Is the decline of birds and amphibians in a steppe lake of northern Patagonia a consequence of limnological changes following fish introduction?

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ABSTRACT

1. Laguna Blanca, in Laguna Blanca National Park, is a lake in Patagonia which has been designated as a Ramsar site since 1971 because of bird diversity and abundance and importance for nesting, particularly for the black neck swan,Cygnus melanocoryphus. It is also valued for its populations of endemic amphibians, Atelognathus patagonicus and Atelognathus praebasalticus.

2. Avian and amphibian populations have decreased dramatically in recent years. Percichthys colhuapiensis, Percichthys trucha (Pisces, Percichthyidae), Salmo trutta and Oncorhynchus mykiss (Pisces, Salmonidae) were introduced into Laguna Blanca in 1965. Since 1986, no Atelognathus frogs have been found. The abundance of swans and coots, which are strongly associated with macrophytes for nesting and feeding, has diminished drastically, whereas piscivorous birds have increased.

3. The fishless condition of some neighbouring small lakes with abundant pond weeds, aquatic birds and endemic amphibians, was assessed in order to compare the physical and chemical characteristics and the quantitative composition of the benthos among lakes. Fish presence at Laguna Blanca and its absence at El Burro, Antiníñ and Jabón lakes, were confirmed. Compared with previous results, it seems that the abundance of Amphipoda (Hyalella), Copepoda and Cladocera at Laguna Blanca has decreased, while Acari has increased and Notostraca has disappeared. Water transparency has diminished in Laguna Blanca and now is lower than that of fishless lakes.

4. P. colhuapiensis were captured only in Laguna Blanca, with the highest captures in the littoral zone. The population shows rapid individual growth in the early years and an absence of fish older than 6 years. The preponderance of benthos and the presence of macrophytes in the gut contents of adult P. colhuapiensis appear to indicate that they are important consumers of these resources.

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This paper concludes that fish introduction in Laguna Blanca led to a complex trophic cascade effect (fish predation on tadpoles, fish competition for avian food, bottom disturbance, zooplankton reduction) producing deleterious effects on the amphibian and bird populations.

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KEY WORDS: Laguna Blanca National Park; Ramsar; fish-avian-plankton-benthos interactions; amphibian decline

INTRODUCTION

Laguna Blanca, in Laguna Blanca National Park (Figure 1), is a lake in northern Patagonia (Argentina) that has been a Ramsar site since 1971 because of bird diversity and abundance and importance for nesting, particularly for the black neck swan, Cygnus melanocoryphus. It is also valued for its populations of endemic amphibians, Atelognathus patagonicus and Atelognathus praebasalticus (Cei and Roig, 1966; Daciuk, 1968; Administración de Parques Nacionales, 1993). Human impact is subtle but present. Terrestrial grazing has affected all the water bodies of this study for a long time (106 cows and horses and 2626 sheep and goats in 1955; Daciuk, 1968), and this continues to the present (159 cows and horses and 2276 sheep and goats in 1994; Siffredi and Vazquez, 1994).

Previous geological, biological and limnological data were recorded by Gollán (1951), Cei and Roig (1966), Daciuk (1968), Marcolin (1968), Ruiz Leal (1972), Correa Luna (1974), Paggi (1981), Quirós et al. (1986), Administración de Parques Nacionales (1993), Dirección Nacional de Recursos Hídricos (1995), and Canevari et al. (1998). Daciuk (1968) reports the illegal introduction of fish: 6000 juvenile Percichthys colhuapiensis (Pisces, Percichthyidae) and an unknown number of Salmo trutta and Oncorhynchus mykiss (Pisces, Salmonidae) were put into the lake in 1965 (Administración de Parques Nacionales, 1993). In addition, Percichthys trucha was observed in Laguna Blanca (Quirós and Baigún, 1986; Mazzucchelli, 1991).

Avian and amphibian populations have decreased dramatically in recent years (Administración de Parques Nacionales, 1993). Since 1986, no Atelognathus frogs have been found in Laguna Blanca (Administración de Parques Nacionales, 1993; Cuello, 2002). During this time, the macrophyte cover (Myriophyllum elatinoides) and the abundance of swans and coots has diminished drastically (Ramilo, pers. comm.), whereas piscivorous birds have increased. There is no evidence of environmental changes or impacts other than fish introduction that could have provoked such consequences.

The aim of this work was to perform a preliminary analysis of possible relationships between fish introductions into Laguna Blanca and subsequent amphibian and avian declines. The main approach adopted was to compare present and past data of Laguna Blanca and to assess the fishless condition of some neighbouring small lakes which have abundant pondweeds, amphibians, and aquatic birds. The qualitative and quantitative composition of littoral benthos was compared among these lakes. Further work will be necessary in order to establish causal relationships linking the declines in amphibians and birds with fish introductions.

METHODS

Laguna Blanca (Figure 1) is situated at an elevation of 1250 m, with a surface area of 1700 ha, a perimeter of 30 km, a maximum depth in different parts of the lake ranging from 8.5 to 10 m, and eutrophic water quality (Daciuk, 1968; Quirós et al., 1986, Table 1). Mean annual air temperature in the area is 10°C, with a minimum of −25 and a maximum of 30°C. In colder winters the surface freezes for up to 2 months during July and August.
Figure 1. Location of Laguna Blanca (39°02' S, 70°21' W), Verde (39°00' S, 70°23' W), Antínir (38°58' S, 70°21' W), Jabón (38°58' S, 70°22' W) and El Burro (39°07' S, 70°25' W) lakes. The rectangle indicates the Laguna Blanca National Park borders. Isolines range from 1100 m a.s.l. (Laguna Blanca shoreline) to 1700 m a.s.l. (equidistance 25 m).
Table 1. Physical, chemical and biological properties of Laguna Blanca and lakes without fish (El Burro, Jabón and Antiñir). Dissolved oxygen was recorded at dusk. Qualitative abundance of *Atelognathus patagonicus*, aquatic birds, and pondweeds (*Myriophyllum* sp.) are indicated. For Laguna Blanca, the fish catch per unit effort is shown.

<table>
<thead>
<tr>
<th></th>
<th>Laguna Blanca</th>
<th>El Burro</th>
<th>Jabón</th>
<th>Antiñir</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latitude, Longitude</td>
<td>39°03' S, 70°49' W</td>
<td>39°06' S, 70°24' W</td>
<td>38°58' S, 70°22' W</td>
<td>38°59' S, 70°23' W</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>1293</td>
<td>1378</td>
<td>1339</td>
<td>1367</td>
</tr>
<tr>
<td>Surface water temperature (°C, March 2001)</td>
<td>14</td>
<td>13</td>
<td>22</td>
<td>19</td>
</tr>
<tr>
<td>Conductivity (μS cm⁻¹, March 2001)</td>
<td>800</td>
<td>450</td>
<td>310 (surface)</td>
<td>290 (1 m depth)</td>
</tr>
<tr>
<td>Secchi depth (m, March 2001)</td>
<td>1</td>
<td>&gt; 2</td>
<td>3</td>
<td>&gt; 1.5</td>
</tr>
<tr>
<td>Maximum depth (m)</td>
<td>11</td>
<td>2</td>
<td>4</td>
<td>1.5</td>
</tr>
<tr>
<td>Chlorophyll-a (μg L⁻¹, March 2001)</td>
<td>23.09 (1 m depth)</td>
<td>0.70 (1 m depth)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total phosphorus (μg L⁻¹, March 2001)</td>
<td>62.84 (3 m depth)</td>
<td>16.76 (1 m depth)</td>
<td>57.83 (0.5 m depth)</td>
<td>48.54 (1 m depth)</td>
</tr>
<tr>
<td>Total dissolved phosphorus (μg L⁻¹, March 2001)</td>
<td>18.07 (1 m depth)</td>
<td>13.39 (1 m depth)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dissolved O₂ (mg L⁻¹, March 2001)</td>
<td>11.0 (1 m depth)</td>
<td>10.5 (0.5 m depth)</td>
<td>8.8 (surface)</td>
<td>11.0 (0.5 m depth)</td>
</tr>
<tr>
<td>Catch per unit effort</td>
<td>46.2, 35.4</td>
<td>0.0, 0.0</td>
<td>0.0, 0.0</td>
<td>0.0, 0.0</td>
</tr>
</tbody>
</table>

* A. patagonicus
  * Absent
  * Present
  * Low
  * High

Additional notes:
- *Administración de Parques Nacionales* 1993,
- Cuello 2002,
- *Administración de Parques Nacionales* 2003,
- E. Ramilo pers. comm.,
- S. Ortubay pers. obs.
In order to compare the status of Laguna Blanca with neighbouring, presumably fishless, lakes four small lakes — Verde, Jabón, Antiñir and El Burro — were surveyed in addition to Laguna Blanca. During an initial sampling of Laguna Blanca and Laguna Verde in January 2001, fish were caught using gill nets (25 mm bar mesh size, 50 m long and 2 m high) placed perpendicular to the shoreline from 0 to 1.5 m depth. Gill nets were left in place overnight. Dip netting also was carried out at two small inlet streams of Laguna Blanca, Pichi-Nireco and Blanco (Figure 1).

During a more extensive second sampling, in March 2001, physical and chemical properties at Laguna Blanca, Jabón, Antiñir and El Burro, were recorded, assaying for phosphorus and chlorophyll in the lake water, and sampling benthos and fish populations. Phosphorus was measured as total phosphorus (TP) and total dissolved phosphorus (TDP) following the ascorbate-reduced molybdenum blue technique (APHA, 1989), using unfiltered and filtered water (through GF/F filters), respectively. Chlorophyll-a concentration was determined by extraction with 90% ethanol following Nusch (1980) and measured in a Turner AU-10 fluorometer.

Benthos was sampled once, at 30, 50 and 80 cm depths. Because of the stony lake beds, the Eckman sampler was inappropriate and a small electric (12 V) centrifuge pump at the end of a plastic tube was used (17 mm inner diameter, 10 m length). Surface sediments and organisms were sucked up while moving the tube end over a square area of 0.25 m² at each depth. The sample was filtered through a 300 μm mesh and the sample fixed in 4% formaldehyde. Once identified and classified into major taxonomic groups, a known number of individuals belonging to each category were weighed (± 2 mg). Data were compared statistically among lakes (using Kruskal–Wallis and Dunn’s test) on the basis of numeric abundance and mass of main taxonomic groups.

Fish were collected with several 60 m long arrangements of gill nets (mesh size 15, 20, 30, 50, 60 and 70 mm between knots, each 10 m long and 2 m high) placed on the bottom at 2, 4 and 10 m depths, following Vigliano et al. (1999). Gill nets were set parallel to the shore and left in place overnight. In the small lakes, gill nets worked only at a depth of about 2 m. Seining and electrofishing assessed the presence of small fish near the shore. Complementary to January and March 2001 samplings, further fish net samplings were performed during May, September and October 2003, for diet study and abundance assessment. The captured fish were identified according to Ringuelet et al. (1967) and Scott and Crossman (1974). They were weighed, measured and sexed, and the gonadal status was estimated according to Milano (1996). The guts were dissected for diet study, and contents fixed in 4% formaldehyde. Scale samples were taken from each fish, washed, and observed under a microfilm reader (Cannon Universal reader 300S, 27 X). Growth rings were counted on the screen. Growth curves were constructed using observed data. Separation of normal distributions (Bhattacharya’s method) and fitting of the von Bertalanffy growth model were performed using FISAT 2 (FAO-ICLARM Stock Assessment Tools). All other statistical analyses were performed with SPSS® and SIGMASTAT®.

RESULTS

Physical and chemical properties

Laguna Blanca is larger, deeper, and less transparent than the other lakes (Table 1).

Benthos composition

Samples differed between Laguna Blanca and fishless lakes (Figure 2). Significant differences were detected among lakes (Kruskal–Wallis) both in number and in weight for Ostracoda (p = 0.03), Hyalella (p = 0.02), Copepoda (p = 0.03), Acarini (p = 0.01), Plecoptera (p = 0.02), Coleoptera adults (p = 0.01), Notonectidae
Figure 2. Composition, mean number (top) and mean weight (bottom) by benthos sample. Main categories are indicated for lakes with fish (Laguna Blanca) and without fish (Antíñir, El Burro, Jabón).
(p = 0.03), and Hemiptera (p = 0.01). Most of these variables also showed significant differences between lake pairs (Dunn’s test, p = 0.05).

The main traits of Laguna Blanca were low number and small mass of benthic organisms, the presence of Acarini and the low abundance in number and mass of Hyalella (undetectable in Figure 2).

Fish

Fish were caught only at Laguna Blanca and its streams. Juvenile S. trutta and O. mykiss were captured in the streams, and juvenile and adult P. colhuapiensis in the lake. Catch per unit effort in March 2001 (number, and mass, of fish per 60 m net arrangement and night), was 46 fish and 35 kg, in the littoral. Six age classes of juvenile and adult P. colhuapiensis were found in a subsample, but only three normal distributions could be separated (N = 38, Figure 3). Adult individuals were larger than 250 mm TL (males) and 270 mm TL (females). Captures performed during May (autumn) and September (late winter) and October (spring) 2003 showed the presence of running males and vitellogenic females, suggesting repetitive breeding events taking into account the already observed summer reproduction in January and March 2001. Both the length-frequency and the von Bertalanffy growth curve showed the absence of age classes older than 6 years, a low recruitment in the year class 2 (175 to 225 mm), a low asymptotic length (368.98 mm) and a high growth rate (K = 0.46, Figure 3).

The diet of P. colhuapiensis showed a strong dependence on sampling date (Figure 4). In early summer (2001), the diet of adult P. colhuapiensis was dominated (in number) by Copepoda and Ostracoda. In late summer (2003), the diet diversity was greater, with high percentages of Planorbidae (Mollusca: Gastropoda) and terrestrial insects. Planorbidae and amphipods clearly predominated in autumn 2003, whereas terrestrial insects disappeared. At the end of winter Planorbidae predominated and in spring almost all the prey were Copepoda. No amphibian was detected in the fish guts in any sampling.

DISCUSSION

Laguna Blanca and the other three lakes show abiotic differences (in area and depth) that constrain the interpretation of other biological differences as consequences of fish introduction (Table 1). Myriophyllum cover was lower in Laguna Blanca than in the other lakes. Benthos composition differed among lakes. Laguna Blanca had lower numbers and a smaller mass of benthic organisms, a lower abundance and mass of Hyalella, and the unique presence of Acarini. Fish were absent at El Burro, Antiñir and Jabón lakes. P. colhuapiensis and a few O. mykiss were captured in Laguna Blanca, with the highest captures of P. colhuapiensis in the littoral zone. The abundances recorded for P. colhuapiensis in Laguna Blanca are the highest, in comparison with other populations of P. colhuapiensis and P. trucha, in Patagonian lakes and reservoirs surveyed with comparable fish gear (Cussac et al., 1998; Ruzzante et al., 1998, 2003; Buria, 2001; Aigo, 2002; Milano et al., 2002). The extremely high abundance of Percichthys in Laguna Blanca agrees with, and even exceeds, the prediction of Quiroñas (1991) concerning the relationship between the abundance of salmonids and Percichthys, and temperature (Figure 5). The K and L0 values for Percichthys showed a faster growth than that observed by Guerrero (1991) for other lakes. Both the high growth rates and the peculiar size structure reflect the enriched trophic state of the lake and the massive periodic fish deaths observed in autumn in Laguna Blanca (Mazzucchelli, 1991). These fish deaths may be related to blooms of cyanophytes (C. Queimalínos, pers. comm., according to preliminary plankton studies). The preponderance of benthos in the gut contents of adult P. colhuapiensis, a major seasonal variation, and the presence of macrophytes showed a clear relationship of these fish with the benthos and littoral dynamics. The absence of Ateleognathus and the low density of birds in Laguna Blanca also showed a remarkable difference compared with the other lakes (Table 1).
Figure 3. Frequency (number of fish), total length (mm), and age (yr) of _Percichthys colhuapiensis_ captured in Laguna Blanca (March 2001). Grey lines indicate mean size at maturity for males (250 mm) and females (270 mm). Dotted lines indicate modal grouping of fish sizes. Continuous lines fit observed (Lowess empty circles) and estimated sizes (von Bertalanffy model, $L_0 = 368$ mm, $K = 0.46$ yr$^{-1}$, solid circles).
The past situation was very different. Daciuk (1968) found very abundant free-living leeches and an extraordinary abundance of amphipods, copepods, ostracods and cladocerans at Laguna Blanca, in his research between 1964 and 1967. Although Daciuk (1968) refers to the presence of piscivorous birds (*Phalacrocorax brasilianus*) at the end of his fieldwork as a novelty, it seems that the presumed effects of fish introduction did not appear immediately or in a dramatic way, but rather progressively. Thus, the first reported change was of *Atelognathus patagonicus*, which was considered scarce in 1984 and absent since 1986 (Administración de Parques Nacionales, 1993). It was previously the most abundant amphibian in the area (290 individuals in 1000 m²; Péfaur and Duellman, 1980). Mazzucchelli (1991) observed high abundance of macrophytes, amphipods, copepods and free-living leeches, and a high abundance of juvenile and adult *P. colhuapiensis* (one adult and 83 large juveniles caught in a 25 m long, 40 mm mesh size net, overnight). Mazzucchelli (1991) observed that the guts of *P. colhuapiensis* were mainly full and had high proportions of amphipods. Comparing the results of the present study with the qualitative observations of Daciuk (1968) and Mazzucchelli (1991), it seems that the abundance of *Hyalella*, Copepoda and Cladocera has diminished in Laguna Blanca while Notostraca has disappeared, and Acari has appeared. From 1995 to the present (Table 1), *Myriophyllum* abundance and avian diversity and abundance decreased dramatically (Administración de Parques Nacionales, 2003; E. Ramilo, pers. obs.).

This synthesis of non-systematic historical data shows a lag of approximately 19 yr between the introduction of a few thousand *P. colhuapiensis*, *S. trutta* and *O. mykiss* juveniles and the first visible record of amphibian decline. This seems to be a very long time, but it may be explained by competition among the introduced species and the time taken for colonization of this 1700 ha lake by a few thousand juvenile fish.
It must be noted that in the 1984–1987 samplings, \textit{Percichthys} catch-per-unit-effort in Laguna Blanca was ca. 50\% of the highest captures recorded in several other Patagonian lakes in the same sampling seasons (Quiros, 1991; Quiros and Baiguén, 1986; Figure 5). The abundance of salmonids, which are almost undetectable these days, were of the same order as \textit{Percichthys}. It seems that the salmonid decline in Laguna Blanca is recent and concomitant with \textit{Percichthys} increase.

Lake productivity can be strongly regulated by fish (Andersson \textit{et al}., 1978; Carpenter \textit{et al}., 1987; Persson \textit{et al}., 1993). Through top-down effects, an increase in planktivorous fish (e.g. juvenile \textit{Percichthys}, Ruzzante \textit{et al}., 2003) may lead to lower densities and small size of zooplankton grazers, and an increase in algal mass (Shapiro and Wright, 1984; Carpenter \textit{et al}., 1985; Reynolds, 1994). Benthivorous and particularly detritivorous fish can affect water quality and development of algae in the water column by releasing nutrients from the bottom (Andersson \textit{et al}., 1978; Tatrai and Istvánovits, 1986; Horpila and Kairesalo, 1990; Tatrai \textit{et al}., 1990; Persson and Hamrin, 1994). A direct effect on turbidity by
re-suspension of bottom particles has also been reported (Meijer et al., 1990; Tolonen et al., 2000). Nowadays, water transparency is markedly lower in Laguna Blanca compared with previous data (4–5 m in Daciuk (1968) and in Quiro’s and Baíguén (1986)), and present values (≤1 m) are lower than those obtained in fishless lakes (Table 1). Both *P. colhuapiensis* and *P. trucha* are benthivorous fish (Cussac et al., 1998; Ruzzante et al., 1998, 2003; Logan et al., 2000) with affinities for eating detritus in the case of *P. trucha* (Ruzzante et al., 2003) and for macrozoobenthos and fish in *P. colhuapiensis* (Cussac et al., 1998; Macchi et al., 1999).

This paper reports preliminary data that are perhaps useful in the design and evaluation of possible restoration programmes. How can a lake be managed for conservation after a significant man-made disturbance when there are insufficient baseline data? In this case it was possible to see how the lake had changed but there were limited historical data and limited possibilities to compare the lake with other similar lakes. Attempts at reconstructing lake history and a diagnosis of the causal relationships of the present situation, led to the conclusion that there have been both top-down and bottom-up changes to the amphibian and bird populations. The frog, *A. patagonicus*, has disappeared from the lake, bottom-feeding coots and swans that rely on submerged vegetation have decreased, and piscivorous birds have increased. The frog may have disappeared from Laguna Blanca owing to these changes in the food and habitat of its tadpoles and young metamorphs, predation by larger fish, or both. The coots and swans most likely have decreased in numbers due to degradation and alteration of their food supplies, and the piscivorous birds have increased in abundance as fish populations have increased. In agreement with these results, M. E. Cuello (pers. comm.) found a small neighbouring lake similar to El Burro with poor macrophyte abundance, no amphibians and *Percichthys* presence. She also observed experimental predation of *P. colhuapiensis* on *A. patagonicus* tadpoles. It must be noted that the first reported change in Laguna Blanca (1984) was the decline of *A. patagonicus* (Administración de Parques Nacionales, 1993). Obviously, direct consequences of predation were observed sooner than other changes related to more complex trophic relationships.

At present, an experimental study is under way in a small bay of Laguna Blanca: a net barrier for fish has been constructed and their numbers are being depleted by intensive fishing (>1.5 t of *P. colhuapiensis* were removed) in the closed bay (ca. 10,000 m², Project Ramsar WFF/02_2/ARG/7). If the trophic structure of the bay is restored (as shown by the recovery of amphibian and aquatic bird habitat), then it might be suggested that an artisanal fishery could be a useful tool for restoring the whole lake. Preliminary results indicate some changes in macrophyte abundance (P. Vigliano, pers. comm.) but previous results of such restoration practices have shown a lapse of 3 to 4 yr before changes occur (Tolonen et al., 2000).

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