



Fish distribution patterns and habitat availability in lakes Moreno Este and Moreno Oeste, Patagonia, Argentina



Magalí Rechencq ^{a,b,*}, Pablo Horacio Vigliano ^{a,b}, Patricio Jorge Macchi ^{a,b}, Gustavo Enrique Lippolt ^a

^a Grupo de Evaluación y Manejo de Recursos Ícticos (GEMaRI), Universidad Nacional del Comahue (UNCo), Quintral 1250, 8400 Bariloche, Río Negro, Argentina

^b Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA), Universidad Nacional del Comahue (UNCo) y Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Quintral 1250, 8400 Bariloche, Río Negro, Argentina

ARTICLE INFO

Article history:

Received 23 January 2014

Received in revised form 10 July 2014

Accepted 11 September 2014

Available online 13 October 2014

Keywords:

Fish distribution

Habitat types

Habitat availability

Oligotrophic lake

Galaxiids

Patagonia

ABSTRACT

Andean Patagonian lakes are ultraoligotrophic and deep, have simple food webs and low fish diversity and abundance. In this work the distributional abundance data of fish was studied in two interconnected Andean Patagonian lakes with varying proportions of contrasting habitat types. Hydroacoustic data (120 kHz) were used to analyze fish abundance and habitat use during the mixis and stratification periods. Three types of habitat (near shore, surface pelagic and deep pelagic) and two groups of fish, based on size (Big Fish >12 cm total length and Fish Larvae and Small Fish <12 cm total length) were defined. The distribution of both fish groups in these lakes revealed differences in habitat use for each lake and period. Fish group abundance was related to the availability of habitat types, according to the morphology of each lake. The Big Fish group showed preference for the near shore habitat during lake stratification and always appeared as individual targets. The Fish Larvae and Small Fish group used mainly the pelagic habitat during mixis, where they formed dense sound scattering layers. However, during lake stratification many individual targets from this group were found both in pelagic and near shore habitats, which would seem to indicate a change in distributional behavior. This is possibly associated with niche changes in the Galaxiids (*Galaxias* spp), a key component of Northern Patagonian lake food webs. Lakes like Moreno Oeste, which are morphologically and structurally more complex, could have more diverse fish ensembles with higher abundances. In contrast, lakes of simple morphology with low development of near shore habitats and ample deep zones, like Lake Moreno Este, could present lower Big Fish abundance. The contrasting habitat availability between lakes accounts for the abundances and distribution patterns of each fish group. While in these lakes fish assemblage species composition could depend on the environmental filter, the particular structure of a fish assemblage in terms of the proportional abundances of species depends on proportional habitat type availability. We can speculate that in Andean Patagonian lakes Galaxiids mediate a habitat coupling process critical for the transfer of energy and matter in oligotrophic lakes. We may also consider that the Small Puyen in this type of lake is a keystone prey species that relieves predation pressure on other potential prey. The existence of deep pelagic habitats in numerous deep lakes in the Northern Patagonian Andean region provides not only daytime refuge for Galaxiids, which allows them to maintain their high numbers in the lakes, but could also, in the long term, act as a Galaxiid source for other water bodies.

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* Corresponding author at: Universidad Nacional del Comahue, GEMaRI, Anexo Pasaje Gutierrez 1490, Cede Central Quintral 1250, 8400 San Carlos de Bariloche, Río Negro, Argentina. Tel.: +54 294 15457 8388/-+54 294 442 8505x452.

E-mail addresses: magalirechencq@gmail.com, magali.rechencq@crub.uncoma.edu.ar (M. Rechencq), pablo.vigliano@gmail.com (P.H. Vigliano), patriciomacchi@yahoo.com.ar (P.J. Macchi), glippolt@yahoo.com.ar (G.E. Lippolt).

¹ Work Postal Address: Quintral 1250, 8400 Bariloche, Argentina.

² Home Postal Address: Lonquimay 3905, 8400 Bariloche, Argentina.

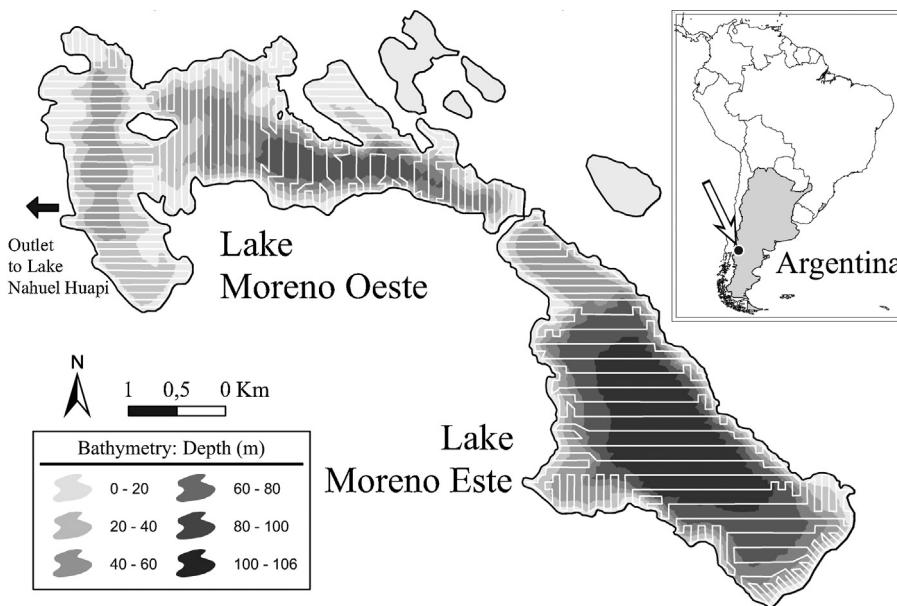


Fig. 1. Moreno Lake System: geographic sampling location (white arrow), flow direction (black arrow) and bathymetry (grays scale), hydroacoustic cruise track (white line).

Introduction

Knowledge of the distribution of organisms in a water body helps in the understanding of how they interact with each other and with the environment, facilitating the study of the roles played by each one in the ecosystem. Organism distribution is a dynamic, complex process, regulated by biological requirements, opportunities and interactions with other organisms and the environment (Beauchamp et al., 2007). Moreover, the environment is not spatially homogeneous: landscapes are dynamic due to processes occurring in the ecosystem (e.g. disturbances, currents, animal food-searching behavior). Populations are not totally synchronized with these processes which affect them and change their daily and seasonal distribution (Pastor, 2008). This heterogeneity offers unequal opportunities and leads to preferred behaviors with regard to habitat selection. Thus organisms group according to their physiological requirements, ontogeny, life history and trophic level, generating distribution patterns reflected in variations in the abundance of these groups in the different types of available habitats (Smith and Smith, 2002).

In lentic water bodies habitat type availability is determined by basin and lakebed morphology, such as the case of the deep Patagonian Andean lakes which are of glacial origin. Habitat types are defined by physicochemical parameters and inhabited by heterogeneous organism assemblages. Habitat borders are dynamic, depending on varying environmental conditions throughout the year. Light availability which depends on depth and transparency, and proximity to the bottom which offers refuge, are factors which affect habitat type borders and are influenced by basin morphology. Argentinian Patagonian Andean lakes of glacial origin are generally located in deep U-shaped valleys with northwest-southeast orientation, steep slopes and an extensive deep pelagic zone (Quirós and Drago, 1985; Mermoz et al., 2009). The presence of bays and peninsulas that typically form long, thin arms, or branches, provoke a shore effect that increases the influence of land on the aquatic environment. These lakes are characterized as being oligotrophic with an extensive euphotic zone, oxygenated lower regions and deep thermoclines which influence the structure of the trophic web (Modenutti et al., 1998, 2010). In these water bodies the relation between light, organic matter and nutrient availability, which is a

limiting factor, affects the structure and dynamics of the food web (Modenutti et al., 2010).

The varying morphology of the lakes conditions the proportions of the different habitat types they offer, which in turn vary in the conditions of the factors that influence their use by fish. According to the environmental filter hypothesis, the different habitat types would determine which organisms or life stages conform the assemblage of each habitat (*sensu* Poff, 1997). Thus, distribution patterns and lake-wide fish abundances would be influenced by lake morphology and habitat type availability. Two interconnected lakes with contrasting habitat type availability and the use of hydroacoustic techniques provided the framework to address the following questions: What are the spatial patterns of fish distribution in deep Patagonian Andean lakes? How are habitats used by fish? Are the fish assemblage structures and their distribution patterns related to proportional habitat availability as determined by lake morphology? In this context the aim of this work is to determine the existence of spatial patterns of fish distribution, and their association with habitat availability during the thermal mixis and stratification periods of two deep Patagonian Andean lakes of glacial origin.

Material and methods

Study area

The Moreno Lake System (Fig. 1) is formed by two interconnected main basins, the Moreno Oeste, and Moreno Este, which are oligotrophic, warm monomictic Northern Patagonian Andean Range Lakes of glacial origin. Morphological and limnological characteristics (Table 1) taken from the literature (Morris et al., 1995; Probst and Eckmann, 2009; Rechencq et al., 2011), measured with an YSI multiparameter sonde (T°) or estimated following standard procedures (Wetzel and Likens, 1991), are similar to those of other deep glacial lakes both in Chile and Argentina. Although the surface areas of lakes Moreno Oeste and Moreno Este are similar ($\sim 6 \text{ km}^2$ each), other morphological and limnological characteristics differ (Table 1), providing differential habitat type availability. The trophic webs in this system are similar to that of other Patagonian Andean Lakes which

Table 1

Morphological and limnological variables of lakes Moreno Oeste and Moreno Este.

Variables	Source	Moreno Oeste	Moreno Este	Ratio Este/Oeste
Morphology				
Surface area (km ²)	a	6.09	6.14	1.01
Fetch (km)	a	5.2	4.7	0.90
Width (km)	a	1.8	2.1	1.17
Coastline (km)	a	23.3	14.1	0.61
Volume (hm ³)	b	208.7	424.2	2.03
Z max (m)	c	88	106	1.2
Z med (m)	c	28	51	1.82
Z term (m) ^d	e	15	11	0.73
Temperature				
T mixis (C°)	e	6.3	7.4	1.17
T stratified (C°)	e	11.4	10.8	0.95
T stratified (min-max) (C°)	e	7.2–20.9	6.6–20.6	0.92–0.99
Light				
Secchi (m)	c	15	16	1.07
Kd par (1 m ⁻¹)	f	0.14	0.16	1.14
Z1% (%)	g	33	29	0.88
Euphotic volume (hm ³)	b	145.2	170.7	1.18
Aphotic volume (hm ³)	b	63.6	253.5	3.99

^a Estimated through GIS.^b (Wetzel and Likens, 1991).^c (Rechencq et al., 2011).^d The thermocline ranges from 15 to 20 m in thickness and is usually present from November to April.^e Measured with YSI multiparameter sonde.^f Kd par (Morris et al., 1995).^g Z1% (Sensu Probst and Eckmann, 2009).

present low species diversity (Macchi et al., 2007; Pascual et al., 2007; Modenutti et al., 2010). Only eight fish species are commonly found in these lakes (Table 2), with varying principal diet components and occurrence patterns associated with ontogeny and fish size (Barriga, 2006; Macchi et al., 2007; Milano et al., 2013).

Hydroacoustic field sampling design and methods

A scientific echosounder (Biosonics DE4000, Split beam, 120 kHz, 3.5 half beam angle) was used, mounted face down. Data were collected with the Visual Acquisition 4.02 software and stored for later analysis. Settings used to collect data were 1 ping per second, a pulse width of 0.4 ms, a collecting threshold of –80 dB, and water temperature. A cruise track was established of spaced out, preplanned rectangular transects (Fig. 1), with transect density adapted beforehand according to the bottom depth (MacLennan and Simmonds, 1992). Because the acoustic beam increases with depth and shallow areas are more structurally complex, where the bottom was lower than 60 m the distance between transects was set at 75 m, and for greater depths at 150 m. The boat used travelled at a relatively constant velocity of 5 km/h. The survey was carried out during daylight hours on consecutive days, with similar cloud cover and wind strength conditions, to minimize the noise of

surface waves. Hydroacoustic sampling took place during daylight hours starting 2 h after sunrise and ending 2 h before sunset. The coastguard prevented us from conducting night sampling because of the risk of navigating in the dark due to the high proportion of heterogeneous coastline, islands, bays, shoals and peninsulas. For the mixis period the data were collected over 7 days, between July 27, 2007 and August 16, 2007. For the lake stratification period sampling was carried out over 7 days between January 16, 2008 and March 03, 2008.

Hydroacoustic data analyses

Hydroacoustic data were analyzed using Visual Analyzer V 4.0.2 (Biosonics, 2004) and Echoview, Sonar Data V 4.1. The echograms were visually explored and analysis areas were defined excluding areas where the organism signals were hidden by ‘noise’ from other sources. The upper first meter of the water column was excluded because of wave surface noise. Bubble areas due to bottom emissions identified through TS individual analysis, and noise areas produced by the transducer lateral lobes and the presence of steep slopes were also discarded. A bottom blanking zone of 50 cm was used to exclude echoes from objects lying on the bottom, thus avoiding overestimation.

Table 2

Principal diet components and occurrence of common fish species present in Argentinian Patagonian Andean Lakes, such as the Moreno Oeste and Este Lakes (Barriga, 2006; Macchi et al., 2007; Milano et al., 2013).

species	Larval/juvenile principal diet	Adult principal diet	Occurrence
Small Puyen (<i>Galaxias maculatus</i>)	Zooplankton	Zooplankton	Very high
Creole Perch (<i>Percichthys trucha</i>)	Fish, benthos	Fish, benthos	High
Rainbow Trout (<i>Oncorhynchus mykiss</i>) ^h	Fish, benthos	Fish, benthos	High
Big Puyen (<i>Galaxias platei</i>)	Zooplankton	Fish, benthos	Medium
Brook Trout (<i>Salvelinus fontinalis</i>) ^h	Fish, benthos	Fish, benthos	Medium
Brown Trout (<i>Salmo trutta</i>) ^h	Fish, benthos	Fish, benthos	Low
Patagonian Silverside (<i>Odontesthes hatcheri</i>)	Zooplankton	Fish, zooplankton	Low
Velvet Catfish (<i>Olivaichthys viedmensis</i>)	Benthos	Fish, benthos	Low

^h No native species.

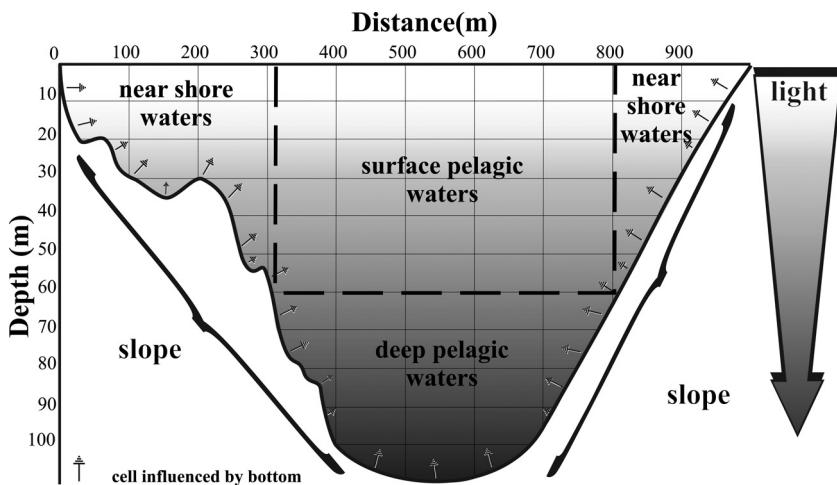


Fig. 2. Vertical profile and habitat type zonation. Cells 100 m long by 10 m deep were classified into three habitat types (near shore, surface pelagic and deep pelagic waters; separated by dashed line) based on depth in m (Y axis), light penetration (shading), and bottom influence (cells with arrows).

Habitat types

Three different types of habitat were defined and used for the present work, considering the varying levels of influence of depth, light penetration and proximity to the bottom: near shore waters, surface pelagic waters, and deep pelagic waters (Fig. 2). In order to analyze the availability of habitat types, their volumes in both lakes were calculated by integrating the areas delimited by the 10 m depth hypsographic curves (Wetzel and Likens, 1991) of each habitat type. Total volume of each lake was estimated by adding up the volumes of all strata and habitats. From these values the percentages of each type of available habitat were calculated for each basin and bar graphs were constructed to represent their depth to volume ratios, and to visualize the proportions of the different types of habitat.

Fish groups

Cross examination analysis of catch and hydroacoustic data allowed us to define two identifiable fish groups using a 12 cm total length (TL) or its associated -46 dB target strength (TS) (Love, 1977) as a cutoff point to separate them. The first group, called Big Fish, was formed by individual echoes with $TS \geq -46$ dB corresponding to fish over 12 cm TL. The second group, called Small Fish and Fish Larvae, was detected both as small fish under 12 cm TL (individual echoes with $TS < -46$ dB) and larval stages, or as small sized fish aggregations forming thick sound scattering layers (SSL).

Seasonal data from fish sampling from an extensive research program (GEMaRI 2000–2008), which used a depth stratified sampling design, was used to determine species and specimens sizes present, and habitat use during both mixis and stratified lake periods. Data from catches at different depths with benthic and pelagic gill nets (15, 30, 40, 50, 60 and 70 mm bar mesh size) set for 12 h in two benthic and one pelagic sampling point in both lakes (Vigliano et al., 1999), coastal seine trawls (5 mm bar mesh size), baited net traps (2 mm bar mesh size), and horizontal and vertical tows of an ichthyoplankton net (280 μ m mesh size) were grouped according to the three habitat types previously described (Table 3). In order to approximate a comparison of habitat use according to the different types of catch gear deployed we used percentual species specific catch composition per catch gear, by fish groups, habitat type, depth strata and lake, during mixis and stratified periods (Table 3). Gill net percentual catch composition was derived from catch per unit of effort in numbers (CPUEN) standardized to 15 h and 100 m^2 of gill net.

For hydroacoustic abundance estimations the TS for each fish group was established by evaluating the size ranges caught and the size which corresponded to the individual echoes detected on the echograms (Table 4). For the Big Fish group TLs caught ranged from 12 to 69 cm with a mean TL of 34.6 cm, corresponding to a TS value of -36.6 dB (Love, 1977) which was used for abundance estimations of Big Fish. For this group, the hydroacoustic estimated abundance values for each species were derived from percentual catch composition by depth strata and habitat (Table 3).

For the Small Fish and Fish Larvae group the criteria used to establish the TS value differed from the one used for the Big Fish group, since the three catch methods used sampled a particular fraction of the size range involved. An average of the pooled catches would be biased due to the differing catchability and selectivity of the different methods. To establish the TS value for abundance estimation of Small Fish and Fish Larvae we considered it more reliable to use the relationship between TS and the backscattering cross section of a target (σ , dB), which is derived from $TS = 10 \log(\sigma/4\pi)$ (MacLennan and Simmonds, 1992). The σ average of all individual targets ($TS < -46$ dB) detected on the echograms gave us an estimated TS value of -58.2 dB (TL = 2.3 cm) (Love, 1977) which was used for the abundance estimation for this group.

Data analysis

Each transect track echogram was analyzed using a grid with rows 10 m in depth and columns 100 m in length. The resulting cells were classified according to the following grouping criteria: lake (Moreno Oeste, Moreno Este), habitat type (near shore waters, surface pelagic waters or deep pelagic waters), time period (mixis, stratified), and/or depth strata. Each fish group abundance [N fish] for each grouping criteria was estimated from the equation: abundance = $\delta \cdot V$, where δ was the average cell fish density [fish per cubic meter] and V was the insonified volume [cubic meter] (MacLennan and Simmonds, 1992) of the corresponding grouping criteria. Each cell's δ was estimated using backscattering strength echointegration from $\delta = \sigma/(4\pi \times 10^{(TS/10)})$, where σ measured the backscattered energy by cell for each group of fish using their respective TS group value. The statistical differences in estimated abundances between habitat types and period between lakes were evaluated using χ^2 ($P < 0.01$). Bar graphs were drawn up of abundance [N fish] and percentual abundance [% of total N fish] estimated for both fish groups, classifying the data by habitat type, lake and time period. In addition, bar graphs of fish abundance according to depth stratum were constructed. In

Table 3

Percentual species composition (%) per catch gear for fish groups, habitat type and lake, during Mixis (Mix) and Stratified (Str) periods: Big Fish (TL > 12 cm); Small Fish and Fish Larvae (TL < 12 cm); and species and/or stages Not Included in the fish groups but present in the lakes. Species: Creole Perch (CP), Salmonids (Sa), Big Puyen (BP), Velvet Catfish (VC), Patagonian Silverside (PS), Small Puyen (SP), larval stage of both *Galaxiids* (Ga).

Big fish (TL > 12 cm)							
Near shore							
Moreno Este							
Species	CP Mix	Str	Sa Mix	Str	BP Mix	Str	
Gill nets: depth (m)							
2.5	0	30	100	70	0	0	
10	14	50	86	50	0	0	
20	0	66	0	33	0	0	
30	40	66	60	33	0	0	
40	0	50	0	0	100	50	
50	25	0	25	44	50	56	
Baited net traps: depth (m)							
1	0	0	0	0	0	0	
10	0	0	0	0	0	0	
30	0	0	0	0	0	0	
50	0	0	0	0	100	100	
Moreno Oeste							
Species	CP Mix	Str	Sa Mix	Str	BP Mix	Str	
Gill nets: depth (m)							
2.5	50	36	50	64	0	0	
10	60	40	40	60	0	0	
20	100	50	0	50	0	0	
30	57	40	43	20	0	40	
40	50	0	0	50	50	50	
50	50	0	0	0	50	100	
Baited net traps: depth (m)							
1	0	0	0	0	0	0	
10	0	0	0	0	0	0	
30	0	0	0	0	0	0	
50	0	0	0	0	0	0	
Surface Pelagic							
Moreno Este							
Species	CP Mix	Str	Sa Mix	Str	BP Mix	Str	
Gill nets: depth (m)							
0	0	0	100	100	0	0	
10	0	100	0	0	0	0	
20	0	0	0	0	0	0	
Moreno Oeste							
Species	CP Mix	Str	Sa Mix	Str	BP Mix	Str	
Gill nets: depth (m)							
0	0	0	100	100	0	0	
10	0	0	0	100	0	0	
20	0	0	0	0	0	0	
Deep Pelagic							
Moreno Este							
Species	CP Mix	Str	Sa Mix	Str	BP Mix	Str	
Gill nets: depth (m)							
80	0.000	–	0.000	–	0.009	–	
90	–	0.000	–	0.000	–	0.113	
Baited net traps: depth (m)							
80	0	0	0	0	100	100	
106	0	0	0	0	100	100	
Moreno Oeste							
Species	CP Mix	Str	Sa Mix	Str	BP Mix	Str	
Baited net traps: depth (m)							
75	0	0	0	0	100	100	
88	0	0	0	0	100	100	
Small fish and fish larvae (TL < 12 cm)							
Near shore							
Moreno Este y Moreno Oeste							
Species	SP Mix	Str	Ga Mix	Str			
Baited net traps: depth (m)							
0	100	100	–	–			
30	100	100	–	–			
50	100	100	–	–			
Coastal Seine Trawl: depth (m)	1	100	100	–	–		
Tows of ichthyoplankton net: depth (m)	25	–	–	100	100		

Table 3 (Continued)

Big fish (TL > 12 cm)						
Surface and Deep Pelagic						
	Moreno Este y Moreno Oeste					
Species	SP Mix	Str	Ga Mix	Str		
Baited net traps: depth (m)	80 106	0 0	0 0	— —	— —	
Tows of ichthyoplankton net: depth (m), coinciding with SSL depths	25 80	— —	— —	100 100	100 100	
Species or fish stages not included in the fish group but present in lakes						
Near Shore, Surface Pelagic and Deep Pelagic						
Moreno Este (ME) and Moreno Oeste (MO)						
	VC (TL > 12 cm)		PS (TL > 12 cm)		VC, PS, CP, S, BP (TL < 12 cm)	
	Mix	Str	Mix	Str	Mix	Str
Gill nets: depth (m)	ME 30 MO 0 Others	0 0 0	<1 0 0	0 0 0	— — —	— — —
Baited net traps, coastal seine trawl or tows of ichthyoplankton net in all depth sampled		0	0	0	0	0

Table 4

Total Length (TL) and Target Strength (TS) relation between catch and acoustic data of fish groups. Theoretical Target Strength (TS t) of species present in catch for each sampling gear and Theoretical Total Length (TL t) used to estimate abundances for each fish group were established from TL and TS theoretical relation ([Love, 1977](#)). Larval stages of Big Puyen and Small Puyen were grouped as Larval Galaxiids.

Fish Group	Species or group	Catch data		Acoustic data	
		TL (cm)	TS t (dB)	TS (dB)	TL t (cm)
Big Fish (TL > 12 cm)				−36.6	34.6
Gill nets					
	Creole Perch	33.5	−36.9		
	Salmonids	45.0	−34.5		
	Big Puyen	21.6	−40.4		
Baited Traps					
	Big Puyen	19.4	−41.2	−58.2	2.3
Small fish and fish larvae (TL < 12 cm)					
Baited traps					
	Small Puyen	5.5	−51.3		
Coastal trawl					
	Small Puyen	4.5	−54.6		
Tows of ichthyoplankton net	Galaxiids	1.3	−62.8		

order to be able to allocate species identity to hydroacoustic estimated fish abundances using the available catch data (GEMaRI 2000–2008) by strata and habitat for the Big Fish group we used gill net proportional species composition where possible. Where only one species was caught regardless of the fishing gear used, the estimated hydroacoustic abundances were assigned only to that species ([Table 3](#)). This approach could not be used with the Small Fish and Fish Larvae group. In the same strata or habitat baited net traps and coastal seine trawls caught only Small Fish while ichthyoplankton nets caught only Galaxiid larvae, thus invalidating proportional allocation. Therefore, hydroacoustic abundances refer to the whole group.

Results

The volume percentages [%] of available habitat types in each lake, and their volumes [hm³] per depth stratum are shown in [Fig. 3](#). Light and bottom proximity are the two factors that exert most influence in Lake Moreno Oeste due to a predominant near shore habitat. In Lake Moreno Este light wields the greatest

influence due to a predominant surface pelagic habitat. This and the less developed coastline and higher percentage of steep slopes in Lake Moreno Este than in Moreno Oeste, account for contrasting habitat type availability.

Big fish distribution

The abundance and relative abundance values for Big Fish ([Fig. 4](#)) show that for both lakes estimated numbers in mixis are lower than during stratification ($\chi^2, P < 0.01$). These results also reveal that the habitat with highest abundance of Big Fish is the near shore one, irrespective of the basin or the sampling period, which means that Moreno Oeste has a greater abundance of this fish group. The abundance of this group during the mixis period in the surface pelagic habitat in both basins and in the deep pelagic habitat in Moreno Este for both periods can also be seen ([Fig. 4](#)).

Big Fish abundance values by 10 m depth strata for habitat types in both lakes are shown for mixis ([Fig. 5](#)) and stratification ([Fig. 6](#)) periods. Note the difference in scales between [Figs. 5 and 6](#) required to represent the large differences in abundance between periods.

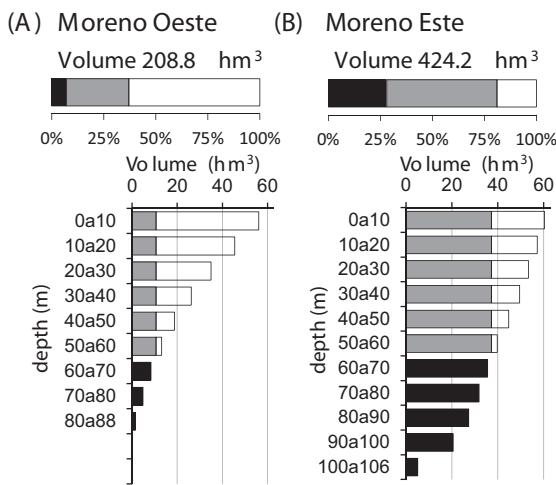


Fig. 3. Total volume and 10 m depth strata volume of available habitat types: volume in lakes Moreno Oeste (A) and Moreno Este (B) for: near shore waters (open bars) surface pelagic waters (grey bars), and deep pelagic waters (black bars).

In near shore waters the highest numbers of Big Fish in both lakes during mixis are deeper than in stratification, corresponding to Creole Perch and Salmonids between 20 and 40 m depths for mixis and between 10 and 30 m for stratification. In the deeper strata of this

habitat in both periods Big Puyen represent the highest numbers. It is also worth noting that in both periods Big Fish abundance in Moreno Este is lower than in Moreno Oeste for all depth strata except in mixis for the 40–50 m depth stratum of Moreno Este. In the surface pelagic habitat the Big Fish group does not have a high number of fish in either of the lakes or periods. Although their highest numbers correspond to Moreno Este, mainly during the stratified period in the 20–30 m depth stratum, this cannot be appreciated in Figs. 5 and 6 due to the x axis scale differences necessary due to the higher numbers in the near shore habitat. Most of the echoes of this fish group in this habitat were recorded between 50 and 60 m depths, in cells influenced by proximity to the bottom (Fig. 2). In the deep pelagic habitat Big Fish numbers are low except for the 90–100 m depth stratum of Moreno Este Lake in both periods, corresponding to Big Puyen, which present higher abundance during the stratification period.

Small fish and fish Larvae distribution

The abundance and relative abundance of Small Fish and Fish Larvae (Fig. 7) was several orders of magnitude higher than that of the Big Fish group. Moreno Oeste has lower fish numbers of Small Fish and Fish Larvae than Moreno Este during both periods in all habitat types. In Moreno Oeste Lake during the mixis period Small Fish and Fish Larvae abundances are much lower than in the stratification period, when most of them are in the near shore habitat. The

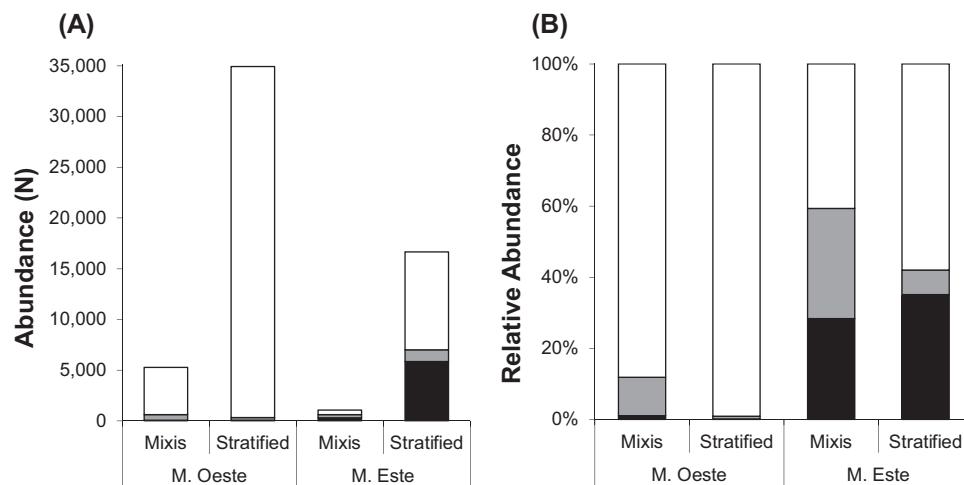


Fig. 4. (A) Abundance (N) and (B) relative abundance (%) of Big Fish for both lakes and periods surveyed by habitat type: near shore waters (open bars), surface pelagic waters (grey bars) and deep pelagic waters (black bars).

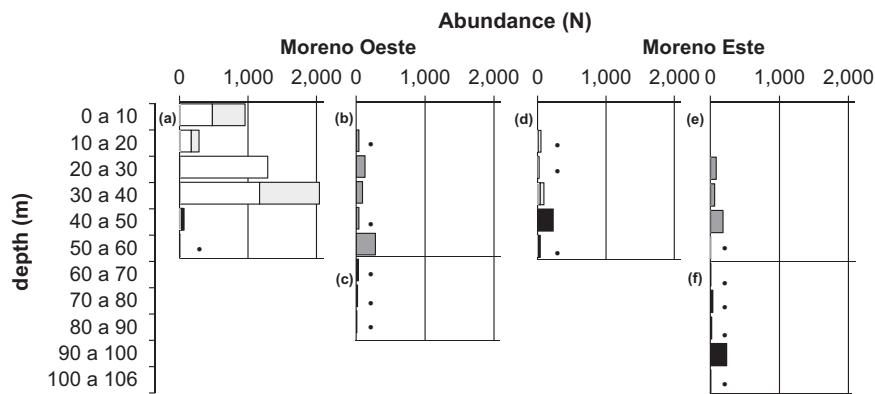


Fig. 5. Distributional abundance of the Big Fish group by depth stratum per lake and habitat type for the mixis period. Abundance for Lake Moreno Oeste in (a) near shore waters, (b) surface pelagic waters, and (c) deep pelagic waters, and for Lake Moreno Este (d) near shore waters, (e) surface pelagic waters, and (f) deep pelagic waters of Creole Perch (open bars), Salmonids (light grey bars), non-identified species (dark grey bars), and Big Puyen (black bars). Non null total values less than or equal to 50 (dot).

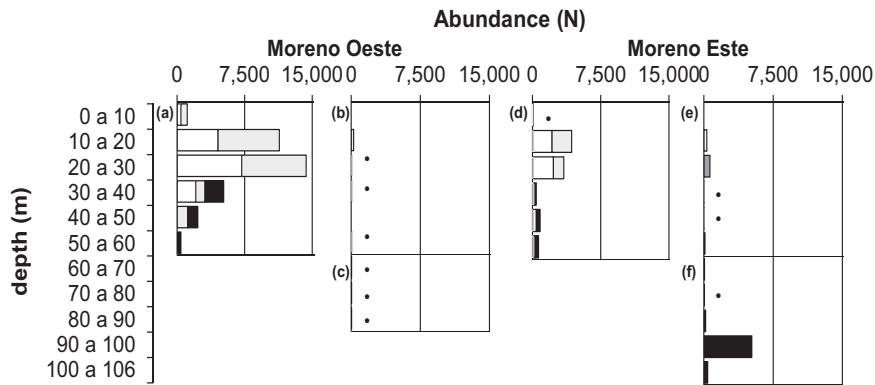


Fig. 6. Distributional abundance of the Big Fish group by depth stratum per lake and habitat type for the stratification period. Abundance for Lake Moreno Oeste in (a) near shore waters, (b) surface pelagic waters, and (c) deep pelagic waters, and for Lake Moreno Este (d) near shore waters, (e) surface pelagic waters, and (f) deep pelagic waters of Creole Perch (open bars), Salmonids (light grey bars), non-identified species (dark gray bars), and Big Puyen (black bars). Non null total values less than or equal to 50 (dot).

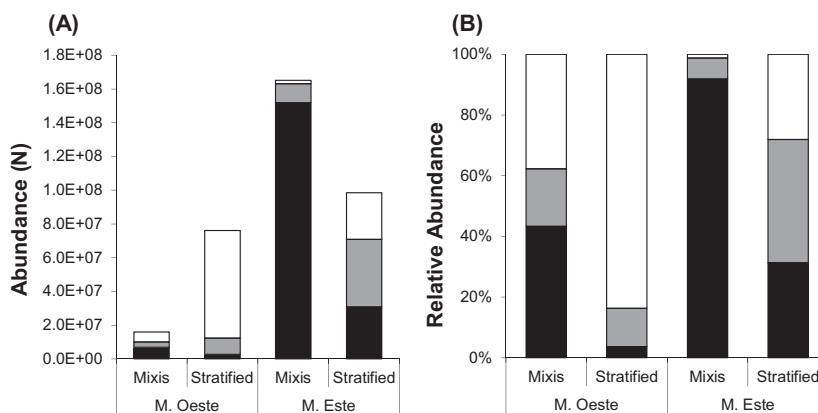


Fig. 7. (A) Abundance (N) and (B) relative abundance (%) of Small Fish and Fish Larvae for both lakes and periods surveyed by habitat type: near shore waters (open bars), surface pelagic waters (grey bars) and deep pelagic waters (black bars).

deep pelagic habitat of Moreno Este in the mixis period presents the highest numbers for this group.

Small Fish and Fish Larvae values by 10 m depth strata for habitat type in both lakes are shown for mixis (Fig. 8) and stratification (Fig. 9) periods. During the mixis period this group is represented in all habitats of both lakes mostly by SSL, while during the stratification period there is higher proportion of individual targets. In both cases acoustic signal characteristics and sampling indicate they correspond principally to larval Galaxiids. In near shore waters the

highest numbers of Small Fish and Fish larvae in both lakes correspond to the stratification period, when most of the individual targets are concentrated between 0 and 30 m depths, with acoustic sizes mostly corresponding to those of juvenile and adults of Small Puyen (Table 4). The surface pelagic habitat shows the lowest numbers of Small Fish and Fish Larvae for both lakes and periods except for Moreno Este during stratification, when considerable numbers can be found between 0 and 30 m depths. The deep pelagic habitat of both lakes shows strikingly different abundance patterns. Moreno

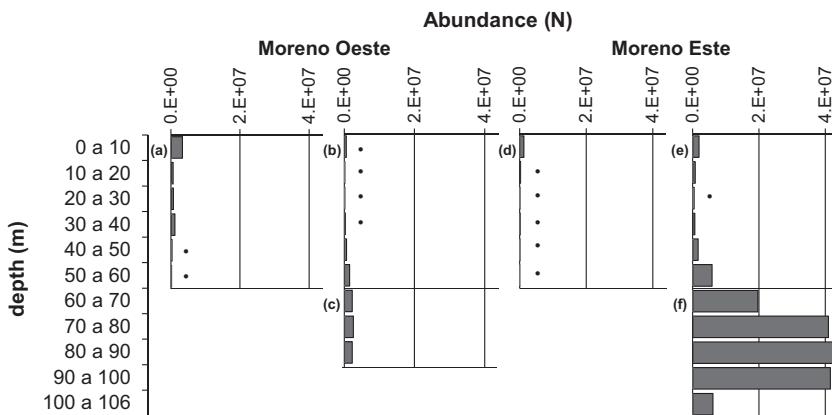


Fig. 8. Distributional abundance of Small Fish and Fish Larvae (Galaxiids) by depth stratum per lake and habitat type for the mixis period. Abundance for Lake Moreno Oeste in (a) near shore waters, (b) surface pelagic waters, and (c) deep pelagic waters, and for Lake Moreno Este (d) near shore waters, (e) surface pelagic waters and (f) deep pelagic waters. Non null total values less than or equal to 5×10^5 (dot).

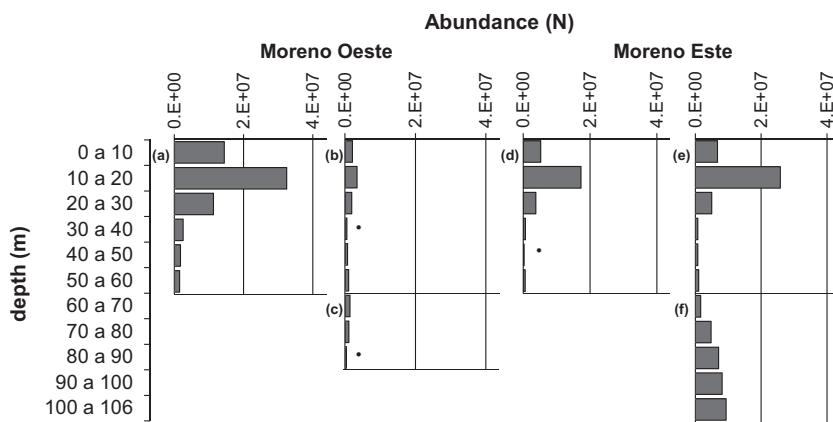


Fig. 9. Distributional abundance of Small Fish and Fish Larvae (Galaxiids) by depth stratum per lake and habitat type for the stratification period. Abundance for Lake Moreno Oeste in (a) near shore waters, (b) surface pelagic waters, and (c) deep pelagic waters, and for Lake Moreno Este (d) near shore waters, (e) surface pelagic waters and (f) deep pelagic waters. Non null total values less than or equal to 5×10^5 (dot).

Oeste during both mixis and stratification shows the lowest abundances for this group, while the deep pelagic of Moreno Este during mixis has the highest abundance of Small Fish and Fish Larvae of both lakes, which form dense SSLs. During stratification the pattern is similar in Moreno Este, although in smaller numbers than in mixis.

Discussion

The distribution of fish in these interconnected lakes revealed differences in the use of habitats between Big Fish and Small Fish and Fish Larvae in relation to both lakes and period of the year. While the Big Fish group predominantly uses the near shore habitat during both mixis and stratified periods, the Small Fish and Fish Larvae group uses mostly the deep pelagic habitat during mixis, and the near shore and surface pelagic habitats during stratification. Results clearly show that irrespective of the period, Big Fish are more abundant in Moreno Oeste Lake and do not form shoals in either of the lakes or periods. Allocation of species to hydroacoustic records for this group show that while Creole Perch and Salmonids use the near shore habitat more, the Big Puyen use the deeper strata of this habitat as well as the deep pelagic. During mixis, the general levels of abundance of this group are lower than in the lake stratification period, for both lakes. This difference between periods coincides with the variations in catches of this group of fish in Patagonian lentic water bodies (Vigliano et al., 2008, 2009; Juncos et al., 2013) and is probably associated with reproductive migrations. Previous studies have shown that Big Puyen have specific morphological and physiological adaptations that allow them to make extensive use of the deep benthic habitat (Milano et al., 2002; Milano, 2003). The present study shows, as a novel result, that it also makes extensive use of the deep pelagic water column. For the Small Fish and Fish Larvae group the results clearly show that for both periods this group is more abundant in Lake Moreno Este, in contrast to that observed for the Big Fish group. The highest concentrations of the Small Fish and Fish Larvae group were found in the surface and deep pelagic habitats. Most of the acoustically recorded abundances in these two habitats correspond to larval Galaxiids, which during mixis concentrate as SSL in the deep pelagic, and during stratification are mostly found as individual targets in all habitats. Use of the deep pelagic by larvae of both Small and Big Puyen, as well as by adults of the latter species, probably provides daytime refuge from visual predation for the larvae, and refuge and foraging opportunities for Big Puyen adults of the Big Fish group. During stratification, greater use of the near shore habitat by the Small

Fish and Fish Larvae group is revealed by a noticeable increase in their abundance. This increase can be explained by the ontogenetic shift of Galaxiids in habitat use, as they migrate from the pelagic towards the near shore waters during metamorphosis (Barriga, 2006; Milano et al., 2013), with acoustical sizes corresponding to those recorded in our samplings. We can conclude that native Galaxiids, in relation to their life cycle and ontogenetic habitats shifts, make more extensive use of all habitats than Creole Perch and Salmonids.

The observed variation between abundances of both the Big Fish and Small Fish and Fish Larvae groups between lakes can be explained by preferential habitat use by the different life stages of fish and by varying proportions of available habitats between lakes, related to lake morphology. The near shore habitat predominates in Moreno Oeste (63%), while in Moreno Este pelagic habitats are dominant (81%). The contrasting habitat availability between lakes accounts for the distribution patterns described for each fish group according to both catches and hydroacoustics. Creole Perch and Salmonids (Big Fish group) in both periods, and adults and juveniles of Small Puyen (Small Fish and Fish Larvae group) use the near shore habitat. Big Puyen adults (Big Fish group) in both periods and larval Galaxiids (Small Fish and Fish Larvae group) in mixis use both pelagic habitats. It would be expected that lakes that are morphologically and structurally more complex where the bottom exerts a high level of influence on the limnetic water column (Fig. 2, cells with arrows) would result in more complex fish communities with higher abundances. In contrast, lakes of simple morphology with low development of near shore habitats and ample deep zones would present lower Big Fish abundance. Fish assemblages of lakes of the Northern Andean Patagonian Region show similar species composition (Macchi et al., 2008), which may indicate a generalized common environmental filter (sensu Poff, 1997). While in these lakes fish assemblage species composition probably depends on the environmental filter, the particular structure of a fish assemblage in terms of species proportional abundance would depend on proportional habitat type availability.

In order to understand fish assemblages or lake-wide processes, the relation between habitat availability, habitat use and fish abundances must be taken into account. So far, habitat use by fish in Patagonian lakes and associated processes have been studied in both shallow and deep lakes in the habitats that we call the nearshore and surface pelagic (Cussac et al., 1992; Barriga et al., 2002; Buria et al., 2007; Aigo et al., 2008). In deep lakes sampling design must consider habitat type availability in order to avoid biases. As an example, the combined use of different fishing methods and hydroacoustic techniques in the ample deep pelagic

waters of Moreno Este Lake revealed previously unknown high abundance of Big Puyen, comparable with those of other species in other habitats. This implies that studies in lakes with high availability of this habitat have probably underestimated the reported abundances of this species and their importance in associated processes, such as their role in the food web and nutrient recirculation. Habitat coupling is an ecosystemic process of great importance in terms of energy, nutrient transport, and recycling between habitats, affecting predator–prey interactions and the structure and stability of food webs (Schindler and Scheuerell, 2002; McIntryre et al., 2006). We can speculate that in Andean Patagonian lakes Galaxiid recirculation of nutrients through excretion (Reissig et al., 2003), mediated by daily and ontogenetic migration between habitats (Rechencq et al., 2011), as well as their high abundance and role as prey (Vigliano et al., 2009; Juncos et al., 2013), conform a habitat coupling process that could be critical considering the oligotrophic nature of the lakes. We may also consider the Small Puyen to be a keystone prey species, that is to say a species that can maintain its numbers despite being subject to predation, controlling predator density and reducing predation pressure on other prey (Holt, 1977). This could be due to the high abundance of both Galaxiid species in the Small Fish and Fish larvae group shown in this paper and their heavy consumption by predators, estimated through bioenergetics modeling (Juncos et al., 2013). Daily migrations of both Galaxiid species, reflecting the use of the deep pelagic as a key daytime refuge from visual predators, and displacement to feeding areas during the night (Rechencq et al., 2011) may contribute to their tolerance to predation. Noy-Meier (1981) stated that under certain circumstances removal of a keystone prey species would diminish overall diversity. This could be the case for New Zealand where Salmonid introductions had devastating effects on galaxiids and other native biota (McDowall, 2003). In Argentine Patagonia Galaxiids do not appear to have suffered as much (*see this paper*). The numerous deep lakes and the availability of deep pelagic habitats and habitat ontogenetic shifts may contribute to predation tolerance. If this is the case, the numerous deep lakes may act as Galaxiid sources within a drainage basin and also relieve predation pressure on potential prey.

Acknowledgements

We wish to thank all the members of the GEMaRI for their field assistance, and also the personnel of the Hydroacoustic Lab of INIDEP, Argentina, for their constant support. Finally, we wish to thank Sonar Data for their support and technical assistance with the use of Echoview. This article was partially supported by the Universidad Nacional del Comahue (CRUB-UNCo B001), ANPCyT PICT 2004 No. 25722, and the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET).

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