Journal of FISH BIOLOGY

fsbi An International Society for Fish Biology

Journal of Fish Biology (2016) **89**, 403–416
doi:10.1111/jfb.12969, available online at wileyonlinelibrary.com

Dispersion of the invasive common carp *Cyprinus carpio* in southern South America: changes and expectations, westward and southward

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Common carp *Cyprinus carpio* possess multiple traits that contribute to their success as an invasive species. They have been introduced across the globe, and abundant populations can have numerous negative effects. Although ecological niche-based modelling techniques have been used to predict the potential range of *C. carpio* invasion in U.S.A., occurrence and abundance patterns have not yet been considered on a regional scale. In the present review new locations are documented, the status of the southernmost population has been studied and the probability of new lakes and reservoirs being colonized by *C. carpio* has been obtained and related to environmental conditions. The new localities for *C. carpio* have expanded its distribution westward, into the Andean Region, and present results from the South American southernmost population have shown a well-established population. Analysis of presence data provided two principal results: (1) the probability of a site being with *C. carpio* can be inferred using environmental variables and (2) the probability of a site being with *C. carpio* is a useful tool for the prediction of future invasions. Selective fishing on the Negro basin could constitute a potential mitigation measure, decreasing the abundance of the species and thus reducing the species' potential for southward expansion. These results reinforce the idea that artisanal fisheries, food production and conservation interests should be taken into account by local government management agencies in any discussion regarding the southern distribution of *C. carpio* in the near future.

Key words: conservation; exotic fish; fresh water; global warming; Patagonia.

INTRODUCTION

The common carp *Cyprinus carpio* L. 1758 is currently considered one of the most ecologically harmful invasive species and is ranked among the eight most invasive fish taxa of the world by the International Union for the Conservation of Nature (Lowe *et al.*, 2000). It possesses multiple traits that contribute to its success as an invasive species, such as broad environmental tolerance, early sexual maturity, high reproductive capacity, short generation times, fast individual growth rates and a generalist diet (Schade & Bonar, 2005; Ahmad *et al.*, 2011). Its effect is mainly due to its ability to alter aquatic habitats through high levels of nitrogen excretion and disturbance of the

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bottom sediments of lakes and reservoirs where it has been introduced. *Cyprinus carpio* can modify the level of chlorophyll-a (Parkos *et al.*, 2003; Chumchal *et al.*, 2005; Matsuzaki *et al.*, 2007), increase turbidity, degrade water quality, reduce macrophyte and benthic invertebrate densities (Zambrano & Hinojosa, 1999; Parkos *et al.*, 2003; Matsuzaki *et al.*, 2007; Kulhanek *et al.*, 2011) and decrease habitat heterogeneity (Perrow *et al.*, 1999). These habitat modifications affect native aquatic species (De Vaney *et al.*, 2009), leading to a decline in endemic species (Koehn *et al.*, 2001; Angeler *et al.*, 2002; Parkos *et al.*, 2003; Tapia & Zambrano, 2003; Pinto *et al.*, 2005; Haynes *et al.*, 2012), even to the point of local extinction (Ogutu-Ohwayo, 1990; Canonico *et al.*, 2005). The severity of these negative effects has been shown to be highly dependent on local *C. carpio* biomass (Jeppesen *et al.*, 2000; Egertson & Downing, 2004; Chumchal *et al.*, 2005; Weber *et al.,* 2010; Kulhanek *et al.*, 2011). Studies have suggested that catchment management practices, which reduce nutrient input, may ultimately hinder *C. carpio* abundance, size structure or growth rates (Egertson & Downing, 2004; Weber *et al.*, 2010).

The native distribution of *C. carpio* encompasses a vast area, stretching eastward from eastern Europe, across Russia and China (Zambrano *et al.*, 2006). This species has been introduced across the globe both intentionally, for aquaculture, commercial and recreational fisheries, and ornamental purposes, and unintentionally, due to the release of live bait and pet fishes (Balon, 1995; Koehn, 2004; Sorensen & Bajer, 2011; Forsyth *et al.*, 2013). *Cyprinus carpio* occupy many different micro-habitats, have high fecundity, spawn in shallow, slow-flowing water (De Vaney *et al.*, 2009) and have high eco-physiological tolerances. They prefer areas with a winter air temperature cold enough to freeze lakes, but where summer water temperatures reach 25° C, the temperature needed for their reproduction (Maitland & Campbell, 1992; Kulhanek *et al.*, 2011). Although *C. carpio* prefer shallow, warm, slow-moving water bodies and exhibit high tolerance to eutrophic waters, populations have been found in a broad range of environmental conditions (Balon, 1995; Koehn, 2004; Schade & Bonar, 2005; Kulhanek *et al.*, 2011). Ecological niche-based modelling techniques have previously been used to predict the full potential invasion range of *C. carpio* in North and South America. Annual maximum air temperature and concentration of chlorophyll-a were the main variables that explained *C. carpio* presence (Zambrano *et al.*, 2006).

Global warming has already affected the distribution of the Patagonian fish fauna, with new southward locations detected in Patagonia for several Neotropical fish species (Aigo *et al.*, 2008). Although the distribution of Neotropical fishes towards high latitudes seems to be limited by thermal constraints (Cussac *et al.*, 2009; González Naya *et al.*, 2011), this appears not to be the case for *C. carpio*. This species has the potential to become established in subtropical and temperate systems, and in the highlands within the tropics (Zambrano *et al.*, 2006; Kulhanek *et al.*, 2011). Zambrano *et al.* (2006) observed that South American areas prone to further invasion are located principally in the south (Argentina, southern Brazil and southern Chile). *Cyprinus carpio* has been recorded in central Chile (Habit *et al.*, 2006) and central Argentina (Colautti, 1997), the Negro River basin being the southernmost recorded location (Alvear *et al.*, 2007).

In the present work, new locations of *C. carpio* in the Andean Region (López *et al.,* 2008) are documented, the status of the southernmost population (Negro River basin) is studied and the probability of new lakes and reservoirs becoming sites with *C. carpio* is assessed and related to environmental conditions and to the physiological variables of the species.

MATERIALS AND METHODS

Although fragmentary, published information about the fishes of Patagonia has been useful for improving understanding of historical biogeographical patterns (Aigo *et al.,* 2008; Cussac *et al.,* 2009; Habit *et al.*, 2010). Following Pascual *et al.* (2002), presence and absence data on *C. carpio* in Argentina were compiled; thus building the most recent distribution database for the species in the region. Information on lakes and reservoirs (depth, area, Secchi disc, total phosphorus, total organic nitrogen and chlorophyll-a) and presence data for *C. carpio* were reviewed from literature for reservoirs and lakes of Argentina (Quirós, 1991; Poi de Neiff *et al.,* 1999; Cabido *et al.,* 2004; Liotta, 2005; Mancini & Grosman, 2008; Mancini *et al.,* 2009; Schwerdt & López Cazorla, 2009; Rosso & Quirós, 2010). In addition, data were considered from a previous survey, performed between 1996 and 2008 within the framework of the U.S. National Science Foundation (NSF) PIRE programme (OISE 0530267) for collaborative research on Patagonian Biodiversity (http://patagonia.byu.edu/). Details of sampling procedures were presented in Ruzzante *et al.* (2011), Unmack *et al.* (2012) and Crichigno *et al.* (2013). To give a brief account, fish were collected in spring and summer sampling, with seines operated during the day and sets of gillnets placed at between three and five sites per lake (two to five nights per lake). Gillnets were set before dusk and hauled after dawn the following morning. Aspects of climate were also used, including 1961–1990 annual means of annual precipitation and maximum (MaxAAT), minimum (MinAAT) and mean (MeanAAT) annual air temperatures (all at 0·5° native resolution *c.* 2500 km^2), obtained from the Intergovernmental Panel on Climate Change (www.ipcc.ch). The final database consists of 20 *C. carpio*-invaded lakes and reservoirs (with at least one positive record) and 86 lakes and reservoirs with no records of *C. carpio* presence (see Table SI, Supporting Information).

The population of the Negro River basin was sampled with seven sets of gillnets of mono (44–180 mm stretch mesh) and polyfilament (30–108 mm stretch mesh), at three neighbouring connected capture sites; Canal Arroyito in Limay River (39° 06′ S; 68° 34′ W), Dique Ballester in Neuquén River (38° 43′ S; 68° 10′ W) and Allen in Negro River (39° 01′ S; 67° 48′ W) from late winter (September) 2011 to autumn (April) 2013. A total of 12 samples were obtained. Standard length (L_S) and mass (M) data ($n = 134$) were recorded and processed in order to obtain estimations of growth and condition factor ($C_F = M L_S^{-3}$). A Von Bertalanffy growth function (VBGF) was fitted to the data. Data of captured individuals ($n = 134$, 80–650 mm L_S, number of samples = 13, size class 5 cm) were fitted with the non-parametric scoring of VBGF fit using the response surface procedure in ELEFAN I [FAO-ICLARM Stock Assessment Tools, Gayanilo *et al.* (1994)]. Allometric growth was studied in terms of a multiplicative model $M = a L_S^b$ in order to estimate parameter b. The existence of seasonal variations of C_F was tested using Kruskal–Wallis one-way ANOVA on ranks (SigmaStat; http://sigmastat.software.informer.com/).

The data were first analysed with principal component analysis (PCA) in order to identify the environmental variables that most explained the variance between capture sites. Following this, discriminant analysis (DA), considering lakes and reservoirs with and without records of *C. carpio* (Fig. 1), calculating previous probabilities using the size of the groups, and including all variables in the analysis (discriminant function, DF), allowed testing of the environmental differences between categories (with and without *C. carpio*) and identification of the variables most closely associated with such differences (Seber, 1984; Norusis, 1986). Also, DA provided the probability of each lake and reservoir being a with *C. carpio* site. The relationship between this probability and the MaxAAT, the main variable explaining the potential distribution of *C. carpio* in the world (Zambrano *et al.*, 2006), was explored using regression analysis.

RESULTS

Five new localities for *C. carpio* were recorded, expanding the known range of the species into the Andean Cuyan Province of López *et al.* (2008) [El Carrizal Reservoir (33° 18′ S; 69° 42′ W), Lake Urrelauquen (38° 06′ S; 66° 48′ W), Ullum Reservoir (31° 30′ S; 70° 36′ W), see Table SI (Supporting Information)] and into the Patagonian

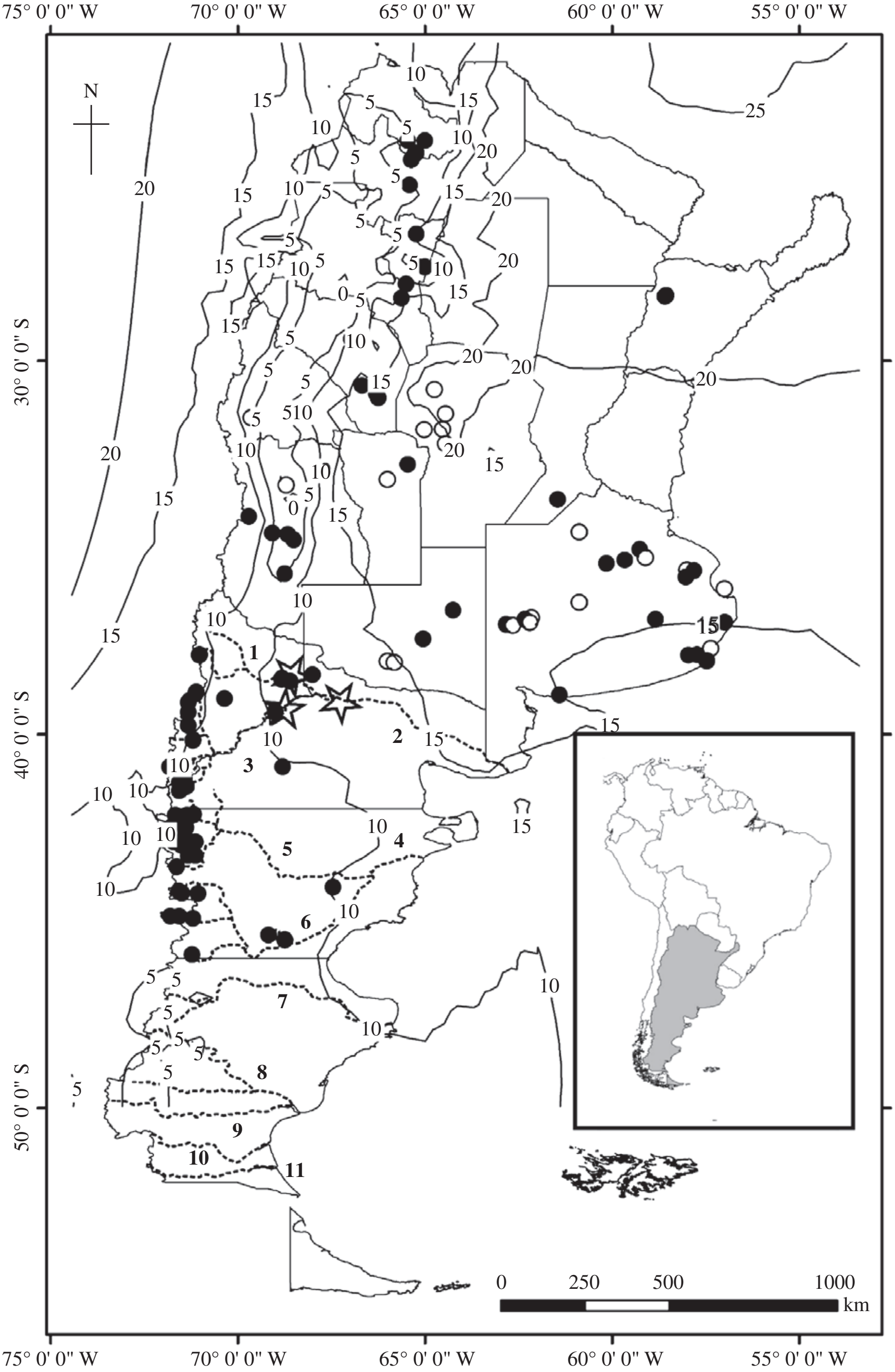

FIG. 1. Isotherms (1961 to 1990 annual means representing mean annual air temperature, MeanAAT, ____, numbers intercalated in °C), lakes and reservoirs with (○) and without (●) *Cyprinus carpio* in Argentina. ------, the major Patagonian rivers, in bold: 1, Neuquén; 2, Negro; 3, Limay; 4, Lower Chubut; 5, Mean and Upper Chubut; 6, Senguer-Chico; 7, Deseado, 8-Chico; 9, Santa Cruz; 10, Coig; 11, Gallegos. ✫, the populations of Canal Arroyito in Limay River (39°06′S; 68°34′W), Dique Ballester in Neuquén River (38°43′S; 68°10′W) and Allen in Negro River (39°01′S; 67°48′W).

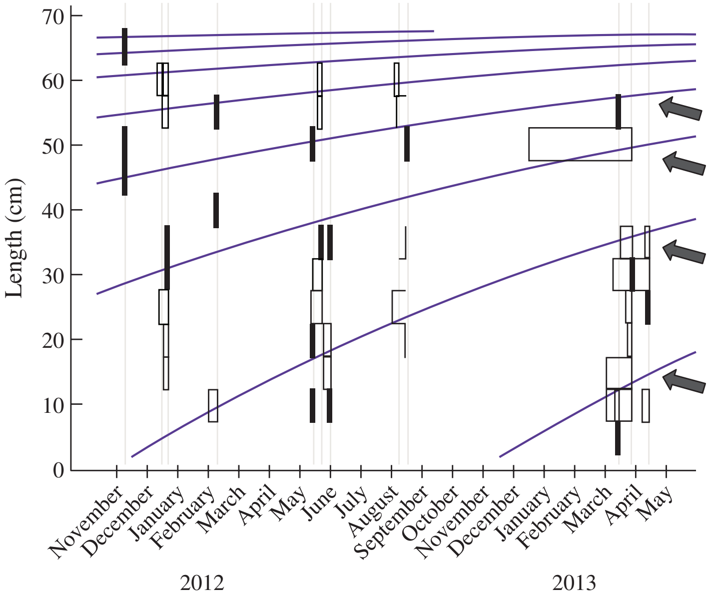

FIG. 2. *Cyprinus carpio* individuals captured in Negro River basin. Standard length (L_S) frequency plot (boxes; $n = 134$) and Von Bertalanffy growth function ($L_\infty = 69.50$ cm, $K = 0.51$) fitted to L_s; date superimposed. ⬅, observed cohorts.

Province, upstream of the records of Alvear *et al.* (2007) in the Negro basin (Canal Arroyito on the Limay River and Dique Ballester on the Neuquén River).

The analysis of L_S frequencies of individuals showed an $L_\infty = 69{\cdot}50$ cm, $K = 0{\cdot}51$, a t_0 rooted in spring (November) and at least four size modes for each sampling date; indicating that the littoral captures consisted of several different cohorts (Fig. 2). Water temperatures at capture showed a range (7·7–21·6° C) that can be compared with previous data from the literature.

Allometric relationships ($M = a\,L_S{}^b$) of the *C. carpio* caught at Canal Arroyito, Dique Ballester and Allen ($a = -4{\cdot}672 \pm 0{\cdot}064$, estimate ± 95% C.I.; $b = 2{\cdot}993 \pm 0{\cdot}044$, estimate ± 95% C.I.) does not allow rejection of the hypothesis of isometry ($b = 3$). No slope changes were observed over the range of body size ($\log_{10} M = \log a + b \log_{10} L_s$, $r^2 = 0{\cdot}993$, $n = 134$), and therefore, no information about the size of first sexual maturity could be proposed. Seasonal variation of the C_F did not show significant differences between seasons (K–W one-way ANOVA on ranks, $n = 134$, $H = 5{\cdot}857$, $P > 0{\cdot}05$).

PCA of the environmental data of all lakes and reservoirs accounted for more than 70% of the total variance, extracting three principal components (PCs). Temperature and variables related to the trophic status of lakes and reservoirs, such as Secchi disc, total organic nitrogen, chlorophyll-a and total phosphorus were the most important (Table I).

DA between sites with and without *C. carpio* produced one discriminant function (DF) with 81·9% of cases correctly classified ($n = 105$, $P < 0{\cdot}01$; Table II). It must be noted that MinAAT, MeanAAT and MaxAAT were the most important variables followed by chlorophyll-a concentration (Table I). DF also produced two new variables: the probability of being a site with *C. carpio* (PSWC) and the predicted membership

Table I. Principal component analysis (PCA, quartimax rotation) of environmental data of lakes and reservoirs. Loading for the environmental variables onto principal components 1–3 (PC1–PC3) and the variance explained. Values in bold indicate the highest contribution of each environmental variable to the three principal components. Discriminant analysis between lakes and reservoirs with and without *Cyprinus carpio* presence. All variables included (DF, Wilks' $\lambda = 0{\cdot}772$, $P < 0{\cdot}01$). Coefficients of each standardized canonical discriminant function (DF1), variance explained and canonical correlation are indicated. Spearman's ρ correlation between each variable and the PSWC. Only significant results are indicated

	PCA			DF	
	PC1	PC2	PC3	DF1	Spearman's ρ/P<
MaxAAT	**0·962**	0·029	−0·019	0·779	0·784/0·001
MeanAAT	**0·957**	0·042	−0·031	1·703	0·770/0·001
MinAAT	**0·898**	0·166	−0·091	−1·922	0·710/0·001
Secchi disc	**−0·790**	−0·332	−0·123	0·059	−0·683/0·001
Mean depth	**−0·582**	−0·352	0·032	−0·283	−0·506/0·001
Mean annual rain	**−0·509**	0·223	−0·455	0·384	−0·266/0·01
TON	0·289	**0·877**	−0·011	0·189	0·491/0·001
Clo-a	0·329	**0·703**	−0·115	0·409	0·728/0·001
TP	0·067	**0·523**	0·080	−0·265	0·520/0·001
Area	−0·029	0·079	**0·910**	0·369	–/–
Variance explained (%)	40	19	11	100	
Total variance explained (%)	40	59	70		
Eigenvalues				0·295	
Canonical correlation				0·447	

MaxAAT, maximum annual air temperature; MeanAAT, mean annual air temperature; MinAAT, minimum annual air temperature; TON, total organic nitrogen; Clo-a, chlorophyll-a; TP, total phosphorous.

for each lake or reservoir (predicted site with or without *C. carpio*). All the sites with PSWC >0·5 were predicted to be sites with *C. carpio*. Significant correlations between the PSWC and environmental variables were observed (Table I). The lakes and reservoirs with *C. carpio* (currently or predicted) have MeanAAT higher than 10–11° C (Fig. 3).

Table II. Classification results, counts and percentages. Original and forecast classification of lakes and reservoir with (yes) and without *Cyprinus carpio* (no). Discriminant function with all variables included (DF) was used

Presence of *C. carpio*		Group forecast Yes	No	Total	Per cent of original cases correctly classified
Original					
Yes	Count	5	14	19	
	%	26·3	73·7	19	
No	Count	5	81	86	
	%	5·8	94·2	100	
					81·9

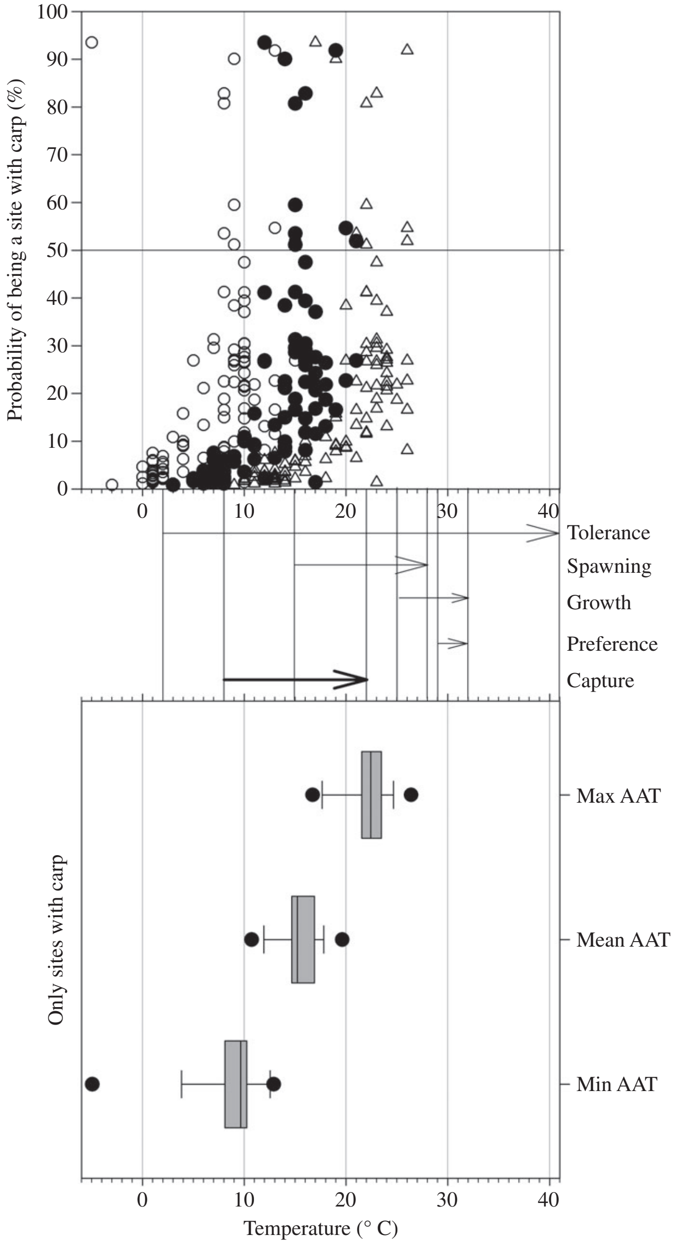

Fig. 3. Presence of *Cyprinus carpio* with regard to temperature. (a) Probability of being a site with *C. carpio* in the discriminant function of 105 lakes and reservoirs of Argentina in relation to mean (●; MeanAAT), minimum (○; MinAAT) and maximum (△; MaxAAT) annual air temperatures. (b) Box and whisker plots (mean, quartiles and data outside of 5 and 95 percentiles) of MeanAAT, MinAAT, and MaxAAT in the 20 lakes and reservoirs with *C. carpio*. Between (a) and (b), the range of water temperature at capture in the confluence of Limay, Neuquén, and Negro Rivers are indicated (⟶) in relation to tolerance (Koehn, 2004), spawning (Koehn, 2004), optimum growth (30 to 32°C, Jobling, 1981; 25°C, Metz *et al.*, 2003) and preferred thermal ranges (29 to 32°C, Jobling, 1981) recorded in the literature (⟶).

DISCUSSION

Cyprinus carpio was introduced in the south of the Neotropical region (López *et al.,* 2008), for ornamental purposes, at the beginning of the 20th century (Mac Donagh, 1948). Ringuelet *et al.* (1967) observed the presence of *C. carpio* in La Plata River, reservoirs and shallow lakes in central Argentina. Although there is no information about the origin of the individuals, the first dispersion into the Andean Region was observed by Cazzaniga (1980) in the Colorado River, and Alvear *et al.* (2007) reported its southward dispersion in three sampling sites downstream in the Negro River. The five new localities for *C. carpio* reported here (from north to south, Ullum Reservoir, El Carrizal Reservoir, Lake Urrelauquen, Dique Ballester on Neuquén River and Canal Arroyito on the Limay River) were foreseeable, as they lie within the latitudinal range previously observed for the species (Liotta, 2005). It is noteworthy that they expand the specific distribution westward, into the Andean region, and upstream in the Negro River basin. It is important to mention that at the northernmost sites (Ullum Reservoir, El Carrizal Reservoir and Lake Urrelauquen) with high abundance of *C. carpio*, the historically abundant native *Percichthys trucha* (Valenciennes 1833) (Cahiza, 2003) was almost absent (Gonçalves *et al.*, 2010). In the Negro River, *C. carpio* showed significant trophic overlap (Schöener index), in summer with *P. trucha* (in only one sampling site)*,* and in spring with the native silverside *Odontesthes hatcheri* (Eigenmann 1909) (Alvear *et al.*, 2007; Crichigno *et al.*, 2013; Conte-Grand *et al.*, 2015). Future studies will be needed in order to identify piscivory of native or other exotic fishes (salmonids) on *C. carpio* in Patagonia.

The present results, upstream from the confluence of the Limay and Neuquén Rivers into the Negro River, show a well-established population, with several cohorts, similar to that observed by Colautti (1997) in the Salado River basin (Provincia de Buenos Aires). The allometric relationships can change between ontogenetic periods. Size intervals for these periods can be estimated by finding the lengths at which these allometric relations changed (Balon, 1990; Kováč *et al.*, 1999; Barriga *et al.,* 2002). Although allometry did not provide information about sexual maturity in this case, it should be taken into account that *C. carpio* attains sexual maturity at age 2+ years in the Salado River basin (Colautti, 1997) and can be sexually precocious, even as young as *c.* 6 months, and sometimes at a mass <100 g (Basavaraju *et al.*, 2002). Colautti (1997) suggested a positive relationship between the gonado-somatic index and C_F in the Salado River basin, but a significant seasonal variation in the C_F was not observed in the Negro River basin population.

As expected, almost all lakes and reservoirs with *C. carpio* studied here are within the thermal tolerance range of the species (Koehn, 2004), and their MaxAATs are within the thermal spawning range (Koehn, 2004). It must be noted, however, that the MaxAAT of almost all lakes and reservoirs with *C. carpio* lie below the thermal range of growth and preference (Jobling, 1981; Metz *et al.*, 2003; Fig. 3). In agreement with the condition of the southernmost population, the range of water temperatures at capture in Canal Arroyito in the Limay River, Dique Ballester in Neuquén River and Allen in Negro River lies within the tolerance range (Koehn, 2004) and partially overlaps with the spawning range (Koehn, 2004), but lies below the range of optimum growth temperature (25–32° C, Jobling, 1981; Metz *et al.*, 2003) and below the range of preferred temperature (29–32° C, Jobling, 1981) (Fig. 3).

PCA results showed that the lakes and reservoirs considered here are clearly ordered by temperature and trophic variables. This fact is relevant since Quirós (1991) and later Aigo *et al.* (2008) showed that the relationship between relative abundances of species and environmental variables (latitude, longitude and area of lakes) was significant in Patagonia. In the same way, the relationship between number of native and alien species and environmental variables (latitude and perimeter area^{-1} ratio) was significant (Aigo *et al.,* 2008). In agreement with Egertson & Downing (2004), DA showed that temperature and chlorophyll-a are important variables for predicting, on a correlative basis, the presence of *C. carpio*. The lakes and reservoirs of Argentina with *C. carpio* (observed or predicted) considered here have MeanAAT higher than 10° C. As expected, all lakes and reservoirs with *C. carpio* lie within the thermal tolerance range of the species, and their MaxAATs are within the thermal spawning range. It must be noted, however, that the MaxAAT of all lakes and reservoirs with *C. carpio* in Argentina are below the thermal range of growth (partially) and the thermal range of preference (Fig. 3).

The DA of presence data provided a PSWC that is a useful tool for prediction of future invasions, but predictions should also consider other factors, such as aquatic connectivity, road access and land use (Habit *et al.*, 2012). Within the Negro River basin, southward expansion seems to be limited by the Arroyito Dam, the first on the Limay River (from downstream to upstream; Fig. 1). No other river system runs from south to north in the area, and so the Arroyito Dam is key to the control of the southward invasion.

Zambrano *et al.* (2006) predicted *C. carpio* distribution throughout Patagonia based on MaxAAT. In addition, minimum annual temperature was a significant predictor of *C. carpio* occurrence, as it affects spawning activity and can also cause winter fish kills, both of which limit the distribution of this species (Balon, 1995). Kulhanek *et al.* (2011) found that low winter temperatures may currently restrict *C. carpio*. Present capture data for the Negro River show water temperatures below preference and optimum growth, but climate warming could help future southward advances in the area (Aigo *et al.*, 2008, 2014; Cussac *et al.*, 2009; Báez *et al.*, 2011). In particular, it should be considered that the present analysis is based on 1961–1990 mean values and that these temperatures have increased in the intervening years by between 0·5 and 1·5° C in Patagonia (www.smn.gov.ar/serviciosclimaticos/?mod=cambioclim&id=1).

Understanding the patterns and population dynamics of freshwater fish invasion is therefore important for predicting the trends, timing and pathways of population expansion, and hence optimizing management action that seeks to minimize range expansion, and to control or eradicate these species (Brown & Walker, 2004; Arim *et al.*, 2006; Forsyth *et al.*, 2013). For example, a significant point regarding *C. carpio* dispersion in the region is the use of live bait. *Cyprinus carpio* is excluded from the list of permissible live bait in central Argentina (Provincia de Buenos Aires, DISPOSICION DPP No. 468; www.maa.gba.gov.ar/pesca/leg_archivos/D468-99.pdf) and the use of live bait is not permitted in Argentine Patagonia (Reglamento de Pesca Deportiva Continental Patagónico; http://desarrollosustentable.tierradelfuego.gov.ar/wp-content/uploads/2013/08/Reglamento-Pesca-2013-2014.pdf/).

Even though it is not allowed, the cultural practice of live bait use could be the way *C. carpio* overcame the obstacle of the Arroyito Dam. Recent observation of the presence of the Neotropical *Cheirodon interruptus* (Jenyns 1842) in the endorheic basin of the Valchetta Stream (H. López, pers. comm.), south of the Negro River basin, and data on the movement of nine species between the Colorado and Negro basins (Aigo *et al.*, 2008), including *C. carpio*, highlight the risk of this practice. In addition to preventing the transport of *C. carpio*, other measures are possible. In northern Argentina several rivers are exploited efficiently through selective fishing, supporting a valuable fishery that exported up to 2403 t of *C. carpio* per year between 2007 and 2012 (Ministerio de Agricultura, Ganadería y Pesca; www.minagri.gob.ar). Similar action on the Negro basin could result in a potential mitigation measure (De Vaney *et al.*, 2009), leading to a decrease in the abundance of this species, thus reducing their potential for southward expansion. It should not be overlooked that *C. carpio* is a major resource in terms of food production in the world (FAO; www.fao.org/fishery/affris/species-profiles/common-carp/natural-food-and-feeding-habits/en) and that their introduction, culture and fishery could be the goal of well-defined government policies regarding national food security (Quirós & Mari, 1999). The stocking of lakes and reservoirs is a practice deeply rooted in government management, including the stocking of *C. carpio* in Argentina (Ministerio de Agricultura, Ganadería y Pesca Argentina, 2011). The present results reinforce the idea that the trade-off between food production and conservation is an issue that should be faced in the near future, with special regard to the southern distribution of *C. carpio* in South America.

We wish to thank J. Allison (University of Nebraska-Lincoln, U.S.A.) and J. Smith (University of Nebraska-Lincoln, U.S.A.) for collaboration in data entry. We would like to acknowledge the following institutions which awarded grants to the present project: Universidad Nacional del Comahue (04B147) and Consejo Nacional de Investigaciones Científicas y Técnicas (PIP 112-200801-00282) of Argentina and the NSF-PIRE award (OISE 0530267, U.S.A.) for support of collaborative research on Patagonian Biodiversity granted to the following institutions (listed alphabetically): Brigham Young University, Centro Nacional Patagónico, Dalhousie University, Darwinian Botanical Institute, Universidad Austral de Chile, Universidad Nacional del Comahue, Universidad de Concepción and University of Nebraska.

Supporting Information

Supporting Information may be found in the online version of this paper:

TABLE SI. Lakes (L) and reservoirs (R) with and without *Cyprinus carpio*. Data include latitude, longitude, chlorophyll-*a* and 1961–1990 means for maximum (MaxAAT), minimum (MinAAT) and mean (MeanAAT) annual air temperatures (all at 0·5° native resolution *c.* 2500 km^2) obtained from the Intergovernmental Panel on Climate Change (www.ipcc.ch). Predicted presence was obtained from DA

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