

Diet of the exotic Rainbow Trout in the critical habitat of the threatened Hooded Grebe

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ABSTRACT

Key-words:
Patagonia,
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The lakes of the basaltic plateaus of Patagonia represent the only reproductive habitat for the critically endangered Hooded Grebe (*Podiceps gallardoi*). More than 50 of these naturally fishless lakes have been stocked with the exotic Rainbow Trout (*Oncorhynchus mykiss*). While the available information suggests that the diet composition of trout and Hooded Grebes could overlap, to date no formal studies of the diet of Rainbow Trout in these aquatic environments have been published. We characterized the diet of trout in one of the primary reproductive areas of the Hooded Grebe based on the analysis of the gut contents of 177 individuals, from 9 lakes. Amphipods were clearly the most dominant group of prey, quantified as frequency of occurrence and proportion by weight. The condition factor of trout and the abundance of amphipods in the stomach contents showed a functional relationship, suggesting that the wellness of trout depends on the availability of this prey. Amphipods also represent a primary prey for the Hooded Grebe, suggesting a strong dietary overlap with the trout. The presence of trout may generate processes of competition that could affect the survival of the Hooded Grebe. This interaction may be particularly relevant in large vegetated lakes, where the Hooded Grebe reproduces.

RÉSUMÉ

Régime alimentaire de la truite arc-en-ciel introduite dans l'habitat essentiel du grèbe mitré menacé

Mots-clés :
Patagonie,
aquaculture,
espèces
exotiques,
interactions
entre espèces,

Les lacs des plateaux basaltiques de Patagonie représentent le seul habitat de reproduction pour le grèbe mitré en danger critique (*Podiceps gallardoi*). Plus de 50 de ces lacs naturellement sans poissons ont été empoisonnés avec la truite arc-en-ciel (*Oncorhynchus mykiss*). Bien que les informations disponibles suggèrent que la composition des régimes alimentaires de la truite et du grèbe mitré pourraient se chevaucher, à ce jour, aucune étude formelle de l'alimentation de la truite arc-en-ciel dans ces milieux aquatiques n'a été publiée. Nous avons caractérisé le régime alimentaire de la truite dans l'une des zones de reproduction principales du grèbe mitré basé sur l'analyse du contenu stomacal de 177 truites, provenant

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chevauchement de régime alimentaire de 9 lacs. Les amphipodes étaient clairement le groupe le plus dominant de proies quantifiées aussi bien par la fréquence d'occurrence que la proportion en poids. Le facteur de condition de la truite et l'abondance des amphipodes dans le contenu de l'estomac ont montré une relation fonctionnelle, ce qui suggère que le bien-être de la truite dépend de la disponibilité de cette proie. Les amphipodes représentent également une proie principale pour le grèbe mitré, suggérant un chevauchement important de l'alimentation avec celle de la truite. La présence de la truite peut générer des processus de concurrence qui pourraient affecter la survie du grèbe mitré. Cette interaction peut être particulièrement importante dans les grands lacs avec végétation, où le grèbe mitré se reproduit.

INTRODUCTION

Most of the fresh water in the southern Patagonian steppe is located in a system of basaltic plateaus (mesetas) that hold the largest lakes of this region, as well as thousands of smaller shallow lakes. These aquatic environments represent the primary habitat for numerous species of waterbirds, including several endemisms and threatened species (Di Giacomo, 2005; Lancelotti *et al.*, 2009a), and are the only reproductive area for the threatened Hooded Grebe (*Podiceps gallardoi*), a diving waterbird considered to be one of the most endangered species in Argentina (Roesler *et al.*, 2012; Birdlife International, 2015). More than 50 of these naturally fishless lakes have been stocked with Rainbow Trout (*Oncorhynchus mykiss*), generating an extensive aquaculture system, and promoting the economic development of this remote region. These introductions also generate concerns about the potential impact on the receiving communities (Roesler *et al.*, 2011, 2012). For instance, the introduction of Rainbow Trout into the Lake Strobel meseta – that historically has represented the core reproductive habitat for the Hooded Grebe (Imberti, 2005) – has been proposed as one of the primary drivers of the species decline (estimated to be more than 80% during the last 30 years; Roesler *et al.*, 2012).

Concerns about the potential effects of trout introductions on Hooded Grebe populations are supported by an extensive literature recording alterations derived from the introduction of exotic fishes in aquatic systems worldwide. These alterations include changes in the composition and abundance of species, nutrient availability and nutrient cycles, the primary productivity and trophic relationships, and the behavior and spatial distribution of prey (Carpenter & Kitchell, 1996; Scheffer, 1998; Donald *et al.*, 2001; Knapp & Matthews, 2001; Schindler & Parker, 2001; Eby *et al.*, 2006; Reynolds, 2011). These effects are more drastic in lakes devoid of native fish (Mallory *et al.*, 1994; Donald *et al.*, 2001; Vredenburg, 2004), as is the case of the lakes of the basaltic plateaus of Patagonia. In the Patagonian steppe the introduction of exotic fishes into lakes has been responsible for local extinctions of cladoceran species, the reduction of size in zooplankton and the homogenization of communities (Modenutti & Balseiro, 1994; Reissig *et al.*, 2006). The translocation of native fish and the introduction of Rainbow Trout into the shallow lake Laguna Blanca (70°22'W, 39°02'S) led to the local extinction of amphibians, and the loss of habitat for waterbirds (Ortubay *et al.*, 2006).

Available information suggests that the diet composition of trout and Hooded Grebes – both visual predators – could overlap. The collection of potential prey for both species is restricted to a small number of species of crustaceans (amphipods, copepods and cladocera) and insect larvae (Fjeldsa, 1986; Beltran *et al.*, 1992). Knowledge about the diet of the Hooded Grebe is poor and limited to a few direct observations of feeding behavior. The literature (see Fjeldsa, 1986) and *in situ* observations suggest that the Hooded Grebe predaes mostly on the few large preys of these lakes, mostly snails and amphipods, and also aquatic insects and their larvae. All of these organisms are potential prey for Rainbow Trout, a typical omnivorous species easily adaptable to local conditions of food availability (Quinn, 2005). However, to date no formal studies of the diet of Rainbow Trout in these aquatic environments have been published. Meanwhile, the number of lakes stocked with trout increases from year to year.

Therefore, the information of the diet composition of this exotic predator is essential to evaluate the potential dietary overlap between the two species and for proposing hypotheses about the effects resulting from trout introduction in this aquatic system. We analyzed the gut contents of 177 individuals of Rainbow Trout from 9 lakes of the Lake Strobel meseta to characterize their diet. Lakes analyzed included the whole range of lake sizes (from 0.13 to 100 km²), and limnological characteristics (e.g. macrophyte abundance) of the stocked lakes, as well as two primary reproductive environments of the Hooded Grebe.

METHODS

> STUDY AREA

The Lake Strobel meseta (71°22'W, 48°26'S, 2500 km², Fig. 1), one of the largest basaltic mesetas in Patagonia, is the focus of most of the aquaculture activity. This meseta holds over one thousand lakes, from small temporary ponds to lakes larger than 100 km² (Lancelotti *et al.*, 2009b). The lakes are natural depressions situated on a basaltic bed of Tertiary and Quaternary origin (Pereyra *et al.*, 2002), which collect water from snow and melting ice. Based on limnological characteristics these lakes have been classified into four categories (Lancelotti *et al.*, 2009b). Those with high conductivity (>2000 µS·cm⁻¹) and characteristically turbid water (Secchi < 0.5 m) represent a distinct lake type (turbid lakes), 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 into 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).

There are few invertebrate species in these lakes (Lancelotti, 2009). Pelagic organisms are largely represented by crustaceans, with a prevalence of calanoid copepods of the genus *Boeckella*, and Cladocera (represented mostly by *Daphnia* spp.). Ostracods have relatively low abundance. Eight species of calanoid copepods have been identified in the Lake Strobel meseta, but no more than three different species are numerically dominant (Lancelotti, 2009). Benthic organisms are primarily represented by oligochaetes, chironomidae larvae, hirudineas and gastropods (this last group is not present in every lake). *Hyalella* represents the only genus of amphipods recorded in the Lake Strobel meseta (Lancelotti, 2009). Aquatic insects are dominated by chironomidae larvae and coleoptera. Neither amphibians nor native fish inhabit the lakes of this basaltic meseta system.

Lakes present a rich waterbird community, with over 20 species, including the near-threatened Magellanic plover (*Pluvianellus socialis*) and Chilean flamingo (*Phoenicopterus chilensis*) (Lancelotti *et al.*, 2009a, 2009b). From October to March the Hooded grebe congregates in the basaltic mesetas to reproduce. Throughout the ample gradient of lake characteristics, Hooded grebes strongly prefer lakes with a combination of emerged macrophytes (dominated by the *Myriophyllum elatinoides*) surrounded by open water areas (Fjeldsa, 1986; Lancelotti *et al.*, 2010). The *Myriophyllum* generate carpets over the water surface, where Hooded Grebes build their nests using the macrophytes as building material. During the reproductive period the parents reside in the colony, feeding the chicks with prey captured in open water areas (Fjeldsa, 1986).

More than 40 fishless lakes of the Lake Strobel meseta have been stocked with Rainbow Trout, generating an extensive aquaculture system, which consists of stocking fry (approximately 6000 individuals per km²) in medium-sized lakes (0.05–0.71 km², mean 0.19 km²). Harvest takes place two to three years after the stocking, when fish reach commercial size (fork length > 20 cm), and then lakes are stocked again, starting a new cycle of production. In general, farmers prefer to stock large unvegetated lakes, where trout harvest with gillnets is the easiest. However, in several of the large vegetated lakes trout have also been stocked at the onset of the aquaculture activity. On the other hand, all small vegetated and turbid lakes

Table 1

Summary of lake characteristics and trout samples. Lakes were classified into types based on their limnological characteristics (Lancelotti, 2009b); LU and LV correspond to large unvegetated and large vegetated lakes, respectively. Lake area (Area) was estimated using satellite images (Landsat 7). Depth corresponds to the maximum depth recorded in each lake. Stocked refers to the year (spring) of the first fish stock. Season is the date of fish capture. N is the sampling size. K is the mean value of the condition factor. NA indicates non-available data.

Lake	Type	Area	Depth	Stocked	Season	N	Trout length	K
Chanchos	LU	0.6	NA	1996	Feb-05	18	34.0–43.6	1.33
Campamento	LU	0.43	16	1996	Dic-04	10	33.0–38.0	1.16
Potrero	LU	0.79	15	2001	Dic-05	37	14.5–45.0	1.6
La Pala	LU	0.47	NA	2003	Mar-05	31	19.0–35.0	1.64
La Española	LU	0.13	NA	2003	Mar-05	12	21.9–28.1	1.62
Rodríguez	LU	0.24	22	2003	Dic-06	14	28.4–36.3	0.89
Herradura	LV	0.17	9	2000	Dic-06	38	18.8–70.0	1.24
Islote	NA	7	>40	2003	Dic-10	8	60.0–72.0	1.5
Strobel	NA	100	>40	1995	Dic-04	9	46.0–62.5	1.7

remain fishless (Lancelotti *et al.*, 2010). Because of habitat restrictions (e.g. lack of permanent streams and adequate spawning beds) trout do not reproduce in most of the shallow lakes of the Lake Strobel meseta. Therefore, trout populations are completely regulated by stocking and fishing.

> SAMPLING

We analyzed the stomach contents of 177 trout captured in nine lakes (Table 1). Lakes analyzed were selected taking into account the wide range of limnological characteristics of the stocked lakes. This array of lakes includes eight lakes used for aquaculture and one large lake used for fly fishing (Strobel). Aquaculture lakes were represented by six large unvegetated lakes, and two large vegetated lakes (Islote and Herradura); the last two represent primary reproductive habitats for the Hooded Grebe (Lancelotti *et al.*, 2009b). Finally, the Lake Strobel is the largest lake of this meseta (100 km²), which sustains sport fishery activity. The trout population of the Strobel lake is self-sustainable through natural reproduction, and was originated through the stocking of the Barrancoso river (in 1997), the only tributary of this lake.

Trout were captured with gillnets, covering a wide range of trout sizes, from 14.5 to 72 cm (fork length, Table 1), during spring and summer, matching with the reproductive period of the Hooded Grebe. Individual trout were measured (fork length, FL), weighed, and their stomachs were conserved in formalin solution (10%). Stomach contents were analyzed with a stereoscopic microscope. Preys were grouped into five general categories: amphipods, copepods, cladocera, ostracoda and insects. For each stomach we counted all individuals of each previously defined group. Additionally, for samples with abundant prey we pooled individuals of the same group to estimate the mean individual weight. Then, for each stomach we estimated the biomass of each group of organisms as the product of the mean individual weight and their frequency.

> DATA ANALYSIS

The proportion of weight in the gut contents for each defined group of prey was calculated as:

$$\hat{W}_i = \frac{W_i}{\sum_{i=1}^n W_i}$$

where W_i is the weight of the prey i and n is the number of prey types in the stomach. Then for each trout population (lakes) we calculated the mean proportion by weight as follows:

$$W_i = \frac{1}{p} \sum_{j=1}^p \frac{W_{ij}}{\sum_{i=1}^n W_{ij}}$$

where p is the number of fish with food in the stomach, and j is the number of fish.

We estimated the confidence interval for the mean proportion by weight for each prey group and each lake by means of bootstrap analysis (Manly, 1991). For each trout population we generated a simulated population, of the original population size, taking a random sample with replacement of individuals. Then, based on the simulated population we estimated and recorded W for each prey item. This process was replicated 5000 times. Based on these 5000 estimations we obtained the confidence interval ($\alpha = 0.05$) of this index for each type of prey and for each trout population.

In a second analysis we evaluated the relationship between the trout condition and diet. We calculated Fulton's condition factor (k ; Pope & Kruse, 2007) as an estimator of the wellness of trout:

$$K_i = \frac{W_i}{FL_i^3} \times 100$$

where K is the condition factor, W is the fish weight, FL is the fork length and i is the i th individual. This index is widely used for fish. For trout, values of K lower than 1 indicate poor condition (lower values of weight than expected for the fish length, assuming an isometric growth model) and values higher than 1 indicate good condition (higher values of weight than expected for the fish length). Finally, we used a linear model to evaluate the relationship between the frequency of amphipods (in weight), which represent the primary prey of trout (see results), and the condition factor. For this analysis we pooled the individual data of all trout populations (lakes) into a single cluster.

RESULTS

Amphipods were present in every single trout stomach collected from the collection of lakes, with the exception of Lake Chanchos (presence in 83% of the individuals; Table II). Cladocera, copepods and insects were also important prey in terms of frequency of occurrence, but these groups showed high variations in the occurrence index, from 0% to 75% for cladocera, 0% to 83% for copepods, and 0% to 90% for aquatic insects. Amphipods and cladocerans were the most numerous preys (Table II), with high variation in numbers, especially for cladocera. Besides, in several lakes trout preyed on a higher number of daphnids than amphipods (e.g. Chanchos, Potrero and La Pala).

The dominance of amphipods in the stomach contents was most manifest in terms of proportion by weight (Figure 2). In eight of the nine analyzed lakes amphipods presented mean values of proportion by weight higher than 60%, and in five of these lakes the values were higher than 90%. The highest values of this index were observed in the two largest lakes, Strobel (99.5%) and Islote (99.6%). Trout of two medium-sized lakes, Potrero and La Pala, also showed a high proportion of amphipods in the stomach (94.2% and 94.7%, respectively). Trout from Lake Rodriguez had a low proportion of amphipods (35.5%) in their stomachs, not significantly different than the proportion of aquatic insects (64%).

The condition factor of trout and the abundance of amphipods in the stomach contents showed a functional relationship (Figure 3). Trout with higher frequency of amphipods in the stomach contents showed higher values of the condition factor. The lowest mean value of the condition factor was obtained in the Lake Rodriguez (Table I), the lake with the lowest proportion of amphipods in the diet.

Table II Summary of the three indices used to evaluate the diet composition of Rainbow Trout in lakes of the Lake Strobel meseta. FO: the frequency of occurrence. FN and CI are, respectively, the range of values of numeric frequency, and the confidence interval of the mean value of proportion by weight (observed values shown in Figure 2). The intervals show the minimum, mean and maximum values, respectively.

	Group	Chanchos	Campamento	Potrero	La Pala	La Española	Rodriguez	Herradura	Islote	Strobel
FO	amphipods	83	100	100	100	100	100	100	100	100
	cladocera	72	30	62	26	75	-	50	75	56
	copepods	50	20	3	39	83	-	26	13	-
	ostracods	-	-	3	-	-	-	45	13	-
	insects	6	90	5	29	67	92	95	-	11
FN	amphipods	0-22-170	51-218-631	4-98-350	1-33-114	40-165-337	2-50-159	1-4-9	125-243-492	1-13-26
	cladocera	0-548-2947	0-22-116	0-23-627	0-6-67	0-79-305	0-61-565	0-0-0	0-49-150	0-1-3
	copepods	0-7-40	0-0-1	0-3-26	0-7-123	0-55-323	0-0-0	0-0-0	0-0-0	0-0-2
	ostracods	0-0-0	0-0-3	0-0-0	0-10-91	0-0-0	0-0-0	0-1-10	0-0-0	0-0-0
	insects	0-0-2	0-0-0	0-3-28	0-13-230	0-8-21	0-0-1	2-22-121	0-0-1	0-9-28
CI	amphipods	54-70-85	45-63-78	89-94-98	92-95-97	80-89-95	33.2-46.8-63.2	72.8-79.2-84.5	99-99.6-99.9	99-99.5-99.9
	cladocera	0-0.1-0.1	20-34-50	2-6-11	0-1-3	0.5-1.2-2.1	0-0-0	0.2-0.5-1.1	0.1-0.4-1	0.1-0.5-1
	copopods	0-0.5-1.3	1.1-3.2-6.1	0-0-0	0.4-2-3	2.5-7.2-15.3	0-0-	0.7-3-7.4	0-0-0	0-0-0
	ostracods	0-0-0	0-0-0	0-0-0	0-0-0	0-0-0	0-0-0	0-0-0	0-0-0	0-0-0
	insects	14-29-46	0-0.2-0.6	0-0.1-0.2	0.7-2.2-4	1.2-2.9-4.9	36.8-53.2-66.8	12.4-17-22.8	0-0-0	0-0-0

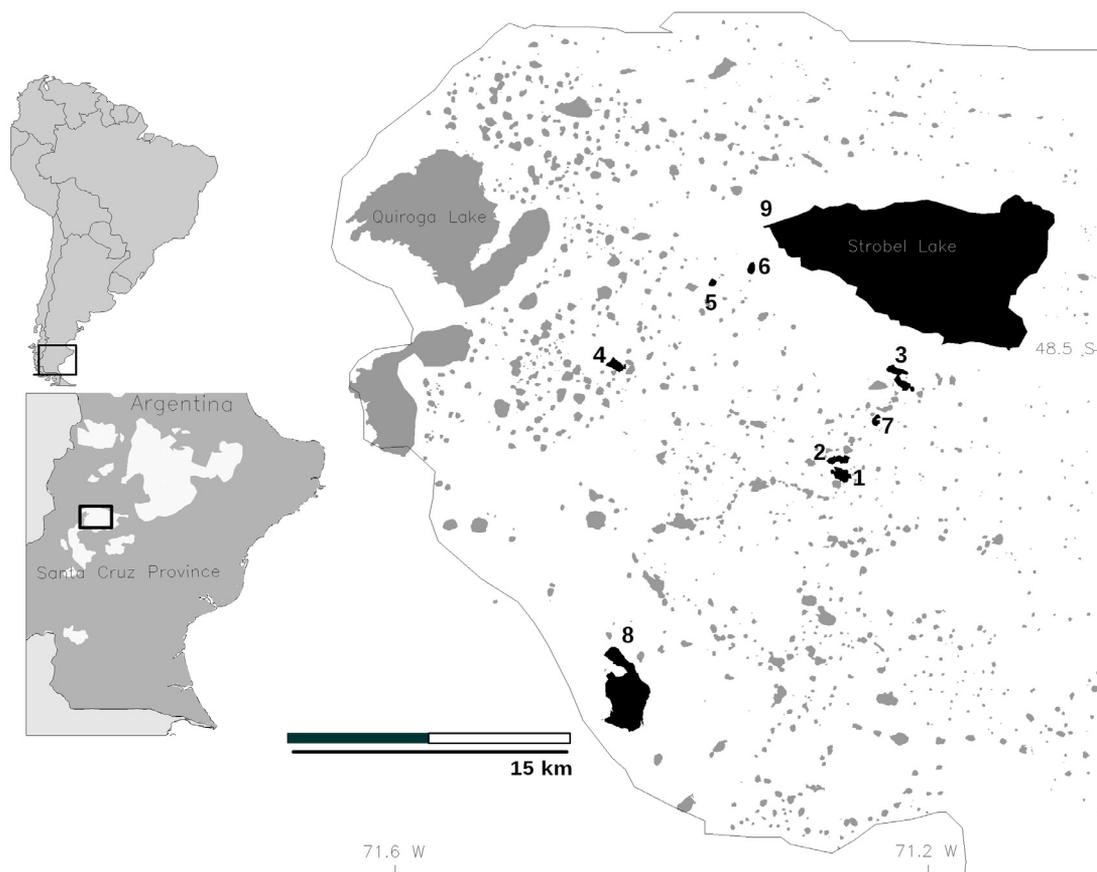


Figure 1

Map of lakes of the Lake Strobel meseta obtained from a satellite image (Landsat7). The satellite image was processed to mask land and highlight water bodies (in gray, surveyed lakes in black and numbered). Inset shows Santa Cruz Province (Argentina), basaltic mesetas in gray and Lake Strobel meseta (black rectangle). Numbers 1 to 9 correspond, respectively, to the surveyed lakes Chanchos, Campamento, Potrero, La Pala, La Española, Rodríguez, Herradura, Islote and Strobel.

DISCUSSION

In the lakes of the basaltic mesetas of Patagonia, copepods and cladocera strongly dominate the communities numerically, and are substantially more abundant than amphipods (Lancelotti, 2009). However, amphipods are among the largest prey in these lakes, where adults and larvae of aquatic insects are restricted to littoral rocks and macrophytes, suggesting that trout selectively predate on amphipods. Additionally, the results suggest that the wellness of trout could depend on the availability of this prey. However, this relationship could respond to other environmental variables not analyzed here, and therefore to evaluate this hypothesis it is necessary to conduct specific experiments; for example, analyzing changes in diet and growth during the fishery history in individual lakes.

Amphipods and snails represent the bulk of the Hooded Grebe diet (Fjeldsa, 1986). However, only a few lakes of the Lake Strobel meseta have snails. Besides, snails were absent in all lakes analyzed in this study, as well as in an array of fishless lakes with similar characteristics, including vegetated and unvegetated lakes, of the Lake Strobel meseta (Lancelotti, 2009). Therefore, amphipods could represent one of the primary prey for Hooded Grebes, especially in unvegetated lakes, where these organisms represent the only abundant large prey. Large unvegetated lakes were frequently used by non-breeding flocks of Hooded Grebes in periods previous to trout introductions (Fjeldsa, 1986), whereas the presence of this species was

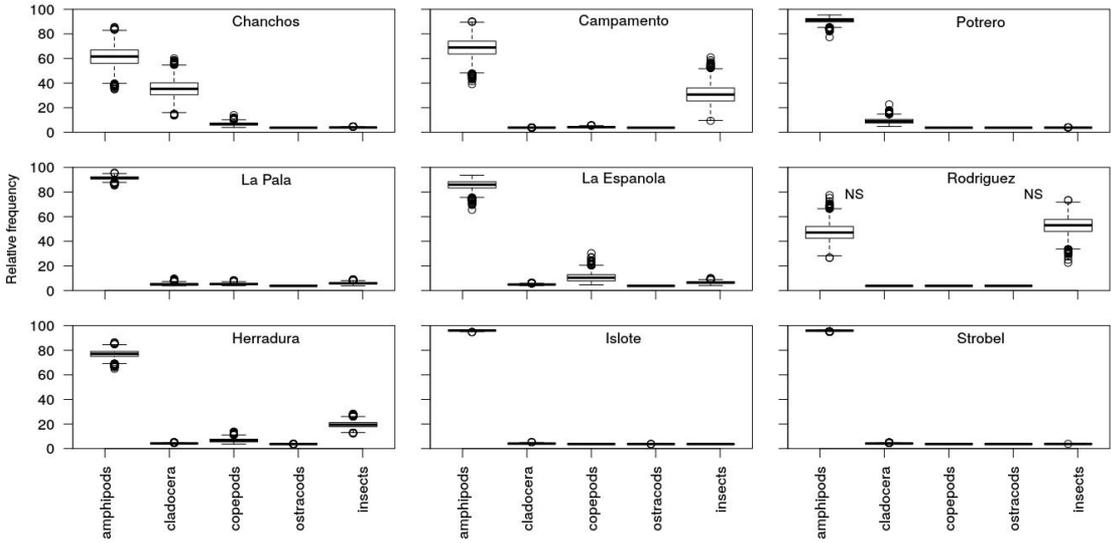


Figure 2

Proportion by weight of prey of trout from nine lakes in the Lake Strobel meseta. The horizontal line represents the median value. The lower and upper hinges represent, respectively, the 25% and 75% percentile. NS labels in the panel corresponding to the Lake Rodriguez indicate no significant differences between amphipods and insects in the gut contents of trout from this lake.

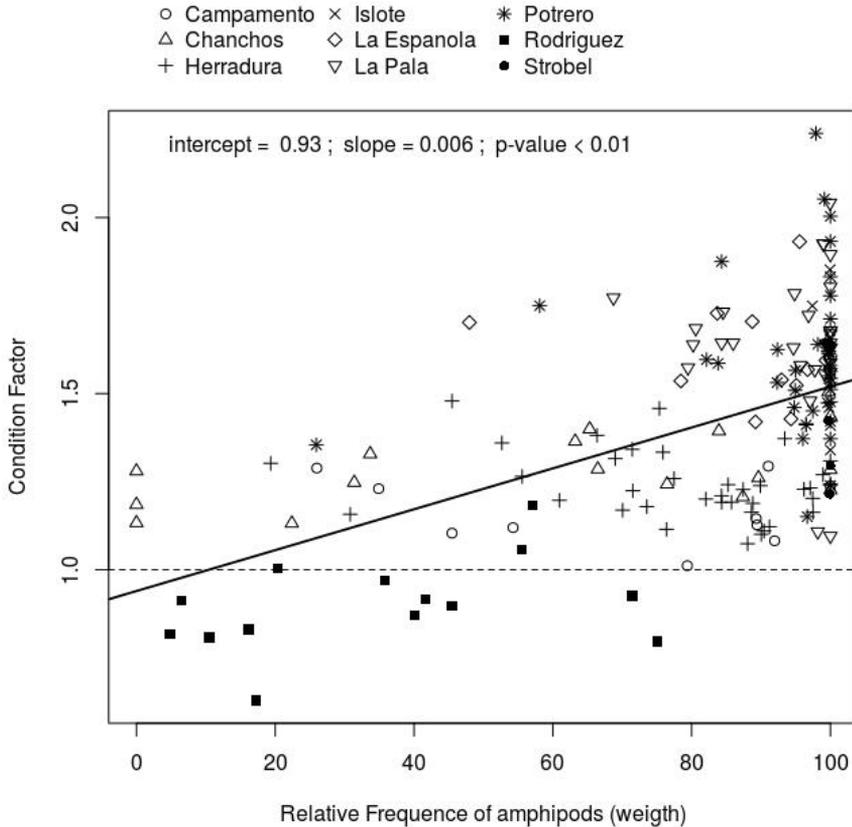


Figure 3

Relationship between the condition factor of trout, and the proportion by weight of amphipods in the stomach contents. For this analysis the samples of trout of all lakes were pooled into a single group. The dashed line indicates the expected value of the condition factor, assuming an isometric model of growth ($k = 1$).

seldom observed after the trout introduction in these lake types (Lancelotti *et al.*, 2010). This observed change in lake use could respond to a decrease in prey abundance as a direct effect of trout predation.

The interaction between Rainbow Trout and Hooded Grebes may be particularly relevant in large vegetated lakes, where the Hooded Grebe reproduces. Amphipods and large coleopterans of the family Dytiscidae are abundant in the macrophyte areas, which represent the main feeding habitat for Hooded Grebes. Coleopterans also represent a sizable and palatable prey for trout, but this item was seldom observed in their stomach contents, suggesting that the abundance of these organisms in the large vegetated lakes stocked with trout has decreased during the aquaculture period. In this context, the diet composition of trout could be varied during the fishery history, and therefore the actual diet could be responding to a modified environment.

The abundance of large prey represents one of the key factors determining the reproductive success of the Hooded grebe (Fjeldsa, 1986). Predation by grebes can generate strong declines in prey in areas next to the colonies, leading to starvation and eventually the abandoning of chicks (Fjeldsa, 1986). This process could be strongly intensified by trout predation, with its derived effects on the reproductive success of the Hooded Grebe.

To date, no legal restrictions are imposed on aquaculture, and this activity could therefore potentially be extended to most of the permanent lakes of the basaltic mesetas of Patagonia. For instance, partially vegetated lakes are likely to be increasingly used as the preferred non-vegetated lakes are used up, which could increase the spatial overlap between trout and the Hooded Grebe (Lancelotti *et al.*, 2010). Besides, two of the most important reproductive habitats for Hooded Grebes, the Islote lake (included in this study) in the Lake Strobel meseta, and Lake El Sello (71°20'W, 46°55'S) in the Lake Buenos Aires meseta, have been stocked with trout in recent years.

In 2014 the Patagonia National Park was created, with the protection of the Hooded Grebe and its habitat as a main objective. This National Park contains the most important known reproductive sites of this species. Meanwhile, in areas with aquaculture, more active directives for conservation are required. The authorization for stocking new sites should be based on previous assessment of the value of target lakes as a habitat for Hooded Grebes, reducing the risk of stocking vegetated lakes. These conservation actions should be complemented by the removal of trout from suitable sites for Hooded Grebe reproduction.

The provincial fishery agency (Subsecretaría de Pesca), responsible for regulating and controlling aquaculture activities, is limited economically and logistically, and is unable to supervise this extensive and remote region. Therefore, managers should motivate the collaboration of fish farmers, stimulating the application of appropriate aquaculture practices through financial incentives, and the diversification of the economic activities (*i.e.* bird watching, ecotourism).

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