

Transgenerational effects of anadromy on juvenile growth traits in an introduced population of rainbow trout (*Oncorhynchus mykiss*)

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Abstract: We determined whether the propensity for anadromy was related to maternal phenotype in a population of partially anadromous rainbow trout (*Oncorhynchus mykiss*). We identified the maternal phenotype (anadromous versus resident) of wild juveniles from two successive cohorts using stable isotope analysis ($\delta^{15}\text{N}$) of muscle tissue and (or) strontium to calcium ratios in the otolith core. We also tested the hypothesis that juvenile size and growth are related to maternal migratory history. For both cohorts, juvenile size at capture and growth, as determined using otolith and scale structural analyses, were strongly related to maternal migratory history. Offspring of anadromous mothers were larger and grew faster than resident offspring. Back-calculated length at age 1 of anadromous and resident adults provided support for a positive association between body size and anadromy, indicating that larger offspring are more prone to displaying anadromy. We conclude that maternal anadromy, which influences adult size and egg quality, affects the propensity of progeny to migrate, thus perpetuating the anadromous tactic across generations and influencing the establishment and persistence of anadromy.

Résumé : Nous avons tenté d'établir si la propension à l'anadromie était associée au phénotype maternel dans une population de truites arc-en-ciel (*Oncorhynchus mykiss*) partiellement anadrome. Nous avons déterminé le phénotype maternel (anadrome ou résident) de juvéniles sauvages de deux cohortes successives par l'analyse d'isotopes stables ($\delta^{15}\text{N}$) de tissus musculaires et (ou) des rapports strontium:calcium dans la partie centrale des otolithes. Nous avons également vérifié l'hypothèse voulant que la taille et la croissance des juvéniles soient reliées à l'historique de migration de la mère. Pour les deux cohortes, la taille au moment de la capture et la croissance des juvéniles, déterminées par l'analyse de la structure des otolithes et des écailles, étaient fortement reliées à l'historique de migration de la mère. Les juvéniles issus de mères anadromes étaient plus imposants que les juvéniles issus de mères résidentes, et leur croissance était plus rapide. Le rétrocalcul de la longueur à un an d'adultes anadromes et résidents a appuyé la présence d'une association positive entre la taille du corps et l'anadromie, ce qui indique que la progéniture de plus grande taille est plus susceptible de faire preuve d'anadromie. Nous concluons que l'anadromie maternelle, qui influence la taille adulte et la qualité des œufs, a une incidence sur la propension de la progéniture à migrer, perpétuant ainsi la tactique anadrome d'une génération à l'autre et influençant l'établissement et la persistance de l'anadromie. [Traduit par la Rédaction]

Introduction

Several species of salmonids exhibit partial anadromy, where one fraction of the population migrates to the ocean (i.e., anadromous tactic), while the other matures in fresh water with no marine migration (i.e., resident tactic) (Jonsson and Jonsson 1993). While the ultimate causes of niche shifts within such populations are more obvious (to maximize fitness), the proximate mechanisms controlling the shifts are under debate. A common observation in studies of partial anadromy in fishes is that migrants and residents differ in body size and growth (e.g., Atlantic salmon (*Salmo salar*): Thorpe et al. 1998; ciscoes (*Coregonus* spp.): Mehner and Kasprzak 2011). In salmonids, under some extraordinary circumstances such as access to abundant resources and stable conditions for development, faster growth early in life can result in early maturation and residency (Olsson and Greenberg 2011; McMillan et al. 2012). In most cases,

however, larger fish migrate to the ocean, while smaller fish stay as residents for 1 or several more years (Nicieza et al. 1991; Hecht et al. 2012).

The expression of alternative migratory tactics in salmonids depends on both genetic and environmental variation (reviewed in Dodson et al. 2013). The influence of environmental factors on fish growth and their propensity to migrate has been reported in several studies. For example, Olsson et al. (2006) found that food availability, through its effect on growth, was highly related to the adoption of anadromy in a brown trout (*Salmo trutta*) population. In rainbow trout (*Oncorhynchus mykiss*), variation in the incidence of anadromy and residency in response to factors such as stream order, water temperature, and elevation (e.g., Narum et al. 2008; Mills et al. 2012) also reveals that life history variation is related to environmental factors. There is also considerable evidence for

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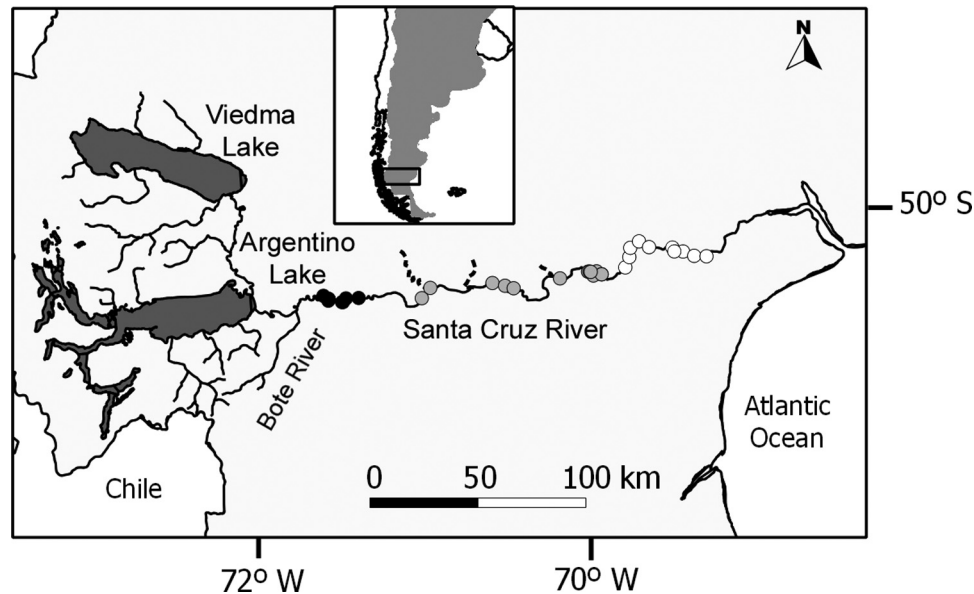
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Fig. 1. Location of study area and sites sampled in the upper (black dots), middle (grey dots), and lower (white dots) sections along the Santa Cruz River.



strong genetic control over growth-related traits and heritability of anadromy. For example, much of the genetic variance in body size is shared with the propensity for anadromy in brook trout (*Salvelinus fontinalis*) (Thériault et al. 2007). In *O. mykiss*, Nichols et al. (2008) and Hecht et al. (2012) found evidence of genetic control on physiological and morphological changes associated with smoltification, such as growth and body morphology.

Another important source of variation in juvenile condition is related to maternal investment and behavior (i.e., maternal effects, Bernardo 1996). As a result of the niche shift from fresh water to the ocean, migration often enables individuals to attain high growth rates, size-at-age, and fecundity (Zimmerman and Reeves 2000; Hendry et al. 2004). The differences between anadromous and resident females can result in profound differences in egg quality, choice of spawning habitats, and breeding time (Fleming and Reynolds 2004). Patterns of offspring provisioning (e.g., lipid storage in eggs) and selection of the biophysical spawning habitat, which determines the offspring's rearing environment following hatching, may affect early phenotypic expression, leading to variation in growth and metabolic rates and pathways of energy utilization (Einum and Fleming 1999; Régner et al. 2010; Houde et al. 2011). Maternal effects and their influence on offspring condition have been detected until advanced juvenile stages. For example, Serbezov et al. (2010) demonstrated that parental effects on their offspring's length-at-age lasted for more than 2 years in *S. trutta*. In turn, such influences on juvenile development may affect the propensity to migrate and, ultimately, the incidence of anadromy in the population.

The Santa Cruz River (Patagonia, Argentina) sustains an introduced population of rainbow trout that has re-created both anadromous and nonanadromous life histories, one of the rare examples of established anadromy outside the species' native range (Pascual et al. 2001). Genetic analyses have revealed that anadromous and resident forms in this population shared a common genetic origin derived from anadromous and nonanadromous sources introduced from rivers in California, USA (Riva-Rossi et al. 2004). The two forms are now genetically indistinguishable (Pascual et al. 2001) and can give rise to either life history (Riva-Rossi et al. 2007). These studies have provided evidence supporting the idea that the re-creation of the anadromous life history has been favored by both the genetic constitution of introduced fish (lineages with a tendency for anadromy) and environmental causes (e.g., free access to the ocean coupled with higher productivity of surrounding marine areas in relation to freshwater

habitats) (Riva-Rossi et al. 2007). However, mechanisms and proximate causes underlying the successful establishment and maintenance of the anadromous tactic in this river remain unknown. The goal of this study was to understand the role of anadromous maternal influences on juvenile body size and growth trajectories and, ultimately, on the persistence of the anadromous life history tactic in the *O. mykiss* population of the Santa Cruz River. Our two main hypotheses are that (i) growth performance and body size of juveniles is related to their maternal tactic (anadromous versus resident) and (ii) faster growth rates and larger body size during the juvenile stage of anadromous progeny are linked to the expression of the anadromous tactic. We combined two complementary analyses to evaluate these hypotheses. First, we used data on juvenile rainbow trout caught in the Santa Cruz River to evaluate the strength of the association between the maternal tactic and body size and growth patterns of their offspring. Second, we also back-calculated juvenile body size at age 1 for adults of known anadromous and resident ecotypes from the same river to examine the relationship between adoption of anadromy and body size during juvenile development.

Materials and methods

Study site and population structure

The Santa Cruz basin in Patagonia, Argentina (Fig. 1), is dominated by two large glacial-fed lakes, Viedma and Argentino; numerous second- to third-order tributaries feed these lakes, and landlocked populations of rainbow trout inhabit most of these streams. The Santa Cruz River (mean flow $690 \text{ m}^3 \cdot \text{s}^{-1}$, range $300\text{--}2000 \text{ m}^3 \cdot \text{s}^{-1}$) flows for 382 km across the Patagonian plateau to drain into the Atlantic Ocean (Fig. 1). River discharge is derived primarily from snow and glacial melt (Consejo Federal de Inversiones 1961), and only one permanent tributary enters the main stem in the upper section (Bote River, 26 km from headwater, Fig. 1). The Santa Cruz River has been described as a homogenous river with overall uniformity in environmental variables (e.g., slope, dissolved oxygen, conductivity) that provides poor conditions for fish growth (i.e., lowest macroinvertebrate density in comparison to 42 other Patagonian rivers; Tagliaferro et al. 2013). There are no barriers to fish migration along the river. Mean water temperature is $9 \text{ }^\circ\text{C}$, with maxima in January ($15.3 \pm 0.6 \text{ }^\circ\text{C}$, mean \pm standard deviation (SD), $N=7$ years) and minima in July ($3.1 \pm 0.1 \text{ }^\circ\text{C}$).

Table 1. Number of individual fish per stage, month of capture, and river section assigned to each alternative maternal origin (anadromous or resident) by stable isotope and otolith microchemical analyses.

Stage	Age (months)	Month of capture (cohort)	Season	Anadromous				Resident				
				U	M	L	Total	U	M	L	Total	
Fry	1–3	Nov. (2008)	Spring	28	10	0	38	15	0	0	15	
		Nov. (2009)	Spring	16	31	—	47	1	0	—	1	
YOY	5–7	Apr. (2009)	Autumn	19	5	—	24	14	8	—	22	
		7–9	June (2008)	Autumn	18	10	8	36	4	2	2	8
			Sept. (2009)	Spring	15	38	15	68	2	6	9	17

Note: River sections are as follows: upper section (U), rkm 55–110; middle section (M), rkm 155–210; and lower section (L), rkm 240–280. A dash (—) denotes that the section was not visited that month.

The rainbow trout population of the Santa Cruz River has been monitored since 1998 using gillnet sampling, radio tracking, and electrofishing surveys coupled with sampling of the sport fishery. Adult surveys throughout 2000, 2001, and 2004 conducted in the upper (rkm 40–70) and midsections of the main stem (rkm 155–210) showed that most areas are inhabited by mature fish of mixed life history ($N = 74$ females plus 77 males), with major contributions of anadromous fish (86% of mature females and 73% of mature males were anadromous) (M. Pascual and C. Riva-Rossi, unpublished data).

These surveys also showed that most of the anadromous fish in this river migrate to sea after 2 years of freshwater residency (age 2+), and reproduction of resident fish occurs predominantly at age 3+ (Riva-Rossi 2004). Life history reconstructions based on strontium:calcium (Sr:Ca) profiles in otoliths ($N = 14$, Riva-Rossi et al. 2007) and scale pattern analysis ($N = 211$, Riva-Rossi 2004) showed that once the anadromous lifestyle is initiated, fish continue migrating annually to and from the ocean and show no tendency to resume residency. During the spawning migration, anadromous adults generally enter the river in March (fall season), but spawning does not begin until July (mid-winter) and peaks in September (spring). No resident spawning aggregations or grounds were registered, but sneaking males were frequently observed in anadromous spawning grounds.

Body length distributions, scale pattern analysis, and reproductive studies indicated that in this river, anadromous fish are much larger (635 versus 350 mm fork length (FL) mean body size), significantly more iteroparous (8 versus 4 mean number of spawning events) (Pascual et al. 2001), and have larger eggs than resident fish (0.12 ± 0.01 g versus 0.07 ± 0.02 g mean egg size and 95% confidence interval (CI) for anadromous and resident fish, respectively) (Liberoff et al. 2011).

Fish collection and sample preparation

We followed two cohorts of juvenile fish in 2009 and 2010 during their first year of life. We captured fish at the fry stage (~1–3 months old) in spring 2008 and 2009 (December in the Southern Hemisphere) and young of the year (YOY) in autumn (June 2009 and April 2010) and spring (September 2010) (Table 1). YOY captured in autumn and spring were born during spring of the previous year, so YOY captured in 2009 are referred to as cohort 2008 and YOY captured in 2010 are referred to as cohort 2009. Fish were collected with electrofishing gear at several sites along the Santa Cruz River (Fig. 1). Fish were euthanized with an overdose of MS-222 (tricaine methanesulfonate, $1 \text{ g}\cdot\text{L}^{-1}$). Samples were immediately frozen at -20°C until laboratory preparation. In the laboratory, fish were measured (FL, nearest mm), and stomach contents of fry were removed to avoid bias in stable isotope analysis because of the presence of prey items in the sample. The carcasses of fry were dried at 60°C until constant mass was achieved. Dried carcasses were ground into a fine powder with mortar and pestle for stable isotope analysis for maternal origin determination. Otoliths were collected for maternal origin determination, and otoliths of fry were used for structural analysis and growth estimation. Scales from an area below the posterior margin of the dorsal fin and five scale rows above the

lateral line were collected to estimate individual growth trajectories for YOY.

To evaluate whether propensity for anadromy is related to body length at the juvenile stage, we estimated length at age 1 for adult fish of known anadromous and resident phenotypes. Adult fish were captured with gillnets at several sampling sites in the upper (rkm 55–110), middle (rkm 155–210), and lower (rkm 240–280) sections of the Santa Cruz River from 1996 to 2005. Anadromous ($N = 152$) and resident ($N = 70$) fish were identified according to morphological differences such as body size and color patterns, and the classification was later confirmed by scale pattern analysis as described in Riva-Rossi et al. (2007). Fish were measured (FL, nearest mm), and scales were collected for back-calculation analysis.

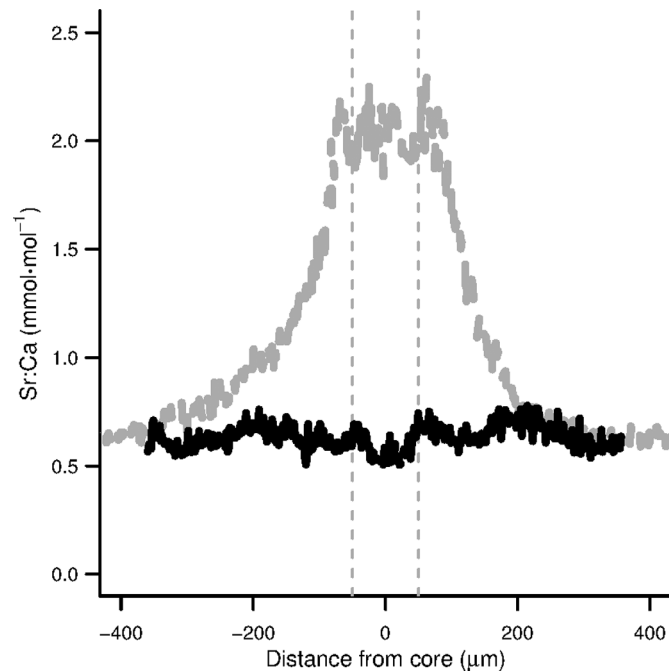
Maternal origin determination

To assess the association between the anadromous or resident maternal tactic and growth and body size variability in the progeny, we determined the maternal origin of juvenile fish with two complementary methodologies. Natural abundance stable isotope analysis of nitrogen in muscle tissue was used to determine maternal origin of fry. The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures in muscle tissue during fish emergence are derived from the yolk sac and should reflect the mother's feeding environment (Doucett et al. 1999). Stable isotope signatures of maternal sources in muscle tissue of anadromous fish are eventually diluted by freshwater dietary input; thus the maternal marine signature in these fish becomes indistinguishable from resident progeny as residence time in the river increases (Doucett et al. 1999). Fry relying on yolk sac and showing no evidence of exogenous feeding in otoliths ($N = 85$; see below in Juvenile growth and body size variability section) were classified as anadromous or resident offspring according to their similarity with adult $\delta^{15}\text{N}$ signatures (adult resident $\delta^{15}\text{N} = 8.4\text{‰} \pm 0.8\text{‰}$, adult anadromous $\delta^{15}\text{N} = 14.9\text{‰} \pm 0.7\text{‰}$, mean \pm SD, Ciancio et al. 2008). For all YOY ($N = 175$) and for fry showing evidence of exogenous feeding and diluted maternal signatures ($\delta^{15}\text{N} < 15\text{‰}$ but $> 8.4\text{‰}$; $N = 16$), maternal origin was determined based on microchemical analysis of the otolith core. Stable isotope analysis is easier, less expensive, and faster to conduct than otolith microchemical analysis; thus, we conducted stable isotope analysis when possible.

For isotopic analyses, 0.1–0.5 mg of ground, dried tissue was placed into 3.5 mm \times 5 mm tin capsules, followed by combustion in an elemental analyzer (Carlo Erba NC2500) coupled to a Thermo Fisher Delta V Plus isotope ratio mass spectrometer at the Geophysical Laboratory, Carnegie Institution, Washington, D.C., USA. Stable isotope ratios are expressed as $\delta^{15}\text{N}$ (Mariotti 1983). The working standard was acetanilide ($\delta^{15}\text{N} = 1.8\text{‰}$). Repeated analyses of the standard during these analyses had a standard deviation of ± 0.16 ($N = 20$).

Maternal origin determination by otolith chemical analysis is based on the fact that the Sr:Ca ratio is typically greater in marine waters than in fresh water (Kalish 1990). Sr:Ca levels in otolith primordia are determined by the Sr and Ca content of the waters where vitellogenesis took place. Therefore, if natal river Sr:Ca

Fig. 2. Typical Sr:Ca ratio ($\text{mmol}\cdot\text{mol}^{-1}$) profile along the otolith growth axis for maternal origin determination. Sr:Ca ratios for a fish of anadromous origin (grey points) and a fish of resident maternal origin (black points) are shown to illustrate typical profiles. Dashed lines enclose the central core region that is influenced by maternal compounds.



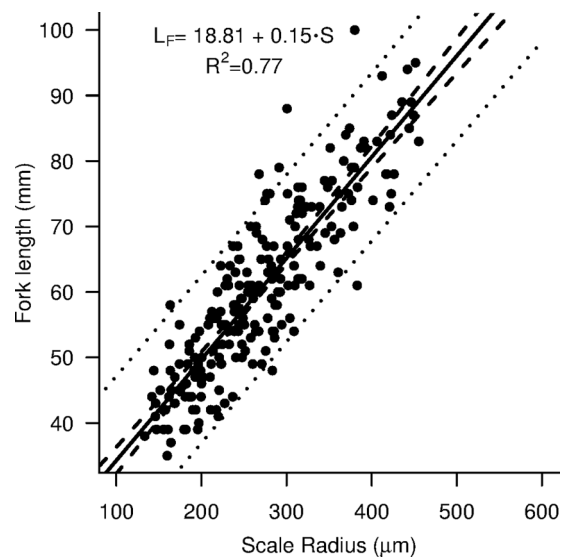
is distinct from marine Sr:Ca, the maternal origin of individual fish can be determined at any age by analyzing the chemical composition of the otolith core. In most systems, Sr:Ca in the otolith core is higher for the progeny of females that mature in sea water and lower for progeny of females that mature in fresh water (Kalish 1990). Microchemical analysis of otolith cores for maternal determination in this population was validated by Riva-Rossi et al. (2007).

For Sr:Ca analysis, one otolith per individual was cleaned, mounted sulcus side down on a glass slide using a transparent mounting medium, and polished using 3 and 9 μm lapping film until all primordia were clearly exposed. Sr and Ca were measured along the otolith growth axis using a Thermo X-series II inductively coupled plasma mass spectrometer and a Photon Machines G2 193 nm excimer laser system with time-resolved data acquisition (WM Keck Collaboratory for Plasma Spectrometry, Oregon State University, Corvallis, Oregon, USA). The laser was set at a pulse rate of 7 Hz with a 40 μm ablation spot size and travelled at 7 $\mu\text{m}\cdot\text{s}^{-1}$. Normalized ion ratios were converted to molar ratios based on our measurements of known mean elemental concentrations of National Institute of Standards and Technology (NIST) 612 glass standards and the molar mass of Sr and Ca. The mean percent relative SDs for glass standards were $^{43}\text{Ca} = 4.2\%$ and $^{86}\text{Sr} = 4.7\%$. Progeny were classified as anadromous or resident according to their Sr:Ca profile along the growth axis (Fig. 2). When the profile showed an abrupt increase in Sr:Ca ratios to levels $\geq 1 \text{ mmol}\cdot\text{mol}^{-1}$ in the core region (central 100 μm), the individual was classified as anadromous progeny. On the contrary, when a homogeneous profile of relatively low levels of Sr:Ca was observed, the individual was assigned as resident progeny (Fig. 2).

Juvenile growth and body size variability

Estimations of growth were completed for both fry and YOY stages. For fry captured in 2008 and 2009, length-at-age was estimated through otolith structural analysis. For this purpose, FL

Fig. 3. Scale radius – body length relationship for YOY *Oncorhynchus mykiss* in the Santa Cruz River used for back-calculation methods. Continuous line represents the regression line ($\text{SE}_{\text{intercept}} = \pm 1.555$, $\text{SE}_{\text{slope}} = \pm 0.005$); dashed lines represent the 5% and 95% confidence intervals, and dotted lines the 5% and 95% prediction intervals.



and age (days) estimated from daily otolith increments were used (Campana 1983). Otoliths polished for Sr:Ca analysis were visually examined under a transmitted light microscope (400 \times magnification) with an image analysis system. Hatching and first-feeding check marks were identified as described in Liberoff et al. (2013). Total number of increments between hatch mark and the edge of the otolith (posthatch age) and total number of increments from first-feeding mark to the edge of otolith (exogenous age) were enumerated. All measurements were conducted along the longest antero-posterior axis.

For YOY stage, we compared lengths at capture of fish assigned as resident and anadromous progeny captured in June 2009 and April and September 2010 with two-way analysis of variance (ANOVA). In addition, to evaluate differences in growth pathways between anadromous and resident offspring, we reconstructed individual growth trajectories of collected YOY in autumn 2009 and 2010 using scale measurements and fitting linear mixed-effects model (LME). Several scales per individual were mounted on a glass slide, projected by a microfiche reader at a magnification of about 55 \times , and photographed. The spacing between successive pairs of circuli was measured along the longitudinal anterior axis, from the midpoint of the focus to the scale edge, with imaging software (ImageJ, National Institutes of Health, Bethesda, Maryland, USA; <http://rsb.info.nih.gov/ij/>). Fork length was regressed against total scale radius in the juvenile stage to examine whether there was a relationship between fish length and scale size, a necessary assumption for estimating fish growth from scale circulus spacing. This relationship was significant and positive (slope = 0.15, $R^2 = 0.77$, $P < 0.001$, Fig. 3), and evaluation of residual plots indicated that the relationship was linear.

Linear mixed-effects model

To contrast our ecological hypothesis of different growth patterns between anadromous and resident progeny, we fitted an LME. Mixed-effects models are especially suitable for growth data, because they are robust when certain assumptions regarding the form of associations within subjects (lack of independence between repeated measurements) are not met. Models were fitted and inferences were done through likelihood-based methods using the nlme package (Pinheiro et al. 2012) in R (version 2.15.1, R Development Core Team 2013).

Table 2. Model selection to evaluate cohort growth variation and maternal origin effects on individual growth trajectories fitted to spacing between circuli data of fish scales as a function of time.

Model	Fixed-term description	Fixed-term structure	df	ΔAIC	AIC weight
M1	Maternal origin and cohort effects on all three parameters; cohort and maternal origin interaction	$(\beta_0 + \gamma_{0k} + \delta_{0i}) + (\beta_1 t_{ij} + \gamma_{1k} + \delta_{1i}) + (\beta_2 t_{ij}^2 + \gamma_{2k} + \delta_{2i}) + (\gamma_k \times \delta_i)$	20	5.8	0.037
M2	Maternal origin effect on intercept and quadratic term; cohort effect on all three parameters; cohort and maternal origin interaction	$(\beta_0 + \gamma_{0k} + \delta_{0i}) + (\beta_1 t_{ij} + \delta_{1i}) + (\beta_2 t_{ij}^2 + \gamma_{2k} + \delta_{2i}) + (\gamma_k \times \delta_i)$	17	0.0	0.670
M3	Maternal origin effect on intercept and quadratic term; cohort effect on all three parameters; no interaction	$(\beta_0 + \gamma_{0k} + \delta_{0i}) + (\beta_1 t_{ij} + \delta_{1i}) + (\beta_2 t_{ij}^2 + \gamma_{2k} + \delta_{2i})$	15	4.0	0.091
M4	Maternal origin effect on slope; cohort effect on all three parameters; cohort and maternal origin interaction	$(\beta_0 + \gamma_{0k} + \delta_{0i}) + (\beta_1 t_{ij} + \delta_{1i}) + (\beta_2 t_{ij}^2 + \delta_{2i}) + (\gamma_k \times \delta_i)$	16	3.0	0.148
M5	No maternal origin effect on growth; cohort effect on all three parameters	$(\beta_0 + \delta_{0i}) + (\beta_1 t_{ij} + \delta_{1i}) + (\beta_2 t_{ij}^2 + \gamma_{2k} + \delta_{2i})$	14	5.0	0.055
M6	No effect of maternal origin or cohort on growth	$\beta_0 + \beta_1 t_{ij} + \beta_2 t_{ij}^2$	11	25.5	<0.001

Note: The growth trajectory was estimated fitting a quadratic curve with intercept (β_0), linear term (β_1), and quadratic term (β_2) parameters. γ_{0k} , γ_{1k} , and γ_{2k} correspond to maternal origin effects on growth parameters, and δ_{0i} , δ_{1i} , and δ_{2i} correspond to variation in growth due to cohort effects. Models incorporate both random (all terms varying randomly with each fish) and fixed terms (mixed-effects models). Akaike information criteria score (ΔAIC), Akaike weight, and degrees of freedom (df) are given for each model.

For this study, growth trajectories of collected YOY were estimated by modeling the incremental circuli spacing across the scale, using a linear quadratic model, with all three parameters varying randomly for each individual: $Y_{ij} = \beta_0 + \beta_1 t_{ij} + \beta_2 t_{ij}^2 + b_{0i} + b_{1i} t_{ij} + b_{2i} t_{ij}^2 + \varepsilon_{ij}$, where Y_{ij} is the incremental circuli spacing (μm); β_0 , β_1 , and β_2 correspond to the population mean intercept, slope, and quadratic term, respectively; and b_{0i} , b_{1i} , and b_{2i} are the individual random intercept, slope, and quadratic term, respectively, assumed to be independent for different i . t_{ij} represents the incremental circuli, and ε_{ij} is the within-group error, assumed to be independent for different i , j , and independent of the random effects. Fixed terms were added to evaluate variation in growth trajectories due to maternal origin, where γ_{0k} , γ_{1k} , and γ_{2k} account for the mean difference in intercept, slope, and quadratic term, respectively, between progeny of anadromous and resident mothers. Similarly, to evaluate growth variation between years, fixed effects accounting for year of birth (cohort) were included in the model, where δ_{0i} , δ_{1i} , and δ_{2i} account for the mean difference in intercept, slope, and quadratic term between cohorts in 2008 and 2009.

The fitting routine consisted of a series of six models that are defined in Table 2. The complex model with maternal influences, year-class variation, and their interaction (M1, Table 2) allowed us to examine the error structure and check assumptions of normality and homogeneity of variance. Given that the analysis of model residuals showed a pattern in measurement variability with the covariate (circulus), we fitted a “power of the covariate” variance structure, which significantly improved model goodness-of-fit (ΔAIC = 39.6). To test the contribution of maternal origin and cohort to overall growth variance, we extracted sequentially one effect at a time (M2 to M5) starting from the complex model (M1) and compared models’ goodness-of-fit using the Akaike information criterion (AIC) and Akaike weights (Akaike 1974; Pinheiro and Bates 2000).

Adult body size back-calculation

To assess whether anadromy in the Santa Cruz River was positively correlated with body size at the end of the first year of life, which is the beginning of spring, 21 September in the Southern Hemisphere, we estimated size at age 1 from adult scale measurements. Several cleaned scales from each specimen were pressed on acetate sheets with heated plates; circuli impressions were highlighted by the application of ink, magnified on a microfiche reader, and photographed. Annual marks (annuli) and migration checks were recognized using general criteria for temperate fish

(Tesch 1971) and experience with Santa Cruz River *O. mykiss* (Riva-Rossi et al. 2007). All anadromous fish included in this analysis showed migration checks at age 2+. The radii corresponding to each annuli were measured from the nucleus and along the longitudinal anterior axis of the scale.

Back-calculation of adults length at age 1 was performed through the regression approach (Campana 1990). This method estimates FL_i at some previous age i through insertion of the measured scale radius into a fish length – scale radius regression derived from samples of the population (Campana 1990). Although this procedure assumes no deviation of individual fish and scale measurements from overall regression, sources of error associated with the estimation of body size at an earlier time (e.g., violation of proportionality between scale and body growth) are reduced, given that no assumptions are made after the estimation interval (after age 1 in this particular case). In addition, the regression method provides a useful tool when mean back-calculated lengths, rather than individual values, are of importance (Campana 1990).

Predictions of length at age 1 given scale radius at first annuli were done using the relationship shown in Fig. 3. Assumption of proportionality between scale and body length was met (regression, $P < 0.001$), and linearity was confirmed by inspection of residual plots.

Results

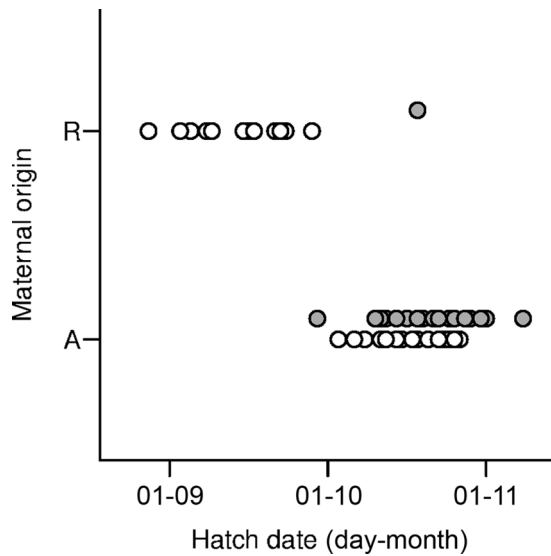
Maternal origin determination

The combination of nitrogen stable isotopes and otolith microchemical analyses allowed us to determine maternal origin for 281 individuals in the first year of development (Table 1). Fry with enriched $\delta^{15}\text{N}$ and no evidence of exogenous feeding were all classified as anadromous progeny ($16.4\% \pm 1.2\%$, mean \pm SD), whereas fry with diluted $\delta^{15}\text{N}$ signatures and YOY were classified according to their Sr:Ca ratio profile. The marine Sr:Ca ratios in the otolith core zone (Fig. 2) was $1.326 \pm 0.046 \text{ mmol}\cdot\text{mol}^{-1}$ (mean \pm 95% CI) for the anadromous group and $0.764 \pm 0.036 \text{ mol}\cdot\text{mmol}^{-1}$ for the resident group.

Early stage development

Fry captured in 2008 and 2009 were predominantly of anadromous origin (84.2% in 2008 and 98% in 2009; Table 1). Fry of anadromous and resident origin showed different spatial patterns; fry of anadromous mothers were captured in the middle and upper sections, while fry of resident mothers were only captured in the upper section (Table 1). In addition, all fry of resident origin

Fig. 4. Hatch dates of anadromous (A) and resident (R) offspring of cohorts 2008 (white dots) and 2009 (grey dots).



captured in 2008 were residing in secondary channels and shallow bays, whereas most of the anadromous offspring were captured along the main stem (100% in 2008 and 68% in 2009). In 2009, the secondary channel in the upper section, where we captured most of the fry of resident offspring the year before, was not carrying water. Therefore, although we covered the same area and sites between years, only one fry was assigned as resident offspring and was captured in the main stem (Table 1).

Otolith analysis of captured fry provided estimates of days since hatch (posthatch age), days since the beginning of the exogenous feeding (exogenous age), and back-calculated hatch date. Fry of resident origin captured in 2008 were significantly older than those of anadromous origin ($t_{17,1} = -9.3$, $P < 0.001$; 70.50 ± 4.61 days, 38.96 ± 2.17 days, mean posthatch age \pm 95% CI, for resident and anadromous progeny, respectively). Posthatch age differences resulted from a significant temporal segregation in hatching dates; resident offspring started hatching at the end of winter, whereas anadromous progeny started later in the spring, with no overlap between them (Fig. 4). In 2009, the only fry assigned as resident offspring did not differ in its hatch date from anadromous counterparts captured that year (Fig. 4).

Anadromous and resident offspring differed in their life stage at capture. One hundred percent of the otoliths of resident offspring displayed exogenous feeding checks, whereas only 35% of fish of anadromous origin were feeding exogenously (Fig. 5). In addition, resident offspring captured in 2008 had been feeding on freshwater items for a longer period than their anadromous counterparts ($t_{19,6} = -18.4$, $P < 0.001$; 39.58 ± 3.21 days, 2.58 ± 1.58 days, mean exogenous age \pm 95% CI for resident and anadromous progeny, respectively) (Fig. 5). Finally, although anadromous and resident progeny differed in estimated age, hatch date, and life stage, they did not differ in length at capture ($t_{20,4} = -1.09$, $P > 0.05$, Fig. 5), with fry of anadromous origin being larger at age than their counterparts.

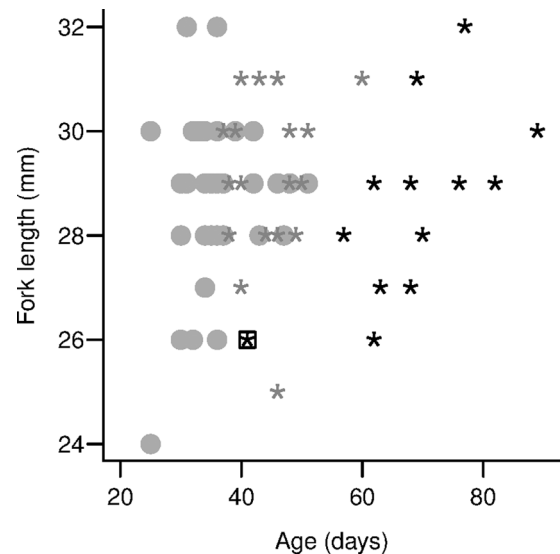
Young of the year

As observed for fry, YOY captured in autumn and spring were predominantly from anadromous mothers (overall 73%, Table 1). However, at this stage, fish of both maternal origins were captured along the entire longitudinal gradient (Table 1).

Body size variability

Size of YOY collected during the first year of development varied between 39–98 mm and 39–83 mm for anadromous and resi-

Fig. 5. Body length against estimated age for anadromous progeny (grey symbols) and resident progeny (black symbols). Asterisks represent fish feeding exogenously, and circles are fish that show no evidence of exogenous feeding. Fry of resident offspring captured in 2009 are indicated by a square symbol.



dent offspring, respectively (Figs. 6a–6c). Anadromous offspring displayed greater variation in size (Figs. 6a–6c) and were larger than resident offspring throughout the first year of development (two-way ANOVA, $F_{\text{maternal origin}, 1} = 43.9$, $F_{\text{month}, 2} = 32.4$, $P < 0.001$; $F_{\text{interaction term}, 2} = 0.1$, $P > 0.05$).

Growth trajectories

Analysis of scale growth increments of YOY captured in autumn ($N = 90$, Table 1) revealed that progeny of anadromous females had larger scale size, and a larger estimated body size, than resident offspring during the first 6 months of development (Fig. 7). Based on LME modeling approach, the model that best described growth trajectories of juveniles included cohort effects on all model parameters, maternal phenotype effects on slope and on the quadratic term and an interaction term between maternal phenotype and cohort effects (M2, Table 2). Judging from the performance criteria, reduced models without an interaction term (M3) and without a maternal origin effect on the quadratic term (M4) received considerably less support ($\Delta\text{AIC} > 5$, Table 2). The extraction of any other fixed effect also resulted in models with less support ($\Delta\text{AIC} > 7$, M5, M6; Table 2). The model selected (M2, $\text{AIC}_{\text{weight}} = 0.67$) suggests that early growth variation is related to maternal origin, but the magnitude of initial advantages varies with cohort (Fig. 7). Growth patterns also differed between years, with cohort 2008 having larger scale size at age and faster growth than cohort 2009 (Fig. 7).

Adult body size back-calculation

Analysis of adult back-calculated length at age 1 was performed on 152 anadromous and 70 resident fish. Capture FL varied from 380 to 820 mm for anadromous fish and from 237 to 440 mm for resident fish, and age ranged from 3 to 10 years for anadromous fish and from 3 to 7 years for resident fish. Back-calculation analysis revealed similar body length patterns to those of juveniles, with anadromous fish exhibiting larger body size at age 1 than resident fish ($t_{127,7} = -4.14$, $P < 0.001$; 66.5 ± 1.6 mm, 60.2 ± 2.51 mm, mean \pm 95% CI for anadromous and resident fish, respectively; Fig. 6d).

Fig. 6. Box plots for fork length of YOY captured in (a) April 2010, (b) June 2009, and (c) September 2010, where “A” and “R” represent progeny of anadromous and resident mothers, respectively, and (d) back-calculated length at age 1 for anadromous and resident adults. The central rectangle spans the first quartile to the third quartile; the segment inside the rectangle shows the median; whiskers show the locations of the minimum and maximum; and points represent outliers.

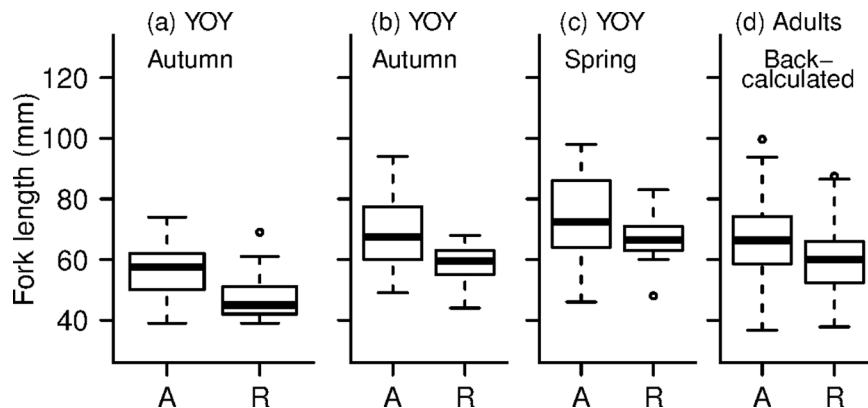
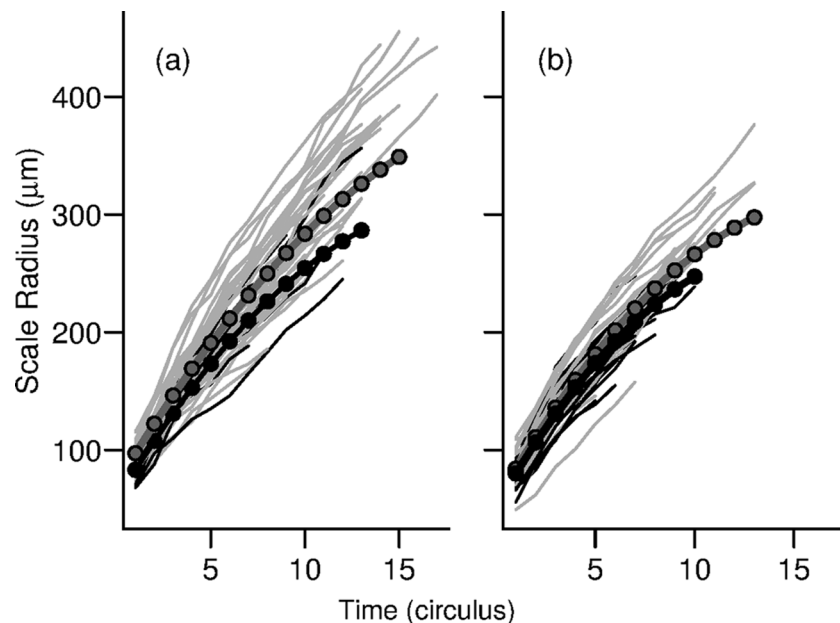


Fig. 7. Observed (thin lines) and estimated (lines with dots) growth patterns (fixed effects extracted from the linear mixed-effects model) for anadromous (grey lines with dots) and resident progeny (black lines with dots) captured in autumn for (a) cohort 2008 and (b) cohort 2009.



Discussion

This study supports the hypothesis of a strong association between maternal anadromy and offspring growth and size; offspring of anadromous mothers were larger at age than their counterparts from very early stages, and body size differences persisted throughout the first year of development. In addition, adult back-calculation showed a positive relationship between the anadromous tactic and body size at age 1. Altogether, these analyses provide evidence of fish propensity for anadromy being related to the maternal migratory phenotype in a wild population of partially anadromous rainbow trout.

The early growth advantages in anadromous offspring detected in the present study have also been reported in other partially anadromous populations of salmonids (e.g., Chernoff and Curry 2007; Jardine et al. 2008). Anadromous offspring size advantages have been linked to nongenetic maternal effects (e.g., Aubin-Horth and Dodson 2004) primarily as a consequence of variation in egg size (e.g., Gilbey et al. 2005; Evans et al. 2010). For example, it has been shown that larger brown trout females produce larger eggs that in turn produce larger juveniles (Einum and Fleming 1999). Because the larger juve-

niles are able to acquire and defend better feeding territories, this size advantage is transferred into a later fitness advantage (higher growth and survival), especially under arduous conditions (Einum and Fleming 1999). Given the striking differences in growth-related egg size differences between anadromous and resident females in the Santa Cruz River, length-at-age differences detected in the fry stage might be a consequence of higher relative maternal investment of anadromous females.

Other mechanisms such as temporal and spatial segregation between anadromous and resident females might have also contributed to variation in their offspring’s body size and growth. Results for fry captured in 2008 suggest great variation in hatch dates, which might have arisen as a consequence of temporal segregation in spawning events. In addition, fry of anadromous mothers were captured predominantly in the main stem, whereas fry of resident mothers were mostly captured in secondary channels. However, given that these segregation patterns were only registered in one season (2008), we can only conclude that partial segregation of spawning might occur at the microhabitat scale, but we cannot assure that isolation mechanisms between life his-

tory forms are present. Moreover, YOY of both anadromous and resident origins were found along the entire longitudinal gradient, indicating that there is spatial overlap in breeding activity at larger spatial scales, as previously indicated by radiotelemetry and spawning surveys in this population (Riva-Rossi et al. 2003; M. Pascual and C. Riva-Rossi, unpublished data).

Microsatellite analysis on 7 loci and 47 individuals in one study (Pascual et al. 2001) and 14 loci and 235 individuals in another (C. Riva-Rossi, unpublished data) provide strong evidence of lack of genetic differentiation ($F_{ST} = -0.003$ and -0.0015 , respectively) between forms in this river. Riva-Rossi et al. (2007) determined the maternal origin of adult anadromous and resident fish and found a high level of life history reversals: four adult anadromous fish out of 14 were from resident mothers, whereas two adult resident fish out of six were from anadromous mothers. These studies suggest that anadromy and residency in this river are alternative phenotypes of a single population and that any individual may potentially adopt the anadromous or resident life history, but as the present study suggests, the probability of expressing either life history is related to maternal origin. In addition, interbreeding between life history forms reported for this (Riva-Rossi et al. 2003) and other populations (e.g., Pearsons et al. 1997) of salmonids might also contribute to high gene flux between forms. Therefore, temporal and spatial spawning segregation patterns reported here might not be strong enough to overcome genetic flux between forms. Alternatively, given that the Santa Cruz River population originated approximately 25 generations ago, it is plausible that alternative life histories are reflecting transitional states (Riva-Rossi et al. 2007). Therefore, we cannot discard the possibility that spatial and temporal segregation mechanisms could potentially lead to future reproductive isolation between the anadromous and resident forms.

Through otolith microchemical analysis we could only identify the maternal origin; therefore, it is unknown whether resident males contributed to the anadromous fraction and vice versa. In sympatric partially anadromous populations, anadromous females mostly breed with anadromous males; however, resident males might successfully breed with anadromous females through a “sneaking” behavior (Pearsons et al. 1997). Given that sire body size has been positively related to size of offspring (Heath et al. 1999; Serbezov et al. 2010), it is possible that anadromous males mating with anadromous females may have contributed to enhanced growth and size of their offspring.

Both maternal and paternal influences could be also attributed to inheritance of growth-related traits (Heath et al. 1999; Olsen and Vøllestad 2001). Evidence of genetic basis of size at hatching and growth rates, mostly during embryonic development, suggests that genetic factors might have also influenced growth in anadromous progeny. However, other studies have concluded that differences between offspring phenotypes, such as those seen in this study, may in fact result from a combination of the propagation of early differences driven by maternal effects, reinforced by direct genetic factors, either paternally or maternally inherited, that are expressed during offspring development (Thériault and Dodson 2003; Hecht et al. 2012). Both maternal effects and heritability of quantitative traits have been shown to vary depending on environmental conditions, with maternal effects increasing in magnitude and some traits having lower heritability in unfavourable habitats (Aubin-Horth and Dodson 2004, reviewed in Carlson and Seamans 2008). The Santa Cruz River basin is an extremely unproductive basin (Miserendino 2001; Tagliaferro et al. 2013) where growth opportunities are limited; therefore, conditions for low heritability in quantitative traits and augmented maternal effects are met.

We also examined the relationship between juvenile body size and the future adoption of anadromy. Estimation of fish size at age 1 from adult scales supports the hypothesis of a positive relationship between body size at the juvenile stage and propensity for anadromy. Adult back-calculated length-at-age showed that larger age 1 fish ad-

opted the anadromous life history, while smaller age 1 fish adopted the resident tactic, a pattern that has been seen in other partial migratory populations of salmonids (e.g., Nicieza et al. 1991; Páez et al. 2011). However, the overlap in back-calculated lengths at age 1 for anadromous and resident adults indicates that even small fish could reach a minimum size for emigration if they accelerated growth during their second year in fresh water. Therefore, progeny of resident mothers could also adopt the anadromous life history and progeny of anadromous mothers could also stay in fresh water, which is consistent with life history reversals reported for this population (Riva-Rossi et al. 2007).

The back-calculation method provided a useful tool for our purpose of comparing groups; however, the comparison of juvenile fish captured in cohorts 2008 and 2009 with cohorts ~10 years apart could introduce variation in our analysis. Although the differences in estimated mean age 1 length between anadromous and resident adults are consistent, it is possible that freshwater growth performance and (or) environmental factors have changed over the years. Such variation could have led to changes in length distributions at age 1, such as the difference observed between YOY captured during spring and adult back-calculated lengths (Figs. 6c–6d). In the future, it will be possible to reconstruct length distributions from 2008 and 2009 cohorts that were sampled as juveniles and provide further information to evaluate population trends and also evaluate the effect of size-selective mortality after age 1.

In many salmonid populations with both anadromous and resident individuals, the larger juveniles usually smolt and migrate to sea, while the smaller individuals often become resident and mature in fresh water (Nicieza et al. 1991; Hecht et al. 2012). In some cases, however, the early-maturing individuals may be larger than nonmaturing fish (Aubin-Horth and Dodson 2004). This variation in the relationship between growth and future life history indicates that not only growth (or body size), but also metabolic rate, lipid stores, social status, and several ecological factors in the local environment influence the individual life history decision to smolt or mature (Rikardsen and Elliott 2000 and references therein). While the relationship between growth and propensity for anadromy may vary between study cases, McMillan et al. (2012) found that, regardless of growth, early male maturity was positively correlated with whole-body lipid content in a partially anadromous population of rainbow trout, where larger males with higher lipid levels had a greater probability of maturing as a resident at age 1+. The authors concluded that total body lipid content was a more direct measure of the individual condition leading to maturation. In this study we exclusively focused on growth-related traits as measures of conditions influencing the propensity to migrate, because in this river emigration occurs predominantly at age 2+, while most individuals that adopt the resident life history mature at age 3+ (Riva-Rossi 2004). Although not reported here, we sampled fish every 3 months during their first 2 years of life, just prior to emigration, and did not find any differences in gonad development nor in whole-body lipid content between larger (smolting) and smaller (rearing, undifferentiated) fish. Lipid reserves are critical for completion of maturation, because a certain amount of surplus energy is needed for gonadal development (Thorpe et al. 1998). The delayed maturation and early sea migration exhibited by Santa Cruz River rainbow trout may actually suggest that under the local environmental conditions the energetic levels needed to reach freshwater maturation are not met until very late in life, resulting in the inhibition of the developmental trajectory towards becoming a mature resident fish.

Finally, the significantly larger contribution of anadromous females to the juvenile stock reflects the fitness advantages accrued by this tactic. Therefore, it is likely that, through maternal provisioning, anadromous females not only affect the growth of their offspring, and thereby their tactic, but also the future fitness of their offspring across generations. Maternal effects thus may well

constitute an adaptive transgenerational trait (e.g., Plaistow et al. 2004), providing a self-perpetuation mechanism for anadromy, whereby anadromous females lay larger eggs and produce offspring with size and growth advantages that tend to express anadromy. To conclude, our results support the hypothesis that maternal anadromy, which influences adult size and egg size, affects the propensity of offspring for anadromy, which would perpetuate the anadromous tactic across generations. Such a maternal effect could influence the incidence of anadromy in the early stages of species introduction in novel environments, thus promoting the early establishment of the anadromous form under certain conditions and contributing to its reinforcement and persistence.

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