ARTICLE IN PRESS
JGLR-00913; No. of pages: 10; 4C:
Journal of Great Lakes Research xxx (2015) xxx–xxx
Contents lists available at ScienceDirect
Journal of Great Lakes Research
journal homepage: www.elsevier.com/locate/jglr

Stable isotope analysis of trophic structure, energy flow and spatial variability in a large ultraoligotrophic lake in Northwest Patagonia

Marina Arcagni [a,*], Andrea Rizzo [a,b], Linda M. Campbell [c], María A. Arribére [a], Romina Juncos [a], Mariana Reissig [d], Kurt Kyser [e], Juan P. Barriga [f], Miguel Battini [f], Sergio Ribeiro Guevara [a]

[a] *Laboratorio de Análisis por Activación Neutrónica, Centro Atómico Bariloche, Comisión Nacional de Energía Atómica. Av. Bustillo 9500, 8400 Bariloche, Argentina*
[b] *Centro Científico Tecnológico – CONICET – Patagonia Norte. Av. de los Pioneros 2350, 8400 Bariloche, Argentina*
[c] *Environmental Science, Saint Mary's University, 923 Robie St., Halifax, NS B3H 3C3, Canada*
[d] *Laboratorio de Fotobiología, Instituto de Investigaciones en Biodiversidad y Medio Ambiente, Universidad Nacional del Comahue, CONICET. Quintral 1250, 8400 Bariloche, Argentina*
[e] *Department of Geological Sciences and Geological Engineering, Queen's University, Miller Hall, Kingston, Ontario, KL7 3N6, Canada*
[f] *Laboratorio de Ictiología y Acuicultura Experimental, Instituto de Investigaciones en Biodiversidad y Medio Ambiente, Universidad Nacional del Comahue, CONICET. Quintral 1250, 8400 Bariloche, Argentina*

ARTICLE INFO

Article history:
Received 3 December 2014
Accepted 11 May 2015
Available online xxxx

Communicated by Michael Sierszen

Index words:
Stable isotope analysis
Patagonia
Mixing model
Trophic relationships

ABSTRACT

The food web structure of the largest lake in northwest Patagonia, Lake Nahuel Huapi (area 557 km^2), was investigated. Fish, benthic macroinvertebrates, plankton and primary producers were analyzed for stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotopes in three sites with contrasting morphometry and environmental characteristics. $\delta^{15}N$ and $\delta^{13}C$ revealed a similar food web structure between basins but with distinct isotopic baselines. The SIAR (Stable Isotope Analysis in R) mixing model was used to study potential food sources (benthic or pelagic) for adult fish. Results indicated that energy flow to fish from both habitats is different for each site and species, and does not depend on the basin morphometry. An ontogenetic shift in the carbon source and trophic level was observed in some of the fish species, revealing a coupling between the pelagic and bentho-littoral habitats of the lake. Our findings complement the existing literature on trophic interactions between introduced and native fish, and provide novel information on plankton composition, food web structure and energy flow in a large lake of North Patagonia that can be extrapolated to other understudied lakes in the area.

Introduction

Lakes are complex ecosystems composed of several distinct subsystems or habitats. The pelagic habitat of lakes includes planktonic organisms, and fish and energy flow is largely through phytoplankton and bacterial pathways (Schindler and Scheuerell, 2002). In contrast, the bentho-littoral habitat is characterized by periphyton, macrophytes, macroinvertebrates, and fish, and the energy flow includes primary production from benthic algae and macrophytes, allochthonous inputs from the terrestrial system and sinking phytoplankton from the epilimnion (Fitzgerald and Gardner, 1993; Covich et al., 1999; Doi, 2009). Ecological interactions between the different habitats, the relative importance of the littoral habitat, and the potential for zoobenthos to contribute to whole-lake secondary production are determined by lake size and lake basin morphometry (Schindler and Scheuerell, 2002). Lake Nahuel Huapi is the largest (557 km^2) and deepest (464 m) lentic water body of glacial origin in North Patagonia to the East of the Andes (Quirós and Drago, 1985; Iriondo, 1989). This lake has complex shoreline topography with seven branching arms, each with its own varying morphometric and environmental characteristics over a terrestrial gradient ranging from wet montane Andean forests in the north-west to dry temperate steppes in the east.

In nutrient-poor lakes, such as Lake Nahuel Huapi (Díaz et al., 1998), where low phytoplankton biomass and high transparency favor benthic primary production, littoral energy mobilization has been suggested to be of considerable importance for fish (Hecky and Hesslein, 1995; Vadeboncoeur et al., 2002). Large and deep lakes tend to have lower perimeter-lake area ratios, thereby reducing the potential contribution of bentho-littoral habitats in comparison with small and shallow lakes (Schindler and Scheuerell, 2002). However, for deep lakes with complex topography, such as Nahuel Huapi, Baikal (Central Asia), Malawi or Tanganyika (East Africa), the bentho-littoral habitats may become more important for certain bays with more shallowly tapering shorelines (e.g. Yuma et al., 2006). In this sense, Queimaliños et al. (2012) found that the neighboring connected lakes (Moreno West and Moreno East) have the same surface area but differential allochthonous indicators in the pelagic zone. This is related to the differences of

* Corresponding author. Tel.: +54 294 444 5240x5297; fax: +54 294 444 5299.
E-mail addresses: marina.arcagni@cab.cnea.gov.ar (M. Arcagni), rizzo@cab.cnea.gov.ar (A. Rizzo), LM.Campbell@smu.ca (L.M. Campbell), arribere@cab.cnea.gov.ar (M.A. Arribére), rominajuncos@gmail.com (R. Juncos), mreissig@crub.uncoma.edu.ar (M. Reissig), kyser@geol.queensu.ca (K. Kyser), juan.barriga@crub.uncoma.edu.ar (J.P. Barriga), miguel.battini@crub.uncoma.edu.ar (M. Battini), ribeiro@cab.cnea.gov.ar (S.R. Guevara).

http://dx.doi.org/10.1016/j.jglr.2015.05.008
0380-1330/

Please cite this article as: Arcagni, M., et al., Stable isotope analysis of trophic structure, energy flow and spatial variability in a large ultraoligotrophic lake in Northwest Patagonia, J. Great Lakes Res. (2015), http://dx.doi.org/10.1016/j.jglr.2015.05.008

perimeter-lake area ratio of both lakes, and the consequent dissimilarities of contact between the lake and the terrestrial environment.

Due to their high mobility, fish function as a strong link between bentho-littoral and pelagic habitats by feeding on prey from both habitats (Schindler and Scheuerell, 2002; Vander Zanden and Vadeboncoeur, 2002; Barriga et al., 2012; Reissig et al., 2015). In Patagonian lakes, exotic salmonids, particularly rainbow trout, play a major role in habitat coupling through predation in both bentho-littoral and pelagic habitats (Juncos et al., 2013). Recent investigations in Lake Nahuel Huapi have focused on the trophic interactions between top predator fish species and their prey through analyses of gut contents (Juncos et al., 2011, 2013; Juárez, 2012). However, there has been little research on whole food-web structure and the role of fish in connecting habitats within this oligotrophic lake. In particular, two native fish, the galaxiids *Galaxias platei* and *Galaxias maculatus*, are also an important link between bentho-littoral and pelagic habitats (Barriga et al., 2012; Reissig et al., 2015). This occurs in two ways: *Galaxias* spp. are an important link between their lower trophic invertebrate prey in both pelagic and bentho-littoral habitats and their piscivorous predators (Rechenq et al., 2011; Milano et al., 2013; Reissig et al., 2015), and *Galaxias* spp. will undergo ontogenetic migration from pelagic juvenile stages to bentho-littoral and deep-benthic adult stages, therefore connecting the two habitats through their lifecycle stages (Barriga et al., 2002).

Over the past two decades, stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope analyses (SIA) have been widely used to study carbon transfer dynamics, food web structure and to estimate trophic position of the organisms in freshwater lacustrine ecosystems around the world (e.g., Post, 2002; Campbell et al., 2003; Solomon et al., 2011). The isotopic composition of the carbon and nitrogen in an animal reflects the nitrogen and carbon isotopic composition of its diet (DeNiro and Epstein, 1978, 1981). Consumers are typically enriched in ^{15}N relative to its diet; therefore, the δ^{15}N values can be used to estimate trophic position. In contrast, δ^{13}C values of consumers change little with trophic transfers (Post, 2002) consequently they can be used to determine original sources of dietary carbon (Layman et al., 2011). This approach has been used in North Patagonian lakes to analyze and compare the food web structure of the double-basin system of Lake Moreno (Arcagni et al., 2013), which is characterized by contrasting hydrogeomorphic characteristics in each basin (Queimaliños et al., 2012). Lake Moreno is an ultraoligotrophic lake that flows through a short river into Lake Nahuel Huapi and possesses a similar food web structure as the larger lake.

The similar species assemblages and the inter-basin differences between each branch of Lake Nahuel Huapi, as well as the use of stable isotope techniques to assess food web structure and energy flow, provided the opportunity to formulate the following questions: Are there differences in the food web structure between basins? Are there differences in the isotopic baselines between the basins? Is the contribution of pelagic and bentho-littoral energy sources to top predator fish related to the morphometry of the basins? In this context the objectives of this work are to characterize through stable isotope analysis the food web structure of Lake Nahuel Huapi in three basins with differential morphometric and environmental features, to compare the δ^{13}C and δ^{15}N values of the organisms between the basins, basins, and to determine the contribution of pelagic and bentho-littoral carbon sources to the top predator fish species in each branch.

Materials and methods

Study Site

Lake Nahuel Huapi (41°03′S, 71°25′W), located in Nahuel Huapi National Park (NHNP, Fig. 1), is an ultraoligotrophic system with a mean annual Secchi depth of 12 m, euphotic zone ($Z_{1\%}$) that extends to 48.8 m, total phosphorus of 5.1 μg L^{-1}, and chlorophyll *a* of 0.6 μg L^{-1} (Alcalde et al., 1999; Caravati et al., 2010). Like all the lakes in Andean Patagonia, Lake Nahuel Huapi is of glacial origin and has been classified as warm monomictic with summer stratification (Quirós and Drago, 1985; Diaz et al., 2007).

Because of the constant west winds and the Andes mountain range that play a crucial role in determining the precipitation regime of the area, there is a strong west–east climatic gradient. As a result, between the westernmost and easternmost margins of Lake Nahuel Huapi, precipitations shift from 3000 mm to less than 700 mm, influencing plant distribution. Hence, while mountain slopes on the west are covered by dense forest, on the east the vegetation is characterized by grass and shrub species typical of the Patagonian steppe.

Three sites were selected in Lake Nahuel Huapi for this study: Brazo Rincón (BR), Bahía López (BL), and Dina Huapi (DH) (Fig. 1). Brazo Rincón is situated on the northwestern part of the lake in the rainiest region of NHNP, with average precipitation of 2800 mm y^{-1} (data provided by the Autoridad Interjurisdiccional de Cuencas (AIC)). This branch is surrounded by the Andino-Patagonic forest characterized by *Nothofagus dombeyi* (Coihue), *Chusquea culeou* (Caña colihue) in the understory, and other native tree and shrub species. The branch is characterized by an extended littoral zone with sandy beaches, and the basin has a regular shape with a maximum depth of approximately 100 m and an area of around 7.7 km^2.

Bahía López is a small, shallow, and closed bay (Fig. 1) with a maximum depth around 50 m and an area of approximately 1 km^2. The average precipitation rates in BL are of 1200 mm y^{-1} (AIC), and the area is surrounded by a mixed forest of *N. dombeyi* and *Austrocedrus chilensis* (Cordilleran cypress). There are a few rocky beaches around the bay and Lake Moreno's connection with Lake Nahuel Huapi is on the south-east margin of the basin.

The third site, DH, is located in the main and largest branch of Lake Nahuel Huapi, near River Limay, the outflow of the lake, and downstream of the city of San Carlos de Bariloche (population 130,000) (Fig. 1). This sampling point is located in the driest region of the lake (500 mm y^{-1}, AIC) with a maximum depth of 236 m. Besides a few tree species that grow near the shoreline of DH, such as *Nothofagus antarctica* (Ñire), *Maytenus boaria* (Mayten), and exotic *Salix* sp. (Willow), the dominant vegetation is typical of the Patagonian steppe.

The fish community of Lake Nahuel Huapi is represented by five native species, namely *Percichthys trucha* (creole perch), *Galaxias maculatus* (small puyen), *Galaxias platei* (big puyen), *Olivaichthys viedmensis* (velvet catfish), and *Odontesthes hatcheri* (patagonian silverside), and three introduced salmonid species: *Oncorhynchus mykiss* (rainbow trout), *Salmo trutta* (brown trout), and *Salvelinus fontinalis* (brook trout) (Juncos et al., 2013). Information on the composition of the macroinvertebrate community of Lake Nahuel Huapi is scarce and the best sources of Nahuel Huapi freshwater invertebrate species are from published fish gut content analysis. Crustacean decapods (*Aegla* sp. and *Samastacus spinifrons*), amphipods (*Hyalella* sp.), gastropods (*Chilina* sp.), bivalves (*Diplodon chilensis*), and insect larvae are all important dietary items for littoral-feeding fish (Juncos et al., 2011; 2013).

The phytoplanktonic community is dominated by the bacillariophyceans *Cyclotella steligera*, *Rhizosolenia eriensis*, and *Synedra ulna*, the dinophycean *Gymnodinium* sp., the prymnesiophycean *Chrysochromulina parva*, and the cyanophycean *Dactylococcopsis raphidioides* (Diaz et al., 1998). Balseiro et al., (2007) included the cladocerans *Bosmina longirostris*, *Bosmina chilensis*, and *Ceriodaphnia dubia* and the copepod *Boeckella gracilipes* as part of the zooplanktonic community.

Sampling and sample preparation

Sampling campaigns were carried out in two seasons, February (summer) and May (fall) 2011. Benthic macroinvertebrates, riparian tree leaves, and biofilm were sampled in summer when organisms are most abundant, fish in fall after the sport fishing season was over, and

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