

Influence of maternal habitat choice, environment and spatial distribution of juveniles on their propensity for anadromy in a partially anadromous population of rainbow trout (*Oncorhynchus mykiss*)

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Abstract – This study evaluated the importance of the environment and spatial distribution of juvenile fish for the adoption of alternative migratory tactics in a partially anadromous population of rainbow trout (*Oncorhynchus mykiss*) from the Santa Cruz River. We captured young-of-the-year fish along the river during autumn 2009, 2010 and spring 2010 and determined their maternal origin (anadromous vs. resident) using strontium to calcium ratios in the otolith core. Relative proportion of anadromous offspring, modelled with logistic regression, increased towards headwaters and in areas with deeper channels and larger substrate composition. Body length, modelled with linear multiple regression, varied positively with site depth, water velocity, substrate size and anadromous maternal origin. Based on evidence for limited juvenile movements (<25 km), the spatial extent of this study (240 Rkm) and the identification of large, contrasting reaches along the river, it is likely that the observed spatial distribution of juveniles and their association to sites with coarse substrate composition reflects maternal spawning activity. Results further indicate that anadromous females breed predominantly in middle and upper river sections in areas with coarse substrate. Given that body size in this system has been positively related to propensity for anadromy, we propose that female spawning choice affects their offspring's spatial distribution, providing the adequate physical template for anadromous offspring to reach or maintain larger body sizes and display anadromy themselves. Relevance of this study is also discussed in the context of alterations in response to future dam construction in one of the latest free-flowing rivers sustaining anadromous *O. mykiss*.

Key words: maternal effects; non-native salmonids; otolith microchemistry; dam construction; Patagonia

Introduction

Spatial variation of organisms in heterogeneous environments is a key driver of ecological processes from individual (e.g. growth, survival) to ecosystem scales (e.g. species assemblages, productivity). The environment experienced by fish in freshwater systems can influence their growth performance and life history traits (e.g. age at first maturation) leading to direct

fitness consequences (Xu et al. 2010). In populations with partial anadromy, the environment plays a key role in the adoption of alternative migratory tactics ('AMTs', anadromy vs. residency). The expression of a migratory tactic is conditional on the individual's state during juvenile development (Thorpe et al. 1998), which is under genetic control and also influenced by the environment (reviewed in Dodson et al. 2013). For example, Olsson et al. (2006) showed that

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juvenile fish became migrants when food levels were low in a *Salmo trutta* population. In addition, Morinville & Rasmussen (2006) suggested that anadromy in *Salvelinus fontinalis* was related to habitat use during the juvenile stage; the authors found that habitats with fast-moving water (i.e. riffles) were occupied more frequently in streams with anadromous fish in comparison to riffle habitats in streams with only resident fish.

Several studies have demonstrated that the environment experienced by juvenile salmon is highly influenced by the breeding location of parents (Finstad et al. 2010; Hudy et al. 2010). By selecting certain breeding areas females may dictate their offspring density (Einum et al. 2008) and the amount and quality of habitat experienced in early juvenile stages (Finstad et al. 2010). Within partially anadromous salmonid populations, anadromous and resident females differ in their spawning habitat requirements. Larger anadromous females tend to spawn in deeper and faster water (Zimmerman & Reeves 2000) and are able to exploit gravel beds with larger substrate size than smaller resident females (Kondolf & Wolman 1993; Zimmerman & Reeves 2000). In fact, anadromous and resident mothers often display different spatial patterns within river networks (McMillan et al. 2007; Narum et al. 2008), potentially leading to offspring of alternative female phenotypes having different environmental experiences.

Rainbow trout (*Oncorhynchus mykiss*) introduced in the Santa Cruz River (Patagonia, Argentina, Fig. 1) established a self-sustaining partially anadro-

mous population which constitutes one of the rare examples of recreation of anadromy outside the species' native range (Pascual et al. 2001). Genetic and otolith microchemistry analyses revealed that anadromous and resident forms in this population shared a common genetic origin (Riva-Rossi et al. 2004) and that the two forms are now genetically indistinguishable (Pascual et al. 2001) and can give rise to either life history (Riva-Rossi et al. 2007). Previous studies in this river also showed that young-of-the-year (YOY) of both anadromous and resident maternal origins were present along the entire river gradient, although not in the same proportion (Liberoff et al. 2014), and both anadromous and resident mature fish were captured in the same river sections throughout the breeding season (Riva-Rossi et al. 2003; C. Riva-Rossi & M. Pascual, unpublished data). These results provide strong support for the idea that in this river anadromous and resident forms are alternative phenotypes of the same genetic population and that the environment plays a key role in the adoption of AMTs.

A recent study showed that propensity for anadromy in this river was positively related to body size during the juvenile stage and that larger fish were mostly progeny of anadromous mothers (Liberoff et al. 2014). Length-at-age differences were present since the time of emergence, but body size and growth differences persisted long after emergence and were detected until the end of first year of life. Although egg provisioning (e.g. lipid storage in eggs) was proposed as the primary mechanism leading to

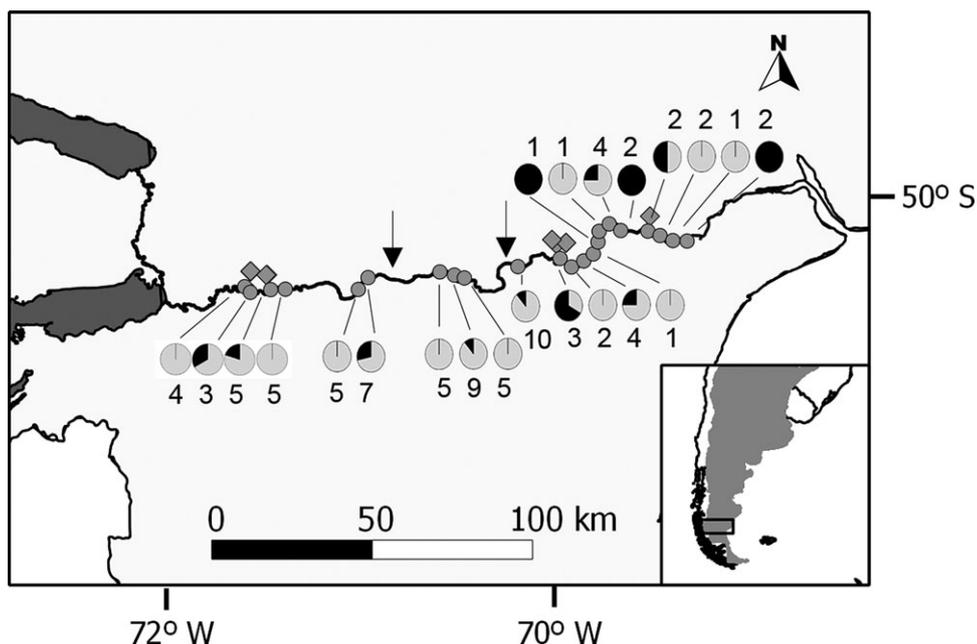


Fig. 1. Study sites sampled in spring (dots) and autumn (diamonds, located above dots artificially to enhance visualisation) along the Santa Cruz River. Arrows show the future location of dams. Pie charts represent the proportion of anadromous (grey) and resident (black) offspring in every site sampled in spring, sample size is shown adjacent to each chart.

early length-at-age differences between progeny of anadromous and resident mothers, the extent to which the spatial distribution and environmental experience influences juvenile growth and contributes to life history adoption in this river remains unknown.

The specific objectives of this study were three-fold; we: (i) determined if the spatial distributions and the riverine environments experienced by juvenile offspring of anadromous and resident mothers were similar, (ii) quantified the relationship between fish size, as a proxy for propensity for anadromy, and specific attributes of the riverine rearing habitat and (iii) modelled the environmental variation along the river and collected information on movement patterns of juvenile salmonids in order to identify which riverine variables analyzed in (i) and (ii) might reflect maternal breeding activity. The rationale for this analysis was that a female's spawning choice would play an important role in their offspring's environmental experience if adequate habitat characteristics are present in some sections of the system and therefore only available for fish that hatched and emerged in proximity to these sections.

In light of the results, we also evaluated future scenarios for anadromy within this population given the forthcoming environmental changes associated with dam construction on the Santa Cruz River.

Materials and methods

Study site

The Santa Cruz River in Patagonia, Argentina, (Fig. 1, average 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. River discharge is derived primarily from snow and glacial melt (CFI 1961). Average water temperature is 9°C with maxima in January ($15.3 \pm 0.6^\circ \text{C}$, mean \pm standard deviation, SD, $N = 7$ years) and minima in July ($3.1 \pm 0.1^\circ \text{C}$).

The Santa Cruz River is one of the last free-flowing and undisturbed rivers inhabited by anadromous *O. mykiss*. This situation will soon change because two dams are projected for construction within 2014–2015. Dams will be located at river km 132 and 197, inundating most of the known anadromous spawning distribution area (Riva-Rossi et al. 2003) and blocking the migratory corridor, leaving only a lower stretch of 49% of current length of regulated river (Fig. 1).

Sampling design and fish collection

We conducted sampling during two seasons: spring (September 2010, in the Southern Hemisphere) and

autumn (June 2009 and April 2010). Spring sampling was designed to describe spatial distribution patterns of anadromous and resident offspring along the entire river and their association with environmental variables. For this purpose, we sampled sites every 6 km from the headwaters to the mouth covering 240 km of river. Young-of-the-year (≤ 12 months old, 70.5 ± 13.2 mm; mean fork length \pm SD) were collected with a backpack electro-fishing gear (LR-24 Electrofisher, Smith Root Inc, Vancouver, WA, USA) walking 52 sites along the shore. Fish collection sites covered a shore area 100 m long and 2–5 m wide and were characterised according to their channel morphology (maximum channel depth, maximum channel velocity, channel width and substrate composition, see below in 'Environmental Survey'). The maternal origin of fish from 22 sites (N fish = 79), considered as representative of the river's longitudinal gradient, was determined (Fig. 1). The decline in the number of fish per site towards the mouth (e.g. sites downstream of the 11th site, Fig. 1) is related to the number of fish captured along the river.

Additionally, we used a different sampling design in autumn to determine if fish body size was related to microhabitat characteristics (i.e. specific conditions where fish were captured which, in this river, defined homogeneous habitats 20–60 m long and 2–5 m wide). In addition to measurements of channel width and substrate composition of fish collection site, in autumn, we also measured the local depth and velocity to capture the microhabitat variation (see below in 'Environmental Survey'). In contrast to the evenly spaced sites sampled in spring, in autumn, we visited specific locations along the river covering the upper, middle and lower river sections (Fig. 1). Within each section, we selected sites to capture the range of habitats with contrasting microhabitat characteristics (e.g. riffles, runs and shallow pools). We captured and determined the maternal origin of 44 YOY in autumn 2009 and 46 in 2010 ($\sim 7\text{--}9$ months old, 59.4 ± 12.9 mm; mean fork length \pm SD) in seven sites in close proximity to the sites sampled in spring. Similar to our spring collections, fish were captured with a backpack electro-fishing gear walking sites along the shore.

After capture, fish were euthanised with an overdose of MS-222 (Tricainemethanesulfonate, $1 \text{ g} \cdot \text{l}^{-1}$) and immediately frozen at -20°C until laboratory preparation. In the laboratory, fish were measured for fork length F_L (nearest mm) and otoliths were collected for microchemical analysis to determine their maternal origin.

Environmental survey

To determine the spatial distribution and characterise the environment of juvenile fish with alternative

maternal migratory tactics along the river gradient (spring sampling), we surveyed variables related to channel morphology. We collected data on maximum channel depth and channel water velocity, which were measured from a boat within the river channel adjacent to the fish collection site, and channel width and substrate composition which were measured from shore at the fish collection site. Maximum channel depth was determined with a LCX-15MT echosounder (Lawrence Electronics Inc, Tulsa, OK, USA). Maximum channel velocity was measured from a drifting boat, with a GPS Garmin Oregon 550 (Garmin International Inc, Olathe, KS, USA). Channel width (wet width) was measured from shore using a TruPulse 200 laser distance meter (Laser Technology Inc, Centennial, CO, USA). Substrate size composition was estimated following the Wolman Pebble count procedure (Wolman 1954), which consisted of walking upstream along a zig-zag line across the fish collection sample area and measuring the width of 50 randomly chosen pieces.

Furthermore, to relate juvenile body size to their rearing habitat (autumn sampling), we surveyed microhabitat scale variables related to the specific site where electro-fishing was conducted, including site depth and site water velocity (referred as 'local depth' and 'local water velocity'), along with substrate size and channel width. Site average depth (local depth) was calculated from three measures within the sample area, average surface water velocity (local water velocity) was obtained from three measurements of the time a half-submerged object lasted to travel 5 m. Substrate size composition and channel width were measured as described for spring sampling. Maximum channel depth and channel water velocity measurements were not available for autumn surveys.

Maternal origin determination

Maternal origin was determined using microchemical analysis of the otolith's core, based on the fact that the ratio of strontium to calcium (Sr:Ca) is typically greater in marine waters than in freshwater (Kalish 1990). Sr:Ca levels in otolith cores are influenced by the strontium and calcium content of the waters where vitellogenesis took place. Therefore, if natal river Sr:Ca 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. Riva-Rossi et al. (2007) verified that otolith core Sr:Ca could be used to differentiate between juveniles with anadromous and resident mothers in this system.

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 9- and 3- μm lapping film until all primordia were clearly exposed. Sr and Ca concentrations along the otolith growth axis were quantified using a Thermo X-series II inductively coupled plasma mass spectrometer (ICP-MS) 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, OR, USA). The laser was set at a pulse rate of 7 Hz with a 40- μm ablation spot size and travelled at 7 $\mu\text{m}\cdot\text{s}^{-1}$. Normalised ion ratios were converted to molar ratios based on our measurements, known average elemental concentrations of National Institute of Standards and Technology (NIST) 612 glass standards, and molar mass of Sr and Ca. The mean per cent relative SDs for glass standards were $^{43}\text{Ca} = 4.2\%$ and $^{86}\text{Sr} = 4.7\%$. Anadromous and resident progeny were assigned according to their Sr:Ca profile along the growth axis as described in Liberoff et al. (2014). 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 assigned as anadromous progeny; in contrast, when a homogeneous profile of relatively low levels of Sr:Ca was observed, the individual was assigned as resident progeny.

Data analyses

Environmental variation of Santa Cruz River

Channel morphology variables were analyzed as a function of river distance to evaluate the availability of habitat for juvenile fish along the river. For this purpose, we evaluated the correlation between environmental variables, by means of Pearson's correlation coefficient, and analyzed the relationship between each channel morphology variable and river distance from headwater for the 52 sites sampled during spring. Given that there is no assumed parametric function associated to the environmental variation, we fitted generalised additive models (GAMs). GAMs are semiparametric extensions of generalised linear models (GLMs), where the linear predictor has been exchanged for a smoothed, additive predictor. GAMs are useful tools to avoid untested assumptions about the relationship between predictor and response variables (Hastie & Tibshirani 1990). GAMs were fitted using the 'gam' function with Gaussian error distribution within 'mgcv' package (Wood 2011) in R (version 3.0.1, R Development Core Team 2013) and the significance of the smooth terms were evaluated.

Spatial and environmental pattern of anadromy

To analyze the environmental and spatial pattern of resident and anadromous offspring along the river,

we developed a generalised linear model (GLM) with a binomial distribution (logistic regression). The dependent variable was the proportion of anadromous offspring in each site sampled during spring. The independent variables were the channel morphology variables and the position of the sampling site in the river measured as the distance from headwater ('Rkm'). Model residuals were analyzed graphically to evaluate assumptions of normality and homogeneity of variance. Models were fitted and inferences were carried out through likelihood-based methods using 'nlme' package (Pinheiro et al. 2013) in R (version 3.0.1, R Development Core Team 2013).

To find the best model describing the distribution of anadromous and resident offspring, we fitted all possible models using the ' dredge ' function within 'MuMIn' package (Barton 2013) and ranked them according to their Akaike Information Criteria (AIC) and their AIC_{weight} (i.e. relative likelihood of model i given the data and all models being compared) (Burnham & Anderson 2002). Although model selection through AIC ranking will include and exclude some variables, it does not allow evaluation of the

importance of each variable in the model. Therefore, to establish the importance of the spatial distribution and each environmental variable, the relative importance (RI) of each independent variable was obtained as the sum of $AIC_{weights}$ over all possible models including the explanatory variable (Burnham & Anderson 2002). Explanatory variables were ranked according to their RI index.

Spatial and environmental pattern of juvenile body size

We used multiple linear regression to determine which factors could account for variation in juvenile size in autumn. The explanatory variables were local depth, local water velocity, channel width and substrate size, fish's position at capture measured as distance from headwater and year of capture (2009 and 2010). In addition, given that in this system juvenile body size is related to their maternal migratory tactic (Liberoff et al. 2014), we also included the maternal origin of each fish as a categorical explanatory variable.

Model selection routine and estimation of relative importance of each variable were performed as described above.

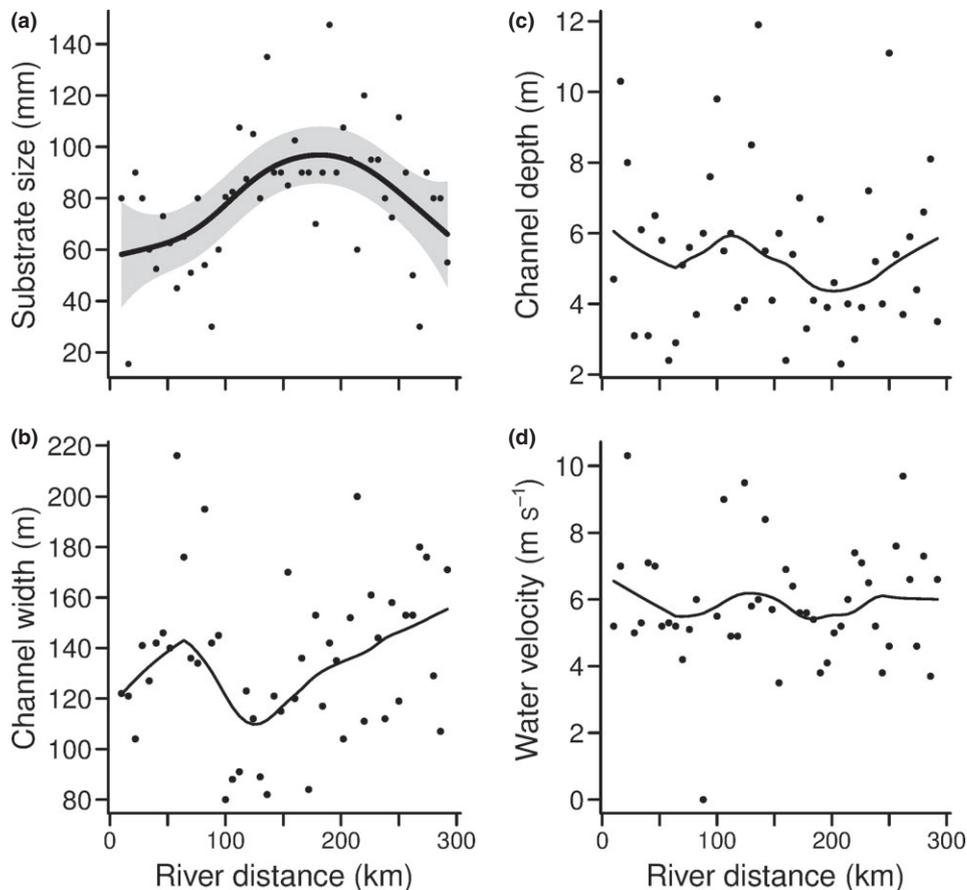


Fig. 2. Longitudinal variation of (a) substrate size, (b) channel width, (c) channel depth and (d) channel water velocity along the Santa Cruz River. The average contribution of river distance to substrate size, estimated with generalised additive models (GAMs), is represented by the continuous line. Shaded areas represent 5 and 95% GAM confidence intervals. For nonsignificant GAMs (b–d) continuous lines are locally weighted polynomial regressions ('lowess').

Results

Environmental variation of Santa Cruz River

Substrate size composition was the only environmental variable that showed a spatial pattern along the Santa Cruz River (GAM, $F_{5,25\text{substrate}} = 4.071$, $P_{\text{substrate}} = 0.003$; Fig. 2a). Middle sections of Santa Cruz River (Rkm ~ 125 to ~ 225) displayed coarse substrate composition (average estimated size 100 mm) whereas upper (Rkm < 50) and lower sections (Rkm > 250) had medium to small substrate (Fig. 2a). Channel depth, width and water velocity, on the other hand, did not display any spatial pattern along the river (GAM, $P > 0.1$, Fig. 2b–d).

Substrate size varied negatively with channel width ($r = -0.45$, $t_{46} = -3.43$, $P < 0.01$), positively with channel depth ($r = 0.33$, $t_{46} = 2.39$, $P < 0.05$) and channel depth correlated negatively with channel width ($r = -0.46$, $t_{46} = -3.57$, $P < 0.001$), although all three correlations were weak. No correlation was found between maximum channel velocity and any of the variables ($P > 0.05$).

Maternal origin

Otolith microchemical analysis allowed determination of maternal origin for a total of 169 fish captured during autumn 2009 ($N = 44$), 2010 ($N = 46$) and spring 2010 ($N = 79$). The Sr:Ca ratios in the otolith core for the anadromous and resident offspring were $1.32 \pm 0.04 \text{ mmol}\cdot\text{mol}^{-1}$, mean \pm 95% confidence interval, CI, and $0.76 \pm 0.04 \text{ mmol}\cdot\text{mol}^{-1}$ respectively.

Relative anadromous contribution to the juvenile stock predominated over resident contribution, 80%

of fish captured in spring and 66.7% of fish captured in autumn were progeny of anadromous mothers.

Spatial and environmental pattern of anadromy

Fish of both maternal origins were captured along the entire Santa Cruz River (Fig. 1). However, the proportion of YOY of anadromous origin predominated over their resident counterparts at most sampled sites (Fig. 1). Probability of maternal anadromy increased towards headwater and in sites with deeper channels and larger substrate size (Fig. 3).

The full logistic model (Model 25, Table 1) with all the explanatory variables of channel morphology and river position of the sampling site accounted for 42.3% of the variation in the proportion of anadromy in the river. Rkm and channel depth were the most important variables explaining the distribution pattern of alternative offspring (RI = 0.751 and 0.747 respectively) followed by substrate size (RI = 0.579) whereas channel width and water channel velocity showed the smallest indexes (RI = 0.335, 0.263 respectively). The selection routine yielded 32 possible models and the best model (i.e. most likely given the data) did not include water channel velocity and channel width (Model 1, Table 1; Table 2). In this model, Rkm, channel depth and substrate size accounted for 41.8% of the variation in the proportion of anadromy along the river.

Spatial and environmental pattern of juvenile body size

Young-of-the-year body length at capture varied between offspring of alternative maternal origin

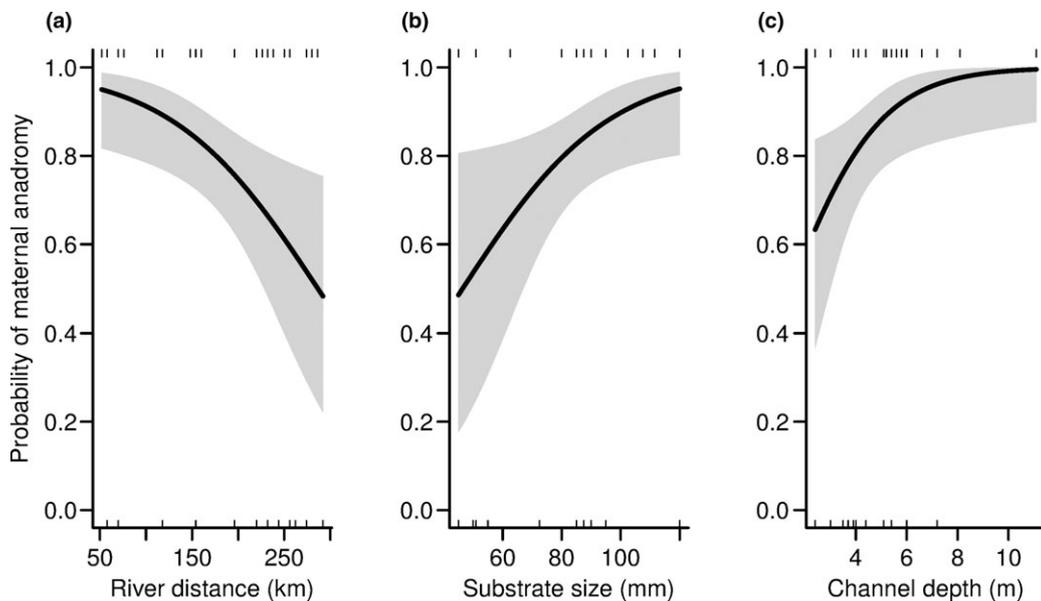


Fig. 3. Logistic regression for maternal anadromy as a function of (a) river distance from headwater, (b) substrate size and (c) channel depth. Lines represent estimated probabilities of maternal anadromy and shaded areas represent the 5 and 95% confidence intervals.

Table 1. Model selection for spatial and environmental patterns of anadromous and resident offspring along the Santa Cruz River. Proportion of anadromy was modelled as a function of river distance from headwater (Rkm), substrate size (Subs), channel depth, channel width and channel velocity (Vel). Model selection routine yielded 32 possible models of which the best seven models and the full model (Model 25) are presented. For each model, model structure, degrees of freedom (d.f.), loglikelihood values, AICc difference (Δ AICc) and Akaike weights, calculated over all possible models, are shown for model selection.

Model	Model structure	d.f.	logLik	Δ AICc	AIC weight
1	Rkm + Subs + Depth	4	-18.6	0.0	0.275
2	Rkm + Depth	3	-21.3	2.3	0.087
3	Width + Rkm + Depth	4	-19.9	2.5	0.078
4	Rkm + Subs	3	-21.7	3.1	0.060
5	Width + Rkm + Subs + Depth	5	-18.6	3.3	0.054
6	Rkm + Subs + Depth + Vel	5	-18.6	3.4	0.051
7	Width + Depth	3	-22.2	4.1	0.035
25	Width + Rkm + Subs + Depth + Vel	6	-18.5	7.1	0.008

Table 2. Parameters of selected logistic model explaining the spatial and environmental pattern of anadromy along the Santa Cruz River.

	Estimate	SE	z value	Pr(> z)
Intercept	-2.405	1.915	-1.26	0.21
Depth	0.559	0.248	2.25	0.02
Subs	0.041	0.019	2.15	0.03
Rkm	-0.013	0.005	-2.54	0.01

and year of capture (two-way ANOVA, $F_{\text{maternal origin,1}} = 40.6$, $P < 0.001$; $F_{\text{year,1}} = 31.1$, $P < 0.001$; $F_{\text{interaction term,1}} = 0.1$, $P > 0.05$). Fish of anadromous offspring were larger at capture than resident offspring in both sampling years (2009: 69.0 ± 3.7 mm, mean \pm CI, 58.4 ± 5.1 respectively and 2010: 56.6 ± 3.8 mm, 47.3 ± 3.2 mm).

Larger fish inhabited deeper and faster water current sites with larger substrate size (Fig. 4). Fish of anadromous mothers were larger than their counterparts even after accounting for environmental effects (Fig. 4). The full regression model with all environmental explanatory variables, river position, maternal origin and year of capture (Model 9, Table 3) explained 66.8% of total variance in fish body length. Relative importance of variables calculated across all possible models yielded the largest relative importance index for maternal origin and local depth (RI = 0.999 for both) followed by local water velocity (RI = 0.989) and substrate size (RI = 0.812); channel width, year of capture and Rkm were the variables with the smallest index (RI = 0.313, 0.280, 0.232 respectively). On the other hand, the model that included only maternal origin (Model 106, Table 3) explained 20.7% of the total variance whereas the model with the most important environmental variables (local depth, local water velocity and substrate size) (Model 46, Table 3) explained 45.3%. The best regression model among 128 possible models contained maternal origin, local depth, local water velocity and substrate size (Model

1, Table 3; Table 4) and accounted for 64.8% of total variance in fish body length.

Discussion

In this study, we characterised the spatial variation of anadromy and residency by determining the proportion of juveniles of anadromous and resident mothers captured throughout the Santa Cruz River. We also identified environmental variables associated with the relative distribution of anadromy and residency and determined which microhabitat characteristics were positively related to juvenile body size. At the basin scale (240 Rkm), anadromy was dominant in the middle and upper sections of the river in areas with deeper channels and larger substrate size. At finer spatial scale (20–60 m), fish were distributed in relation to their body size: larger fish inhabited deeper sites with faster water currents and larger substrate size.

The probability of capturing the offspring of anadromous mothers increased towards headwaters and in areas with deeper channels and larger substrate size. These features are consistent with the habitat selection and behaviour of breeding anadromous females. Higher relative abundance of anadromous offspring in deeper channels with larger substrate composition is in accordance with anadromous female's capacity to exploit deeper sites with larger substrate composition (Zimmerman & Reeves 2000; Hendry et al. 2001). The use of upper river sections might be the result of the large spawning migrations reported for anadromous females in this (Riva-Rossi et al. 2003) and other populations of *O. mykiss* (Brannon et al. 2004).

Substrate size is an important feature for most stages of stream-dwelling fish. Availability of suitably sized substrate can influence spawning success, influence egg to fry survival (Rubin & Glimsäter 1996), and affect the amount of shelter for advanced juvenile stages (Teichert et al. 2011). The association between larger fish and anadromous offspring and

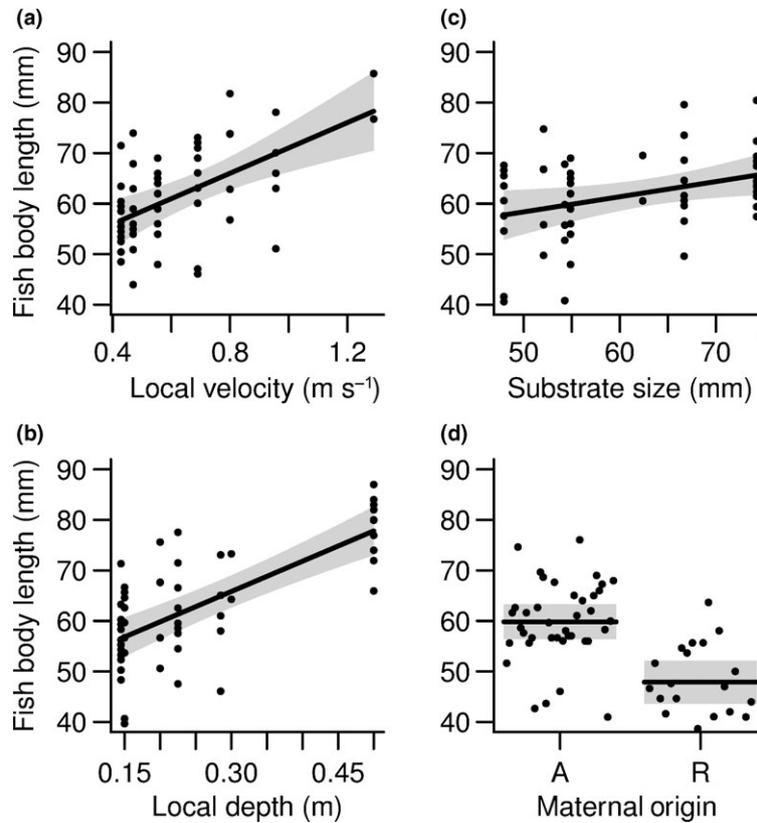


Fig. 4. Partial regression plots showing the partial correlation of (a) local velocity, (b) local depth, (c) substrate size and (d) maternal origin with the dependent variable (fish body length) after removing the linear effects of the other independent variables in the model. Shaded areas represent the 5 and 95% confidence intervals.

Table 3. Model selection for spatial and environmental patterns of juvenile body size variation. Body size was modelled as a function of Maternal Origin (MO), substrate size (Subs), Local Depth (Depth_L), Local velocity (Vel_L), channel width, year of capture (Yr) and river distance from headwater (Rkm). Model selection routine yielded 128 possible models of which the best six models, the full model (model 9), model only accounting for environmental variation (model 46) and model accounting only for maternal origin (model 106) are shown. For each model, model structure degrees of freedom (d.f.), loglikelihood values, AICc difference (Δ AICc) and Akaike weights, calculated over all possible models, are shown for model selection.

Model	Model structure	d.f.	logLik	Δ AICc	AIC weight
1	MO + Subs + Depth _L + Vel _L	6	-203.1	0	0.314
2	Width + MO + Subs + Depth _L + Vel _L	7	-202.6	1.66	0.137
3	MO + Subs + Depth _L + Vel _L	7	-202.8	2.15	0.107
4	MO + Rkm + Subs + Depth _L + Vel _L	7	-203.1	2.58	0.086
5	MO + Depth _L + Vel _L	5	-205.6	2.66	0.083
6	Width + Yr + MO + Subs + Depth _L + Vel _L	8	-202.0	3.2	0.063
9	Width + Yr + MO + Rkm + Subs + Depth _L + Vel _L	9	-201.4	4.73	0.029
46	Subs + Depth _L + Vel _L	5	-216.1	23.7	0.000
106	MO	3	-227.1	40.8	0.000

coarse substrate composition might be due to active habitat selection or to inheritance of habitat selected by their mothers during spawning. The Santa Cruz River consists of long and contrasting reaches according to the substrate composition (~100 km). Although juveniles may have moved hundreds of kilometres in search of coarse substrate habitats, it is perhaps more likely that they have been restricted to these sections since hatching. These analyses suggest that the distribution and environmental experience of

YOY are strongly influenced by their maternal spawning activity.

Several studies on salmonids have detected influences of maternal activity on the spatial distribution of their offspring until advanced stages (Einum et al. 2008; Foldvik et al. 2010, 2012). For example, Einum et al. (2008) conducted field experiments manipulating *Salmo salar* nest distributions over 250 m reaches and found that juvenile distribution patterns were influenced by female breeding activity

Table 4. Parameters of selected multiple regression model explaining the spatial and environmental pattern of fish body size in the Santa Cruz River.

	Estimate	SE	t value	Pr(> t)
Intercept	17.48	11.73	1.49	0.1419
Maternal origin	-11.94	2.18	-5.482	0.0000
Local velocity	25.08	6.17	4.065	0.0002
Local depth	59.98	8.50	7.061	0.0000
Substrate size	0.30	0.14	2.217	0.0308

until the second year of life. Effects of spawning activity on juvenile spatial distributions until advanced stages have been also studied at larger scales (i.e. subwatershed or watershed). Foldvik et al. (2012) studied the spatial distribution of juvenile *S. salar* in a study site 5125 m long and showed that spatial distribution of juveniles (1+ years old) largely followed the distribution of the same cohort during the previous year. Other species of salmonids have not been studied as extensively as *S. salar* but there is also evidence of small movements for *O. kisutch* (<6.3 km) (Anderson et al. 2013) and *O. mykiss* (<20 km) during juvenile stages (Tattam 2006; Mills et al. 2012). The results from this study, in conjunction with existing evidence for limited juvenile movement and maternal effects in other salmonid species, provide additional support for the idea that the relative abundance of anadromous and resident offspring along a river reflects their parent's breeding activity.

In populations with condition-dependent tactics (i.e. conditional strategies, Gross & Repka 1998), such as partial anadromy, identification of environmental variables that affect juvenile growth and body size are necessary to identify environmental controls over the adoption of AMTs. In this study, we identified habitat preferences in relation to fish length. Larger fish, which in this system are more prone to adopt anadromy (Liberoff et al. 2014), occupied deeper sites with larger substrate size composition and faster water currents. Therefore, this study provides further evidence of the link between habitat use, fish condition, and the migratory tactic adoption in *O. mykiss*. The use of costly habitats (i.e. faster water velocities) by juvenile salmonids has been previously linked to adoption of anadromy (Finlay et al. 2002; Morinville & Rasmussen 2006). For example, Morinville & Rasmussen (2006) proposed that migrants occupied habitats with faster water velocities than residents during juvenile stages in brook trout (*S. fontinalis*). Furthermore, for both *S. fontinalis* (Morinville & Rasmussen 2003) and *S. trutta* (Forsyth et al. 1999), migrants and residents displayed different energy allocation during the juvenile stage; migrants had higher consumption rates and higher total metabolic costs than residents. This study in conjunction with results reported by Liberoff et al.

(2014) support the idea that *O. mykiss* show a behaviour similar to other salmonids, where juvenile fish adopting the anadromous life history inhabit faster waters than future residents.

To summarise, we propose that maternal breeding activity strongly affects juvenile distribution and their rearing habitat, which can influence juvenile development. Given that fish body size is related to fish propensity to migrate (Nicieza et al. 1991; Páez et al. 2011; Liberoff et al. 2014), this study provides a link between maternal activity and the adoption of alternative migratory tactics, which is partly due to the maternal influence on the spatial distribution and rearing habitat experienced by her offspring. The fit of several alternative regression models (Table 3) showed that the effect of maternal origin on offspring body size was present even after accounting for environmental variation in physical habitat, accounting for the 20% of body size variation (Model 106, Table 3, see 'Results'). This highlights the likely importance of mechanisms associated with the maternal phenotype, independent of juvenile environmental experience, such as egg provisioning as proposed by Liberoff et al. (2014). The present study provides another key element that strengthens support for the idea that the presence of large maternal effects in this population which may have reinforced the establishment of an anadromous tactic during the early stages of this species introduction.

The Santa Cruz River is one of the latest free-flowing and undisturbed rivers inhabited by anadromous *O. mykiss*. However, dam construction will alter the composition, structure and functioning of the Santa Cruz basin. These alterations will lead to an accumulation of fine sediments in the area above the dam, destroying spawning habitats, and likely modifying the coarse substrate composition currently found within the middle and upper river sections, which have been identified as the critical areas for anadromy. In addition, discharge and temperature cycles will also change leading to further alterations in the biotic communities (NRC 1996). These environmental changes coupled with increased cost of migration will probably lead to a decrease in the anadromous fraction in this population within a few years. New selection pressures and evolutionary changes are expected to occur after dam construction (Angilletta et al. 2008) and probably, after the dam placement, upstream resident fish will genetically diverge from downstream resident and anadromous fish. Future research comparing the situation pre- and post- dam construction will enhance our understanding of evolutionary changes driven by human impacts regarding the interaction between life history forms. Future scenarios will also provide the opportunity to test the

strength of maternal effects, like egg provisioning and selection of spawning habitat, for the maintenance of the anadromous tactic.

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References

- Anderson, J.H., Pess, G.R., Kiffney, P.M., Bennett, T.R., Fauds, P.L., Atlas, W.I. & Quinn, T.P. 2013. Dispersal and tributary immigration by juvenile coho salmon contribute to spatial expansion during colonization. *Ecology of Freshwater Fish* 22: 30–42.
- Angilletta, M.J. Jr, Steel, E.A., Bartz, K.K., Kingsolver, J.G., Scheuerell, M.D., Beckman, B.R. & Crozier, L.G. 2008. Big dams and salmon evolution: changes in thermal regimes and their potential evolutionary consequences. *Evolutionary Applications* 1: 286–299.
- Barton, K. 2013. MuMIn: multi-model inference. R package version 1.9.5. Available at: <http://CRAN.R-project.org/package=MuMIn>.
- Brannon, E.L., Powell, M.S., Quinn, T.P. & Talbot, A. 2004. Population structure of Columbia River Basin Chinook salmon and steelhead trout. *Reviews in Fisheries Science* 12: 99–232.
- Burnham, K.P. & Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. New York, NY: Springer-Verlag.
- Dodson, J.J., Aubin-Horth, N., Thériault, V.E. & Páez, D.J. 2013. The evolutionary ecology of alternative migratory tactics in salmonid fishes. *Biological Reviews of the Cambridge Philosophical Society* 88: 602–625.
- Einum, S., Nislow, K.H., Mckelvey, S. & Armstrong, J.D. 2008. Nest distribution shaping within-stream variation in Atlantic salmon juvenile abundance and competition over small spatial scales. *Journal of Animal Ecology* 77: 167–172.
- Finlay, J.C., Khandwala, S. & Power, M.E. 2002. Spatial scales of carbon flow in a river food web. *Ecology* 83: 1845–1859.
- Finstad, A.G., Einum, S., Sættem, L.M. & Hellen, B.A. 2010. Spatial distribution of Atlantic salmon (*Salmo salar*) breeders: among- and within-river variation and predicted consequences for offspring habitat availability. *Canadian Journal of Fisheries and Aquatic Sciences* 67: 1993–2001.
- Foldvik, A., Finstad, A.G. & Einum, S. 2010. Relating juvenile spatial distribution to breeding patterns in anadromous salmonid populations. *Journal of Animal Ecology* 79: 501–509.
- Foldvik, A., Teichert, M.A.K., Einum, S., Finstad, A.G., Ugedal, O. & Forseth, T. 2012. Spatial distribution correspondence of a juvenile Atlantic salmon *Salmo salar* cohort from age 0+ to 1+ years. *Journal of Fish Biology* 81: 1059–1069.
- Forseth, T., Naesje, T.F., Jonsson, B. & Harsaker, K. 1999. Juvenile migration in brown trout: a consequence of energetic state. *Journal of Animal Ecology* 68: 783–793.
- Gross, M.R. & Repka, J. 1998. Stability with inheritance in the conditional strategy. *Journal of Theoretical Biology* 192: 445–453.
- Hastie, T. & Tibshirani, R. 1990. Generalized additive models. London: Chapman & Hall.
- Hendry, A.P., Berg, O.K. & Quinn, T.P. 2001. Breeding location choice in salmon: causes (habitat, competition, body size, energy stores) and consequences (life span, energy stores). *Oikos* 93: 407–418.
- Hudy, M., Coombs, J.A., Nislow, K.H. & Letcher, B.H. 2010. Dispersal and within-stream spatial population structure of brook trout revealed by pedigree reconstruction analysis. *Transactions of the American Fisheries Society* 139: 1276–1287.
- Kalish, J.M. 1990. Use of otolith microchemistry to distinguish the progeny of sympatric anadromous and non-anadromous salmonids. *Fishery Bulletin* 88: 657–666.
- Kondolf, G.M. & Wolman, M.G. 1993. The size of salmonid spawning gravels. *Water Resources Research* 29: 2275–2285.
- Liberoff, A.L., Miller, J.A., Riva-Rossi, C.M., Hidalgo, F., Fogel, M.L. & Pascual, M. 2014. Transgenerational effects of anadromy on juvenile growth traits in an introduced population of rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* 71: 398–407.
- McMillan, J.R., Katz, S.L. & Pess, G.R. 2007. Observational evidence of spatial and temporal structure in a sympatric anadromous (winter steelhead) and resident rainbow trout mating system on the Olympic Peninsula, Washington. *Transactions of the American Fisheries Society* 136: 736–748.
- Mills, J.S., Dunham, J.B., Reeves, G.H., McMillan, J.R., Zimmerman, C.E. & Jordan, C.E. 2012. Variability in expression of anadromy by female *Oncorhynchus mykiss* within a river network. *Environmental Biology of Fishes* 93: 505–517.
- Morinville, G.R. & Rasmussen, J.B. 2003. Early juvenile bioenergetic differences between anadromous and resident brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* 60: 401–410.
- Morinville, G.R. & Rasmussen, J.B. 2006. Does life-history variability in salmonids affect habitat use by juveniles? A comparison among streams open and closed to anadromy. *The Journal of Animal Ecology* 75: 693–704.
- Narum, S.R., Zendt, J.S., Graves, D. & Sharp, W.R. 2008. Influence of landscape on resident and anadromous life history types of *Oncorhynchus mykiss*. *Canadian Journal of Fisheries and Aquatic Sciences* 65: 1013–1023.
- National Research Council (NRC) 1996. Upstream: salmon and society in the Pacific Northwest. Washington, DC: National Academy Press. 452 pp.
- Nicieza, A.G., Braña, F. & Toledo, M.M. 1991. Development of length-bimodality and smolting in wild stocks of Atlantic salmon, *Salmo salar* L., under different growth conditions. *Journal of Fish Biology* 38: 509–523.

- Olsson, I.C., Greenberg, L.A., Bergman, E. & Wysujack, K. 2006. Environmentally induced migration: the importance of food. *Ecology Letters* 9: 645–651.
- Páez, D.J., Brisson-Bonenfant, C., Rossignol, O., Guderley, H.E., Bernatchez, L. & Dodson, J.J. 2011. Alternative developmental pathways and the propensity to migrate: a case study in the Atlantic salmon. *Journal of Evolutionary Biology* 24: 245–255.
- Pascual, M.A., Bentzen, P., Riva-Rossi, C.M., Mackey, G., Kinnison, M. & Walker, R. 2001. First documented case of anadromy in a population of introduced rainbow trout in Patagonia, Argentina. *Transactions of the American Fisheries Society* 130: 53–67.
- Pinheiro, J.C., Bates, D.J., DebRoy, S., Sarkar, D. & R Development Core Team. 2013. Linear and nonlinear mixed effects models. R package version 3.1-109. Available at: <http://CRAN.R-project.org/package=nlme>.
- R Development Core Team. 2013. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Riva-Rossi, C.M., Arguimbau, M. & Pascual, M.A. 2003. The spawning migration of anadromous rainbow trout in the Santa Cruz River, Patagonia (Argentina) through radio – tracking. *Ecología Austral* 13: 151–159.
- Riva-Rossi, C.M., Lessa, E.P. & Pascual, M.A. 2004. Origins of introduced rainbow trout in the Santa Cruz River as inferred by mitochondrial DNA. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 1095–1101.
- Riva-Rossi, C.M., Pascual, M., Babaluk, J.A., Garcia Asorey, M.I. & Halden, N.M. 2007. Intrapopulation variation in anadromy and reproductive life span in rainbow trout introduced in the Santa Cruz River, Argentina. *Journal of Fish Biology* 70: 1780–1797.
- Rubin, J.-F. & Glimsäter, C. 1996. Egg-to-fry survival of the sea trout in some streams of Gotland. *Journal of Fish Biology* 48: 585–606.
- Tattam, I. 2006. Seasonal life history of *Oncorhynchus mykiss* in the South Fork John Day River Basin, Oregon. Master of Science. Newport, OR: Oregon State University. 145 pp.
- Teichert, M.A.K., Foldvik, A., Forseth, T., Ugedal, O., Einum, S., Finstad, A.G., Hedger, R.D. & Bellier, E. 2011. Effects of spawning distribution on juvenile Atlantic salmon (*Salmo salar*) density and growth. *Canadian Journal of Fisheries and Aquatic Sciences* 68: 43–50.
- Thorpe, J.E., Mangel, M., Metcalfe, N.B. & Huntingford, F.A. 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. *Evolutionary Ecology* 12: 581–599.
- Wolman, M.G. 1954. A method of sampling coarse river-bed material. *Transactions American Geophysical Union* 35: 951–956.
- Wood, S.N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society. Series B, Statistical Methodology* 73: 3–36.
- Xu, C.L., Letcher, B.H. & Nislow, K.H. 2010. Size-dependent survival of brook trout *Salvelinus fontinalis* in summer: effects of water temperature and stream flow. *Journal of Fish Biology* 76: 2342–2369.
- Zimmerman, C.E. & Reeves, G.H. 2000. Population structure of sympatric anadromous and nonanadromous *Oncorhynchus mykiss*: evidence from spawning surveys and otolith microchemistry. *Canadian Journal of Fisheries and Aquatic Sciences* 57: 2152–2162.