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Reciprocal trophic niche shifts in native and invasive fish: salmonids and galaxiids in Patagonian lakes

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SUMMARY

1. Rainbow (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) are widespread and invasive salmonids with important lethal effects as predators, although indirect effects are also possible. We used stable isotope analyses ($\delta^{15}N$, $\delta^{13}C$) to explore how the density of invasive trout in 25 Patagonian lakes alters the trophic niche (TN) of a widespread native fish, *Galaxias platei* (Galaxiidae). We also explored how the density of the galaxiid influences the TN of invasive trout.
2. We quantified two aspects of the TN: (i) the proportion of littoral carbon (PL) and (ii) trophic height (TH) (i.e. the 'height' at which the fish feeds in the food web). We related these measures of TN in a given species to the density of other species (as estimated by catch-per-unit-effort).
3. As *G. platei* body size increased, their PL increased (increasing littoral feeding) in several lakes. However, none of the fish species investigated showed changes in PL with increasing density of the other fish species. TH increased with body size in all three species. In addition, the TH of large *G. platei* declined with increasing trout density and, reciprocally, the TH of large *S. trutta* decreased with decreasing *G. platei* density.
4. The reciprocal effects of native and the invasive fish on TH were as large as a shift of one trophic level. This pattern is consistent with an exhaustion of galaxiid prey for both piscivorous *G. platei* and *S. trutta* in lakes with high trout density.
5. These finding support the suggested management strategy of culling trout from overpopulated lakes, which should simultaneously protect native fish and enhance a lucrative sport fishery for large trout.

Keywords: food-web complexity, generalist predators, linear mixed models, ontogenetic diet shift, trophic plasticity

Introduction

A consistent effect of introduced predators is a decline in the density of native prey populations owing to the lethal effect of predation (Elton, 1958; Preisser, Bolnick & Benard, 2005; Salo *et al.*, 2007), although indirect effects can also be dramatic (Werner & Peacor, 2003; Bolnick & Preisser, 2005; Preisser *et al.*, 2005; Sih *et al.*, 2010). One such effect is a change in the trophic niche (TN) of native species, which might be brought about via exploitative competition or behavioural interactions (Preisser *et al.*, 2005; Bøhn, Amundsen & Sparrow, 2008; Sih *et al.*, 2010). Because native species were presumably sufficiently well adapted to their original niches before invasion, niche shifts induced by invaders might reduce growth and survival and thereby contribute to population decline in the natives. Interestingly, reciprocal effects of natives on invaders are also likely. For instance, variation in the abundance, distribution and behaviour of native prey can cause shifts in the TN of an invader (Sidorovich, Polozov & Zalewski, 2010), which might then influence its growth, survival and population dynamics. Our goal was to evaluate the potential reciprocal effects on the TNs of natives and invaders in a simple food web, where such effects should be most easily detected (Elton, 1927; Strong, 1992; Moyle & Light, 1996; Duffy *et al.*, 2007; Sih *et al.*, 2010).

Our study focussed on interactions between a native galaxiid fish and introduced salmonids in post-glacial

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lakes of Chilean Patagonia. Galaxiids are confined to the Southern Hemisphere and are evolutionarily naive with respect to the salmonid predators that have been deliberately introduced from the Northern Hemisphere (Cox & Lima, 2006; Mcdowall, 2006). These salmonids, particularly brown trout (*Salmo trutta* L.) and rainbow trout (*Oncorhynchus mykiss* [Walbaum]), are extremely disruptive invasive top predators (Cambray, 2003; Casal, 2006) known to have negative effects on galaxiid populations (Mcdowall, 2006; Young *et al.*, 2010; Correa & Hendry, 2012). Although direct predation is probably the leading cause of these negative effects, some indirect effects have also been documented, including habitat shifts (Mcintosh, Townsend & Crowl, 1992; Edge, Townsend & Crowl, 1993; Penaluna, Arismendi & Soto, 2009) and reduced growth (Young *et al.*, 2008). Here we test hypotheses about postulated reciprocal effects: that is, invasive salmonids should influence the TN of galaxiids and native galaxiids should influence the TN of trout. To evaluate these hypotheses, we consider two dimensions of TN (e.g. Matthews *et al.*, 2010): (i) a 'vertical' dimension indicating the 'height' in the food web at which consumers assimilate nutrients [measured as trophic height (TH)] and (ii) a 'horizontal' dimension indicating the importance of littoral versus pelagic food-web resources [measured as proportion of littoral carbon (PL)].

Potential shifts in TNs resulting from interactions between native and invasive species need to be considered in the context of natural ontogenetic niche shifts. For example, TH increases with body size in many fish species, because larger individuals can consume prey over a wider size range (e.g. Werner & Gilliam, 1984; Hjelm *et al.*, 2001; Post, 2003). In addition, PL should increase with body size in *Galaxias platei* that change from planktonic to littoral habitats, or decrease for *G. platei* that change from planktonic or littoral habitats to a profundal benthic mode of life (Barriga *et al.*, 2002; Habit *et al.*, 2010; Correa & Hendry, 2012). The question remains as to how such natural ontogenetic niche shifts might be modified by interactions between native and invasive species? First, we predicted that small *G. platei*, which are particularly susceptible to predation by trout, might show an earlier shift in PL (a switch to littoral resources) in invaded lakes as they avoid the risk of trout predation in open water lacking refugia (Barriga *et al.*, 2002; Macchi, Pascual & Vigliano, 2007; Stuart-Smith *et al.*, 2007; Aigo *et al.*, 2008). Second, we predicted that the TH of small *G. platei* would decrease (they would feed at a lower TH) if foraging for small fish larva and predatory invertebrates is suppressed at high trout abundance (Vander Zanden, Casselman & Rasmussen, 1999), or if the exploitation of littoral and benthic resources becomes more important (Matthews *et al.*, 2010). Third, we predicted that large *G. platei* would show a decrease in TH in invaded lakes because a reduced density of conspecifics limits cannibalism, a behaviour that can otherwise be common (Milano *et al.*, 2006). On the other hand, we predicted that trout would show a decrease in their TH as populations of native fish decline. We tested these predictions by analysing stable isotope (SI) ratios of carbon ($^{13}C/^{12}C$; denoted by $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$; $\delta^{15}N$).

Methods

In principle, the $\delta^{15}N$ and $\delta^{13}C$ signatures of consumers in lakes can be used to calculate time-integrated quantitative measures of TH and PL, respectively. In particular, snails that scrape periphyton from littoral substrates are typically enriched in $\delta^{13}C$ relative to mussels that filter pelagic phytoplankton, and predatory fish that exploit both the pelagic and littoral food webs show intermediate $\delta^{13}C$ (PL) and higher $\delta^{15}N$ (TH) compared to the molluscs (Vander Zanden & Rasmussen, 1999; Post, 2002; Matthews *et al.*, 2010). TH and PL should be calculated relative to lake-specific isotopic baselines, particularly if inter-lake comparisons are required. Here we follow the recommendations of Post (2002) in using long-lived primary consumers (snails and mussels) as calibration baselines, coupled to a two-end member mixing model to estimate PL and TH of fish.

We used the snail *Chilina* sp. Gray (Basommatophora: Chilinidae) and the mussel *Diplodon chilensis* (Gray) (Unionacea: Hyriidae) as calibration baselines, because they are abundant and widely distributed in Patagonia (Parada & Peredo, 2006; Valdovinos, 2006). These taxa (i) frequently coexist in our study lakes (13 of 25 lakes in the present analysis), (ii) capture pelagic or littoral primary productivity and detritus because of their feeding habits [scraper- (snail) and filter-feeder (mussel)] (Estebenet, Cazzaniga & Pizani, 2002; Lara *et al.*, 2002; Post, 2002), and (3) are long-lived compared to most other primary consumers (>30 years for *D. chilensis*; Parada *et al.*, 1989; 1 year for *Chillina sp*. Bosnia, Kaisin & Tablado, 1990). We collected these species by hand from the littoral zone of all lakes that contained them.

Study area

Our study took place in 25 lakes of the Aysén region in western Patagonia, Chile (*c.* 46°S) [Table 1; also see Correa & Hendry (2012) for a map and further description of study area]. Trout were first introduced into the region in

Table 1 Lake descriptors and sample sizes* of the molluscs and fish analysed

ID	Lake	Latitude (°S)	Longitude (°W)	Invasion	Area (ha)	Shore. dev. index†	Altitude (m)	Order‡	Depth (*m*)	Spec. cond. (µS cm^{-1})	Deforestation (%)§	*Diplodon chilensis*	*Chilina* sp.	*Galaxias platei*	*Salmo trutta*	*Oncorhynchus mykiss*
1	Alta	45.5347	72.7086	Uninvaded	89.4	1.38	80	2	55	26.9	9	5	4	8	0	0
2	Barroso	45.7396	72.2451	Invaded	56.4	1.87	334	2	43	32.9	55	10	10	13	13	0
3	Brava	45.0997	71.8272	Invaded	77.5	1.59	840	1	41	50.7	68	0	4	0	9	0
4	Burgos	45.7128	72.2185	Invaded	22.9	2.04	375	2	30	58.8	93	3	3	0	2	8
5	Castor	45.6003	71.7815	Invaded	432.3	2.67	696	2	52	78.7	49	5	5	24	0	9
6	Cea	45.6744	72.2378	Invaded	23.1	1.50	289	2	11	31.8	40	5	5	18	15	0
7	Chacano	46.1728	72.1933	Invaded	15.4	1.87	510	2	14	112.1	64	0	3	0	12	5
8	Escondida	45.5324	71.8259	Uninvaded	74.2	2.04	695	1	17	99.0	29	0	5	9	0	0
9	Espejo	45.7407	72.204	Invaded	9.6	1.18	336	2	21	75.5	84	0	1	0	11	0
10	Frio	45.6675	71.9438	Invaded	396.7	1.58	513	4	15	73.5	47	5	5	9	0	12
11	Gemela	45.5463	71.8162	Uninvaded	25.7	1.54	759	0	14	92.9	57	0	5	12	0	0
12	Juncos	45.6336	71.8509	Uninvaded	6.9	1.15	748	0	3	56.9	44	0	5	11	0	0
13	Leon	45.6161	71.8405	Uninvaded	29.3	1.85	756	0	8	61.6	57	0	2	11	0	0
14	Mercedes	45.7361	72.2173	Invaded	18.9	1.53	349	1	22	75.0	76	0	4	0	10	0
15	Monreal1	45.6369	71.8696	Uninvaded	34.2	1.54	753	0	14	48.8	50	5	5	9	0	0
16	Monreal2	45.8725	72.0209	Invaded	232.2	1.90	603	2	51	52.8	37	0	5	6	17	8
17	Palos	45.3209	72.7027	Invaded	539.5	1.62	0	3	60	23.6	10	4	5	2	4	0
18	Pollux	45.6763	71.8627	Invaded	872.3	2.52	679	3	55	71.6	42	5	5	17	0	24
19	Portales	45.5353	72.5904	Invaded	571.0	2.13	53	3	150	24.2	30	5	5	12	8	0
20	Quijada	45.7177	71.911	Invaded	32.3	1.24	727	0	10	65.4	63	0	3	11	2	0
21	Rengifo	45.6176	72.5113	Invaded	187.2	1.69	110	1	20	24.9	40	3	4	3	8	0
22	Thompson	45.6467	71.7929	Invaded	111.0	2.12	748	1	15	72.3	44	3	4	8	0	6
23	Toro	45.5299	71.8535	Uninvaded	27.3	1.06	686	0	NA	NA	NA	0	2	10	0	0
24	Yulton	45.118	72.9022	Uninvaded	6111.1	2.60	488	3	170	25.0	4	0	5	18	0	0
25	Zenteno	45.5921	72.5482	Invaded	656.1	2.47	95	2	50	25.3	41	5	5	15	2	0

Lake descriptors follow Correa & Hendry (2012).

*Sample sizes are after the removal of nine isotopic outliers distributed among fish and molluscs in six lakes. Lake Sepulveda (Correa & Hendry 2012) was also excluded due to uncertainty in isotopic baselines.

†Shoreline development index quantifies the development of the littoral zone relative to open waters. It is defined as the perimeter of a lake divided by the perimeter of a circle of equal area.

‡Lake order describes lake position in a river network and is measured as Strahler stream order at the lake outlet (endorheic lakes were indexed as order = 0).

§Deforestation is the proportion of lake basin deforested during the twentieth century.

1968, when 78 000 rainbow trout were released into Lago Pollux (Sakai, 1989). Two years later, brown trout were introduced into Lago Elizalde and elsewhere in the region (Shiraishi 1985, cited in Blumberg-Muñoz, 1996). Both species quickly became established and spread (naturally or artificially) to colonise most lakes. Some lakes, however, remained uncolonised, either because obstacles to trout dispersal made them inaccessible or because they were lacking streams that could support trout reproduction (Correa & Hendry, 2012). Across lakes, the density of galaxiids is currently negatively correlated with the density of trout, and in several lakes, galaxiids have apparently gone extinct (Correa & Hendry, 2012). This variation among lakes in the density of trout and galaxiids provides us with an opportunity to investigate TNs along an invasion gradient.

As our goal was to study the effect of trout and galaxiids on each other, we sought to minimise variation among lakes in other environmental variables. Therefore, we chose invaded lakes (i.e. trout were detected) and uninvaded lakes (i.e. trout were not detected) that were otherwise similar. To confirm this similarity, we compared invaded ($n = 17$) and uninvaded lakes ($n = 8$) with respect to lake area [ln(ha)], shoreline development index, maximum depth [ln(m)], specific conductivity ($\mu S\ cm^{-1}$), altitude (m), stream order at lake outlet and proportion (arcsine $\sqrt{p}$) of deforested area within a lake basin (Table 1). Six of the seven variables showed no differences between invaded and uninvaded lakes (Student's t-tests, d.f. = 23, $P > 0.05$). Lake order was significantly higher in invaded than uninvaded lakes [mean (SD) 1.9 (1.0) versus 0.7 (1.2); Student's t-test, d.f. = 23, $P = 0.03$], although considerable overlap was evident. Uninvaded lakes were often of lower order because they were less likely to be connected to streams that were appropriate for trout reproduction. Lake order, however, had no significant effect on the density of *G. platei* after controlling for the negative effect of trout density (Correa & Hendry, 2012). Thus, any differences in TNs between invaded and uninvaded lakes are expected to be the result of trout invasion rather than confounding environmental variables.

Fish collections and density indicators

Our sampling methods are detailed elsewhere (Correa & Hendry, 2012), and so here we describe them only briefly. During the austral summer and early autumn (January–May) of 2007 and 2009, we conducted quantitative fish sampling with three types of fishing gear. (i) Multipanel survey gillnets targeted large fish (>50 g), particularly trout and large *G. platei*. Two gillnets were usually set per lake: one in the littoral zone and one in a deep location at the lake bottom (demersal). (ii) Minnow traps, usually 20 per lake, targeted smaller *G. platei* in a broad range of microhabitats from the littoral to the demersal zone. (iii) Electrofishing targeted small trout and galaxiids in the shallow littoral zone of all lakes, and owing to logistical constraints, this was the only fishing method used in Toro Lake. This combination of approaches secured samples including a broad range of body sizes of each species, allowing an analysis of ontogenetic, interspecific and inter-lake variation in TN.

Correa & Hendry (2012) calculated and analysed multivariate indices (PC1 across the three gear types) of capture-per-unit-effort (CPUE) as a proxy for the densities of *G. platei* and trout. Here, however, we use univariate CPUE data, because this allowed us to target more precisely the demographic classes most relevant to our specific hypotheses, such as large predatory trout or small (prey) *G. platei*. As the explanatory variable for testing the effects of trout on the TN of *G. platei*, we used trout CPUE from gillnets (pooling data from *O. mykiss* and *S. trutta*): ln(number of trout gill netted/number of overnight gillnets + 1). As the explanatory variable for testing the effects of *G. platei* on the TN of trout, we used *G. platei* CPUE from minnow traps: ln(number of *G. platei* trapped/number of overnight traps + 1). *Post hoc* analyses using other univariate and multivariate CPUE-based proxies for fish density led to the same conclusions as reached here. In short, our results are robust to variation in the specific fish density indices, which were in any case correlated with each other (Correa & Hendry, 2012).

Elemental analysis and correction for preservation bias

Shortly after collection in the field, fish were killed with an overdose of MS222 or clove oil. A small portion of muscle tissue (*c.* 3–5 mm in cross-section and 1 cm in length) was then removed from the anterodorsal region of the fish, avoiding dorsal spines. A similar quantity of muscle was obtained from the foot of mussels and snails. These tissue samples were preserved and stored in 95% denatured ethanol (see below): the denaturing agent was 0.02% diethyl phthalate (Cruz Verde). Individual samples were kept in 1.5 mL Eppendorf tubes, whereas samples from several invertebrates of different species were kept together in 25-mL scintillation vials. In the laboratory, the samples were dried at 50 °C for 24 h, and 1.0–1.3 mg (analytical balance Mettler Toledo, Mississauga, ON, Canada; model AB104) of subsamples were removed and placed in tin-capsules. The dried samples were then sent to the Stable Isotope Facility of the University of California, Davis, where they were analysed for ^{15}N and ^{13}C using a PDZ Europa ANCA-GSL elemental analyser attached to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, U.K.). Stable isotope values were specified in δ notation: $\delta^{15}N$ or $\delta^{13}C = [(R_{sample}/R_{standard}) - 1]1000$, where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$ relative to international standards (Vienna PeeDee Belemnite for carbon and atmospheric air for nitrogen).

Ethanol preservation is not ideal for stable isotope analysis because it can produce systematic bias in isotopic values. In our study, however, ethanol preservation was necessary because sampling took place in remote areas where no better preservation method was available. Fortunately, the bias can be corrected through experiments contrasting an ethanol preservation treatment to a control treatment (Kelly, Dempson & Power, 2006; Barrow Lindy, Bjorndal Karen & Reich Kimberly, 2008; Yoshino *et al.*, 2010). Correa (in press) conducted such an experiment by comparing, for a sample of each species, stable isotope measurements from tissue preserved in ethanol (treatment) versus tissue preserved by freezing for <5 day and then drying (control). These data were used to develop bias correction factors that corresponded to mean isotopic deviations between the control and treatment groups, adjusting for individual variation (i.e. repeated measures design) within each species. To correct for preservation bias in the full data set, we then subtracted these bias correction factors from the measured stable isotope values of each ethanol-preserved sample.

Data analyses

We analysed the stable isotope signatures of 411 fish and 172 molluscs across the 25 lakes (Table 1; Fig. 1). Isotopic calibration baselines were calculated as the average $\delta^{13}C$ and $\delta^{15}N$ values by mollusc and lake. All snail baselines, and 13 mussel baselines, were calculated directly from the data. However, mussels were absent from 12 lakes and the average baseline values in those cases had to be inferred indirectly. To do so, we regressed $\delta^{13}C_{(mussels)}$ on $\delta^{13}C_{(snails)}$ for the 13 lakes where they co-occurred and the fitted model was used to predict the missing $\delta^{13}C$ values [$\delta^{13}C_{(mussels)} = -16.63 + 0.56{*}\delta^{13}C_{(snails)}$, ANOVA, $F_{1,11} = 26.7$, $P < 0.001$, $R^2 = 0.71$]. Similarly, we regressed $\delta^{15}N_{(mussels)}$ on $\delta^{15}N_{(snails)}$ for the 13 lakes and the fitted model was used to predict missing $\delta^{15}N$ values [$\delta^{15}N_{(mussels)} = 0.80 + 0.68{*}\delta^{15}N_{(snails)}$, ANOVA, $F_{1,11} = 10.8$, $P = 0.007$, $R^2 = 0.50$]. Lake area sometimes explains variation in isotopic calibration baselines (Post, 2002) but that was not the case in the present study (results not shown), and so it was ignored when inferring missing values.

The TH of each fish was calculated according to (Post, 2002) the following formula: $TH = \lambda + (\delta^{15}N_{(fish)} - [\delta^{15}N_{(snails)}{*}PL + \delta^{15}N_{(mussels)}{*}(1 - PL)])/\Delta_n$, where λ is the TH of the molluscs used as isotopic baselines ($\lambda = 2$ for the primary consumers used) and Δ_n is the enrichment in $\delta^{15}N$ per trophic level (assumed to be 3.4%; Post, 2002). The PL (constrained to vary in the range [0, 1]) of each fish was calculated as the proportion of fish mass derived from the littoral (snails) as opposed to the pelagic (mussels) food web (parameter alpha in Post, 2002): $PL = (\delta^{13}C_{(fish)} - \delta^{13}C_{(mussels)})/(\delta^{13}C_{(snails)} - \delta^{13}C_{(mussels)})$. In our study, $\delta^{15}N$ values were similar between same-lake isotopic baselines (see Results), and so the estimated PL values had little effect on the estimated TH values. TH and PL were treated as response variables separately by species: *G. platei*, *S. trutta* and *O. mykiss*. Alternative analyses that pooled *S. trutta* and *O. mykiss* reinforced our findings for *S. trutta* by itself (results not shown).

To model variation in TH, we used hierarchical, varying intercept, varying slope, mixed-effect models (Gelman & Hill, 2007). To evaluate our hypotheses, the deterministic portion of the model included CPUE of the relevant species (i.e. trout for a model predicting galaxiid TH and vice versa), individual mass (of the fish whose TH is being predicted) and their interaction, the latter allowing for ontogenetic TH shifts that could vary as a function of fish CPUE. The random portion of the model included the random effect of lake identity (unexplained between-lake variation) and variation among individual fish (after accounting for mass), which were nested within lakes (residual variation). The (full) model thus can be written as $TH = 1 + CPUE + \ln(g) + CPUE : \ln(g) + (1 + \ln(g) \mid lake)$, where 1 represent intercepts, CPUE is the relevant lake fish density index (see above), g is the mass of individual fish in grammes and lake is the identity of the lake (see syntax details in Zuur *et al.*, 2009). The model for each species was fitted by restricted maximum likelihood using the function 'lmer' of the R package 'lme4' (Bates & Maechler, 2010). Predictions were evaluated by testing the significance, and visualising the effect size, of the interaction term between mass and CPUE. Statistical significance was tested by fitting through maximum likelihood the full model and a reduced model with no interaction term, which were then compared using the likelihood ratio test (LRT) implemented in the R function 'ANOVA' (Zuur *et al.*, 2009; R Development Core Team, 2010).

In contrast to TH, PL is a proportion and so was analysed in a two-stage generalised linear model (GLM) (Gelman & Hill, 2007). In the first stage, we fitted models

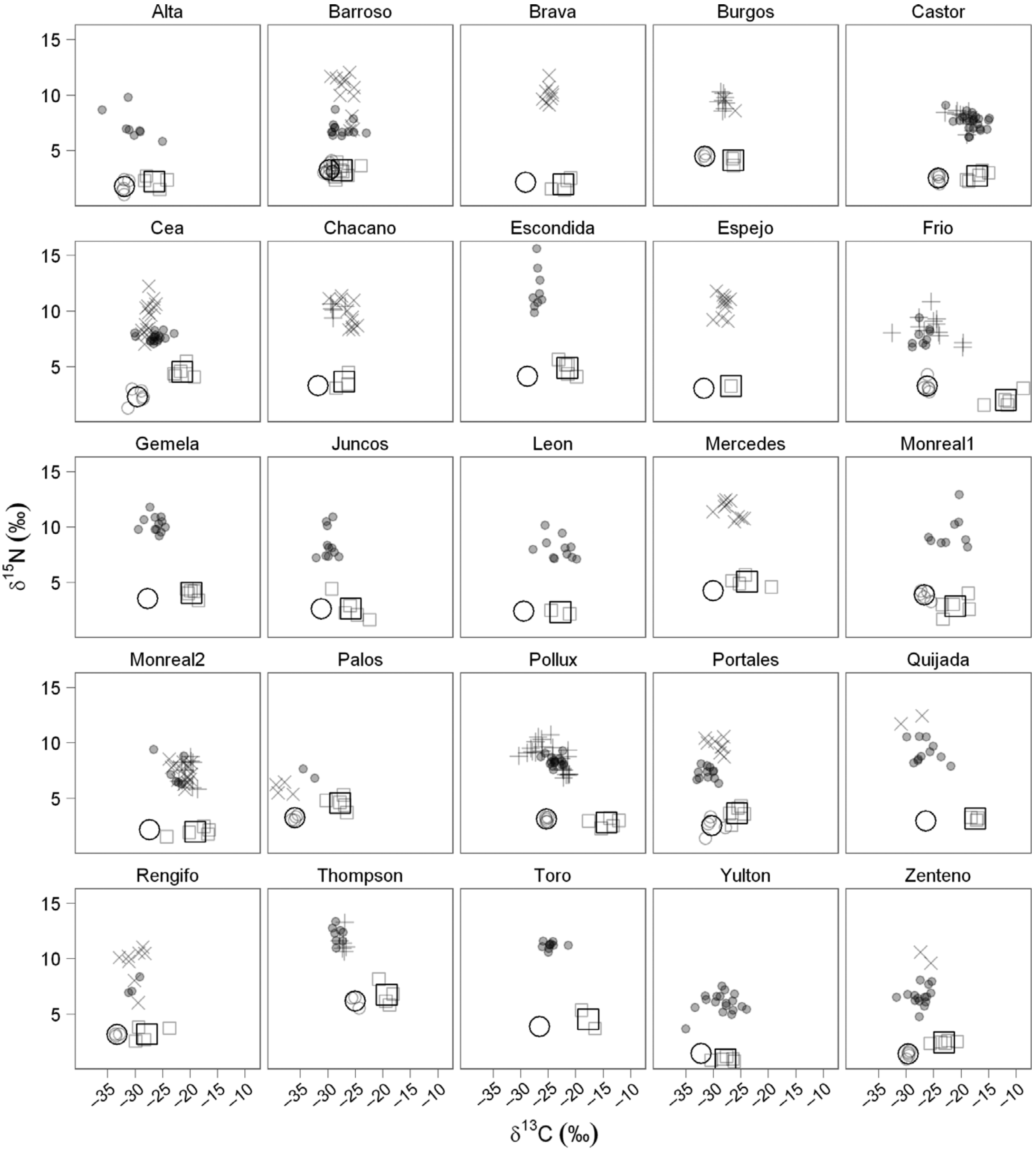

Fig. 1 Stable isotope data for each lake (sorted alphabetically). The snail *Chilina* sp. (□) is taken to represent the isotopic baseline for the littoral food web, and the mussel *Diplodon chilensis* (○) is taken to represent the same for the pelagic food web (means and inferred values, used to calculate fish trophic height and proportion of littoral carbon, are shown with larger, darker symbols). The remaining symbols represent individuals of *Galaxias platei* (•), *Oncorhynchus mykiss* (+) and *Salmo trutta* (×). Values were corrected for preservation bias (see Methods for details).

to the data (individual mass predicting PL) for each lake and species separately using a GLM with a quasibinomial error structure (logit link) implemented in the R function 'glm' (R Development Core Team, 2010). The quasibinomial was preferred over binomial error structure because the data were often overdispersed (i.e. when using the binomial error structure, residual deviance/d.f. >> 1; Crawley, 2007; p. 573–578). In the second stage, we looked for correlations between the resulting coefficients (slopes and elevations) and the relevant fish density index, that is, trout CPUE predicting slopes and intercepts for galaxiid PL and vice versa. We set the significance level to $\alpha = 0.05$ for all statistical tests. R code is available from the corresponding author.

Results

In the 13 lakes where both mollusc species were present, the δ^{13}C values of snails were significantly enriched compared to the δ^{13}C values of mussels [one-tailed paired *t*-test, $t_{(12)} = 8.135$, $P < 0.001$], and fish generally had intermediate δ^{13}C values (Fig. 1). Fish were also substantially enriched in δ^{15}N relative to these primary consumers, which were similar to each other (Fig. 1; two-tailed paired *t*-test, $t_{(12)} = 1.208$, $P = 0.250$). Relative to lighter individuals, heavier fish fed higher in the food web (a greater TH) and sometimes also differed in the PL. These results are consistent with general expectations that fish consume a mixture of pelagic and littoral resources, are at a higher trophic position than primary consumers and show ontogenetic diet shifts.

Ontogenetic shifts in the TH of *G. platei* were related to the presence/absence (Fig. 2) and CPUE (Fig. 3) of trout. Small *G. platei* (*c.* 1 g) had relatively similar TH across the entire gradient of trout CPUE (Fig. 3a). In contrast, large *G. platei* (*c.* 150 g) fed approximately one trophic level higher in lakes where trout were not detected than in lakes with abundant trout (Fig. 3a). Accordingly, the effect of *G. platei* mass on TH (i.e. slope) was negatively correlated with trout CPUE (Fig. 3b; LRT $\chi^2 = 6.781$, d.f. = 1, $P = 0.009$). In an information theoretic context, this full model was the best (AIC = 16.63) followed by a reduced model lacking the interaction term (AIC = 21.43).

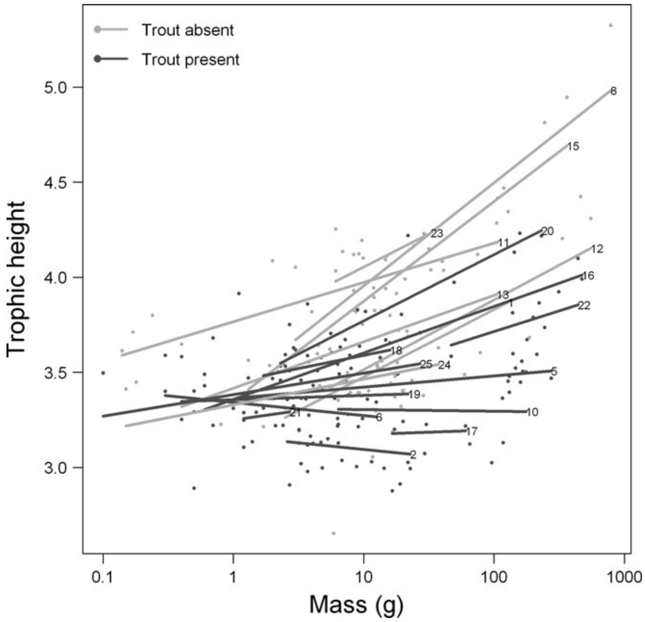

Fig. 2 Ontogenetic shifts in trophic height for the native *Galaxias platei* in the 20 lakes where they were found. Lines represent the fitted model for height on ln-mass in lakes with (dark lines) and without (light lines) invasive trout. Points represent the values for individual fish from all the lakes (for clarity, individual lake membership is not shown). Numbers associated with the fitted lines correspond to the alphabetical order of lakes in Fig. 1 and Table 1, and model coefficients are displayed in Fig. 3.

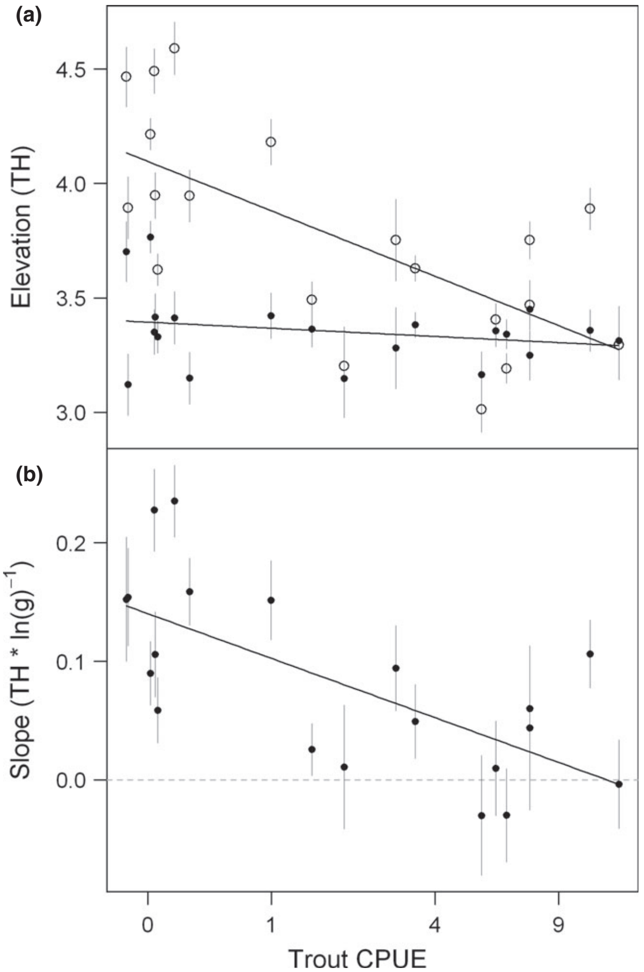

Fig. 3 Multilevel model coefficients for the trophic height (TH) of *Galaxias platei* as a function of trout-catch-per-unit-effort (trout CPUE) (from model in Fig. 2). (a) Elevation represents the TH evaluated at a fish mass of 1 g (•) and 150 g (○) in each lake. (b) Slope represents the coefficients for the effect of ln-mass on TH in each lake. Vertical lines represent 95% confident intervals. Coefficients corresponding to CPUE = 0 were slightly dispersed along the *x*-axis for increased clarity.

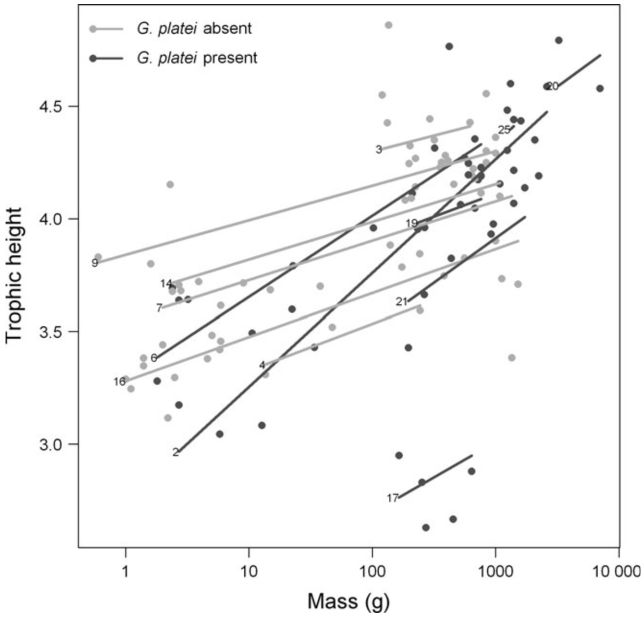

Fig. 4 Ontogenetic shifts in trophic height for the invasive *Salmo trutta* in the 13 lakes where they were found. Lines represent the fitted model for height on ln-mass in lakes with (dark lines) and without (light lines) native *Galaxias platei*. See Fig. 2 for additional details.

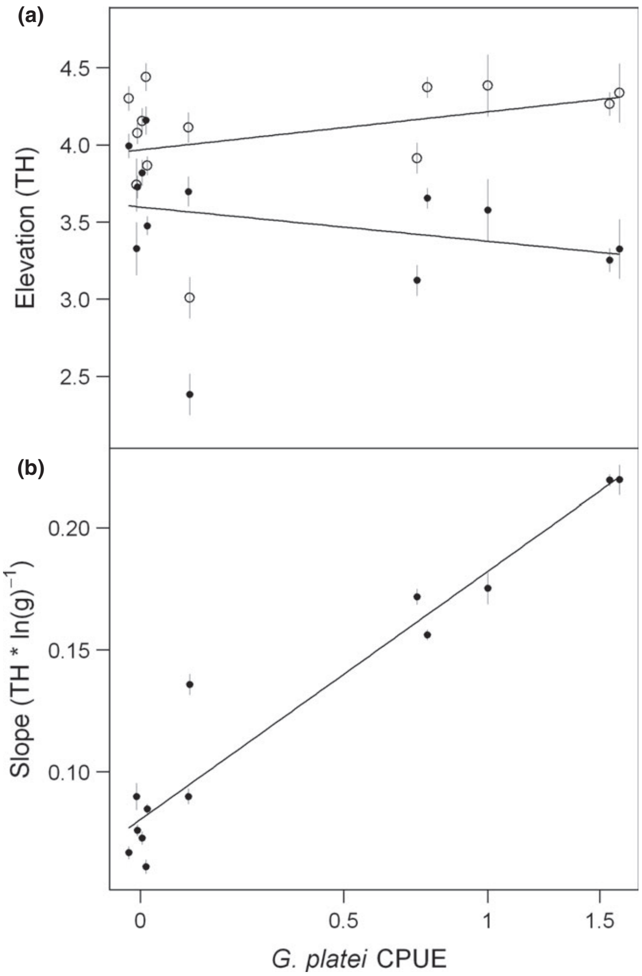

Fig. 5 Multilevel model coefficients for the trophic height (TH) of *Salmo trutta* as a function of *Galaxias platei* catch-per-unit-effort (from model in Fig. 4). (a) Elevation represents the TH evaluated at a fish mass of 10 g (•) and 1000 g (○) in each lake. (b) Slope represents the coefficients for the effect of log-mass on TH in each lake. See Fig. 3 for additional details.

Similarly, ontogenetic changes in the TH of *S. trutta* were related to the presence/absence (Fig. 4) and CPUE (Fig. 5) of *G. platei*. Small *S. trutta* (*c.* 10 g) had a relatively similar or slightly lower TH as *G. platei* CPUE increased (Fig. 5a). In contrast, large *S. trutta* (*c.* 1000 g) fed approximately one TH higher in lakes with abundant *G. platei* than in lakes where *G. platei* were not detected (Fig. 5a). Accordingly, the effect of *S. trutta* mass on TH (i.e. slope) was positively correlated with *G. platei* CPUE (Fig. 5b; LRT $\chi^2 = 7.092$, d.f. = 1, $P = 0.008$). This full model was the best (AIC = 35.95) followed by a reduced model lacking the interaction term (AIC = 41.04).

Oncorhynchus mykiss also showed an ontogenetic increase in TH (see below), but the interaction between *O. mykiss* mass and *G. platei* CPUE was not significant (LRT $\chi^2 = 3.087$, d.f. = 1, $P = 0.079$). Nor was there a significant effect of *G. platei* CPUE without the interaction term in the model (LRT $\chi^2 = 1.785$, d.f. = 1, $P = 0.182$), which leads to a simplified model involving only the effect of *O. mykiss* mass and the random effect of lake identity (LRT $\chi^2 = 21.004$, d.f. = 1, $P < 0.001$). The simplified model was the best fit (AIC = 15.38) followed by the full model (AIC = 18.29). It must be noted, however, that only seven lakes could be included in the analyses involving *O. mykiss*, and hence statistical inference is tenuous. At the individual level, however, the numbers of fish in lakes where they were present were always large enough to detect the expected ontogenetic TH shifts (i.e. the effect of mass).

In contrast to these clear patterns for TH, ontogenetic shifts in the PL were highly variable and seemingly idiosyncratic for all three species. For *G. platei*, slopes of the generalised linear regressions between ln-mass and PL were positive for six lakes, negative for one and non-significantly different from zero in the rest of the 20 lakes in the first stage of the analysis (*t*-tests on slope coefficients). This result suggests a common ontogenetic shift from pelagic larvae to more littoral juveniles and adults. Moreover, the slope coefficients between ln-mass and PL in *G. platei* within lakes were unrelated across lakes to trout CPUE in the second stage of the analysis (ANOVA, $F_{1,18} = 1.058$, $P = 0.317$). For *S. trutta* and

O. mykiss, the slopes of the generalised linear regressions between ln-mass and PL occasionally differed from zero in either direction, and no significant interaction with *G. platei* CPUE was observed (results not shown).

Discussion

Trophic height

Our data reveal shifts in TH in co-occurring native galaxiids and invasive salmonids. For the native species, the results suggest that the indirect, non-lethal impacts of invasive trout prevent their normal ontogenetic shift to feeding higher in the food web with increasing body size. For the invader, these results suggest that the reduction they cause in the density of native species (Correa & Hendry, 2012) hampers their own normal ontogenetic shift to feeding higher in the food web as body size increases. These shifts in TH might be caused in at least two (non-exclusive) ways: (i) the alteration of available food (exploitative competition hypothesis) and (ii) the alteration of feeding behaviour because of predator avoidance (predator avoidance hypothesis).

The outcome of exploitative competition might be affected by ecological differences between *G. platei* and trout. *G. platei* completes its life cycle within lakes (Barriga *et al.*, 2002; Habit *et al.*, 2010; data in Correa & Hendry, 2012) whereas trout spawn in streams where their emerging fry grow for several months or years before entering lakes (Forseth *et al.*, 1999; Arismendi, Sanzana & Soto, 2011c). This spatial segregation between *G. platei* and trout makes *G. platei* in lakes more vulnerable to predation than salmonids (Mcdowall, 2006; Milano *et al.*, 2006; Macchi *et al.*, 2007). Indeed, small *G. platei* are frequently found in the diet of large trout and large *G. platei* (cannibalism), whereas small trout are seldom found in these diets (Macchi *et al.*, 1999; Milano *et al.*, 2006; Vigliano *et al.*, 2009; unpublished data). Thus, the TH of trout may be higher in the presence of galaxiids because the latter are a food source of unusually high TH, whereas the TH of galaxiids may be lower in the presence of trout because of exploitative competition forcing large galaxiids to feed lower in the food web than they otherwise would.

The predator avoidance hypothesis has received support from the demonstration of TN shifts in other systems (Crowder & Crawford, 1984; Schmitz & Suttle, 2001; Preisser *et al.*, 2005). For example, many species modify their foraging behaviour according to the perceived predation risk (Sih *et al.*, 2010 and references therein). Although galaxiids can certainly sense trout and try to avoid them (Stuart-Smith, White & Barmuta, 2008; Penaluna *et al.*, 2009), the observed TH reductions were actually greatest for the least vulnerable large *G. platei* (150 g, *c.* 225 mm SL)(Keeley & Grant, 2001). An alternative behavioural interpretation that could result in this pattern is progressive learning by galaxiids to avoid trout (with consequences for the diet) in response to previous non-lethal interactions (Lundvall *et al.*, 1999; Kelley & Magurran, 2011). Trout, on the other hand, have little to fear from *G. platei*. Therefore, we conclude that the shifts in TH observed in both native *G. platei* and introduced trout are consistent mainly with the exploitative competition hypothesis, although other behavioural interactions are also plausible (see also Rechencq *et al.*, 2011).

The shifts in TH observed in our study (about one trophic level) were quite large in relation to similar effects observed in a classical example from Canadian lakes. There, lake trout decreased its TH by about half of a trophic level after the introduction of smallmouth bass (*Micropterus dolomieu* Lacepède) and rock bass (*Ambloplites rupestris* Rafinesque) (Vander Zanden *et al.*, 1999). We attribute the especially large effect in our system to one property of the organisms and one property of the environment. With respect to the organisms, both *G. platei* and *S. trutta* are generalists (Milano *et al.*, 2006; Casaux & Diprinzio, 2007; Arismendi *et al.*, 2011a). Upon changes in feeding conditions (food availability or foraging behaviour), native generalists can readily engage in potentially adaptive diet shifts. Similarly, invasive generalists can rapidly exploit a variety of food resources across their new range (Clavel, Julliard & Devictor, 2011). With respect to the environment, the food webs we studied are relatively simple, and 'major community effects of invasions are most often observed where the number of species is low' (Moyle & Light, 1996). It is thus likely that fishes in the species-poor communities of post-glacial Patagonian lakes are especially susceptible to the direct and indirect effects of invasive predators (see also Elton, 1927; Strong, 1992; Duffy *et al.*, 2007; Sih *et al.*, 2010).

Proportion of littoral carbon

Observed patterns in the PL were rather variable and idiosyncratic. Some of this variation might be the result of methodological issues surrounding the estimation of PL, including heterogeneity in lipid concentration (Post *et al.*, 2007; Fagan *et al.*, 2011), missing baseline values for mussels in some lakes and inadequate baseline spatio-temporal representation (Guzzo *et al.*, 2011). An even more fundamental issue is that tracing the origins of carbon using one stable isotope (i.e. δ^{13}C) means that only two potential basal sources can be evaluated reliably (reviewed in Boecklen *et al.*, 2011). We based our PL analysis on the assumption that much of the consumer biomass in lakes ultimately comes from the pelagic and littoral food webs (Post, 2002). However, other potentially important sources include allochthonous (i.e. terrestrial) inputs and profundal production (Post, 2002; Cole *et al.*, 2011). Although we cannot assess the contribution of these sources in our study, the last at least seems unlikely to be important given that profundal carbon sources tend to have low δ^{13}C signatures and yet the majority of the fish analysed were enriched in δ^{13}C relative to the pelagic calibration baseline (but see Thompson Lake in Fig. 1). Similarly, the signatures of 191 fish from 25 North American temperate lakes suggest this source is unimportant (Post, 2002).

Assuming the above methodological issues are not too problematic (further discussion in Correa, in press), here we consider ecological factors influencing variation in PL. In six of seven lakes where *G. platei* showed significant PL shift with body size, the shifts were positive indicating an ontogenetic transition towards greater exploitation of the littoral food web, even in deep, invaded lakes. This finding contrasts with the common contention that *G. platei*, after completing its pelagic larval development (especially in invaded lakes), becomes a deep-benthos dweller (Milano & Vigliano, 1997; Barriga *et al.*, 2002; Cussac *et al.*, 2004; Milano *et al.*, 2006). Indeed, Correa & Hendry (2012) collected juvenile *G. platei* in the shallow littoral zone of every lake where the species was detected, and the same was true for adults in many lakes. Therefore, we suggest that the littoral zone might offer food and structural complexity, enabling *G. platei* to evade trout predation to some extent (Aigo *et al.*, 2008). It is also possible that some *G. platei* perform extensive diel migrations between the littoral and the profundal zones (Rechencq *et al.*, 2011).

Management implications

Our results are of potential significance for management. Trout decrease the TH of native *G. platei*, particularly of the largest individuals. In principle, this effect could reduce the food intake rates, limit the growth rates, lower the reproductive potential of adults and thereby reduce the population productivity of the native species (Jonsson *et al.*, 1999; Post, 2003; Vigliano *et al.*, 2009; Britton, Davies & Harrod, 2010). Thus, the indirect effects of invasive trout on the native *G. platei* (and presumably other galaxiids) might exacerbate the lethal effects caused by predation (see Sih *et al.*, 2010). Despite these potential fitness costs, trophic plasticity might be necessary to avoid predation (Schmitz & Suttle, 2001). Thus, the observed TH shift in *G. platei* could have profound and contrasting evolutionary implications ranging from accelerated local extinctions to allowance of long-term persistence and adaptation to the invader (Strauss, Lau & Carroll, 2006). Invasive trout, on the other hand, feed at a higher TH when native galaxiids are present than when they are absent and so could experience fitness costs following the collapse of native fish populations (Jonsson *et al.*, 1999; Post, 2003; Vigliano *et al.*, 2009). These costs could include poor condition, small size, smaller size at maturity, slower growth and slower metabolic rate, especially in oligotrophic lakes. In short, the depletion of native galaxiids is likely to be bad for invading salmonids, pointing directly to a valuable management strategy.

Patagonia is a world-class destination for trout sport fishing and the economic benefits are great (Arismendi & Nahuelhual, 2007; Vigliano, Alonso & Aquaculture, 2007; Pascual *et al.*, 2009; Vigliano *et al.*, 2009) – and angler satisfaction increases with fish size (Loomis, 2006). Arismendi, Penaluna & Soto (2011b) suggested that some lakes in Northern Chilean Patagonia are overpopulated with salmonids, resulting in food shortage and poor body condition of *O. mykiss*. Similarly, our results suggest that overpopulation of trout and the associated decline of *G. platei* probably cause suboptimal ontogenetic trajectories of TH in *S. trutta*. The likely reduction in trout growth would thus compromise the value of the fishery. Therefore, an excellent management strategy for Patagonia might be to reduce trout population density. The resulting increase in native fish density would simultaneously help to conserve a rare endemic group while also enhancing economic opportunities provided by the invader (see also Arismendi *et al.*, 2011b; Correa & Hendry, 2012).

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