Wu et al. 2000).

2.2. Environmental characteristics

Daily air temperature, rainfall, and solar radiation data during the study period were automatically recorded by the meteorological station set up at ~ 1 km from each study lake. Water chemistry parameters including water temperature (Temp, ˚C), pH, total dissolved solid (TDS, mg/L), conductivity (Cond, μS/cm), and oxidation-reduction potential (ORP, mV) of each study lake were measured using YSI Pro-plus multimeter during the study period. An instrumented buoy was installed at the central area of each study lake (Figure 1) for automatic measurement of water temperature, dissolved oxygen (DO, mg/L), and chlorophyll-*a* (Chl-*a*, μg/L) concentrations. Water temperature was recorded automatically at 1-hour intervals by a thermistor probe (Templine; Apprise Technologies, Duluth, MN, U.S.A.). The dissolved oxygen was recorded automatically at 1-hour interval by a Greenspan DO100 dissolved oxygen sensor at the water depth between 0 – 50 cm from the surface. The chlorophyll-*a* concentration was recorded automatically at a 10-minute interval by an in-vivo Chlorophyll-*a* sensor (minimum

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detection limit = 0.025 μg/L; range = 0 – 500 μg/L) of the Turner Designs C3™ submersible fluorometer at the water depth between 0 – 50 cm from the surface. In addition, three water samples were taken at each study lake and transported to laboratory at 4 °C for the concentration of NH_4-N (mg/L), PO_4-P (mg/L), and NO_3-N (mg/L). In the laboratory, the water samples were analyzed for the nutrient concentrations within 24 h. The concentrations of NH_4-N, PO_4-P, and NO_3-N were determined using colorimetric methods by test kit no. 114752, 114848, and 109713 respectively on a Merck Spectroquant® Pharo 100 spectrophotometer. Water samples for dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC) were stored in the cold and dark for < 3 days before being analyzed using a 1010 Total Organic Carbon Analyzer (O.I. Analytical, College station, TX, USA).

2.3. Collections and preparations of biological samples

All major potential food sources including mixed leaf litter, FPOM (fine particulate organic matter), bacteria, phytoplankton and periphyton and their potential consumers including zooplankton, benthic macroinvertebrates, fish, and amphibians were collected during winter (December 2014, January, February, and March 2015) and summer (July 2015) in TFL and YYL. All the samples were for stable carbon and

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nitrogen isotope analysis and determination of the seasonal variation of food web structure in the two study lake ecosystems. Three replicates were collected for each potential food source at each site during each study season.

2.3.1. Potential food sources

The mixed leaf litter were sampled with a hand net (mesh size = 0.5 mm) swept along the water surface at both lakes. They were carefully brought to the surface, any sediment on the leaf surface were removed by washing with lake water and placing in the labelled plastic bags. For FPOM sampling, 0.5 L water was collected at the water depth between 0 – 50 cm from the surface after the sediment was disturbed. Bacteria were collected by scraping the surface of glass slides (25 × 8 cm) from 1-mm meshed cages preinstalled (depth = 50 cm) for 1 month. Periphyton was sampled by brushing the surfaces of cobbles collected along lake shore at about 10 – 20 cm below the water surface. Phytoplankton was collected by passing 2 L water collected at 0 – 50 cm water depth from surface through a sieve (mesh size = 1 mm). The five major potential food sources were collected at both sites in winter and summer during the study period between 2014 and 2015 except that no phytoplankton sample was collected during winter. Since previous study reported that the carbon isotopic signatures of phytoplankton did not have obvious seasonal difference (Gearing et al. 1984), same values of the carbon and nitrogen isotopic signatures of phytoplankton collected in summer were used in winter.

2.3.2. Potential consumers

Zooplankton sample was collected in each study lake by hauling a vertical zooplankton sampling net (mesh size = 330 μm) from lake bottom to surface. Three replicates of zooplankton samples were collected at each study lake during winter and summer. Benthic macroinvertebrates (e.g. Chelicerata, Chironomidae, Hemiptera, Anisoptera, Coleoptera, Oligochaeta, Trichoptera, Corydalidae, and Turbellaria) were collected by sweeping a D-net along aquatic vegetation and the lake bottom in combination with direct picking from the bottom substrate. Additional samples of benthic macroinvertebrates were collected by retrieving macroinvertebrate individuals from three sets of colonization tiles (23 × 6 × 0.6 cm) in 0.5-mm meshed bags pre-deployed 3 – 6 weeks prior to collection. All fish and amphibians samples including tadpoles of *Bufo bankorensis* (Tadpole-B), tadpoles of *Rana adenopleura* (Tadpole-R), adults of *Bufo bankorensis* and *Rana adenopleura*, *Cyprinus carpio*, *Carassius auratus*, *Misgurnus anguillicaudatus*, and *Silurus asotus* were collected using fish traps (3.6 ×

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0.4 × 0.23 m, L × W × H; mesh = 15 mm) and shrimp cages (0.30 × 0.08 m, L × D; mesh = 0.2 cm). Three fish traps and three shrimp cages were installed at about 0 – 1 m below the water surface at different locations at each study lake overnight. Additional samples of fish were collected using three seine nets with different mesh sizes (i.e. 4.55 cm, 2.73 cm and 0.91 cm). All the biological samples were placed in labelled bags or vials, transported them to the laboratory at 4 °C, and frozen at -20 °C before further processing.

In the laboratory, the leaf litter samples were gently rinsed with deionized water to remove any sediment and benthic macroinvertebrates from their surfaces. Each FPOM samples was collected by filtering 500 ml water sample through GF/F filters (Whatman). The zooplankton samples were identified into three taxa, i.e. Copepoda, Cladocera, and Rotifera under a 80x stereo-microscope. The abundance of individuals of each taxon were calculated and recorded. The benthic macroinvertebrate samples were identified to class level (Oligochaeta, Arachnida, Bivalvia), order level (Cladocera, Copepoda, Ostracoda, Trichoptera, Hemiptera, and Plecoptera), infraorder level (Anisoptera) or family level (Chironomidae, Corydalidae) under a 80x stereo-microscope. The abundance of each taxon were calculated and recorded. All fish and amphibian samples were identified to species. All fish and amphibian individuals were measured to nearest

0.01 cm (fork length for fish and body length for amphibians) and wet weight to nearest 0.01 g. To assess the ontogenetic shift in the diet of the fish species in YYL and TFL, the fish were classified according to their body length. All fish were dissected and sex of each individual was identified based on the gonad structure. At least three replicates of each species collected at each site during each season and then back muscle of each fish and leg muscle of each amphibian were separated for stable carbon and nitrogen isotope analysis. Also, the stomach of individual fish and amphibian samples were dissected and preserved in 10 % formalin for further gut content analysis. Prior to the stable carbon and nitrogen isotope analysis, all animal samples were processed so that each sample contained either one individual with dry mass ≥ 2 mg or pooled individuals of the same taxon of dry mass ≥ 2 mg. All processed biological samples were freeze-dried and homogenization with liquid nitrogen using an agate mortar and pestle. All samples were for stable carbon and nitrogen isotope analysis.

2.4. Gut content analyses

Since amphibians and fishes were top predators of the lake ecosystem, it was important to investigate their gut content to understand the food utilization and furthermore to understand the variation of food web structures. The food component in the preserved gut content of individual of amphibians and fishes were classified using a stereo-microscope to lowest taxonomic levels including class level (Oligochaeta, Arachnida, Bivalvia), order level (Cladocera, Copepoda, Ostracoda, Trichoptera, Hemiptera, and Plecoptera), infraorder level (Anisoptera) or family level (Chironomidae, Corydalidae). The prey fishes, sediment, algae, and leaf litter found in the gut content were categorized as fish, sediment, algae, or leaf litter. The relative volumetric quantity of food items and percentage of prey in the predatory fishes and amphibians in the gut was calculated.

2.5. Stable carbon and nitrogen isotope analyses

Stable isotope analyses have been commonly used as tracers in environmental studies in recent decades, ratios of $\delta^{13}C$ and $\delta^{15}N$ have been used to examine aquatic food webs by providing information on the contribution of available food sources and the trophic level of the consumer organisms (Cabana & Rasmussen 1994, Cabana & Rasmussen 1996, Vander Zanden & Rasmussen 2001, Post 2002, Binning et al. 2009, Kelleway et al. 2010, Matuszak et al. 2011, Winemiller et al. 2011). Previous studies indicated that 3 – 4 ‰ and 0 – 1 ‰ enrichment of $\delta^{15}N$ and $\delta^{13}C$ respectively, of a consumer relative to its prey (DeNiro & Epstein 1978, Minagawa & Wada 1984,

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Peterson & Fry 1987, Kling et al. 1992, Hesslein et al. 1993, Cabana & Rasmussen 1994, Gu et al. 1994, Vander Zanden et al. 1997). The ratio of $\delta^{15}N$ can be used to estimate trophic position (Post 2002, Kelleway et al. 2010). The nitrogen composition is influenced by the diet of an organism, and the individuals of the same species that have the similar diet contribution would result in the consistent $\delta^{15}N$ value (DeNiro & Epstein 1981). Therefore, the trophic enrichment fractionation factors were 2.4 ± 0.42 ‰ for $\delta^{15}N$ and 0.4 ± 0.28 ‰ for $\delta^{13}C$ for consumers with vascular plants as primary diet type, whereas 2.2 ± 0.20 ‰ for $\delta^{15}N$ and 0.5 ± 0.14 ‰ for $\delta^{13}C$ for predators with mixed diets (McCutchan et al 2003). Since the ratio of carbon isotopes changes little as carbon moves through food webs, the $\delta^{13}C$ values were used to determine the sources of organic carbon for an organism when the isotopic signature of the sources are different. Also, $\delta^{13}C$ have been used to identify the energy sources of consumers in various ecosystems (DeNiro & Epstein 1978, Peterson & Fry 1987). The ratio of carbon stable isotopes is often used to differentiate between diets based on plants with different photosynthetic (e.g. C3 vs. C4) pathways in terrestrial ecosystems (Rounick & Winterbourn 1986, Oleary et al. 1992). In lake ecosystems, $\delta^{13}C$ is used to distinguish between two major sources of available energy sources including littoral production from periphyton and detritus, and pelagic production from phytoplankton. Since the

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$\delta^{13}C$ which base on the littoral food web tends to be enriched in $\delta^{13}C$ value, or means less negative $\delta^{13}C$, relative to the base of the pelagic food web (France 1995). Since some aquatic producers are able to use bicarbonate ions for photosynthesis, while CO_2 must be taken into the terrestrial plant for photosynthesis. Peterson & Fry (1987) and Hecky & Hesslein (1995) further explained that bicarbonate with CO_2 in air was enriched in $\delta^{13}C$ by 6.0 to 10.8 ‰ relative to the atmosphere CO_2. Therefore, $\delta^{13}C$ could be an indicator to determine the carbon source of a consumer. Stable carbon and nitrogen isotopes of all potential food sources and animal consumers were analyzed by the continuous flow system in which an elemental analyzer (NA 1500, Fison, Italy) was connected to an isotope ratio mass spectrometer (Delta S, Finnigan Mat, Germany) in the Plant Ecophysiological Lab of National Taiwan University. The results were calculated as:

$$\delta^{13}C = \left(\frac{{}^{13}C/{}^{12}C_{\text{sample}}}{{}^{13}C/{}^{12}C_{\text{standard}}} - 1\right) \times 1000$$

$$\delta^{15}N = \left(\frac{{}^{15}N/{}^{14}N_{\text{sample}}}{{}^{15}N/{}^{14}N_{\text{standard}}} - 1\right) \times 1000$$

The international standards were *Vienna Pee Dee Belemnite* (VPBD) (Craig 1957) for carbon and atmospheric nitrogen air for nitrogen (Junk & Svec 1958).

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2.6. Data analyses

2.6.1. Zooplankton and fish abundance and biodiversity

The zooplankton and fish biodiversity was evaluated by taxon richness and species richness respectively. Also, the zooplankton abundance was determined as the number of individuals whereas the abundance of each fish species was recorded as catch-per-unit-effort (CPUE) during winter and summer at each site. The spatial and temporal variation of abundance and biodiversity measures of zooplankton were analyzed using two-way ANOVA. The CPUE of *C. carpio* was analyzed using two-way ANOVA because *C. carpio* was the only fish which was collected at both sites and seasons. Statistical analyses were performed with Minitab® 16 package.

2.6.2. Gut content analysis of fish and amphibians

After analyzing the gut contents and the numeric percentage of each fish (NP, the percentage of individual prey type eaten by each fish) was calculated according to Hyslop (1980) and Blanco et al (2003). Schoener’s index was also used to analyze the diet overlap among male and female adults and juveniles to determine the variation of food utilization pattern between sex and different body sizes of fish based on the diet composition. The diet overlap between different predators in each study season and

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between sexes of the same fish species was calculated with Schoener’s index (Schoener 1970):

$$\mathrm{D} = 100(1 - 0.5 \times \sum_{i=1}^{n} |p_{x,i} - p_{y,i}|)$$

where $p_{x,i}$ = the proportion (0 – 1) of diet category i from the stomach of predator x, $p_{y,i}$ the same for predator y, and n = number of diet categories. D > 60 referred to a significant overlap according to Wallace (1981).

Similarity percentages – species contribution (SIMPER) was used to determine which dietary categories typified the diets of particular species and made the greatest contributions to any dissimilarities between species (Clarke 1993). The seasonal and inter-site variation of gut content of the aquatic predators were analyzed using SIMPER analysis to understand the similarity of gut content between seasons and sites.

2.6.3. Stable isotopic mixing model (SIAR) and food web structures

The SIAR mixing model resolved proportions of different basal food sources in the diet of primary consumers, secondary consumers, and predators. The stable isotope mixing model SIAR v 4.0 (Stable Isotope Analysis in R) of Parnell et al. (2010) was used to determine the contribution of the various potential primary basal food sources to the diet of animal consumers at both TFL and YYL during the study periods. This model allowed the inclusion of carbon and nitrogen isotopic signatures and trophic fractionation ratios with the uncertainty of these values within the model, SIAR also allowed the user to consider variation within and between consumers. This was achieved by incorporating into a single analysis multiple isotopic measurements from each individual (Inger et al. 2010, Parnell et al. 2010). The information required to input into the model included all isotopic data of consumers, mean, and standard deviation (SD) of each source contributing to the consumers, trophic enrichment factors, and elemental concentration values of each basal food source (% C and % N). Prior to modeling, the trophic enrichment factors were calculated for each primary consumer [Coleoptera (Scirtidae), Chironomidae, Chelicerata, Oligochaeta, Trichoptera, zooplankton and tadpole] and secondary consumer [*Cyprinus carpio*, *Carassius auratus*, *Misgurnus anguillicaudatus*, *Silurus asotus*, *Bufo bankorensis*, *Rana adenopleura*, Coleoptera (adult Dytiscidae), Corydalidae, Hemiptera (Gerridae), Hemiptera (Notonectidae), Anisoptera, and Turbellaria]. The organisms were divided into different categories (e.g. primary consumers, secondary consumers, omnivorous fish and carnivorous fish) based on the functional feeding group and their diet habits (Yada & Furukawa 1999, Cordova et al. 2001, García-Berthou 2001, Xie et al. 2001, Varga 2003, Rautio & Vincent 2006, Chen et al. 2008, Rueckert & Giani 2008, Balachandran et al.

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2012, Patrick 2014, Norris 2015, Perbiche-Neves et al. 2016). Moreover, the trophic level was identified as 1 for primary consumers; 2 for secondary consumers; 2.5 and 3 for top predators (2.5 for omnivorous fish and 3 for carnivorous fish) based on the functional feeding group, their diet habits from previous studies and the gut content analyses. The values of SIAR allochthony of the aquatic organisms were calculated as the sum of mode contribution of leaf litter and FPOM, while the values of SIAR autochthony of the aquatic organisms were calculated as the sum of mode contribution of periphyton and phytoplankton.

As δ^{15}N values could provide an indication of the trophic position of a consumer (Minagawa & Wada, 1984), trophic level (TL) was determined for each trophic component (i.e. taxon or species) according to their δ^{15}N ratios as follows:

$$\text{Trophic level (TL)} = \left(\frac{\delta^{15}\mathrm{N}_{Species} - \delta^{15}\mathrm{N}_{Base}}{\delta^{15}\mathrm{N}}\right) + TL_{Base}$$

Where δ^{15}N = the trophic enrichment factors i.e. 2.4 for consumers with vascular plants as primary diet type, whereas 2.2 for predators with mixed diets (McCutchan et al 2003); $\delta^{15}\mathrm{N}_{\mathrm{Species}}$ = the δ^{15}N value of the species in question; $\delta^{15}\mathrm{N}_{\mathrm{Base}}$ = the δ^{15}N value of the representative baseline; $\mathrm{TL}_{\mathrm{Base}}$ = the trophic level of that baseline. In this study, all the primary producers were considered as the representative basis level of trophic structure, i.e. $\mathrm{TL}_{\mathrm{Base}} = 1$. The number of nodes of each food web were calculated as the taxon or

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species of each study lake with the links directly joining the connected trophic levels. The food webs were established by the number of nodes and links of each lake according to the results from both gut content analysis and stable carbon and nitrogen analysis. Linkage density of a food web could represent the web feature and the calculation of linkage density was the number of links divided by the number of nodes (Pimm et al 1991). Food chain length was estimated according to the maximum trophic level of food webs.

3. Results

3.1. Environmental characteristics in the study sites

Both sites exhibited strong seasonality, the solar radiation was ~ 1.7 times higher in summer than in winter, also the solar radiation was higher in TFL than in YYL (Figure 2A). During the study period between 2014 and 2015, annual total precipitation in TFL and YYL were 3038.5 mm and 2295.5 mm respectively, and the annual total number of rainy days at both sites were recorded as 207 days. At both TFL and YYL, the total number of raining days were similar between the two study seasons (winter: YYL = 60 days, TFL = 52 days; summer: YYL = 48 days, TFL = 55 days; Table 1). But the seasonal variation was detected for mean daily rainfall which was ~ 2x higher in

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summer than that in winter (winter: YYL = 6.5 mm, TFL = 5.5 mm; summer: YYL = 12.1 mm, TFL = 14.9 mm; Table 1). Almost continuous precipitation pattern was observed in both study mountain lakes throughout winter and summer, but the intensity of precipitation was higher in summer (Figure 2A). During winter, both the total precipitation and the maximum daily rainfall were similar between TFL and YYL. The maximum daily rainfall was 31.5 mm in TFL, and was 28.0 mm in YYL during winter. The total precipitation was 285.0 mm in TFL, and was 392.0 mm in YYL during winter. During summer, the value of the total precipitation and the maximum daily rainfall were not highly consistent between sites that the maximum daily rainfall in YYL was 2 times higher than it in TFL, but the total precipitation was higher in TFL than in YYL. Yet, the value of the total precipitation and the maximum daily rainfall both were strongly higher in summer than in winter. The maximum daily rainfall was 69.5 mm in TFL, and was 140.0 mm in YYL during summer. The total precipitation was 817.0 mm in TFL, and was 580.0 mm in YYL during summer. Water temperature was generally higher in summer (YYL = 14.1 – 21.3 ^{o}C; TFL = 14.9 – 21.1 ^{o}C) than winter (YYL = 9.6 – 14.9 ^{o}C; TFL = 10.2 – 16.3 ^{o}C) (Figure 2B; Table 1). DO concentration was higher in winter than in summer in both sites (Figure 2B).

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The water chemistry characteristics of the two study lakes are summarized in Table 1. Both lakes were slightly acidic with similar pH measured during the study period (range = 5.19 – 6.30). An obvious inter-site difference in DO concentration was determined during two study seasons that DO concentration was higher in TFL than in YYL. The DO measured in TFL was 9.11 ± 0.16 mg/L during summer and was 9.16 ± 0.35 mg/L during winter. And it was 7.41 ± 0.33 mg/L in YYL during summer and was 8.47 ± 0.41 mg/L in YYL during winter. The mean chlorophyll-*a* concentration (Chl-*a*) in TFL was ~ 200 times higher than that in YYL (winter: TFL = 2.54 ± 1.47 μg/L, YYL = 0.01 ± 0.02 μg/L; summer: TFL = 2.27 ± 0.52 μg/L, YYL = 0.01 ± 0.03 μg/L; Table 1; Figure 3). Low nutrient concentrations were observed in both TFL and YYL during the study periods. The mean NH_4-N concentration was higher in TFL than YYL during winter, but it was lower in TFL than YYL during summer (winter: TFL = 0 – 0.010 mg/L, YYL = 0 mg/L; summer: TFL = 0 – 0.014 mg/L, YYL = 0.010 – 0.025 mg/L). During winter, the mean concentration of nitrate-nitrogen (NO_3-N) was higher in YYL than in TFL (TFL = 0 – 0.35 mg/L, YYL = 0.13 – 0.48 mg/L). During summer, the mean NO_3-N concentration was higher in TFL than YYL (TFL = 0 – 0.10 mg/L, YYL = 0 mg/L). Mean concentration of phosphorous (PO_4-P) were higher in TFL than YYL during both winter and summer (winter: TFL = 0.011 – 0.126 mg/L, YYL = 0 – 0.795

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mg/L; summer: TFL = 0.014 – 0.067 mg/L, YYL = 0.006 – 0.026 mg/L). The mean total dissolved solid (TDS) were higher in YYL than in TFL during both winter (TFL = 3.90 ± 0.37 mg/L, YYL = 15.51 ± 4.40 mg/L) and summer (TFL = 3.57 ± 0.32 mg/L, YYL = 8.55 ± 1.43 mg/L). The mean conductivity were higher in YYL than in TFL during the study periods (winter: TFL = 4.69 ± 0.52 μS/cm, YYL = 17.77 ± 5.21 μS/cm; summer: TFL = 5.09 ± 0.12 μS/cm, YYL = 11.42 ± 1.79 μS/cm). Both DOC and DIC concentrations were generally higher in YYL than in TFL (Figure 2C), but the DOC concentration was generally higher than the DIC concentration in the two study sites during the study periods.

3.2. Potential food sources

The C/N ratios showed clear difference among the five food sources between seasons and sites. The C/N ratios of leaf litter (27.56 – 46.85) were larger than all the other food sources (FPOM: 8.08 – 23.99; bacteria: 6.05 – 20.14; phytoplankton: 13.89 – 18.71; periphyton: 9.26 – 14.15) in the two study lakes during the study periods. The C/N ratios of most of the food sources showed strong inter-site difference. All food sources had significant inter-site variation during both summer and winter except periphyton (one-way ANOVA, $p < 0.05$). In TFL, the C/N ratios of all food sources were slightly higher in winter than summer. In YYL, the C/N ratios of FPOM and bacteria were higher in winter, but that of leaf litter and periphyton were higher in summer. Mean C/N ratios of bacteria were higher in winter in both YYL and TFL with significant seasonal difference revealed by one-way ANOVA (TFL: $p < 0.01$, YYL: $p < 0.05$). But, other food sources in YYL had no significant seasonal difference through one-way ANOVA (leaf litter: $p > 0.05$; FPOM: $p > 0.05$; periphyton: $p > 0.05$). In TFL, the C/N ratios of leaf litter and FPOM had significant difference between season (leaf litter: $p < 0.01$, FPOM: $p < 0.05$), whereas periphyton was the only food sources that had no significant seasonal difference ($p > 0.05$).

The δ^{13}C signatures of the food sources had little seasonal shifts but a clear inter-site variation. Leaf litter was the most δ^{13}C-depleted food source in TFL both during winter and summer whereas bacteria were the most δ^{13}C-depleted food source in YYL during both winter and summer. Results of one-way ANOVA showed the significant seasonal difference of δ^{13}C values of all the primary producers in TFL but only leaf litter and FPOM had significant seasonal difference in YYL. In TFL, the δ^{13}C values of all the primary producers had significant difference between seasons with higher δ^{13}C values during winter (periphyton: $p < 0.05$; bacteria: $p < 0.001$; FPOM: $p < 0.05$; leaf litter: $p < 0.01$). In YYL, only leaf litter and FPOM had the significant seasonal difference of $\delta^{13}C$ values between winter and summer. The mean $\delta^{13}C$ values of FPOM were more $\delta^{13}C$-depleted during summer but mean value of $\delta^{13}C$ signatures of leaf litter was more $\delta^{13}C$-enriched during summer in YYL. The $\delta^{13}C$ values of FPOM ($p < 0.05$) and leaf litter ($p < 0.01$) were significantly different between seasons. However, periphyton ($p > 0.05$) and bacteria ($p > 0.05$) had relatively similar $\delta^{13}C$ signatures between winter and summer. Moreover, the $\delta^{13}C$ values of all the primary producers had significant inter-site difference. During winter, the $\delta^{13}C$ values of primary producers were significantly different between sites with YYL had the more depleted $\delta^{13}C$ signatures (periphyton: $p < 0.01$; bacteria: $p < 0.001$; FPOM: $p < 0.001$; leaf litter: $p < 0.001$). Similar pattern also occurred during summer that all the $\delta^{13}C$ signatures of food sources were more $\delta^{13}C$-depleted in YYL except for leaf litter (periphyton: $p < 0.001$; bacteria: $p < 0.001$; FPOM: $p < 0.001$; leaf litter: $p < 0.05$).

The $\delta^{15}N$ signatures of the food sources had slightly seasonal variation but strong inter-site difference. The mean $\delta^{15}N$ values of leaf litter had seasonal variation at both TFL and YYL with higher $\delta^{15}N$ values in summer (TFL: $p < 0.001$; YYL: $p < 0.05$). The $\delta^{15}N$ signatures of FPOM only had significant seasonal variation in YYL with higher $\delta^{15}N$ signatures in summer (YYL: $p < 0.05$). The $\delta^{15}N$ values of bacteria and periphyton were not significantly different between the two study sites. The mean value of $\delta^{15}N$

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signatures of leaf litter had inter-site variation during both summer and winter with lower δ^{15}N signatures in YYL (summer: $p < 0.01$; winter: $p < 0.01$). In addition to leaf litter, no other δ^{15}N signatures of food sources had inter-site variation during winter. During summer, both FPOM and periphyton had significant difference of δ^{15}N signatures between sites with higher δ^{15}N values in TFL (FPOM: $p < 0.01$; periphyton: $p < 0.01$), whereas the δ^{15}N values of bacteria had no inter-site variation.

3.3. Primary consumers

The C/N ratios of the primary consumers in the two lakes were different among seasons and sites. Mean C/N ratios of Chelicerata were slightly higher in TFL (4.82) than YYL (4.21 – 4.46). The mean C/N ratios of Chironomidae were higher in TFL than YYL (TFL: summer = 6.13, winter = 10.39; YYL: summer = 4.64, winter = 4.89). Tadpole-R and Trichoptera were only collected in YYL during the study periods and had small seasonal shifts in YYL. Mean C/N ratio of tadpole-R was higher in summer (summer = 5.68; winter = 5.45) and the mean C/N ratio of Trichoptera was higher during winter (summer = 5.06; winter = 5.55). The mean C/N ratios of zooplankton was higher in winter in TFL (summer = 3.87; winter = 5.59), whereas it was lower in winter in YYL (summer = 4.93; winter = 4.04). In general, all the aquatic consumers in YYL were more δ^{13}C-depleted than TFL (YYL: -28.55 to -38.43 ‰; TFL: -21.87 to -26.93 ‰). The mean δ^{15}N signatures of Chelicerata was enriched in YYL than in TFL during winter (TFL = 1.16 ‰; YYL = 1.76 ‰), whereas the mean δ^{13}C signatures was depleted in YYL than in TFL during winter (TFL = -26.93 ‰; YYL = -28.55 ‰). The mean δ^{15}N signatures of Chironomidae were higher in TFL than YYL during both winter and summer (winter: TFL = 4.54 ‰, YYL = 0.06 ‰; summer: TFL = 3.19 ‰, YYL = 2.13 ‰). Mean δ^{15}N signatures of zooplankton were higher in TFL than YYL during both winter and summer (winter: TFL = 8.61 ‰, YYL = 3.47 ‰; summer: TFL = 3.54 ‰, YYL = 3.51 ‰). The mean δ^{15}N and δ^{13}C signatures of tadpole-R in YYL were similar between seasons (δ^{15}N: winter = 5.85 ‰, summer = 5.57 ‰; δ^{13}C: winter = -34.66 ‰, summer = -34.68 ‰). Both the δ^{15}N and δ^{13}C signatures of all the primary consumers had no significant seasonal and inter-site variation in our study through one-way ANOVA ($p > 0.05$).

The SIAR mixing model indicated strong seasonal variation in the food utilization pattern of primary consumers in TFL. Most of the consumers in TFL depended on autochthonous food sources (e.g. phytoplankton and periphyton) during both summer and winter (Figure 5A – B). During winter, phytoplankton was the most important food source of zooplankton, contributing up to 48.1 % and followed by periphyton (3.2 %)

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(Figure 5A). During summer, periphyton had the highest relative contribution to all primary consumers in TFL (zooplankton = 25.3 %, Chironomidae = 30.4 %, Oligochaeta = 28.8 %, Figure 5B), while leaf litter had the lowest contribution to all primary consumers (zooplankton = 8.4 %, Chironomidae = 0.8 %, Oligochaeta = 0.2 %, Figure 5B). Contribution of different food sources to Chironomidae was relatively constant between winter and summer in TFL that except for leaf litter, other four food sources shared almost equal contributed to Chironomidae. Moreover, phytoplankton (34.9 %) and periphyton (23.5 %) had the highest relative contribution to *B. bankorensis* tadpole in winter (Figure 5A). During winter, phytoplankton was the most important components of all primary consumers except Chelicerata in TFL (zooplankton = 48.1 %, Chironomidae = 26.8 %, Tadpole-B = 34.9 %, Figure 5A). The food sources contributed to Chelicerata were different from other primary consumers that leaf litter contributed the greatest proportion to Chelicerata in TFL during winter (27.7 %, Figure 5A). Moreover, the similar contribution of food sources was found in YYL that bacteria showed the highest mode relative contribution to most consumers except for Chelicerata in YYL during winter (zooplankton = 53.8 %, Chironomidae = 77.2 %, Trichoptera = 50.0 %, Coleoptera (Scirtidae) = 60.2 %, Oligochaeta = 30.9 %, Tadpole-R = 62.7 %, Figure 5C). Bacteria were the least important food source of Chelicerata in YYL (1.5 %).

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Since bacteria had highest relative contribution to most primary consumers in YYL during both winter and summer, the proportion of other food sources to primary consumers in YYL still had seasonal variation (Figure 5C – D). Contribution of different food sources to Trichoptera, Chironomidae and tadpole of *R. adenopleura* were relatively constant between winter and summer in YYL. Bacteria contributed the greatest proportion to Trichoptera and Chironomidae (Trichoptera: summer = 82.8 %, winter = 50.0 %; Chironomidae: summer = 93.4 %, winter = 77.2 %; Tadpole-R: summer = 84.2 %, winter = 62.7 %; Figure 5C – D). The contribution of different food sources to zooplankton varied seasonally, bacteria were the most important food source in winter (53.8 %), while each available food sources contributed ~ 20 – 25 % to zooplankton during summer. The results for Chelicerata revealed a varied proportion between seasons. Bacteria were the least important food source that contributed to Chelicerata in winter (1.5 %), but all five food sources showed similar contributions during summer (Figure 5C – D). During winter, bacteria were the most important components to Coleoptera (Scirtidae) and Oligocaeta, contributing up to 60.2 % and 30.9 %, respectively (Figure 5C). Also, bacteria were the most important food sources in tadpoles of *B. bankorensis* in summer (74.0 %).

The relative abundance of the composition and three zooplankton taxa (i.e.

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Copepoda, Cladocera, and Rotifera) varied between seasons and sites in our study (Figure 7). The most dominant taxon was Rotifera during both summer and winter in TFL, and the abundance of all three taxa were higher in summer. However, Copepoda was most abundant in winter, and there was no obvious dominant taxon during summer in YYL (Figure 7). Only Cladocera and Rotifera demonstrated higher abundance in YYL during summer. In YYL, Rotifera was 1.7 times higher in summer than in winter. Significant interaction between sites and seasons was observed in the total abundance of zooplankton ($p < 0.01$, Table 3), and was significantly different in season with higher total zooplankton abundance during summer ($p < 0.001$, Table 3; Figure 8D). The abundance of Copepoda had significant interaction between sites and seasons ($p < 0.01$, Table 3), and it had the inter-site variation during the study periods ($p < 0.001$, Table 3; Figure 8A). The abundance of Cladocera showed significant interaction between sites and seasons ($p < 0.01$, Table 3), and had significant seasonal difference with higher abundance during summer than winter ($p < 0.001$, Table 3; Figure 8C). However, there was no significant interaction between sites and seasons of the Rotifera abundance ($p > 0.05$, Table 3), but it had the significant inter-site variation and significant seasonal variation separately (inter-site variation: $p < 0.001$, seasonal variation: $p < 0.001$, Table 3). The mean Rotifera abundance was higher in TFL than YYL, and it was higher during

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summer than winter (Figure 8B).

3.4. Secondary consumers and predators

3.4.1. Benthic macroinvertebrates

The C/N ratios of the secondary consumers were different between season and sites. During winter, mean C/N ratios of all organisms of secondary consumers were higher in YYL than TFL. In YYL, mean C/N ratios of Corydalidae and Hemiptera (Gerridae) were higher during summer than winter (Corydalidae: summer = 4.79, winter = 4.29; Hemiptera (Gerridae): summer = 4.59, winter = 4.40). In TFL, the mean C/N ratios of Turbellaria was higher in winter (4.80) than summer (4.16). But there were no significant seasonal or inter-site variation through one-way ANOVA ($p > 0.05$). All the secondary consumers in YYL were much more δ^{13}C-depleted than in TFL during the study periods (YYL: -25.42 to -34.78 ‰; TFL: -21.73 to -26.46 ‰). Both Anisoptera and Coleoptera (adult Dytiscidae) had inter-site variation of mean δ^{13}C signatures that the higher δ^{13}C signatures were showed in TFL than YYL during winter (Anisoptera: TFL = -22.00 ‰, YYL = -34.46 ‰, $p < 0.05$; Coleoptera (adult Dytiscidae): TFL = -24.36 ‰, YYL = -30.68 ‰, $p < 0.01$). Mean δ^{13}C signatures of Hemiptera (Gerridae) had significant seasonal variation in YYL with higher δ^{13}C values during summer than

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winter ($p < 0.05$). There was no seasonal variation in δ^{15}N values of Turbellaria in TFL (winter = 6.18 ‰, summer = 6.04 ‰, $p > 0.05$). The seasonal variation of δ^{15}N signatures of secondary consumers in YYL varied among taxon. Coleoptera (adult Dytiscidae) and Hemiptera (Gerridae) were more δ^{15}N-enriched during winter than summer (Coleoptera (adult Dytiscidae): winter = 4.50 ‰, summer = 3.63 ‰; Hemiptera (Gerridae): winter = 4.51 ‰, summer = 2.67 ‰), whereas Corydalidae was more δ^{15}N-enriched during summer (Corydalidae: winter = 4.49 ‰, summer = 5.70 ‰). But only Hemiptera (Gerridae) had significant difference in YYL between seasons ($p < 0.05$). Also, the significant difference of δ^{15}N signatures between sites only observed in Coleoptera (adult Dytiscidae) ($p < 0.05$).

The relative proportions of the basal food sources contributed to Turbellaria in TFL changed slightly from winter to summer, with bacteria (32.4 %) being the most important item followed by periphyton (29.9 %) in winter, and periphyton was the greatest contribution (36.5 %) followed by bacteria (20.8 %) in summer (Figure 5A – B). Bacteria were the most important basal food sources to Anisoptera in TFL during winter (35.3 %), followed by periphyton (31.8 %). Similarly, the basal food sources contributed to Anisoptera remained relatively unchanged between sites that bacteria were the most important basal food sources contributed to Anisoptera in YYL (57.5 %).

During winter, leaf litter (5.9 %) was the relatively unimportant basal food source for Coleoptera (adult Dytiscidae) but the contribution of other four sources were relatively even. In contrast, leaf litter had higher contribution than other food sources to Hemiptera (Notonectidae) in TFL during winter (28.8 %). The contribution of different basal food sources to Corydalidae in YYL varied seasonally that bacteria (27.2 %) and phytoplankton (47.3 %) were the most important basal food sources during winter and summer respectively. Bacteria contributed the highest proportion to Coleoptera (adult Dytiscidae) during both winter (25.5 %) and summer (32.1 %). Bacteria made minor contributions to Hemiptera (Gerridae) in YYL during both winter and summer (Figure 5C – D). During winter, bacteria represented the most important basal food source to Anisoptera and Hemiptera (Notonectidae) in YYL during summer. Two different species of Hemiptera (i.e. Notonectidae and Gerridae) were collected in YYL during summer. They had the different pattern of basal food sources utilization that bacteria had the greatest contribution (66.8 %) to Hemiptera (Notonectidae) whilst bacteria was the least important proportion (3.8 %) to Hemiptera (Gerridae).

3.4.2. Fishes and amphibians

The mean C/N ratios of *B. bankorensis* ranged from 3.19 to 3.25. *Rana*

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adenopleura was only sampled in YYL during summer and the range of mean C/N ratio was 2.96 to 3.03. *Carassius auratus* and *C. carpio* were the only collected fish species in TFL during winter, while *S. asotus* was collected in addition to these two species during summer. The sampled fishes in YYL were *M. anguillicaudatus* and *C. carpio* during both summer and winter (Table 4; Figure 9). Results of CPUE of *C. carpio* through two-way ANOVA showed no significant difference between seasons and sites ($p > 0.05$, Table 5). The mean C/N ratio of *C. auratus* in TFL ranged from 3.17 to 3.30, and the mean C/N ratio of *C. carpio* ranged from 3.05 to 3.13 in the two lakes during winter and summer. The mean C/N ratio of *M. anguillicaudatus* in YYL were similar between season (winter = 3.38, summer = 3.39), and the mean C/N ratio of *S. asotus* in TFL during summer was 2.97. Only *C. carpio* had significant inter-site variation of C/N ratios during winter ($p < 0.05$). The mean $\delta^{13}C$ values of fishes and amphibians were all more depleted in YYL than in TFL (YYL: -24.78 to -33.73 ‰, TFL: -21.07 to -23.20 ‰, Table 8). The mean $\delta^{13}C$ signatures of *C. carpio* had significant difference between sites during both winter and summer (winter: $p < 0.01$; summer: $p < 0.001$). The fishes had the higher mean $\delta^{15}N$ signatures than the amphibians (fishes: 7.10 – 9.45 ‰; amphibians: 4.19 – 5.74 ‰), with the only carnivorous fish, *Silurus asotus*, had the highest mean $\delta^{15}N$ values (9.45 ‰). All the $\delta^{15}N$ values of fishes and amphibians were

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similar between season and sites (p > 0.05).

During winter, phytoplankton was the most important basal food sources that contributed to both *C. carpio* and *C. auratus* in TFL (Figure 5A). Phytoplankton was the most important basal food sources to *C. carpio* (30.6 %) in winter, next important contribution were bacteria (27.3 %), and leaf litter (0.8 %) made the minor contributions. According to SIAR model, *C. carpio* and *C. auratus* showed similar basal food sources utilization pattern in TFL during winter such that the highest contribution of *C. auratus* was phytoplankton (29.5 %), followed by periphyton (28.9 %) and bacteria (27.1 %). *Cyprinus carpio* and *M. anguillicaudatus* had different basal food sources utilization pattern in winter so that phytoplankton (52.0 %) were most important food sources of *C. carpio*, but bacteria had the key to *M. anguillicaudatus* in YYL during winter (Figure 5C). Bacteria were the most dominate basal food sources that contributed to *M. anguillicaudatus* both during winter (70.8 %) and summer (80.6 %), other basal food sources had relatively little contribution (< 10 %) to *M. anguillicaudatus* in YYL. In TFL, leaf litter was the lowest basal contribution to *B. bankorensis*, while other four basal food sources had an average contribution during winter (FPOM = 24.6 %; bacteria = 27.6 %; phytoplankton = 23.1 %; periphyton = 26.6 %; Figure 5A).

During summer, periphyton played the greatest supporting role to both *C. carpio*

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(33.9 %) and *C. auratus* (29.7 %), and leaf litter had the lowest basal contribution in TFL (Figure 5B). Leaf litter was also the least important basal food sources that contributed to the carnivorous fish, *S. asotus*, in TFL during summer and phytoplankton (39.5 %) had the highest proportion to *S. asotus*, followed by periphyton (4.3 %). However, bacteria were the most important basal food sources that contributed to both *M. anguillicaudatus* (80.6 %) and *C. carpio* (68.1 %) in YYL during summer (Figure 5D). The basal food sources contributed to *M. anguillicaudatus* in YYL remained relatively unchanged between seasons (Figure 5C – D). SIAR models indicated relatively little contribution (< 10 %) of bacteria to both two amphibian species (*B. bankorensi*s and *R. adenopleura*) in YYL during summer.

All fishes from the two study lakes were primarily omnivorous except for *S. asotus* which was the only carnivorous species. The fish assemblages showed dietary difference among lakes and seasons. The diet of omnivorous *C. auratus* collected in TFL had seasonal variation. Leaf litter (1.6 %), algae (8.2 %), Chelicerata (0.5 %), prey fish (1.6 %), and digested food (88.0 %) were found in the gut content of *C. auratus* during winter, while leaf litter (42.9 %) and zooplankton (57.1 %) were found in the gut content of *C. auratus* during summer (Figure 10A). In TFL, Anisoptera and leaf litter were the dominant components in the gut content for *C. carpio* during winter, while leaf

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litter, Anisoptera, Trichoptera, Ostracoda, Cladocera, and fish were found in the gut content of *C. carpio* in summer (Figure 10B). Moreover, *C. carpio* had a feeding behavior consuming leaf litter, algae, Chironomidae, and Chelicerata in YYL during winter, and the prey in the gut content of *C. carpio* consisted of zooplankton (Ostracoda, Cladocera, and Copepoda) and macroinvertebrates in YYL during summer (Figure 10). In YYL, leaf litter (25.0 %) and macroinvertebrates (5.0 %) were found in the stomach of *M. anguillicaudatus* during winter, whereas there was a wide diet diversity of *M. anguillicaudatus* in summer (Figure 10). *Misgurnus anguillicaudatus* consumed only Chironomidae during winter, but various prey items including Chironomidae, Chelicerata, Anisoptera, Hemiptera, Plecoptera, Bivalvia, fish, and zooplankton (Ostracoda, Cladocera, and Copepoda) were found in the diet during summer (Figure 10). However, *S. asotus* was the only collected piscivorous species in TFL during summer, and the digested food was the most dominant item that was found in its gut content. According to the percentage of prey calculated in the gut content of *R. adenopleura* in YYL during summer, Anisoptera (25.0 %) and Cladocera (25.0 %) represented the largest proportion of the diet, followed by Hemiptera (17.5 %), Chironomidae (13.5 %), Plecoptera (2.5 %), and Chelicerata (1.3 %) respectively (Figure 10B). The percentage of prey calculated in the gut content of *B. bankorensis*

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contained Trichoptera (30.2 %), Corydalidae (25.0 %), Chelicerata (4.2 %), and Oligocaeta (4.2 %). The amphibians in YYL showed a broad range of prey items during summer (Figure 10B). In TFL during winter, leaf litter (50.0 %) was largely found in the diet of *B. bankorensis*. The diet richness of fishes and amphibians during summer were more abundant than that during winter in both YYL and TFL (Figure 10B). Result showed the percentage of prey in *C. carpio* merely based on one to two items, and the gut contents of *C. carpio* mainly consisted of leaf litter, macroinvertebrates, and algae during winter in both TFL and YYL (Figure 10A). Also, the gut content of other predators (i.e. *C. auratus*, *M. anguillicaudatus*, and *B. bankorensis*) only included one to two items (Anisoptera, Trichoptera or prey fish) during winter in both TFL and YYL. However, our results showed a wider diversity of food sources in gut contents of predators during summer in YYL than TFL. In summer, the gut content analysis showed that predators in YYL consumed a wide diversity of food items but aquatic prey constituted the major part of its food. The major prey items of *M. anguillicaudatus* included Cladocera (18.4 %), Chironomidae (18.0 %), Ostracoda (15.0 %), and Anisoptera (13.5 %) (Figure 10B). The gut content of *C. carpio* mainly consisted of macroinvertebrates and zooplankton in YYL during summer.

In TFL, the results indicated dietary overlap apparently existing between *C. carpio*

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and other fish species during winter, while the diet between *C. carpio* and other fish species were not overlap during summer. The results had the similar pattern in YYL that the two species of fishes only showed the significant diet overlap (i.e. D > 60) in winter (Table 6).

SIMPER analysis indicated that the dietary differences were observed both between sites and seasons (Table 7). The diet of predators in YYL substantially differed from that in TFL (mean dissimilarity = 70.87 %, Table 7), largely due to the higher percentage of digested food and leaf litter and with an absence of Chironomidae in TFL. Also, there was strong seasonal variation of the diet of predators in the two study sites. Since the predators consumed leaf litter and algae more frequently and the higher percentage of Chelicerata during winter, this resulted in the dietary differences between seasons (mean dissimilarity = 77.51 %, Table 7).

3.5. Food web structures

The $\delta^{15}N$ and $\delta^{13}C$ signatures of all food sources, primary consumers, secondary consumers, and predators were summarized in Figure 4 so that all food web components in YYL were more $\delta^{13}C$-depleted group but all components were more $\delta^{13}C$-enriched in TFL. It was obvious that leaf litter was not the major food sources utilized by any

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consumers and predators in TFL during both winter (Figure 4A) and summer (Figure 4C). All the basal food sources in YYL showed equally contributed in the food webs relatively (Figure 4B & D). One major trophic pathway was observed in TFL and the trophic position of the top predators were similar between winter and summer (Figure 4A & C). In contrast, two major trophic pathways of which one supported by autochthonous food sources and the other one supported by allochthonous food sources determined in YYL during both seasons. During winter, the top predator of the autochthonous trophic pathway was *C. carpio* and the top predator of the allochthonous trophic pathway mainly based on bacteria was *M. anguillicaudatus* and Anisoptera. However, the top predator of the autochthonous and allochthonous trophic pathways were aquatic insect predator Corydalidae and fish predators (i.e. *C. carpio* and *M. anguillicaudatus*) respectively (Figure 4B & D).

Result of the SIAR allochthony and SIAR autochthony showed that most of the aquatic organisms in TFL mainly relied on autochthonous basal food sources except Hemiptera (Notonectidae) and Chelicerata during winter (Figure 6). In YYL, most aquatic consumers did not directly relied on either autochthonous or allochthonous basal food sources, but showed strong dependence on bacteria as the most important basal food source (Figure 6).

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In TFL, the food chains were slightly longer during summer. In TFL, the maximum trophic levels of fishes were 5.5 and 5.4 respectively during summer and winter (Table 8). In YYL, the food chains were slightly longer during winter. In YYL, the maximum trophic level of fishes was 5.4 during summer and was 5.8 during winter (Table 8). The inter-site variation revealed that the food chain length was similar between sites during summer, and was slightly longer in YYL than in TFL during winter. The food web structures were more complex in YYL than TFL during both winter and summer. In the food webs, the number of nodes was higher in YYL than in TFL during winter (YYL = 18, TFL = 16, Figure 11A – B). This case also appeared during summer (YYL = 19, TFL = 12, Figure 11C – D). The number of links in the food webs was more in YYL than in TFL during both winter and summer (winter: YYL = 36, TFL = 32; summer: YYL = 40, TFL = 24; Figure 11). The linkage density of food webs was similar between seasons both in TFL and YYL (TFL: summer = 2.0, winter = 2.0; YYL: summer = 2.1, winter = 2.0; Table 8, Figure 11).

3.6. Food-resource partitioning of fish

3.6.1. Sex-specific feeding behavior of fish (top predator)

Results of the SIAR models indicated that only *C. carpio* revealed sex-specific

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feeding behavior in YYL during winter (Figure 12). Phytoplankton contributed the greatest proportion to female *C. carpio* (46.5 %), and none of the other sources was identified as important basal food sources (> 10 %), whilst male *C. carpio* appeared to have fed on a relatively even mixture of the available basal food sources except leaf litter (FPOM = 19.5 %; bacteria = 25.9 %; phytoplankton = 26.3 %; periphyton = 23.4 %; Figure 12). Other fish species had no sex-specific feeding behavior. Results of SIAR showed that *M. anguillicaudatus* had no sex-specific feeding behavior that bacteria were the most important basal food sources of both male and female in YYL during both summer and winter. Leaf litter was relatively unimportant basal food sources for both male and female *C. carpio* and *C. auratus*, while other four sources were relatively even contributed in TFL during summer. During winter, the contribution of male and female *C. auratus* were similar in TFL that the highest contribution of both male and female *C. auratus* was phytoplankton, followed by bacteria and periphyton.

Results of gut content analysis indicated that the sexual diet-overlap occurred mainly in TFL during winter and summer. The Schoener’s index values of *C. auratus* in TFL during winter and summer showed significant diet overlap (D > 60) between male and female (winter = 61.75, summer = 90.00, Table 9). The Schoener’s index value of *C. carpio* (17.50) showed that the diet overlap was not significant between genders in TFL

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during summer (Table 9). Yet, the sexual diet-overlap between males and females were not observed in YYL during both winter and summer. The values of Schoener's index of *C. carpio* and *M. anguillicaudatus* in YYL were both < 60 in the study period (winter: *C. carpio* = 40.00, *M. anguillicaudatus* = 40.00; summer: *C. carpio* = 36.67, *M. anguillicaudatus* = 52.50; Table 9).

3.6.2. Fish body size and feeding habits

Results from gut content analysis showed that the gut content of fishes were different with different body size (Figure 13). The small sized (L < 10 cm) *C. auratus* in TFL fed mainly on algae, while Chelicerata and zooplankton was the major component remaining in the stomach of the large size (L > 15 cm) *C. auratus*. *Cyprinus carpio* with different body size in TFL also showed the different gut content. Small fish (L < 20 cm) had (10 %) sediment and medium fish (25 cm > L > 20 cm) had macroinvertebrates in the gut content. Large *C. carpio* (L > 25 cm) fed mainly on macroinvertebrates, zooplankton, and prey fish. A similar pattern was also obtained in YYL so that leaf litter was the major component in the gut content of *C. carpio* with small body size (L < 20 cm), but zooplankton and macroinvertebrates were found in the stomach of medium *C. carpio* (25 cm > L > 20 cm). For *M. anguillicaudatus*, leaf litter was represented major

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diet items of small (L < 10 cm) and medium (15 cm > L > 10 cm) individuals, but macroinvertebrates were the dominant element component of large *M. anguillicaudatus* (Figure 13). Hence, there was a clear association between size of diet items and size of consumer body size so that small-sized fish only fed on smaller items such as sediment, algae, and leaf litter. But, large-sized fish was capable of utilizing larger prey items such as zooplankton, macroinvertebrates, and prey fish in their diet.

4. Discussion

4.1. Primary energy source contributed to subtropical mountain lake ecosystems

The densely distributed leaf litter around the shore of YYL was considered as an abundant food source in YYL. However, our results showed that leaf litter was not the major food source directly contributing to the aquatic ecosystem of YYL despite its high abundance. This was different from previous findings which suggested that allochthonous sources could partially (40 – 55% of particulate organic carbon and 22 – 50% of zooplankton carbon) support the lake metabolism (Jones et al. 1998; Karlsson et al. 2003; Pace et al. 2004) and dystrophic lakes were commonly supported by substantial terrestrial subsidy (Cole et al. 2000, Matthews & Mazumder 2006).

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Moreover, previous study indicated that for lakes with low primary production compared to terrestrial DOC input, bacterial production should be highly dependent on allochthonous carbon (Kritzberg et al. 2005), and allochthonous organic matter would support aquatic food chains and the allochthonous dissolved organic carbon (DOC) could be metabolized by bacteria (Tranvik 1988, Moran & Hodson 1990, Kritzberg et al. 2005). In our study, most consumers in YYL showed strong dependence on bacteria as the basal food sources according to the SIAR mixing model, this could be owing to the high DOC concentration in YYL during the study periods (Figure 2C). Previous study showed that the heavy rainfall events would cause higher inputs of both particulate and organic carbon into the lake during typhoon seasons (Yang et al. 2011). Moreover, leaching of large quantity of DOC would occur in the initial phase (first 6 month) of decomposition in YYL despite the slow decomposition rate of leaf litter in YYL such that the mass loss was only 35 % after 469 days (Rees et al. 2006). Therefore, bacteria were the relatively important basal food sources that directly contributed to the aquatic organisms in YYL. Earlier studies also illustrated that canopy cover suppressed primary production of periphyton by decreasing light intensity and weakened the importance of the autochthonous food chain (Hill et al. 2001, Doi et al. 2007).

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Furthermore, the bacterial assemblage in YYL were dominated by methane-oxidizing bacteria (MOB) because of the δ^{13}C-depleted values of bacteria in YYL during the study periods. The δ^{13}C signature of bacteria in YYL was more negative compared to other basal food sources (bacteria = -34 to -36 ‰), therefore, the carbon isotopic values of bacteria in our study proved the consequence with previous research that CH_4 was much depleted in δ^{13}C, low δ^{13}C values in organisms of aquatic food webs have been considered to indicate their consumption of CH_4-derived carbon (Jones & Grey 2011, Sanseverino et al. 2012). Previous study revealed that biogenic methane produced in anoxic sediments could subsidize food webs as an alternative energy source. A large proportion of the methane diffusing from the sediment and reaching an oxic–anoxic interface can be exploited by MOB in lakes (Jones & Grey 2011, Agasild et al. 2014). Even in shallow lakes, the dense macrophyte beds could limit the oxygen diffusion into the sediment establishing a hypoxic environment which was suitable for methane production in the surface sediment or even in the overlying water (Agasild et al. 2014). MOB carbon could be transferred through the food web up to the fish level, thus CH_4 could be a significant food source not only for the microbial food web and invertebrates, but also for consumers from higher trophic levels (Deines et al. 2007, Sanseverino et al. 2012, Agasild et al. 2014). In our study, *M.*

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anguillicaudatus represented one of the major predator in the food webs of YYL. Our findings agreed with prior studies that that bacteria represented the most important basal food source contributed to *M. anguillicaudatus* during both winter and summer in YYL (Sanseverino et al. 2012, Agasild et al. 2014).

TFL was a relatively unshaded mountain lake and was represented a typical autochthonous ecosystem dependent on autochthonous food sources during both winter and summer. The solar radiation into the water body of TFL was higher than the densely shaded YYL. Since the light intensity of the lake surface was not measure in this study, the value of light intensity of lake surface in both YYL and TFL was used from the previous study that monthly mean light intensity of the water surface were measured from November 2009 to April 2010 (Cheng 2010).This study showed that the mean light intensity were approximately 2 times higher in TFL than in YYL (TFL = 718.9 ± 469.7 μmole/m^2/s; YYL = 372.6 ± 387.3 μmole/m^2/s; Cheng 2010). Moreover, the Chl-*a* concentration in TFL was obviously higher than in YYL indicating that phytoplankton was the more dominant food sources in TFL both during winter and summer comparing to YYL. This agreed with previous findings that the autochthonous community was simple with phytoplankton as the major producer in dystrophic high mountain lakes (Medina-Sánchez et al. 1999, Villar-Argaiz et al. 2001, Carrillo et al.

2002). The carbon and nitrogen stable isotope signatures of aquatic organisms in TFL confirmed that leaf litter was not the major basal food source used by the consumers (Figure 4A & C). The SIAR model output also suggested that leaf litter was least important in contributing to the food webs (Figure 5C – D) and the lake ecosystem would tend to be autochthonous aquatic ecosystem (Figure 6). With lower C/N ratios, autochthonous foods were more valuable foods than allochthonous foods. Our results showed that leaf litter had the highest C/N ratios than all other basal food sources in TFL both during winter and summer, and this could be the reason that the individuals in aquatic food webs did not consumed leaf litter as their main food sources in TFL. Moreover, the SIAR results indicated that the majority of consumers and predators depended on autochthonous food sources (i.e. periphyton and phytoplankton) in the relatively unshaded TFL during different seasons.

Jansson et al. (2000) illustrated that production of autochthonous systems primarily depended on photosynthesis in clear-water lakes with high light penetration, while the energy source based from allochthonous sources mainly dominated in lakes with high concentrations of colored organic substances and low primary productivity. The food web components were found more δ^{13}C-enriched in TFL than in YYL (Figure 4). The primary producers except leaf litter in the two study lakes during both winter and

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summer also showed the mean $\delta^{13}C$ values were more enriched in TFL with significant differences. As consistent to previous study (Pulido-Villena et al. 2005), our results supported that the food web components were more $\delta^{13}C$-depleted in the densely-forested mountain lake than unshaded lake. Finding from earlier studies also matched with our results that the $\delta^{13}C$ values were more enriched in autochthonous food sources (periphyton and phytoplankton) than in allochthonous food sources (leaf litter) (Thimdee et al. 2004, Yam and Dudgeon 2005, Lau et al. 2009, Medeiros & Arthington 2011, Jardine et al. 2013).

4.2. Seasonal variation of availability and characteristic of energy sources

Most environmental parameters including rainfall, solar radiation, and water temperature showed strong seasonality (Figure 2A – B), but not the seasonal variations of all environmental parameters was associated with the ecosystem structure. Despite the large amount of allochthonous food sources would be washed out into YYL owing to the heavy rainfall events during summer (Yang et al. 2011), our results indicated the terrestrial input would not be directly used by aquatic fauna because FPOM and leaf litter were relatively unimportant basal food sources contributed to the organisms in YYL through SIAR analysis. The mean water temperature, solar radiation, and the concentration of Chl-*a* had strong seasonal variation. The higher solar radiation could result in the higher water temperature and the higher Chl-*a* concentration. Prior studies also pointed out the presence of solar radiation would increase the Chl-*a* concentration by increasing the photosynthesis rates (Cabrera et al. 1997, Edwards et al. 2016). Also, when the aquatic ecosystems with the unlimited solar radiation, the higher water temperature could also enhance the efficiency of photosynthesis. Results of SIAR analysis in this study also showed that the aquatic organisms in both TFL and YYL tended to more depend on autochthonous food source during summer than winter. Therefore, light penetration and water temperature would be the key factors influencing the seasonal variation of food web structures in the studied mountain lakes, YYL and TFL.

4.3. Contribution of basal energy sources to primary consumers

The SIAR showed leaf litter was not an important basal food source contributed to all the consumers in TFL during summer. And leaf litter also was not an important basal food source contributed to most of the consumers in TFL except Chelicerata during winter. In YYL, bacteria represented the most dominant basal food sources for most consumers during both winter and summer. However, bacteria were not the most important basal food sources for Chelicerata during the study periods. As the major detritivores in the study lakes, Chelicerata was commonly collected from the sediment both in TFL and YYL and it was possible that Chelicerata had the higher relative dependence on leaf litter and FPOM.

Moreover, the scatter plot of $\delta^{13}C$ and $\delta^{15}N$ showed that there could be a missing basal food source in YYL during both winter and summer (Figure 4B & D). The five sampled basal food sources in our study could not trace back the possible basal food sources of Coleoptera (Scirtidae) and Chironomidae in YYL during winter (Figure 4B) and Trichoptera and Chironomidae in YYL during summer (Figure 4D). Yeh et al. (1995) indicated that the $\delta^{13}C$ isotopic values of an abundant filamentous algae (*Spirogyra* sp.) ranged between -44.8 and -44.9 ‰ (Yeh et al. 1995), this could be the available basal food sources for the $\delta^{13}C$-depleted organisms (i.e. Coleoptera (Scirtidae), Trichoptera and Chironomidae) in YYL during the study periods. Furthermore, the $\delta^{15}N$ value of zooplankton in TFL during winter was higher than all the other aquatic organisms in the ecosystem (Figure 4A). Since previous studied indicated that NO_3-uptake could approach saturation in the high-N lake, but not in the low-N lake, and the phytoplankton enrichment factor for $\delta^{15}N$ would also higher in the high-N lake than in the low-N lake (Nydick et al. 2004). Also, the NO_3-N concentration in TFL during

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winter was slightly higher comparing to other oligotrophic mountain lakes (Kopàcöek et al. 2000, Nydick et al. 2004). Therefore, the results of high δ^{15}N value of zooplankton agreed with prior literature that zooplankton could be most enriched in δ^{15}N when the phytoplankton was taking up NO_3^- primarily and the enrichment of δ^{15}N between phytoplankton and zooplankton was greater when NO_3^- is important (Mullin et al. 1984).

4.4. Contribution of basal energy sources to secondary consumers

The results of basal food sources contributed to secondary consumers were similar to the contribution of energy sources to primary consumers that the autochthonous food sources (e.g. phytoplankton and periphyton) had the highest contribution to fishes in TFL during both winter and summer, whereas bacteria were the most important food sources contributed to fishes in YYL except the *C. carpio* during winter (Figure 5C). Leaf litter was the most dominant basal food sources to Hemiptera (Notonectidae) in TFL during winter, the reason could be that Hemiptera (Notonectidae) mainly fed on Chelicerata. It is noteworthy that leaf litter contributed to the diet of adult amphibians (*B. bankorensis* = 34.7 % and *R. adenopleura* = 28.8 %) in YYL during summer. Hou et al. (2010) showed that the habitat of *B. bankorensis* was open grassland, still water or sides of creeks, while the habitat of *R. adenopleura* was still water or places with rich hydrophilic plants. Since the life cycle of amphibians would not only inhabit in aquatic lake ecosystem, but also crossed to terrestrial area, that leaf litter could contribute to both *B. bankorensis* and *R. adenopleura* in YYL during summer.

4.5. Importance of zooplankton in mountain lake food webs

4.5.1. Effect of inter-site variation to the assemblage of zooplankton

The abundance of different taxon of zooplankton were analyzed to investigate the seasonal and inter-site variation. Also, the abundance and dominant species of zooplankton was related to the availability and characteristic of food sources and the habitat structures in lake ecosystems. During winter, total zooplankton abundance was higher in YYL than in TFL, and the principal cause was that the abundance of Copepoda and Cladocera were both significantly higher in YYL than in TFL. It is noteworthy that Copepoda was the dominant taxon in YYL during winter, this was in accordance with several other reports that Copepoda was dominant in tropical and subtropical lakes (Fetahi et al. 2011, Ortega-Mayagoitia et al. 2011, Kehayias et al. 2013). Moreover, Perbiche-Neves et al. (2016) showed that Copepoda could feed on phytoplankton and even detritus. Since YYL was an allochthonous ecosystem with

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abundant detritus that the available food sources for Copepoda were sufficient.

During summer, total zooplankton abundance was higher in TFL than YYL. The major difference between sites was the higher abundance of Rotifera in TFL than YYL during summer (Figure 8). Since the most important food resources for herbivorous planktonic rotifers were small phytoplankton (Cordova et al. 2001), this observations could be owing to the increasing water temperature and irradiance in relatively unshaded TFL during summer. The higher water temperature and the higher solar radiation were observed in TFL than in YYL in this study (Figure 2A – B). Moreover, Branco et al. (2002) also supported that the rotifer taxa had higher densities associated with increasing water temperature and Chl-*a* concentration.

4.5.2. Effect of seasonal variation to the assemblage of zooplankton

Total zooplankton abundance was higher during summer than winter at both YYL and TFL. Since both food availability (e.g. phytoplankton) and water temperature were the two most important factors controlling zooplankton abundance (Pothoven & Fahnenstiel 2015), the biomass of zooplankton in the study lakes would therefore be higher in both lakes during summer when food abundance and ambient temperature were higher.

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In TFL, the zooplankton abundance during summer was higher than winter (Figure 8A – D), this could be resulted from the stronger light intensity and longer day length during summer. The higher water temperature, solar radiation, and Chl-*a* concentration were observed during summer than winter in the two study lakes. Previous studies showed that both Cladocera and Rotifera were fed on phytoplankton (Cordova et al. 2001, Rautio & Vincent 2006, Rueckert & Giani 2008, Perbiche-Neves et al. 2016), therefore the higher production of phytoplankton caused by the higher light penetration could explain the seasonal variation of zooplankton abundance in this study. Some studies showed that detritus, phytoplankton and even Rotifera would be the food sources of Copepoda (Brandl 2005, Fetahi et al. 2011, Perbiche-Neves et al. 2016). Therefore, it was the reason that Copepoda abundance was higher in TFL during summer.

In YYL, only the Rotifera abundance had significant seasonal variation that the abundance of Rotifera during summer was 13.3 times higher than winter (Figure 8B). Even though the dense canopy covered around YYL, the increasing solar irradiance during summer would enhance the abundance of Rotifera which mainly fed on phytoplankton. The result was in agreement with prior studies that the increasing Rotifera density was with associated with increased of water temperature and Chl-*a*

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concentration (Branco et al. 2002).

4.6. Importance of fish in mountain lake food webs

The resources partitioning by fish in mountain lakes was discussed through stable carbon and nitrogen analysis and gut content analysis. The fishes were observed to consume different categories of food sources based on their body sizes at both TFL and YYL during the study period. Small sized fishes mainly fed on leaf litter, algae, and sediment, while zooplankton, macroinvertebrates, and even prey fish were contained in the gut content of medium and large size of fishes (Figure 13). These was compatible with prior studies, as fishes are known to have ontogenetic patterns of feeding habits, different size classes of a species are suggested to be considered as different ecological units in its habitat (Stoner & Livingston 1984, Barth et al. 2013). Doulka et al. (2013) also pointed out that the relation between gut content and food availability of fish practiced some specialized predation, fish would select different prey categories in respect to their body size and even gender. The main reason of ontogenetic patterns of feeding habits could be found in previous studies that difference in diet within a population was related to differences in morphology (Robinson et al. 1993, Hjelm et al. 2001). Our results showed that the ontogenetic patterns of fish feeding habits would not

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only because of avoidance of the intraspecific competition, but also the differences in morphology of fish. In order to understand the inter-gender diet overlap of the fishes in TFL and YYL during the study period, the analysis of SIAR was analyzed and the Schoener's index were calculated as a supplementary. Results of gut content analysis analyzed via Schoener's index indicated significant diet overlap between fish with male and female only occurred in *C. auratus* in TFL during both winter and summer (Table 9). However, results of SIAR based on carbon and nitrogen stable isotopic signatures revealed that *C. carpio* in YYL during winter had sex-specific feeding behavior (Figure 12). Our results of SIAR indicated that phytoplankton contributed the greatest proportion to the female *C. carpio* while male had a relatively even mixture of the available basal food sources except leaf litter (Figure 12). Male *C. carpio* with larger body size (mean wet weight: male = 222.1 g, female = 177.3 g; mean body length: male = 19.9 cm, female = 17.7 cm) had the ability to feed on a wider variety of prey. Our results matched with previous studies that sexual dimorphism in body size between sexes was the major determinant of diet variation, and sexual differences in diet were suggested to be favored by natural selection with morphology or behavior constrained each species to a limited range of resource (Laufer et al. 2009, Marshall et al. 2009, Isermann et al. 2010). Moreover, other studies indicated that the dietary of gender bias could be influenced by natural selection for different ecological roles in males and females (Houston & Shine 1993), this could be due to avoid intra-specific competition for the available food sources in the habitat (Adewumi et al. 2014).

4.7. Food web structure in mountain lake ecosystems

It was identified that the gut content of fishes could reflect the food source availability of aquatic ecosystems in this study. Since mountain lakes were dystrophic ecosystems and all the fish species in the study sites were opportunistic generalists (Stein et al. 1975, Wysujack & Mehner 2005, Safer 2014, Norris 2015), diet richness analyzed through gut content analysis could represent the available food sources in the environment. Previous studies also indicated that an opportunist predator was capable of modifying its feeding strategies in response to environmental changes (Chapman et al. 1989, Dominguez & Pena 2000), De Sostoa & Lobon-Cervia (1989) found a significant correlation between diet diversity of fishes and abundance of prey. Functional response to prey abundance was also observed in this study.

4.7.1. Effect of inter-site variation to food web complexity and food chain length

During winter, the comparison of inter-site variation of fish diet composition illustrated that the percentage of prey in the predators had less difference between TFL and YYL that the gut content included 1 to 2 categories of food sources in both TFL and YYL (Figure 10). The lower diet richness in both YYL and TFL during winter would be affect by lower water temperature and irradiance causing lower productivity. In addition, Dominguez & Pena (2000) also showed fish had minimum feeding intensity during winter, and the authors speculated fish had a minimum feeding intensity during pre-spawning period and feeding began when breeding occurred. This could rationalize the lower fish diet richness in both study sites during winter.

During summer, the percentage of prey in the predators were more abundant in YYL than in TFL that the gut content of predators in YYL included ~ 3x categories of food sources than TFL (Figure 10). Moreover, the categories of gut content were different between sites through SIMPER analysis. The diet richness was higher in YYL than TFL which could be owing to the higher habitat complexity in YYL. Previous literatures pointed out that habitat complexity in particular the presence of macrophyte could enhance faunal richness and abundance in lake habitats (Meerhoff et al. 2007, St Pierre et al. 2014, Ding et al. 2015). In particular, in freshwater systems were demonstrated that macrophyte complexity was positively correlated with faunal richness and abundance (Taniguchi et al. 2003, Thomaz et al. 2008, Mormul et al.

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2011).According to the theory of spatial heterogeneity (Tews et al. 2004, Cai et al. 2012), the more heterogeneous and complex the habitat, the more complex and diverse was the fauna. The spatial variation of macroinvertebrate community biomass could also be explained by an analysis of multiple habitat heterogeneity scales (Shostell & Williams 2007, St Pierre et al. 2014). YYL had greater habitat complexity than TFL due to the dense macrophyte-bed present and the abundant species richness of algae in YYL (Wu et al. 2000) but aquatic plant was generally absent in TFL. In agreement with previous literatures that the greater diet richness of fish, which meant the greater abundance of prey in the ecosystems, would be due to the higher habitat complexity. This could also explain the slightly longer food chain length in YYL than TFL during winter (Table 7) and the more nodes and links of the food web structures in YYL than TFL during the study periods (Figure 11).

4.7.2. Effect of seasonal variation to food web complexity and food chain length

In TFL, the diet diversity of the predators showed that the available food sources in the ecosystem were more abundant during summer than winter (Figure 10). Also, the longer food chain was also observed during summer than winter. TFL was an autochthonous ecosystem that the organisms mainly depended on autochthonous food

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sources (e.g. periphyton and phytoplankton) in TFL (Figure 5A – B). The stronger light penetration during summer could increase photosynthesis of both periphyton and phytoplankton and then increased the productivity of the entire ecosystem. Prior study also pointed out the presence of UV radiation would increase the Chl-*a* concentration (Cabrera et al. 1997, Edwards et al. 2016). Thus, the higher productivity of lake ecosystems caused by the higher light penetration would be the main factor that increased food availability owing to the higher energy base in TFL during summer. Furthermore, the fish richness was slightly higher during summer than winter in TFL (Figure 9). Carnivorous *S. asotus* was only sampled in TFL during summer. One possible reason could be the higher diet richness during summer showed that the lake ecosystem would provide more available food sources during summer. Hayden et al. (2014) supported our results that strong seasonality often resulted in a high diversity and abundance of prey in summer and resource limitation in winter. Bobori et al. (2013) also found that the number of fish species caught varied among seasons, with the most numbered species being recorded in summer.

In YYL, the diet diversity of the predators also showed the available food sources in the ecosystem were more abundant during summer than winter (Figure 10). Also, the categories of gut content were different between seasons through SIMPER analysis. In

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our study, bacteria were the most available basal food source that contributed to the aquatic fauna in YYL during the study periods (Figure 5C – D). Previous studies showed that allochthonous organic matter could be metabolized by bacteria and would furthermore support the aquatic food chains (Tranvik 1988, Moran & Hodson 1990, Kritzberg et al. 2005). In addition to the higher productivity of autochthonous food sources owing to the stronger light penetration during summer, the more terrestrial food sources input by heavy rainfall events also enhanced the allochthonous productivity in YYL. Previous study also illustrated the higher inputs of both particulate and organic carbon into YYL during summer (Yang et al. 2011). Hence, the productivity of both phytoplankton and bacteria would be higher that caused the greater diet richness in YYL during summer. Moreover, the more links, nodes, and linkage density of the food web structure in YYL were observed during summer than winter (Table 7), which could also be owing to the higher bacteria productivity.

5. Conclusion

- The high availability of the two most dominance allochthonous food sources, i.e. FPOM and leaf litter in the densely shaded ecosystems, they were least utilized by neither aquatic primary consumers directly nor secondary consumers indirectly. Instead, some bacteria, in particular methane-oxidizing bacteria (MOB), was considered as the most important energy basis for the allochthonous mountain lake ecosystems. In contrast, the typical autochthonous dystrophic mountain lakes with relatively unshaded ecosystems would depend on autochthonous (periphyton and phytoplankton) basal food sources.
- One major trophic pathway was observed in the autochthonous mountain lake and the trophic positions of top predators were similar between winter and summer. In contrast, two major trophic pathways which one supported by autochthonous food sources and the other one supported by allochthonous food sources were represented in the allochthonous mountain lake during both seasons.
- Strong seasonal variation in the food web structures in both study mountain lake ecosystems were determined. Both in autochthonous and allochthonous mountain lakes, the available food sources of lakes reflected by diet richness of fish were higher during summer. This could be attributed to the increased light intensity and

water temperature due to increased intensity of solar radiation in summer, furthermore increased the Chl-*a* concentration. Thus, the rate of photosynthesis of primary producers and the lake metabolism in summer could enhance the faunal biomass production resulting in higher complexity food web structures in summer.

- Clear inter-site difference in food web structures and food chain length was found between the two mountain lake ecosystems because of the intrinsic difference in the environmental conditions between sites. The higher habitat complexity due to the preserved macrophyte bed and leaf litter mass on lake bottom of the allochthonous mountain lakes resulting in higher habitat heterogeneity. This could also provide refuge for consumer community including Chelicerata, Chironomidae, Trichoptera and even tadpoles from predation.

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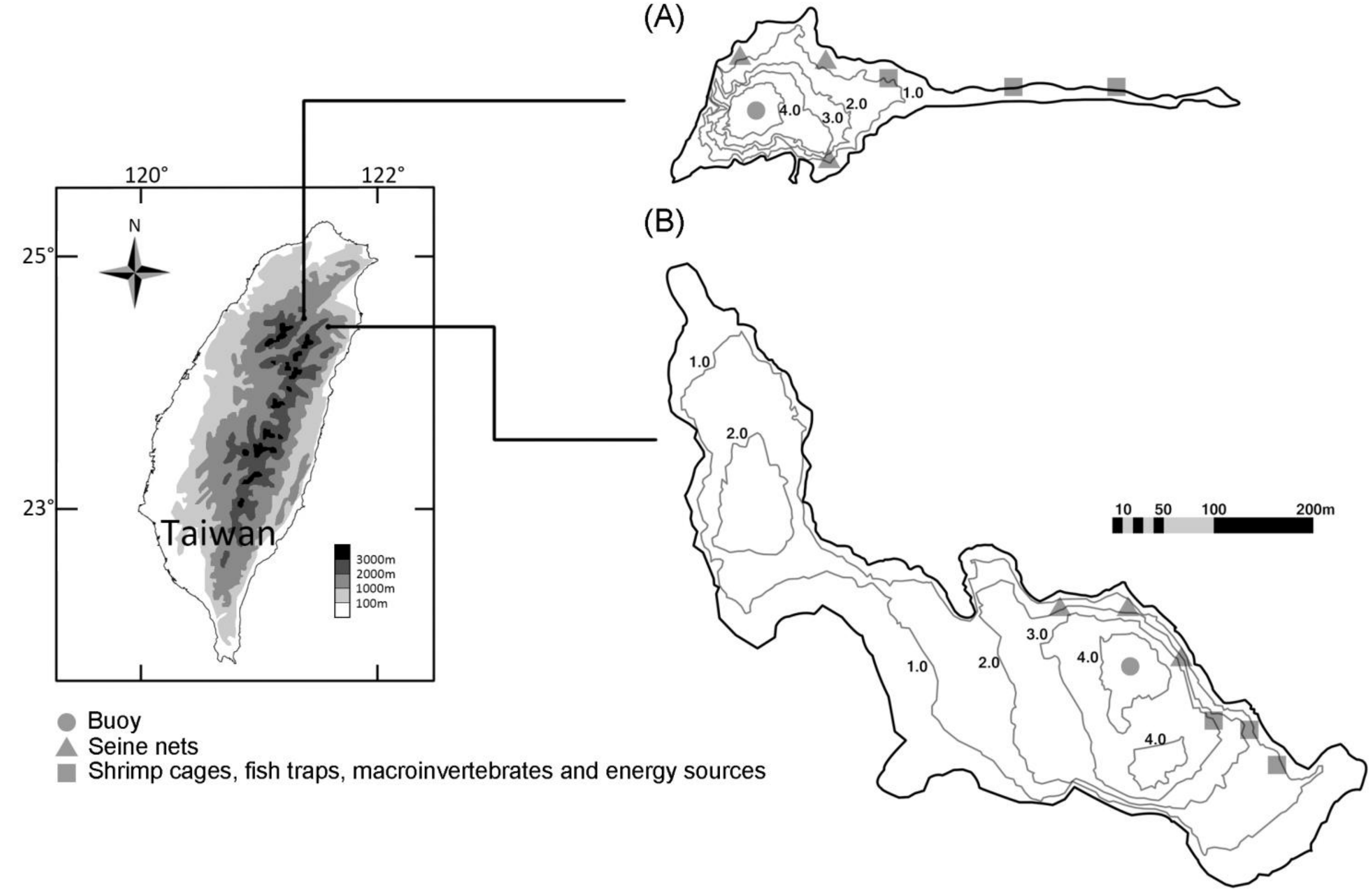

Figure 1 Location of the study lakes, (A) Lake Yuanyang (YYL) and (B) Lake Tsuifong (TFL), in Taiwan

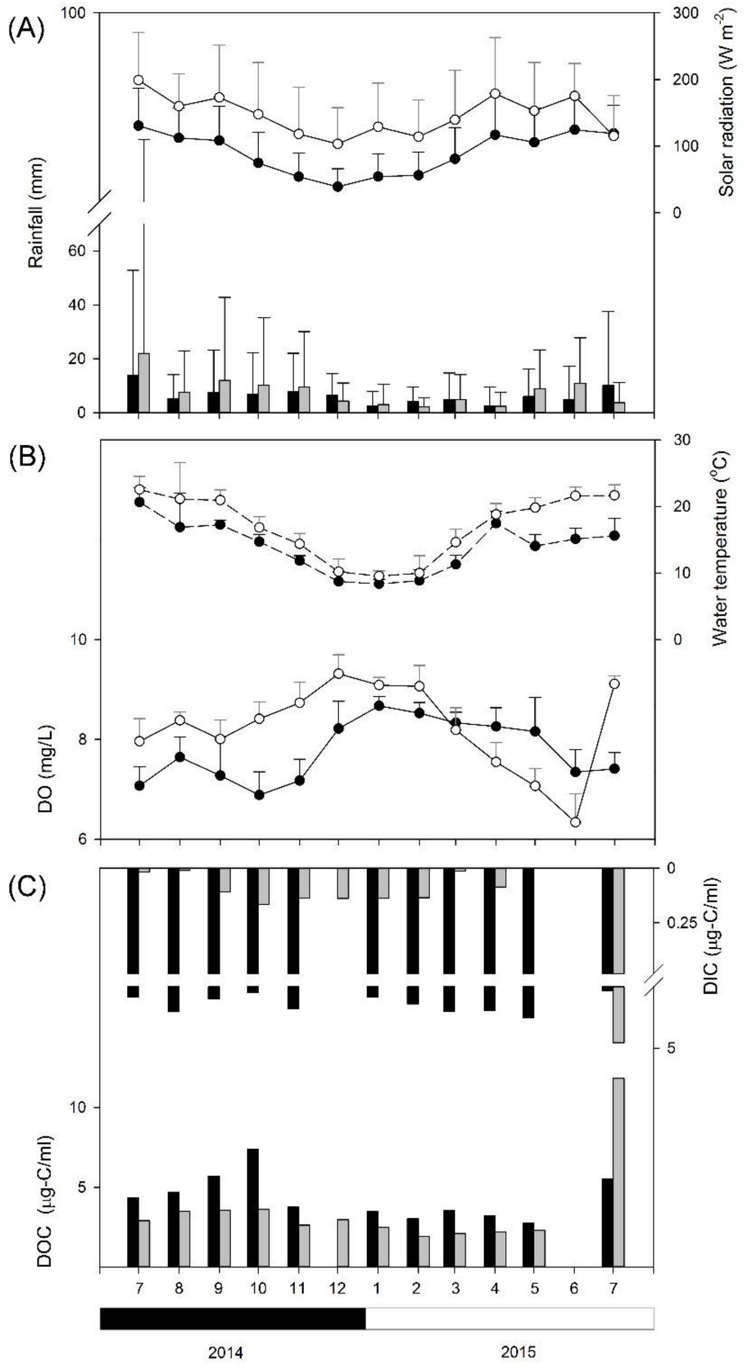

Figure 2 (A) Monthly variation of mean (±SD) solar radiation and mean (±SD) precipitation of the two study lakes during the study periods. Black and white circles indicated mean values of solar radiation measured at YYL and TFL respectively. Black and grey bars represented the mean monthly rainfall at YYL and TFL respectively. (B) Monthly variation of mean (±SD) DO and mean (±SD) water temperature of the two study lakes during the study periods. Black and white circles with solid lines indicated mean values of DO measured at YYL and TFL respectively. Black and white circles with dash lines indicated mean values of water temperature measured at YYL and TFL respectively. (C) Monthly variation of mean DOC and DIC of the two study lakes during the study periods. Black and grey bars represented the mean DOC and DIC at YYL and TFL respectively.

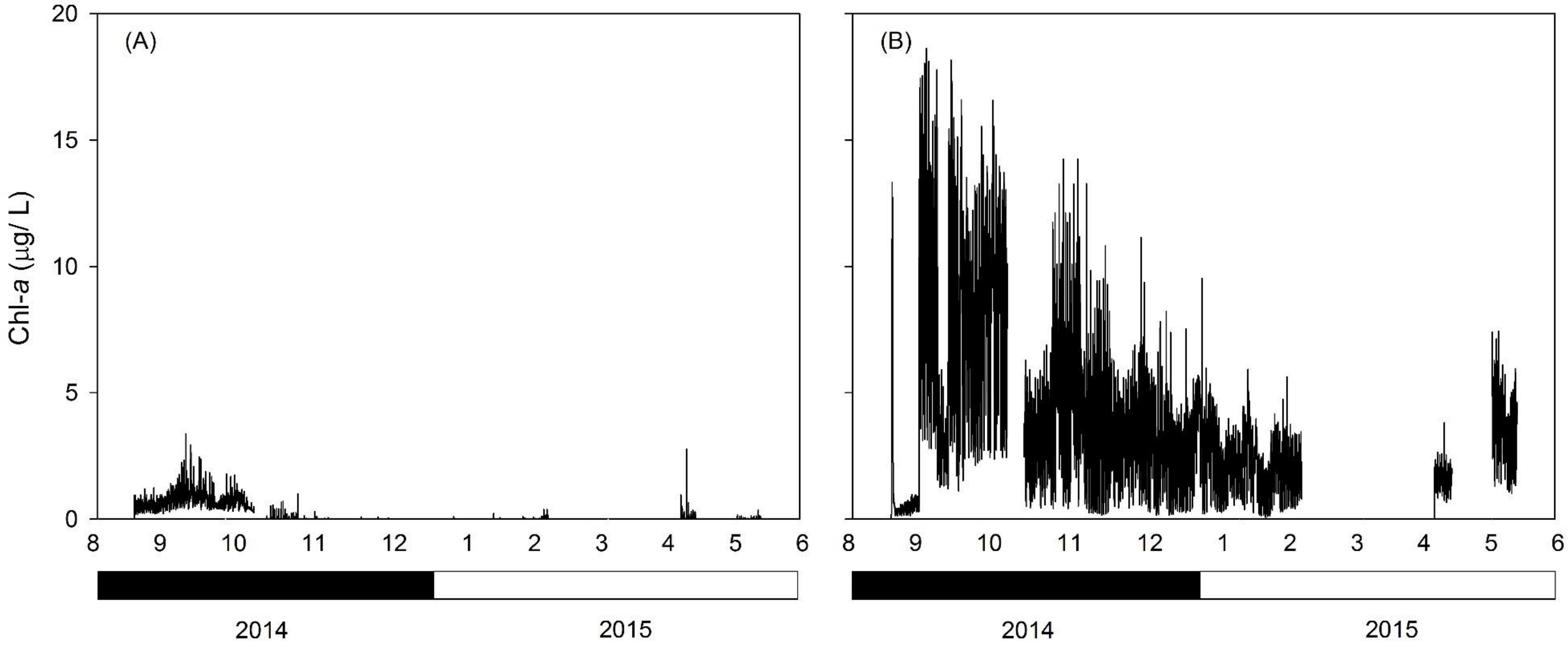

Figure 3 Chlorophyll-*a* concentration recorded by the Turner Designs C3™ submersible fluorometer in YYL (A) and TFL (B) during the study periods between 2014 and 2015. No data was recorded during March – May 2015

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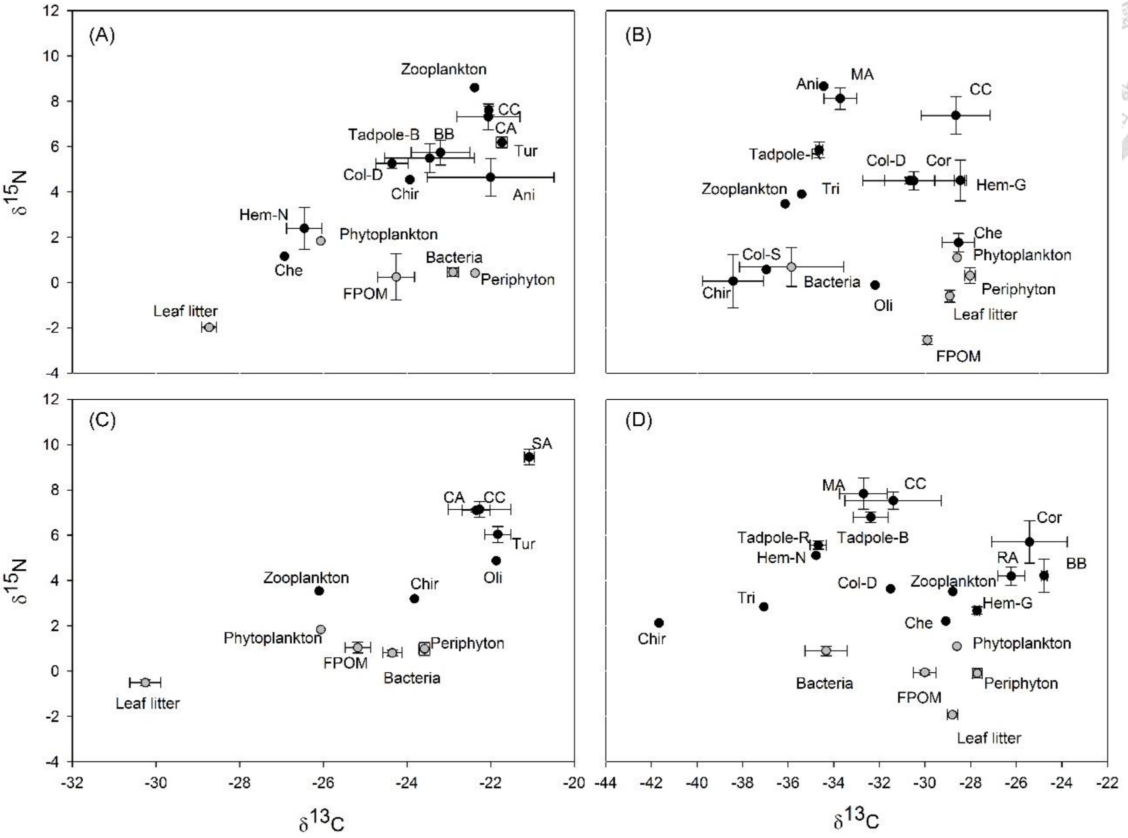

Figure 4 Scatter plots of δ^{13}C and δ^{15}N of major food web components in the two study lakes (TFL: A, C & YYL: B, D) during winter (A, B) and summer (C, D), Data points represent single samples with duplicate sample standard deviations. Grey circle indicates basal energy sources whereas black circles indicates consumers and predators. CC = *Cyprinus carpio*; CA = *Carassius auratus*; MA = *Misgurnus anguillicaudatus*; SA = *Silurus asotus*; BB = *Bufo bankorensis*; RA = *Rana adenopleura*; Tadpole-B = Tadpole (*B. bankorensis*); Tadpole-R = Tadpole (*R. adenopleura*); Ani = Anisoptera; Che = Chelicerata; Col-D = Coleoptera (adult Dytiscidae); Col-S = Coleoptera (Scirtidae); Cor = Corydalidae; Chir = Chironomidae; Hem-G = Hemiptera (Gerridae); Hem-N = Hemiptera (Notonectidae); Oli = Oligochaeta; Tri = Trichoptera; Tur = Turbellaria

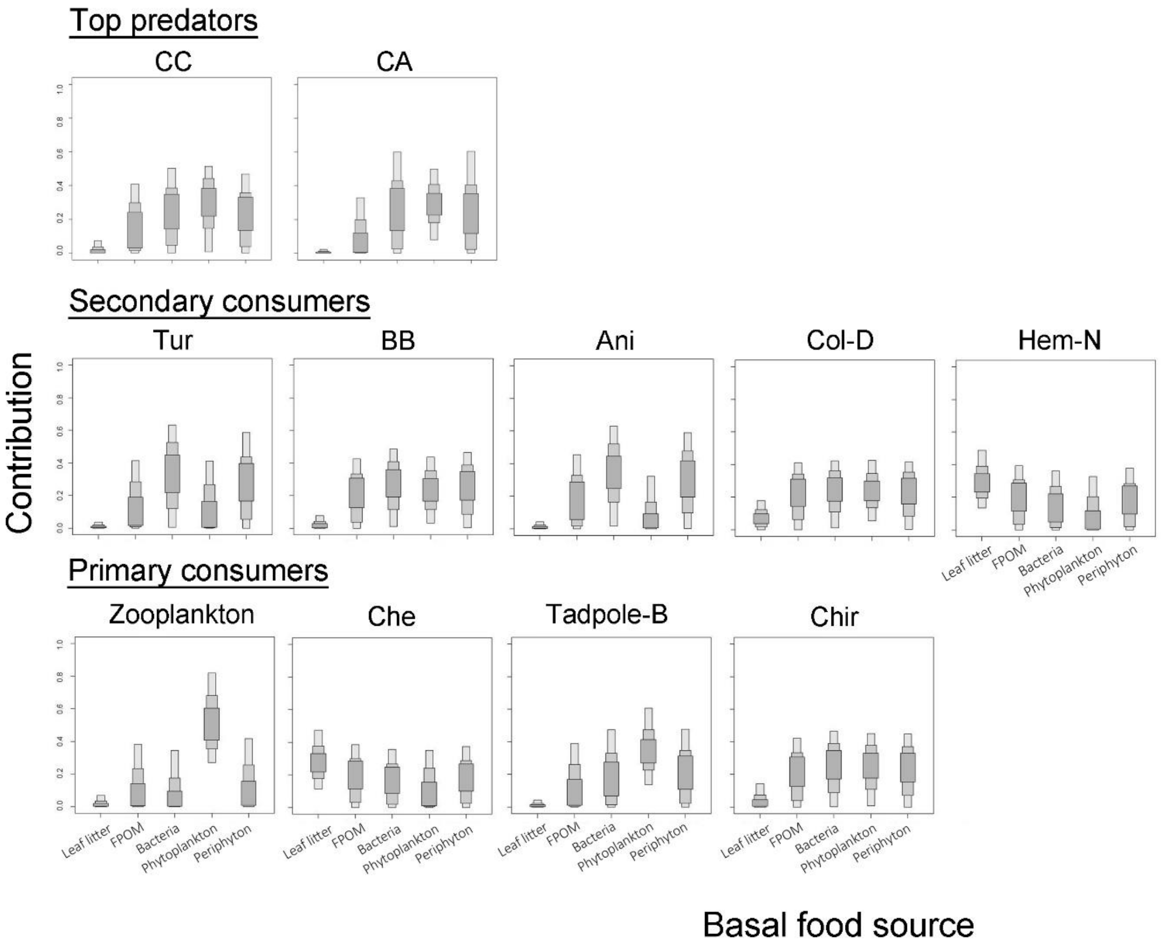

Figure 5A Results of SIAR (95, 75, and 25 % credibility intervals) showing estimated contribution of various basal food sources to consumers and predators in TFL during winter (Coding of species refer to Figure 4)

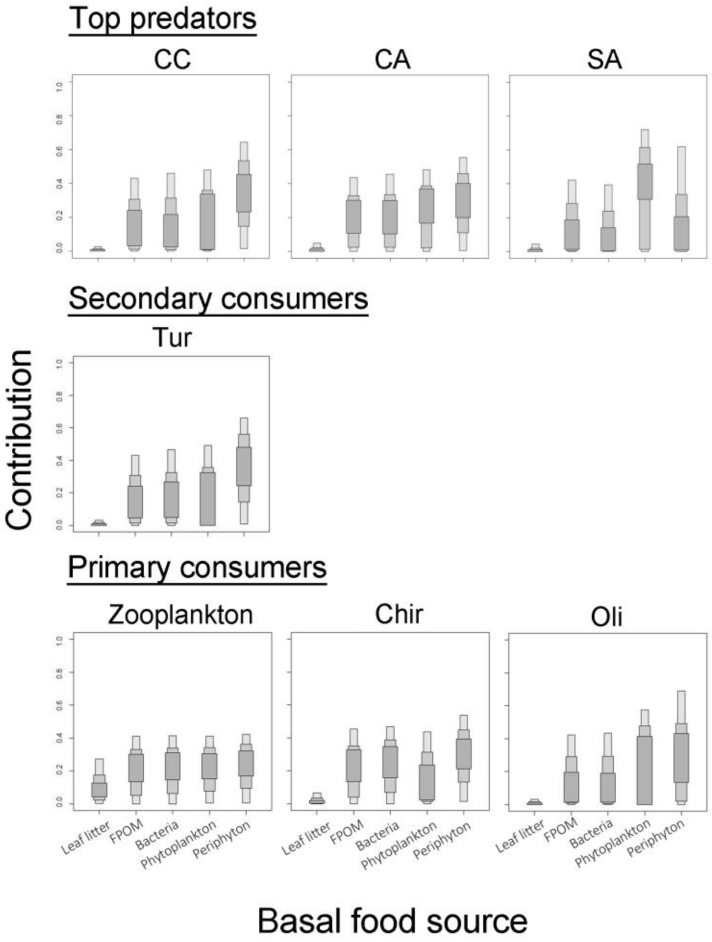

Figure 5B Results of SIAR (95, 75, and 25 % credibility intervals) showing estimated contribution of various basal food sources to consumers and predators in TFL during summer (Coding of species refer to Figure 4)

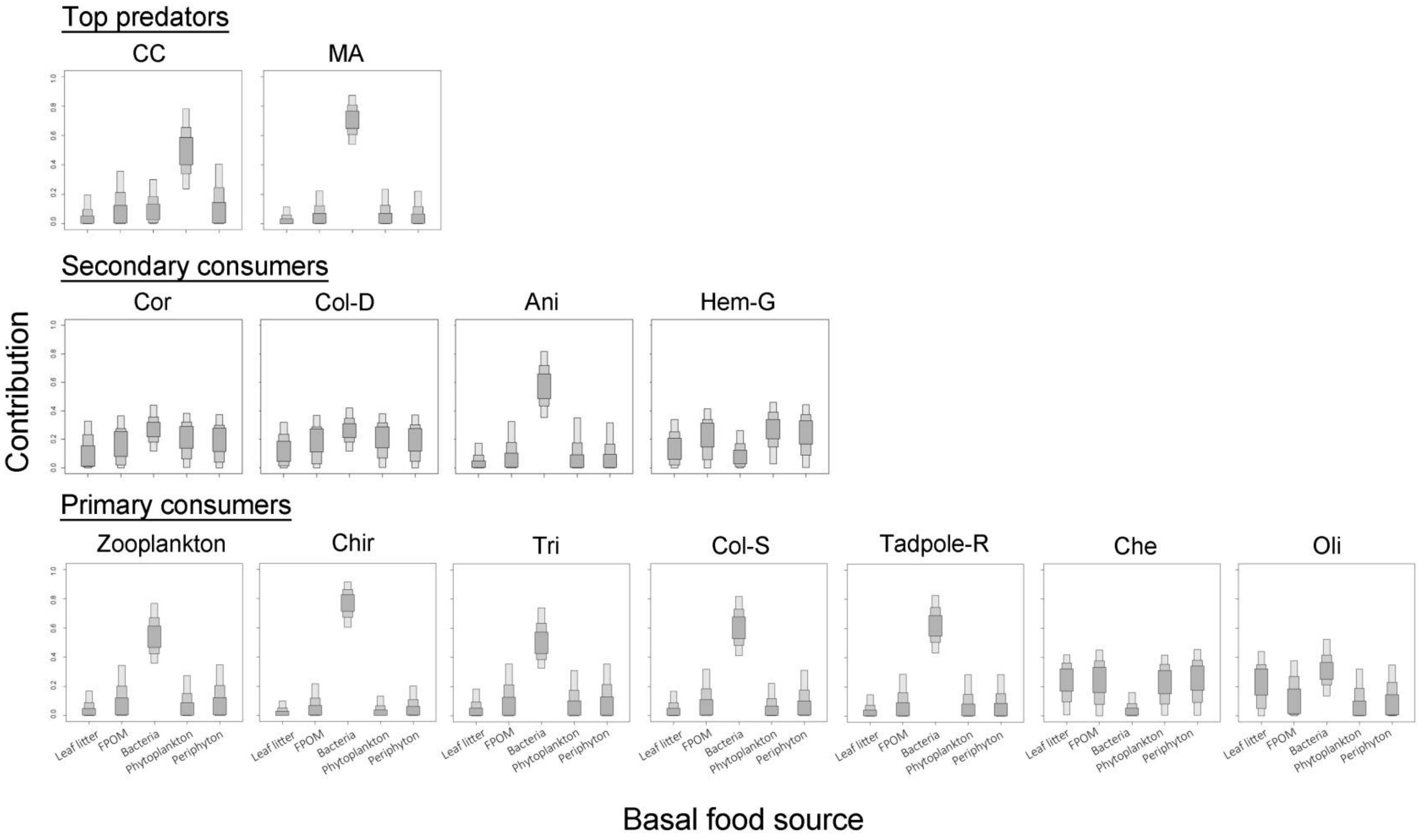

Figure 5C Results of SIAR (95, 75, and 25 % credibility intervals) showing estimated contribution of various basal food sources to consumers and predators in YYL during winter (Coding of species refer to Figure 4)

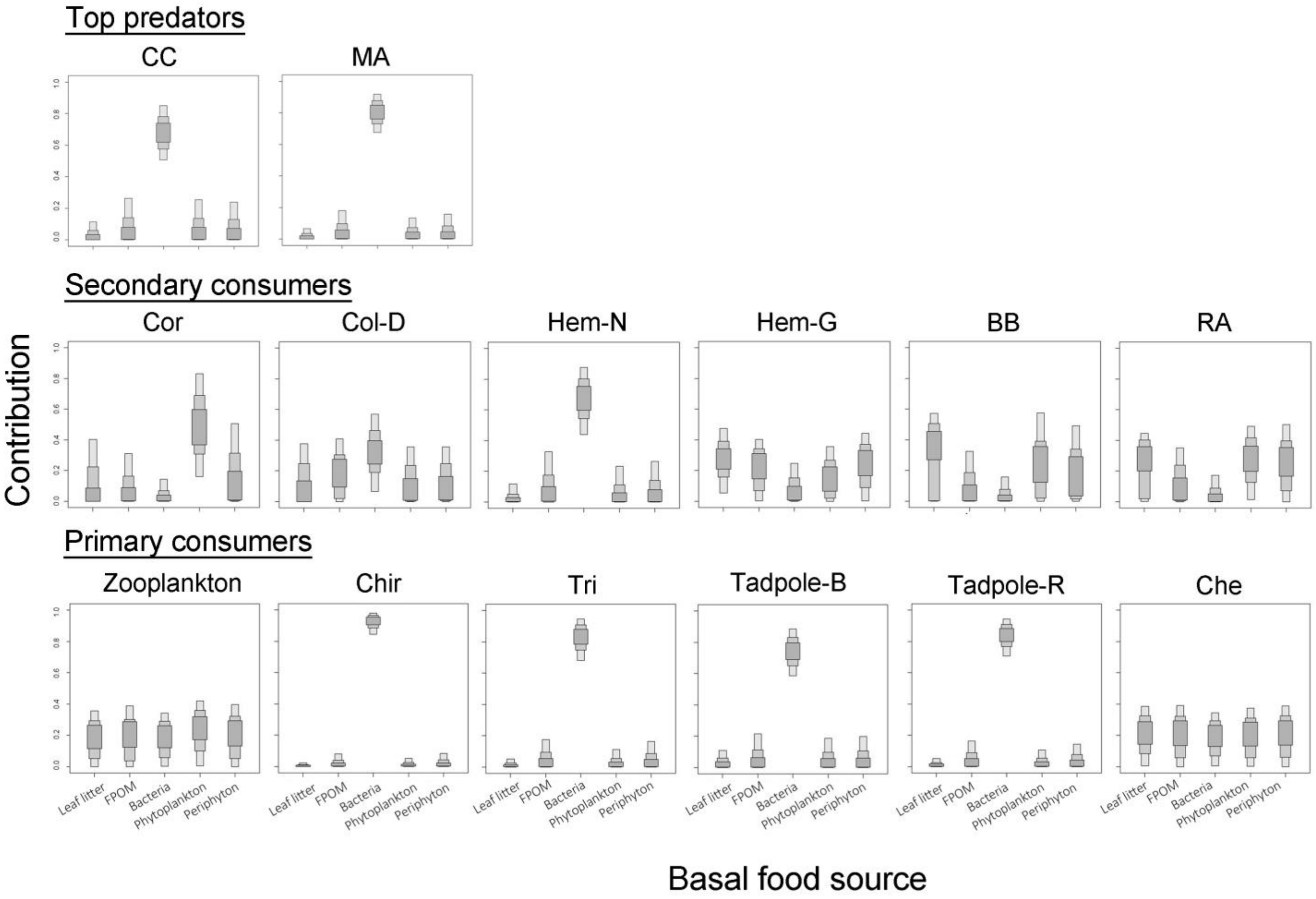

Figure 5D Results of SIAR (95, 75, and 25 % credibility intervals) showing estimated contribution of various basal food sources to consumers and predators in YYL during summer (Coding of species refer to Figure 4)

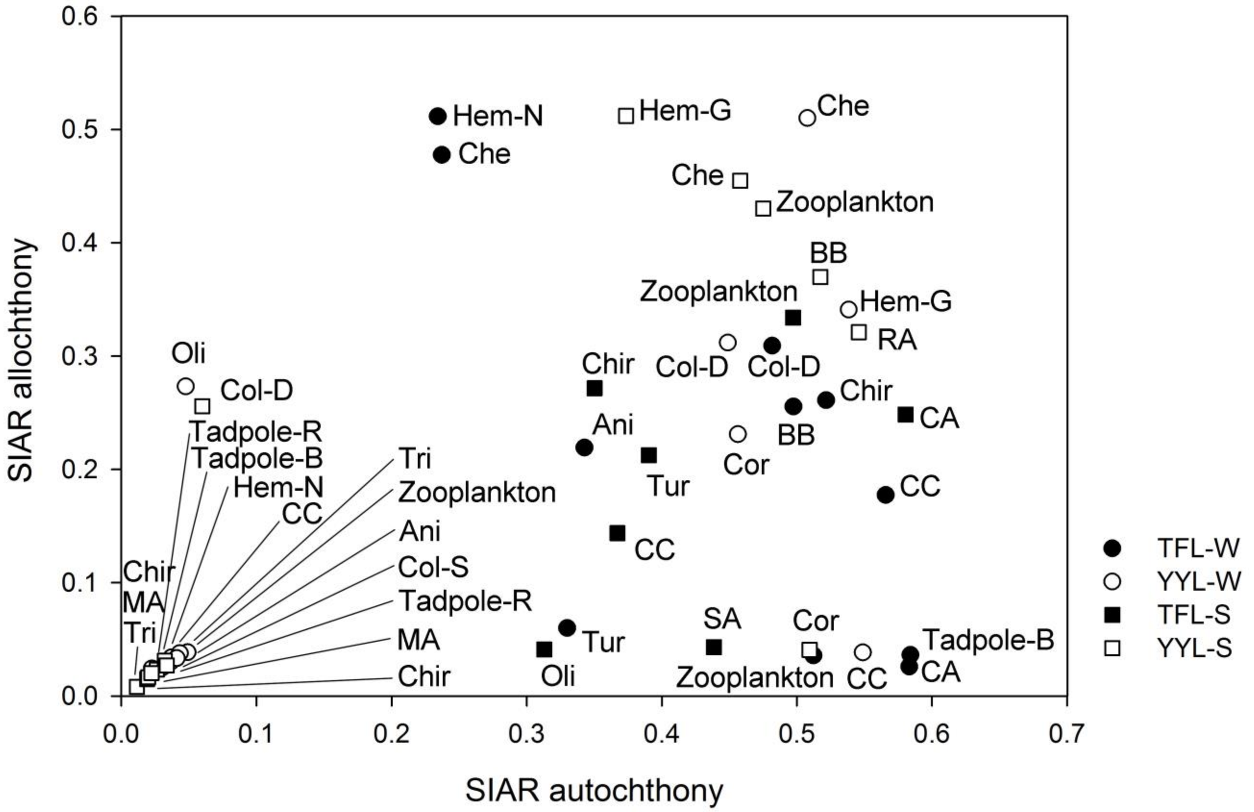

Figure 6 SIAR allochthony and SIAR autochthony mode contributions to aquatic organisms in YYL and TFL during the study periods

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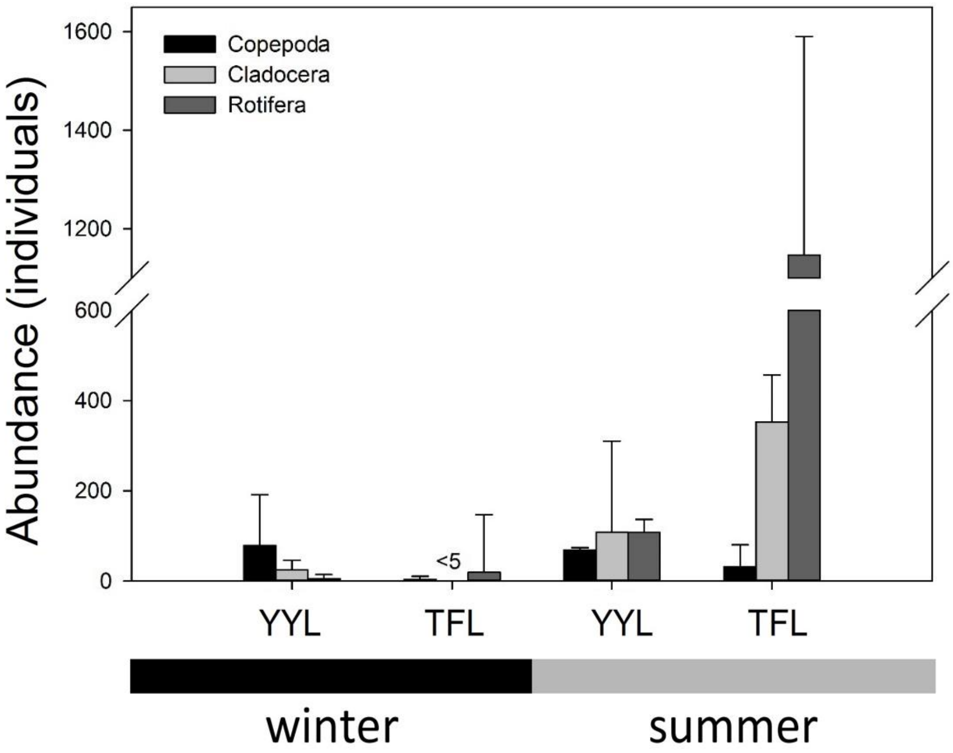

Figure 7 Abundance of zooplankton in the two study lakes during winter and summer

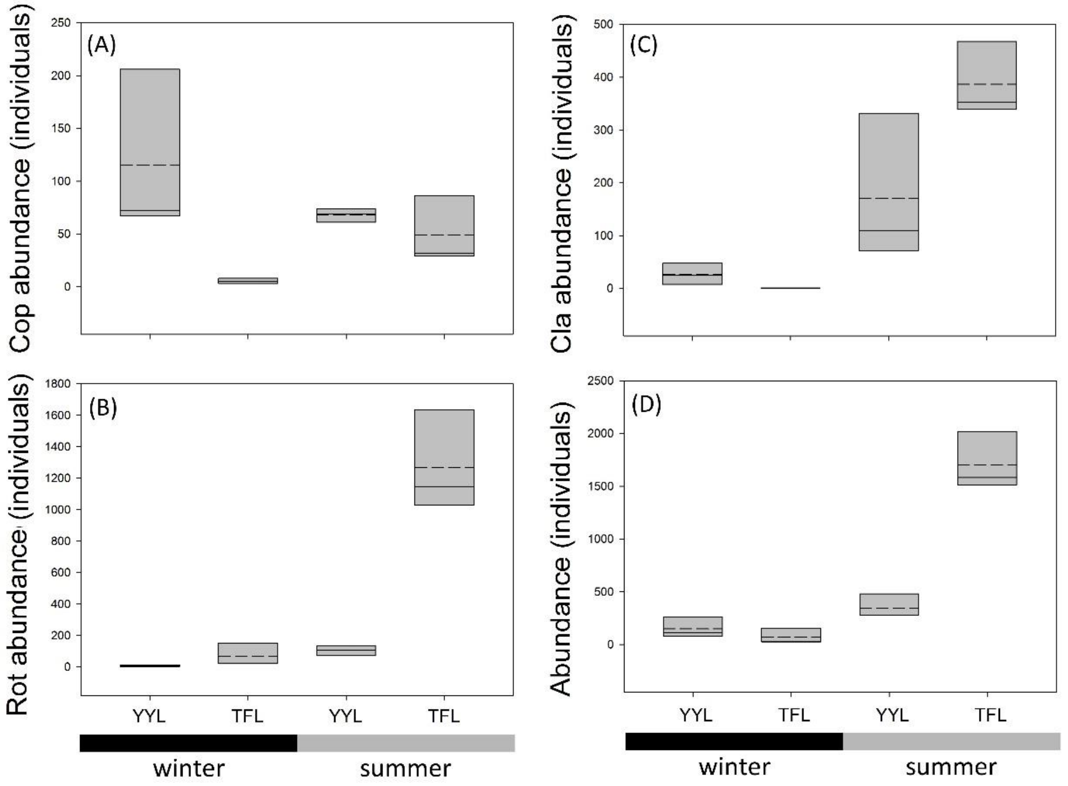

Figure 8 Boxplot of comparison of seasonal variation of zooplankton abundance in the two study lakes during winter and summer (Solid line: Median; short dash line: Mean; Cop: Copepoda; Cla: Cladocera; Rot: Rotifera)

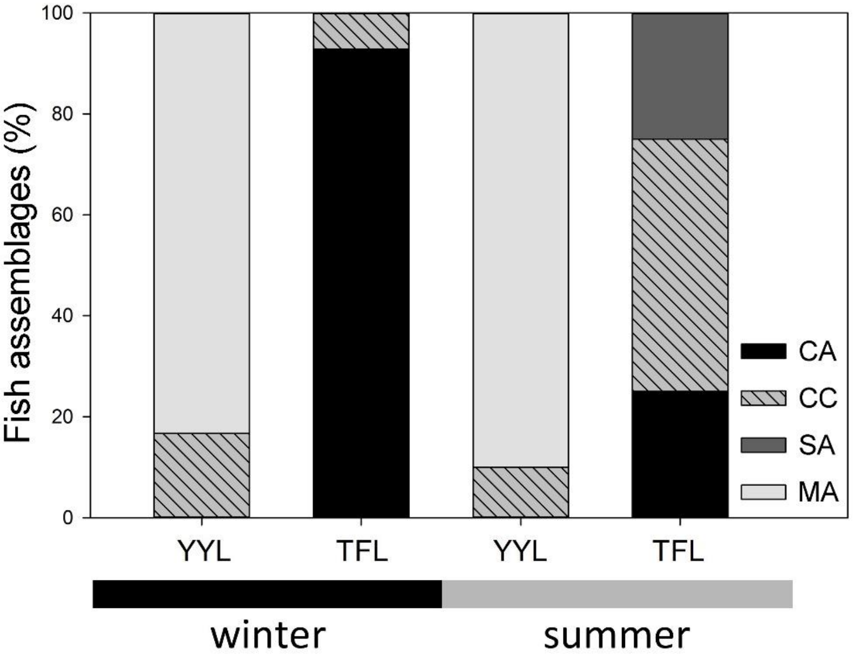

Figure 9 Composition of fish assemblage in the two study lakes during winter and summer (CC = *Cyprinus carpio*; CA = *Carassius auratus*; MA = *Misgurnus anguillicaudatus*; SA = *Silurus asotus*)

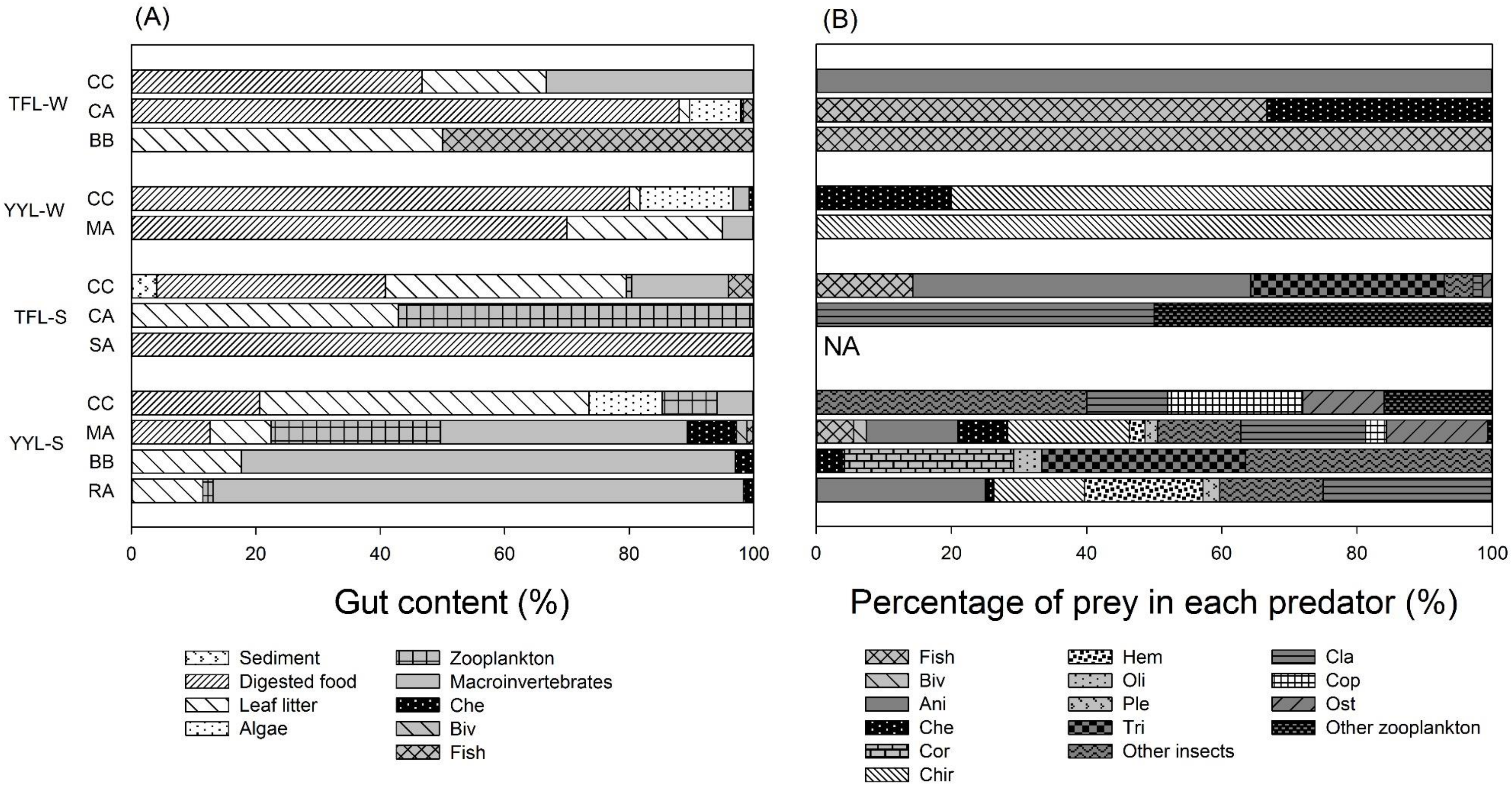

Figure 10 Comparison of seasonal variation of (A) fish diet composition and (B) percentage of prey for each predators (Biv = Bivalvia; Ple = Plecoptera; Refer to Figure 4 for codes of other organisms)

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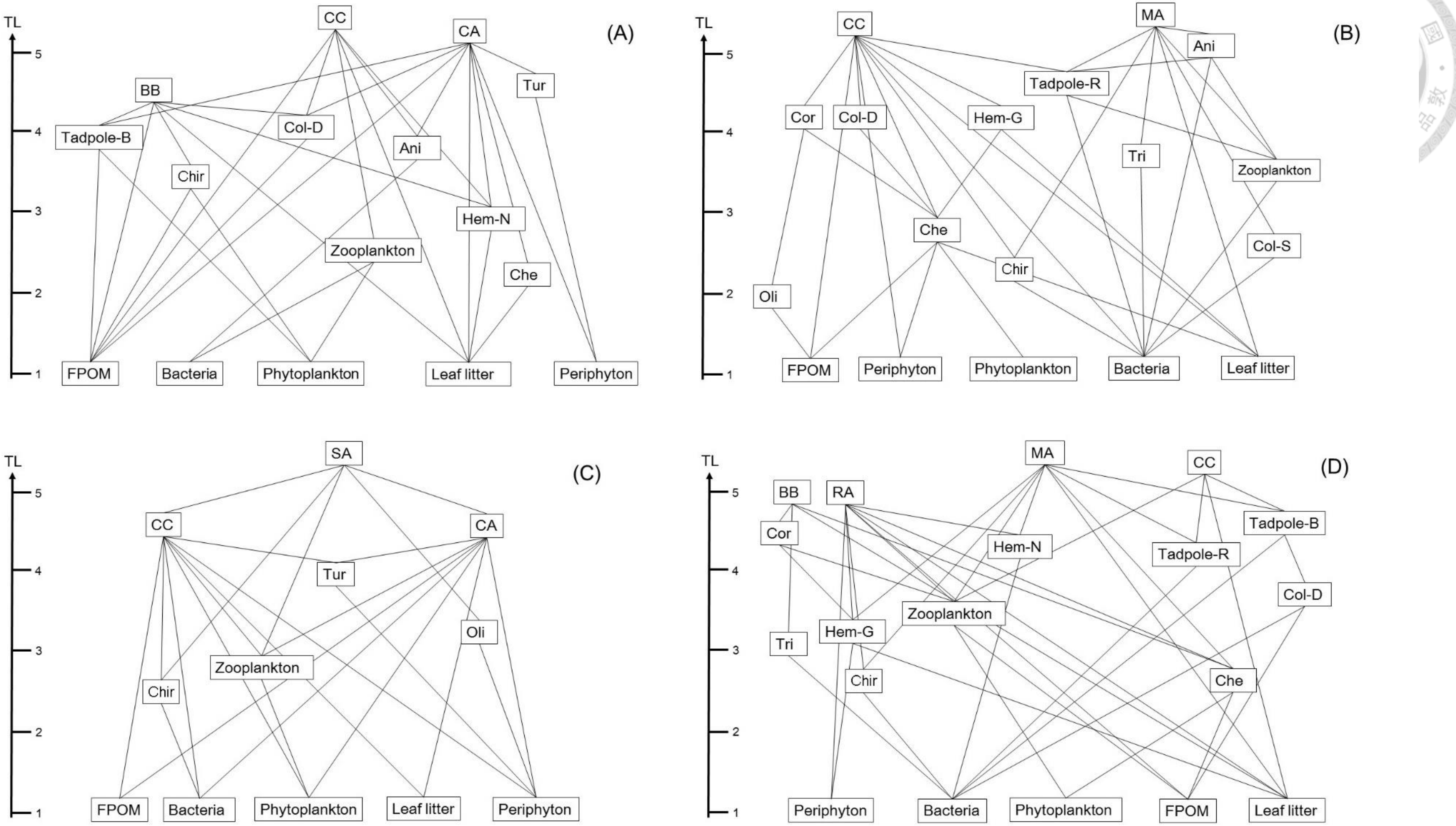

Figure 11 Trophic model of food web in the two study lakes (TFL: A, C & YYL: B, D) during winter (A, B) and summer (C, D) (TL: trophic level, refer to Figure 4 for codes of organisms)

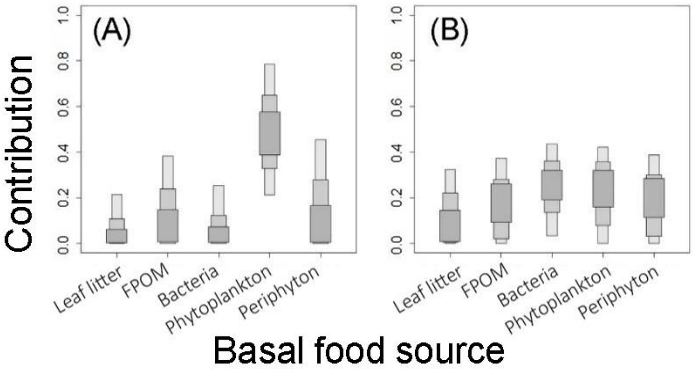

Figure 12 Results of SIAR (95, 75, and 25 % credibility intervals) showing estimated contribution of various basal food sources to female (A) and male (B) *C. carpio* in YYL during winter with sex-specific feeding behavior

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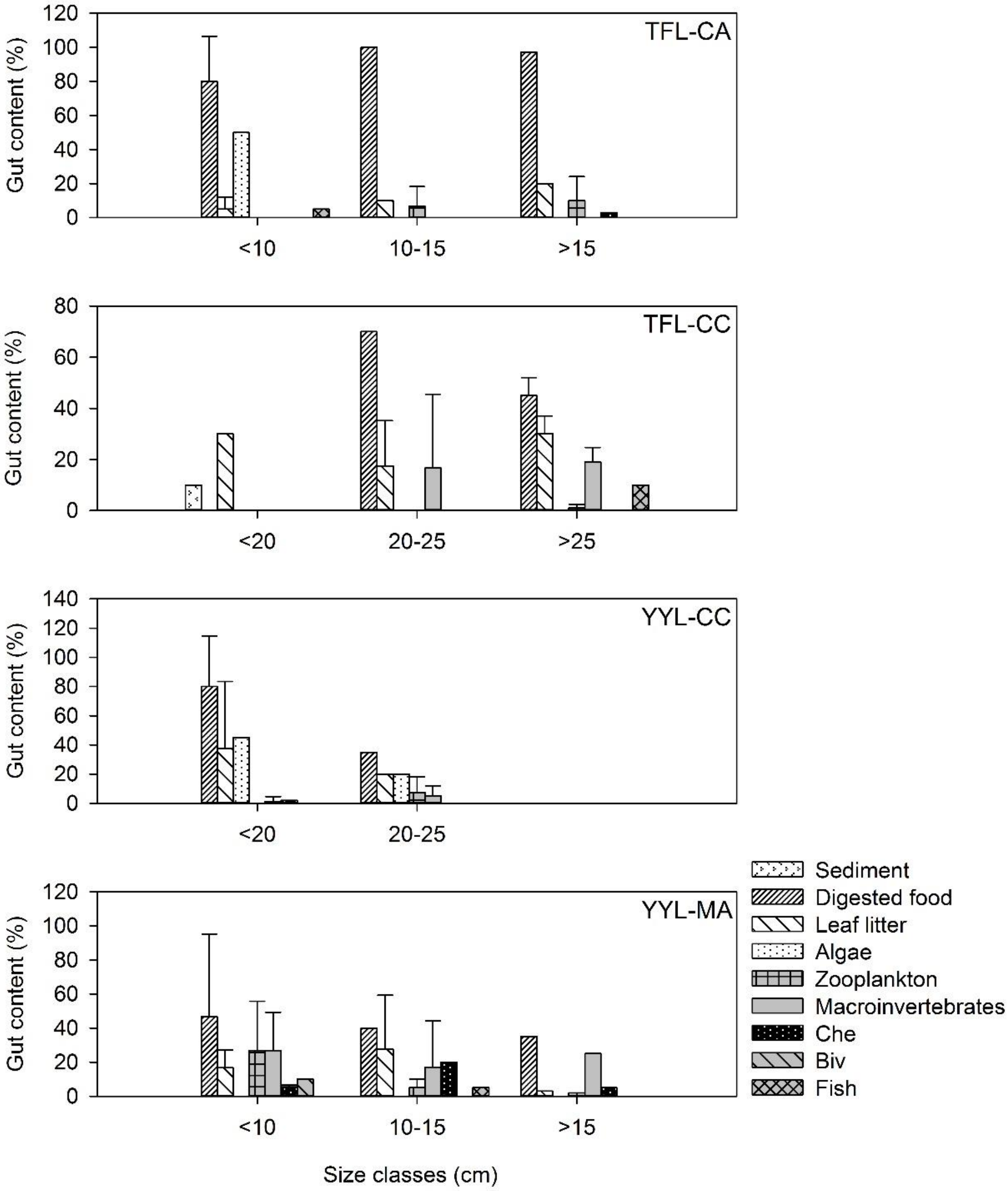

Figure 13 Percentage mean food contributions of prey organisms consumed by predators at different size classes in the two study lakes during winter and summer (Refer to Figure 9 for codes of fishes)

Table 1 Results of the climatic factors and water-quality characteristics of TFL and YYL between winter and summer (DO = dissolved oxygen, ORP = oxidation-reduction potential, TDS = total dissolved solid)

	YYL				TFL			
	Summer		Winter		Summer		Winter	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Maximum daily rainfall (mm)	140	-	28	-	69.5	-	31.5	-
Total precipitation (mm)	580	-	392	-	817	-	285	-
Annual total number of rainy days (numbers of days)	48	-	60	-	55	-	52	-
Mean daily rainfall (mm)	12.1	23.5	6.5	7.1	14.9	18.2	5.5	7.4
Conductivity (μS/cm)	11.42	1.79	17.77	5.21	5.09	0.12	4.69	0.52
TDS (mg/L)	8.55	1.43	15.51	4.4	3.57	0.32	3.9	0.37
DO (mg/L)	7.41	0.33	8.47	0.41	9.11	0.16	9.16	0.35
ORP (mV)	258.22	81.63	249.22	50.16	270.17	19.51	157.33	94.51
pH	5.19	1.15	5.61	0.7	5.22	0.39	6.3	0.56
Water temperature (^{o}C)	18.8	2.9	11.6	1.6	21	0.1	12.6	2.4
Chl-a (μg / L)	0.01	0.03	0.01	0.02	2.27	0.52	2.54	1.47
NH_4-N Conc. (mg/L)	0.015	0.01	0	0	0.002	0.002	0.002	0.002
NO_3-N Conc. (mg/L)	0	0	0.27	0.185	0.018	0.031	0.132	0.19
PO_4-P Conc. (mg/L)	0.014	0.011	0.013	0.023	0.034	0.029	0.019	0.009

Table 2 Results of one-way ANOVA showing the seasonal variation of climatic parameters in the two study lakes during winter and summer

	Summer		Winter			
	Mean	SD	Mean	SD	F	
Air Temperature (^{o}C)	17.8	1.9	5.5	3.3	1672.94^{***}	Summer > Winter
Maximum daily rainfall (mm)	104.75	49.85	29.75	2.47	4.52^{NS}	Summer = Winter
Total precipitation (mm)	698.50	167.60	338.50	75.70	7.67^{NS}	Summer = Winter
Total raining days (days)	51.50	4.95	56.00	5.66	0.72^{NS}	Summer = Winter
Mean daily rainfall (mm)	13.47	1.96	6.01	0.74	25.34^{***}	Summer > Winter

*p<.05; **p<.01; ***p<.001; ^{NS} No significant difference

Table 3 Results of two-way ANOVA showing the inter-site and seasonal variation of zooplankton biodiversity (log transformed) in the two study lakes

	Site			Season			Site × Season		
	SS	MS	F	SS	MS	F	SS	MS	F
Total abundance	0.9621	0.9621	1.57^{NS}	27.2030	27.2030	44.48***	9.1084	9.1080	14.89**
Abundance (Cop)	8.6321	8.6321	26.82***	1.2890	1.2890	4.00^{NS}	4.0966	4.0966	12.73**
Abundance (Cla)	0.0459	0.0459	0.09^{NS}	40.8766	40.8766	84.40***	6.9220	6.9220	14.29**
Abundance (Rot)	19.7749	19.7749	34.74***	38.9062	38.906	68.35***	2.4204	2.4204	4.25^{NS}

*p<.05; **p<.01; ***p<.001; ^{NS} No significant difference

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Table 4 Mean values (± SD) of body length (BL, cm) and wet weight (WW, g) of fish samples collected from the two study lakes during winter and summer (CC = *Cyprinus carpio*; CA = *Carassius auratus*; MA = *Misgurnus anguillicaudatus*; SA = *Silurus asotus*; W = winter; S = summer)

					WW (g)		BL (cm)	
Lake	Season	Family	Species	n	mean	SD	mean	SD
YYL	S	Cobitidae	MA	36	7.05	5.32	10.40	2.42
		Cyprinidae	CC	5	120.45	67.22	18.02	2.96
YYL	W	Cobitidae	MA	28	5.95	4.17	9.56	2.12
		Cyprinidae	CC	4	170.29	46.96	18.43	1.62
TFL	S	Cyprinidae	CA	2	61.40	20.60	15.35	0.92
		Cyprinidae	CC	4	242.30	152.20	24.20	4.76
		Siluridae	SA	2	520.70	60.20	43.85	1.91
TFL	W	Cyprinidae	CA	99	27.58	33.72	9.42	3.26
		Cyprinidae	CC	2	221.37	25.41	21.30	0.99

Table 5 Results of two-way ANOVA showing the CPUE of *C. carpio* (log transformed) in the two study lakes during winter and summer

Source	DF	SS	MS	F
Site	1	0.01964	0.01964	0.69 ^{NS}
Season	1	0.02676	0.02676	0.95 ^{NS}
Site × Season	1	0.00369	0.00369	0.13 ^{NS}

*p<.05; **p<.01; ***p<.001; ^{NS} No significant difference

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Table 6 Comparison of inter-specific diet-overlapping of the dominant fish and amphibian collected in the two study lakes during winter and summer (Refer to Table 4 for the codes of species; W = winter; S = summer; RA = *Rana adenopleura*; BB = *Bufo bankorensis*)

Site	Season	Species	Schoener's index (D)
YYL	W	CC vs. MA	74.30
	S	CC vs. MA	52.80
		RA vs. BB	16.54
TFL	W	CA vs. CC	60.00
	S	CA vs. CC	54.25
		CA vs. SA	65.00
		CC vs. SA	53.75

D > 60: significant overlap (Schoener 1970)

Table 7 The contribution of gut content to predators in TFL and YYL during winter and summer by SIMPER analysis

Taxon	Mean percentage		Cumulative percentage (%)
YYL vs. TFL: Mean dissimilarity = 70.87%			
	YYL	TFL	
Digested food	0.48	0.6	40.57
Leaf litter	0.16	0.34	27.53
Ani	0.11	0.05	65.15
Chir	0.09	0.00	71.06
Cla	0.05	0.01	74.89
Algae	0.05	0.09	78.71
Other insect	0.06	0.00	82.42
Winter vs. Summer: Mean dissimilarity = 77.51%			
	Summer	Winter	
Digested food	0.61	0.33	31.98
Leaf litter	0.15	0.45	58.32
Algae	0.01	0.22	72.19
Che	0.02	0.15	78.14
Ani	0.09	0.05	83.44

(Ani = Anisoptera; Che = Chelicerata: Cla: Cladocera; Chir = Chironomidae)

Table 8 Food web features and analyses in the two study lakes (YYL and TFL) during winter (W) and summer (S)

	YYL(S)	YYL(W)	TFL(S)	TFL(W)
Number of nodes	19	18	12	16
Number of links	40	36	24	32
Linkage density	2.1	2	2	2
Max trophic level (fish)	5.4	5.8	5.5	5.4

Table 9 Comparison of sexual diet-overlapping between male vs. female of the dominant fish in the two study lakes during winter and summer (Refer to Table 4 for the codes of species; W = winter; S = summer)

Site	Season	Species	Schoener's index (D)
YYL	S	CC	36.67
		MA	52.5
	W	CC	40
		MA	40
TFL	S	CA	90
		CC	17.5
	W	CA	61.75

D > 60: significant overlap (Schoener 1970)

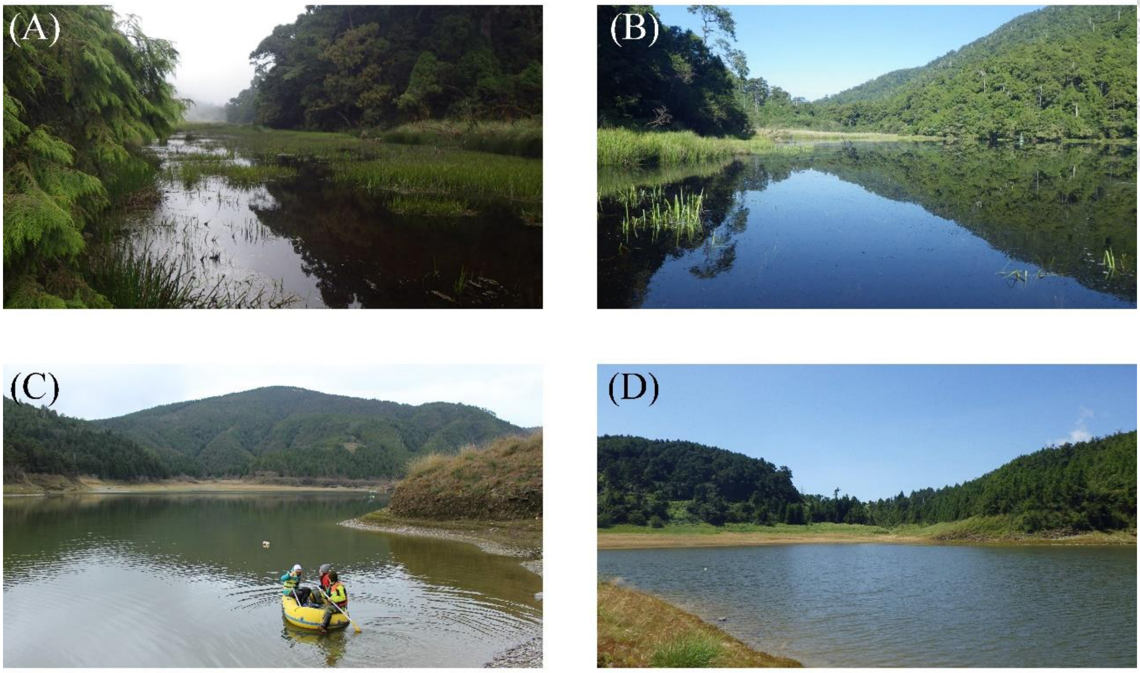

Plate 1 The two study lakes, (A-B) Lake Yuanyang (YYL) and (C-D) Lake Tsuifong (TFL), during winter (A, C) and summer (B, D) in Taiwan

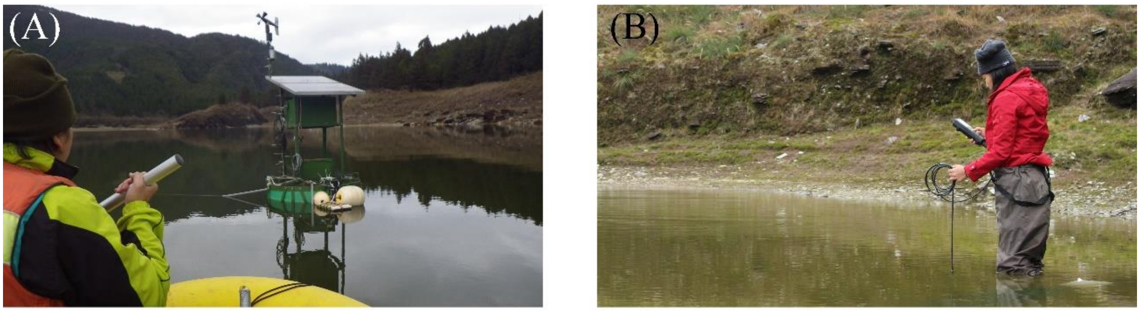

Plate 2 Environmental parameters recorded by (A) the Turner Designs C3™ submersible fluorometer and the Greenspan DO100 dissolved oxygen sensor on the buoy which deployed above the deepest spot of lakes and by (B) the YSI Proplus multimeter

Plate 3 Sampling fish and amphibians with (A-C) fish traps, (D-E) shrimp cages, and (F-H) seine nets

Plate 4 (A-B) Sampling the benthic macroinvertebrates with (A) direct picking from the bottom substrate and (B) retrieving macroinvertebrate individuals from sets of colonization tiles in meshed bags pre-deployed 3 - 6 weeks prior to collection. (C) Zooplankton sample was collected by hauling a vertical zooplankton sampling net from lake bottom to surface

Plate 5 Potential food sources sampling: (A) leaf litter was sampled with a hand net swept along the water surface, (B) periphyton was sampled by brushing the surfaces of cobbles collected along lake shore, (C-D) bacteria were collected by scraping the surface of glass slides from meshed cages preinstalled for 1 month, (E) water sample collection for FPOM

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