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Fishless shallow lakes of Southern Patagonia as habitat for waterbirds at the onset of trout aquaculture

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ABSTRACT

1. The Strobel Meseta, a basaltic plateau of Patagonia (Santa Cruz Province, Argentina), holds thousands of shallow fishless lakes that are prime habitat for many species of waterbirds, including some considered 'near threatened'. In recent years, several lakes have been stocked with trout which has created uncertainty about the potential effects on the recipient ecosystem.
2. Limnological and topographical analyses were performed in a group of 32 lakes of the Strobel Meseta in order to characterize and classify individual lakes of the meseta based on their limnological and topographic features, analyze the association between lake type and use by aquatic birds in general and by the endemic hooded grebe (*Podiceps gallardoi*) in particular, and evaluate the overlap between trout aquaculture and critical habitat for waterbirds.
3. The lakes were classified by multivariate analyses into four characteristic types: turbid, high conductivity lakes (T), small vegetated lakes (SV) and larger lakes which were subdivided into either vegetated (LV) or unvegetated (LU). In general, macrophyte cover was the main classificatory variable, whereas conductivity, pH, surface, and depth contributed moderately. Large vegetated lakes were generally found to be important for waterbirds and provided critical habitat for the hooded grebe, whereas trout farmers largely favoured large unvegetated lakes. However, since some large vegetated lakes have already been stocked, there is some level of geographical overlap between waterbird habitat and trout farming.
4. The existence of some level of spatial segregation between production and critical waterbird habitat affords opportunities for designing a spatially-based management system for trout aquaculture.

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KEY WORDS: waterbird assemblages; hooded grebe; trout aquaculture; Strobel Meseta lakes; Patagonia; lake classification

INTRODUCTION

In many arid regions of the world, waterfowl can be found at high densities in isolated wetlands. These systems provide prime habitat for feeding and breeding and represent the stepping-stones for moving waterbirds, from regional dispersers to long-distance migrants (Weller, 1999). Many species exploit mosaics of wetland habitat and their survival is likely to depend on a wetland network rather than on individual water bodies (Skagen and Knopf, 1994). Therefore, it is critical to consider wetland quality and availability at a regional scale in order to derive habitat-based waterbird conservation management. A fitting first stage of such research is to analyse the association between wetland characteristics and their suitability as habitat for waterbirds.

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The Patagonian steppe, in southern Argentina, receives less than 300 mm of rain per year, thus representing one of the most arid extensions in the country (Cabrera, 1976). Whereas permanent water bodies are scarce in this region, some areas contain natural depressions that collect water from snow and ice melt (Iriondo, 1989) and sustain a rich aquatic biodiversity, including several endemic species of vertebrates and invertebrates (Canevari *et al*., 1998; Menu Marque *et al*., 2000; Reissig *et al*., 2006).

In the Province of Santa Cruz, in particular, 10 different basaltic plateaux or 'mesetas' hold arrays of thousands of endorheic shallow lakes (Figure 1). These mesetas were formed during tectonic episodes in the Miocene-Pliocene periods (Panza and Franchi, 2002). The sinking of the mantle over the underlying substrates produced a rich collection of hollows with a wide diversity of sizes, shapes and configurations (Pereyra *et al*., 2002). The physicochemical characteristics of water appear to be mainly controlled by the composition of underlying sediments. The water regime is mostly determined by the balance between precipitation and evaporation (Paruelo *et al*., 1998). High irradiance levels and the exposure to winds increase evaporation dramatically, conditioning the hydroperiod duration in shallower wetlands. In addition, the exposure to strong winds may have profound ecosystem-wide implications because continuous mixing prevents the formation of thermal compartments in the pelagic zone, favouring nutrient recirculation and increasing productivity. Many of these lakes, naturally devoid of fish (Fjeldsa, 1986; Julio Lancelotti, unpublished data), are covered by dense macrophyte stands and sustain a rich aquatic biodiversity. The research described here focused on one of these plateaux, the Strobel Meseta (48°50′S, 71°20′W, 900 m.a.s.l. 2500 km^2), which holds over a thousand lakes of various shapes and sizes (Figure 1). This meseta comprises prime habitat for hooded grebe, *Podiceps gallardoi*, an endemic and charismatic waterbird discovered in 1974 (Rumboll, 1974), and considered 'Near Threatened' (Beltran *et al*., 1992; BirdLife International, 2004), as well as for other threatened and endemic species such as the Magellanic Plover (*Pluvianellus socialis*) and the Chilean Flamingo (*Phoenicopterus chilensis*) (Scott and Carbonell, 1986; Imberti, 2005). The Strobel Meseta and most of the lakes are privately owned, placed within the boundaries of seven ranches or estancias, and to date does not have any special conservation status. The hooded grebe, however, is protected by a specific law (Provincial law: 2582), that requires the conservation of this species and its habitat.

Starting in the 1940s, and more intensely in recent years, shallow lakes of arid Patagonia have been stocked with rainbow trout (*Oncorhynchus mykiss*), generating a growing aquaculture activity, as well as concerns about potential impacts on native communities. A bitter debate is taking place between those concerned about the potential effects of trout stocking on environmental integrity and those promoting economic development through aquaculture. Fish stocking in fishless lakes has provided some of the best-known examples of trophic cascades and regime shifts to be found in the ecological literature. Effects involve changes in species composition and their relative abundance and behaviour as well as in nutrient cycles and primary production (Hurlbert *et al*., 1986; Carpenter and Kitchell, 1993; Matthews, 1998; Scheffer, 1998; Schindler *et al*., 2001).

In Patagonia the introduction and translocation of both exotic and native fish species have been identified as primary causes of ecological disturbance in aquatic ecosystems in general (Modenutti and Balseiro, 1994; Ortubay *et al*., 2006; Reissig *et al*., 2006; Buria *et al*., 2007), and in shallow lakes in particular (Modenutti and Balseiro, 1994; Ortubay *et al*., 2006; Reissig *et al*., 2006; Buria *et al*., 2007). As a case in point, the introduction of perch (*Percichthys* sp.) in Laguna Blanca, a shallow lake of northern Patagonia, resulted in a dramatic shift in macrophyte cover, and in the loss of bird and amphibian diversity (Cuello *et al*., 2006; Ortubay *et al*., 2006).

The debate surrounding trout stocking of shallow lakes is rooted in contrasting views about development and environmental integrity, and it is clearly fuelled by the lack of locally relevant scientific information (Pascual *et al*., in press). The body of knowledge emerging from regional studies of shallow lakes provides an excellent illustration of the overall consequences of fish introductions, as well as some functional hypotheses for Patagonia's shallow lakes. At the same time, it refers to the impact of different introduced fish species, from typically planktivorous species (*Odonthestes bonariensis*,

Figure 1. Satellite image of the Strobel Meseta (Landsat 7) processed to mask land and highlight water bodies (in grey) and surveyed lakes (in black). Inserted map is Santa Cruz Province (Argentina), basaltic mesetas were highlighted (grey) and black rectangle identifies the Lake Strobel Meseta.

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Odonthestes hatcheri), to more benthivorous species (*Percichthys trucha*, *Percichthys colhuapiensis*) in a set of diverse environments spread throughout 10° of latitude, mostly in North Patagonia. Yet shallow lakes of Patagonia are far from homogeneous (Quiros, 1997). Even at a local scale lakes differ widely in size, chemistry, and macrophyte cover as well as in community structure and functioning.

This paper assesses the variation in lake characteristics at the scale of the Strobel Meseta and its relationship with the value of individual lakes as habitat for waterbirds and trout aquaculture. This information provides a critical background for designing specific models to aid management; it is also a logical first step in identifying spatial strategies to minimize conflicts between conservation and production.

METHODS

Study area

The Strobel Meseta holds over 1500 shallow lakes, including small temporary ponds and lakes larger than 700 ha (Figure 1). The region is mainly represented by enclosed lakes, but a few of them are connected by a temporary stream. Basins are fed by snowmelt, with a significant inter-annual hydrological variability and also showing a wide spectrum of water characteristics related to the nature of the recipient sediments. Even lakes that are similar in their general characteristics comprise a broad range of colour and salinity, from clear fresh water to brackish lakes. Many of the small lakes, and some of the medium size lakes (12 ha, 6 m depth) dry out during low precipitation years. Macrophyte cover, largely composed of *Myriophyllum elatinoides* (locally called 'vinagrilla'), is conspicuous and strongly affected by water dynamics. In some lakes vinagrilla reaches the water surface forming a dense carpet. All lakes remain frozen from early autumn to late spring. Owing to the turbulence caused by strong winds, these lakes do not stratify during summer, although some of them are as deep as 25 m. Strong winds in the region are pervasive, and storms with wind speeds reaching up to 150 km h^{-1} are frequent (Correa, 1998; Paruelo *et al.*, 1998).

More than 20 waterbird species inhabit the Lake Strobel Meseta. The Family Anatidae is particularly well represented, with 12 species. The most conspicuous waterbirds are the black-necked swan (*Cygnus melancoryphus*), the Chiloe widgeon (*Anas sibilatrix*), and the red shoveler (*Anas platalea*) (Lancelotti *et al.*, unpublished data). Previous studies in the Strobel Meseta counted more than 1200 hooded grebes and 65 000 other waterbirds in 119 lakes, leading to an estimate of 200 000 waterbirds and 3100 hooded grebes for the whole meseta (Scott and Carbonell, 1986).

Field data collections

Six surveys were conducted on the Lake Strobel Meseta: two in late spring (2004, 2005), two in the summer (2005, 2006), and two in the early autumn (2005, 2006). A total of 59 lakes were visited and inspected. Based on an overall assessment of these lakes and the examination of satellite images of the area, 32 lakes were selected for the analysis in order to cover the greatest apparent environmental heterogeneity (Table 1). Because of practical difficulties, not all lakes were visited on each survey.

Lake area, maximum axis length (great linear axial dimension), and the axis length of the predominant wind direction (west–east axis) were calculated by analysing satellite images (Landsat 7 ETM) of the area using the software Erdas Imagine 8.5. Lake depth, macrophyte cover, water physical and chemical variables and waterbird species abundances, were obtained *in situ*. Conductivity, temperature and total dissolved oxygen were measured at each sampling site and occasion, using a multiparameter probe (YSI 85, YSI Incorporated, Ohio, USA). Macrophyte cover was recorded as percentage of total lake area in two categories: submerged macrophytes (vegetation completely under water) and emergent macrophytes (upper part of vegetation reaching water surface). Macrophyte cover was estimated *in situ* through visual inspection and mapping. Water samples (250–1000 mL) were taken using a vanDorn bottle and poured into 5 L plastic containers for further analyses. On the same day of collection, water samples were filtered through pre-burned GF/F filters (45 μm pore size, Whatmann^{TM}), which were maintained in a freezer and transported to the laboratory in refrigerated containers for the estimation of total suspended solids and particulate organic matter concentration.

Waterbird censuses

Waterbird counts were conducted from one or more vantage points, using 8 × 40 binoculars and a 25 × spotting scope. Waterbirds were identified to the species level, based on a field identification guide (Narosky and Yzurieta, 1987). In cases in which estimations were imprecise due to waterbird movement, high waterbird number or dense aggregations, two or more counts were made and the mean recorded. Surveys covered a total lake area of 2306 ha; in 230 h of waterbird censuses, a total of 20 275 individual waterbirds were counted, including 490 hooded grebes.

Lake classification

A priori observations of the lake characteristics suggested that general types could be identified. For instance, lakes with high conductivity (more than 2000 μs cm) are turbid and devoid of macrophytes while those with low conductivity have several combinations of macrophyte cover, depth, and lake area. A multivariate analysis was carried out to reduce the large variability observed in the field to a discrete number of groups. A principal component analysis (PCA; Manly, 1994) was conducted first using a subset of 18 lakes to explore the general ordination of lakes. This ordination was expected to provide a set of lake assemblages sharing similar and meaningful traits with respect to the environmental requirements of waterbirds. Variables included in the correlation matrix for the PCA were morphometric (lake area, maximum depth, maximum axis, west–east axis), physico-chemical (water conductivity, pH, total suspended solids and particulate suspended organic matter) and biological (percentage macrophyte cover) (Table 1). For lakes that were surveyed more than twice, the mean value for each variable was used.

The lake ordination was plotted along the two first component axes of the PCA and four lake types were visually identified (see Results for details). Subsequently, a

Table 1. Variables measured in 32 lakes of Lake Strobel Meseta: conductivity (cond), pH, emergent macrophytes (cover), and submerged macrophytes (subm), lake area (area), total suspended solids (solids), total suspended organic matter (organic), maximum depth (h-max), maximum axis length (A-max) and maximum axis in the east–west direction (west)

Lake	Type	Primary variables					Secondary variables				
		Cond (us)	pH	Cover %	Subm %	Area (ha)	Solids (mg L^{-1})	Organic (mg L^{-1})	h-max (m)	A_max (m)	West (m)
Herradura	LV	201	9.3	20	50	16.806	0.0041	0.0037	9	610	413
Martinez_4	LV	285.5	9.2	50	30	16.847	0.0055	0.0038	12	614	452
Potrero	LU	380	9.16	1	1	78.562	0.0044	0.0044	15	1653	983
Satelital_7	SV	164.3	8.6	3	97	5.134	0.0065	0.0047	0.75	368	294
Alvarez_7	LU	190.2	8.4	5	5	59.954	0.0073	0.0056	8	1091	818
Potrerito	SV	501	9.11	40	60	6.254	0.0075	0.0056	1.5	320	253
Ocho	LV	129.4	8.12	65	20	23.042	0.0100	0.0060	8.6	925	921
Rodriguez_19	LU	227	8.58	0	0	18.374	0.0177	0.0094	5	566	451
Puesto	SV	980	10.42	40	40	4.327	0.0160	0.0100	1.3	313	303
Vega	SV	535	10.02	40	60	9.212	0.0240	0.0128	2	477	328
Rodriguez_16	LU	142.4	8.4	5	5	47.231	0.0197	0.0130	5	1126	1024
Cardielito	T	7370	10.7	0	0	26.99	0.0366	0.0162	3.6	701	590
Campamento	LU	81.6	8.4	1	3	42.825	0.0260	0.0205	16	1310	1193
Oliva	T	4542	9.14	0	0	8.858	0.0531	0.0306	1.5	480	321
Alvarez_9	LU	268.2	8.4	0	0	18.339	0.0643	0.0521	8	581	505
Martinez_2	T	9930	10	0	0	13.98	0.1300	0.0600	1.5	625	407
Grabados	T	6510	9.99	0	0	7.006	0.6380	0.2560	0.3	326	282
Loggers	SV	1125	8.88	40	60	3.484	1.3040	0.3720	1.5	293	264
Independent lake subset											
Alvarez_10	LU	177.2	8.7	5	10	17.3					
Alvarez_101	SV	612.0	10.4	10	90	5.0					
Alvarez_103	SV	612.0	10.4	10	90	4.5					
Casco	SU	2602.0	9.8	0	100	21.2					
Chanchos	LU	75.9	9.6	0	1	60.4					
Compuerta	SV	155.5	10.0	70	30	4.7					
Gallaretas	SV	971.0	9.1	55	42	3.6					
Martinez_29	T	3135.0	9.8	0	0	9.1					
Martinez_3	T	2280.0	10.1	0	0	15.8					
Patos	SV	454.5	9.7	30	70	7.4					
Rodriguez_18	LU	170.8	8.8	0	0	7.6					
Rrodriguez_20	LU	60.3	8.0	1	0	18.3					
Rodriguez_51	LU	161.8	8.4	0	0	17.0					
Rodriguez_8	LU	83.8	9.5	0	0	7.4					

For lakes surveyed more than twice the mean values of all measures for each single variable were calculated. Lake types: LU (Large unvegetated lakes), LV (large vegetated lakes), SV (small vegetated lakes), T (turbid lakes).

forward stepwise discriminant analysis (DA; Manly 1994) was performed for the same subset of lakes to validate the inclusion of individual lakes to the groups resulting from the PCA, and to explore the contribution of individual variables to reducing inter-group variance. With the aim of developing a quick assessment of lake type, the original set of environmental variables was reduced by dropping from the analyses those considered redundant and/or costly to obtain (referred to as 'Secondary' in Table 1). The performance of the reduced model (including only the 'Primary' variables) was tested by applying a classification function obtained from the DA, to reassign an independent subset of 15 lakes to the previously defined groups (Legendre and Legendre, 2003). These classification functions were used to determine the most probable association of each lake to a given group. Functions compute classification scores for each case for each group by applying the formula:

$$S_i = a_i + c_{i1}X_1 + c_{i2}X_2 + c_{in}X_n$$

where the subscript i denotes the respective group; the subscripts $1, 2, \ldots, n$ denote the n variables; a_i is a constant for the ith group, c_{ij} is the weight for the jth variable in the computation of the classification score for the ith group; x_j is the observed value for the respective case for the jth variable. S_i is the resultant classification score. The highest classification score between all classification functions (one for each lake type) was considered to reassign lakes to particular groups (Legendre and Legendre, 2003).

Waterbird habitat suitability

The number of species, density of waterbirds, and waterbird abundance for each individual lake were calculated as a measure of habitat suitability. Total waterbird abundance was calculated as the sum of the individuals of all species (excluding the hooded grebe, which was analysed separately). Lakes were grouped according to the lake types identified by the multivariate analysis. Finally, total waterbird abundance, mean waterbird density (individuals ha^{-1}) and mean number of species for each lake type were summarized. In lakes surveyed more than twice the mean values of waterbird species and their abundances were used. Bird species number and density were compared across lake type by means of one-way ANOVA (Zar, 1999). Statistical analyses were carried out using the software STATISTICA (version 6.0).

RESULTS

Contrasting differences in size, depth, macrophyte cover and water characteristics were found within the collection of lakes analysed in the Strobel Meseta. The analysis of satellite images showed that more than 1100 lakes are smaller than 5 ha and over 420 lakes exceed 5 ha.

The PCA based on 10 variables measured on 18 lakes showed that macrophyte cover explained most of the data variability while conductivity, pH, lake area and depth contributed moderately (Table 2). The collection of lakes was grouped in four classes (defined by ellipses in Figure 1, Table 2). Those with high conductivity ($>2000\,\mu$s) and characteristically turbid water (Secchi <0.5 m) clustered as a distinct lake type (turbid lakes, T), which includes lakes of variable size (9–27 ha) and generally low depth (<3 m). The remaining lakes all have clear water and, depending on size and bathymetry, differ in their macrophyte cover and were classified in three different types. Small vegetated lakes (SV) (<9 ha and <2 m deep) are fully vegetated, while the other two groups comprise larger lakes (>7 ha and 3–16 m deep) which are either heavily vegetated (large vegetated, LV, 15–30% emergent macrophyte cover) or sparsely vegetated (large unvegetated, LU, $<15\%$ emergent macrophyte cover). A discriminant analysis (DA, Figure 2) validated these groups by assigning all 18 lakes to the groups assigned by the PCA. Then the model was simplified considering the emergent macrophytes, submerged macrophytes, conductivity, and pH which had a significant effect on group classification. Lake area, although it did not have a significant effect, was also included because it is easy to measure from satellite images and improves model performance. The ability of the reduced model to classify meseta lakes was tested on an independent subset of 15 lakes. Each of these lakes was assigned *a priori* to one of the four lake types by the set of rules related to conductivity ($<2000\,\mu$s), the combination of area (<5 ha) and depth (<9 ha;<2 m) and emergent vegetation cover (>15) previously identified as breakpoints separating lake types. The discriminant analysis based on the reduced model reassigned all 15 cases correctly (Table 3).

Waterbird abundance varied widely between lake types (Table 4). LU lakes comprised more than 50% of the total area surveyed. However, the number of individual waterbirds (all species except hooded grebes) observed in LU lakes was much lower than those in other lake types (less than 5% of total waterbirds counted). SV lakes represent less than 10% of the area surveyed; however, more than 35% of the waterbirds were found there. These differences are clearly expressed by mean waterbird density, which was 35 times higher in SV than in LU lakes. T and LV lakes presented similar waterbird densities (around 12 and 17 individuals ha^{-1}, respectively), which represented nearly half of the abundances recorded in SV. The mean number of waterbird species was significantly higher in LV, SV, and T lakes than in LU lakes ($P<0.001$). T lakes presented a significantly lower number of species than LV and SV lakes ($P<0.001$). The highest waterbird densities were found in SV lakes and the lowest values in LU lakes, both significantly different from all other lake types ($P<0.001$). LV and T lakes presented similar waterbird densities ($P>0.05$).

Hooded grebe counts by lake type reflected a well differentiated lake use of this species compared with other waterbirds (Table 3). Over 88% of individuals of this species were counted in LV lakes, while in lakes with high densities of other waterbirds, such as SV lakes, hooded grebes rarely occurred (Figure 3). The preferential use of LV lakes by the hooded grebe is also indicated by the number of counts with positive observations. Up to 85% of all counts conducted in LV lakes included hooded grebes. In contrast, the species occurred only in 18% of other lake types surveyed.

Waterbird abundance showed a high seasonal variability in all lake types at the level of individual lakes (Figure 3). Waterbird density fluctuated widely between consecutive seasons in several lakes. For instance, density variations were more than 10-fold in the T lakes Martinez-3, Martinez-29 and Oliva and in DV lakes such as Martinez-4. T lakes presented the highest waterbird abundance during spring, decreasing in summer and autumn, a pattern that was not evident in other lake types. Some SV lakes were found to maintain similar abundances at all seasons (i.e. Vega, Potrerito, Satélite and Puesto), whereas other lakes of this group showed high variation (i.e. Loggers, Alvarez-101). LU lakes presented the lowest abundances regardless of season and did not show any evident fluctuation pattern.

Table 2. Summary of the principal component analysis (PCA) and discriminant analysis (DA)

Variable	Principal component analysis			Discriminant analysis		Classification function coefficients			
	Factor 1	Factor 2	Factor 3	F-remove	*p*-level	LV	LU	SV	T
Cond	0.030	0.343	0.019	6.725	0.011*	−0.011	−0.008	−0.01	−0.002
Subm	0.055	0.242	0.002	82.401	0.000**	9.046	4.076	10.54	4.480
Cover	0.015	0.235	0.002	57.472	0.000**	8.388	3.644	9.64	3.960
pH	0.054	0.103	0.107	4.724	0.030*	98.806	59.140	113.18	64.308
Area	0.177	0.017	0.015	2.264	0.150	−2.033	−0.838	−2.29	−1.039
Hmax	0.156	0.012	0.017	2.095	0.171	2.478	0.749	1.72	0.124
Amax	0.196	0.009	0.013	0.160	0.920				
West	0.185	0.001	0.025	0.091	0.963				
Solid	0.065	0.011	0.412	0.268	0.847				
Org	0.067	0.028	0.388	0.244	0.863				
Eigenvalue	4.563	2.063	1.618	–	–				
Variance explained %	45.632	20.632	16.179	–	–				
Constants						−771.525	−246.719	−1015.69	−307.568

Left panel corresponds to eigenvalues, variance and coordinates for the first three principal components. Middle panel shows the variable significance on the discriminant model based on Fisher statistic (df = 18, 25). Right panel shows the classification function coefficients obtained with the DA for each lake type. Lake types: LU (large unvegetated lakes), LV (large vegetated lakes), SV (small vegetated lakes), T (turbid lakes).

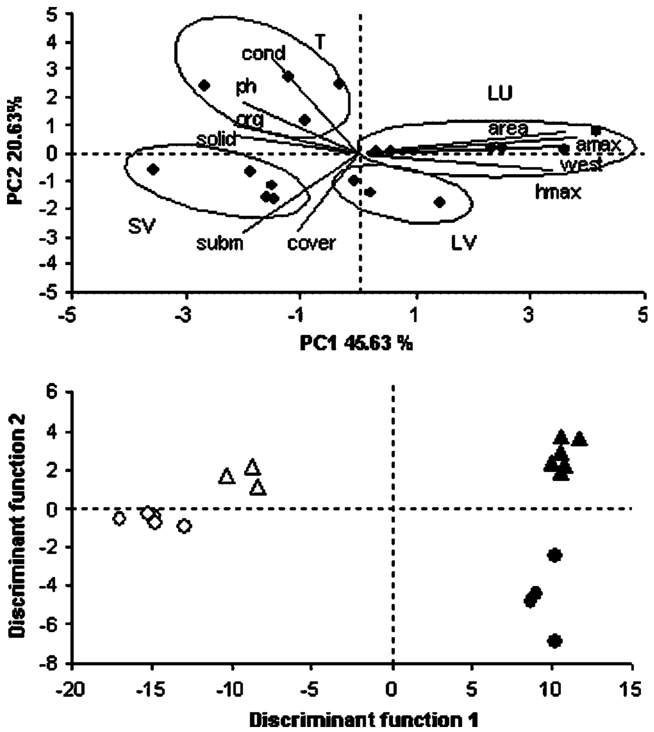

Figure 2. Lake classification based on the principal component and discriminant analyses. Upper panel corresponds to ordination of lakes for the two first components (PC) which explained over 65% of data dispersion, solid lines represent the individual weight of variables (see codes in Table 1). Ovals enclose proposed groups: LU (large unvegetated lakes), LV (large vegetated lakes), SV (small vegetated lakes), T (turbid lakes). Bottom panel shows the relative position of lake groups LU (black triangles), LV (open triangles), SU (black circles) and SV (open circles).

Table 3. Classification of an independent lake subset

Lake	Observed	Classification function scores				
		DV	DU	SV	SU	Assigned
Alvarez_10	LU	183.3	**310.9**	80.7	298.2	LU
Chanchos	LU	62.4	**273.9**	−58.0	251.4	LU
Rodriguez_18	LU	80.6	**266.0**	−39.3	250.1	LU
Rodriguez_20	LU	−10.6	**214.2**	−143.3	191.7	LU
Rodriguez_51	LU	22.0	**234.5**	−106.0	214.6	LU
Rodriguez_8	LU	151.1	**308.2**	41.5	295.5	LU
Casco	T	124.3	294.9	13.1	**295.6**	T
Grup	T	176.5	318.6	74.1	**337.9**	T
Martinez_29	T	142.8	300.9	34.3	**307.1**	T
Martinez_3	T	168.6	319.7	63.4	**321.1**	T
Alvarez_101	SV	1137.0	762.6	**1187.8**	797.6	SV
Alvarez_103	SV	1138.2	763.1	**1189.1**	798.2	SV
Compuerta	SV	1063.8	716.9	**1094.8**	741.9	SV
Gallaretas	SV	950.7	652.5	**967.5**	678.0	SV
Patos	SV	1051.7	711.9	**1087.1**	740.1	SV

A classification function was obtained for each lake type from the discriminant analysis. The highest classification function score (numbers in bold) were considered to include each single lake in to *a priori* defined groups. Lake types: LU (large unvegetated lakes), LV (large vegetated lakes), SV (small vegetated lakes), T (turbid lakes).

Lakes currently used for trout production are dominantly represented by LU types in which the lowest waterbird densities were recorded (Table 4). However, some of the LV lakes most intensively used by hooded grebe have also been stocked with trout.

Table 4. Number of lakes, total lake area and waterbirds surveyed for the four lake types identified by multivariate analyses

	LU	LV	SV	T
Lakes				
Number of lakes	12	3	10	7
Mean area (ha)	43.17	19.00	5.40	15.23
Total area surveyed (ha)	1,251.87	379.98	199.87	426.56
Number of surveys	29	20	37	28
Lakes with trout	8	2	0	0
Waterbirds				
Total waterbirds counted	943	4,417	7,181	7,422
Maximum number of waterbirds observed	191	1,116	704	1,361
Mean number of waterbirds per lake	33.0	242.5	194.8	265.7
Mean waterbird density (ind/ha)	1.02	12.31	36.79	17.55
Mean number of species	3.28	7.25	6.05	5.29
Hooded grebe				
Lakes with positive observations	3	3	3	2
% Lakes with positive observations	25	100	30	28.57
Total counted	15	432	25	18
Maximum hooded grebe observed	6	90	10	7
Mean number of grebes per lake	0.52	21.60	0.68	0.64
Mean number per lake with positive observations	3	25.4	5	4.5

Lake types: LU (large unvegetated lakes), LV (large vegetated lakes), SV (small vegetated lakes), T (turbid lakes). Total waterbird abundance was calculated as the sum of the individuals of all species jointly (hooded grebe was analysed separately) and density of waterbirds by dividing waterbird abundance by lake area.

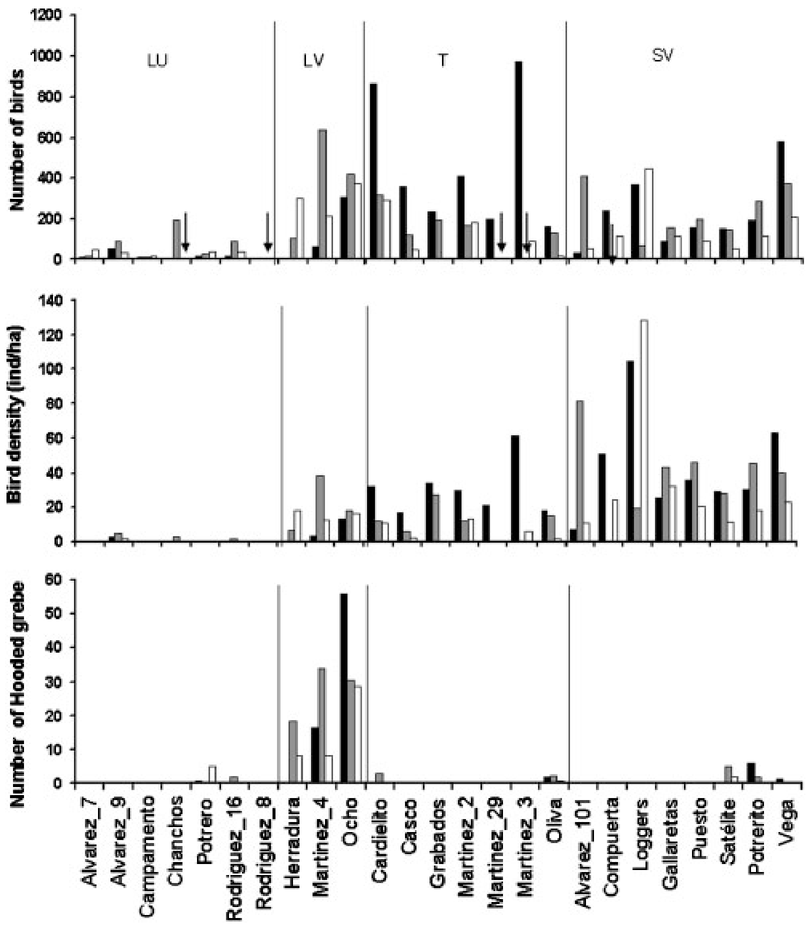

Figure 3. Seasonal occurrence (number and density of individuals) of waterbirds (excluding the hooded grebe) and hooded grebes in the different lakes surveyed. Black, grey and crossed bars correspond to late spring, summer, and early autumn, respectively. Arrows indicate lack of data. Lake types: LU (large unvegetated lakes), LV (large vegetated lakes), SV (small vegetated lakes), T (turbid lakes).

DISCUSSION

The conservation value of shallow lakes in the Patagonian central steppe is illustrated by the diversity and abundance of the wildlife they sustain and the presence of endemic species (Perrotti *et al.*, 2005). However, more geographic and biological information is needed to characterize Patagonian wetlands in terms of their contribution to global biodiversity, and to recognize the variation in ecological patterns and processes characteristic of these environments.

The analysis revealed a substantial variability in size, depth, vegetation and water characteristics of lakes in the Strobel Meseta. The importance of these particular features for wetland classification has been discussed extensively in the literature and highlighted as important factors affecting the distribution and abundance of waterbirds (Scheffer, 1998; Weller, 1999 and references therein). The differences emerging from combinations of conductivity, pH, lake area, and macrophyte cover are strong enough to classify lakes into four distinct classes which, in turn, appear to determine the suitability of a particular site as waterbird habitat. Small and turbid lakes sustained the highest densities of waterbirds followed by large vegetated lakes, with similar species number for all three lake types. On the other hand, large unvegetated lakes held the lowest species number, waterbird abundance, and waterbird densities.

The summer distribution of hooded grebe is restricted to basaltic mesetas in the Santa Cruz Province (Beltran *et al.*, 1992; Johnson, 1997). In contrast to other waterbirds, this species was strongly associated with large vegetated lakes in the Meseta throughout the study period. This preferential use may be related to its reproductive requirements, as hooded grebes are largely dependent on the dominant macrophyte *M. elatinoides* ('vinagrilla') as a platform for nest construction (Lange, 1981; Fjeldsa, 1986). In addition, breeding hooded grebes gather food for their chicks by diving in deeper, open waters associated with macrophytes (Fjeldsa, 1986). Indeed, in this study their colonies were observed exclusively in the three large vegetated lakes surveyed, with such a combination of vegetated and deeper water areas.

Lakes stocked with trout are larger than 6.5 ha and more than 3 m deep. Within large lakes, producers show a preference for unvegetated lakes due to the constraints that macrophytes impose on navigation and gillnet setting. Nevertheless, some deep vegetated lakes, important for waterbirds in general and hooded grebe in particular, have been stocked with trout. Grebes in general are highly vulnerable to gill nets (Fjeldsa, 2004) and the fishery activity could have significant

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population-level effects. To date there is one LV lake under production, which only supports sport fishing; however, more LV would be stocked if the fishery demand were to increase. A certain level of geographical overlap exists between waterbird habitat and trout farming. Given the lack of specific information about the environmental effects of trout stocking on these lakes and the vulnerability of grebes to gill nets, the establishment of precautionary rules appears to be the logical option at this stage of aquaculture development in the Strobel Meseta. For instance, restricting the activity to large unvegetated lakes provides a direct approach to minimize the overlap between trout and waterbirds, including hooded grebe. The set of five primary variables that readily and accurately classified individual lakes in the field may enhance the selection of lakes for farming, thus reducing potential overlap between waterbird habitat and trout production. As a next stage, the analysis of sample lakes should be expanded to the whole meseta. A geographical assessment of critical waterbird habitat and a complete survey of exploitable lakes will provide a full-scale assessment of the degree of conflict between aquaculture and waterbird conservation. In addition, it will supply fundamental information to develop precautionary management rules until more is known about the impacts of trout at an ecosystem level.

Going beyond precautionary management will demand a better understanding of the ecological requirements of waterbirds and other native species within the environmental mosaic provided by meseta lakes. It is quite possible that waterbird species' habitat preferences are arranged along a continuum of characteristics, only discernible through species-specific analyses. Waterbird habitat characterization should be sustained by more specific information on waterbird status within lake food webs. The contrasting characteristics of lakes, together with their differential use by different waterbird species, suggest that community assemblages along the environmental gradient of the Strobel Meseta lakes may be rather variable. The introduction of trout may produce alternative environmental scenarios depending on the intrinsic characteristics of the lake being stocked. Future research should consider the environmental heterogeneity of meseta lakes, as well as food web structure and community assemblage rules, when generating functional models to support the management of the increasing aquaculture sector.

From a legal point of view, restrictions to aquaculture would be supported by the provincial law created to protect hooded grebe and their habitat. From a practical point of view, however, the current production-based ownership system of the Meseta suggests that success of any conservation plan will depend strongly on the degree of cooperation and support obtained from land owners. We recognize some incentives for the establishment of sustainable practices (Pascual *et al.*, in press). This paper shows that restricting aquaculture to large lakes would have marginal effects on current production levels. Moreover, poor management practices would feed back negatively on alternative activities to aquaculture, such as ecotourism and bird watching. Whether these incentives contribute to rational environmental use or not will depend on how aware land-owners and authorities become of them. In order to contribute to management, ecological research should go beyond documenting impacts, to raising awareness through the evaluation of the costs and benefits associated with alternative aquaculture practices.

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