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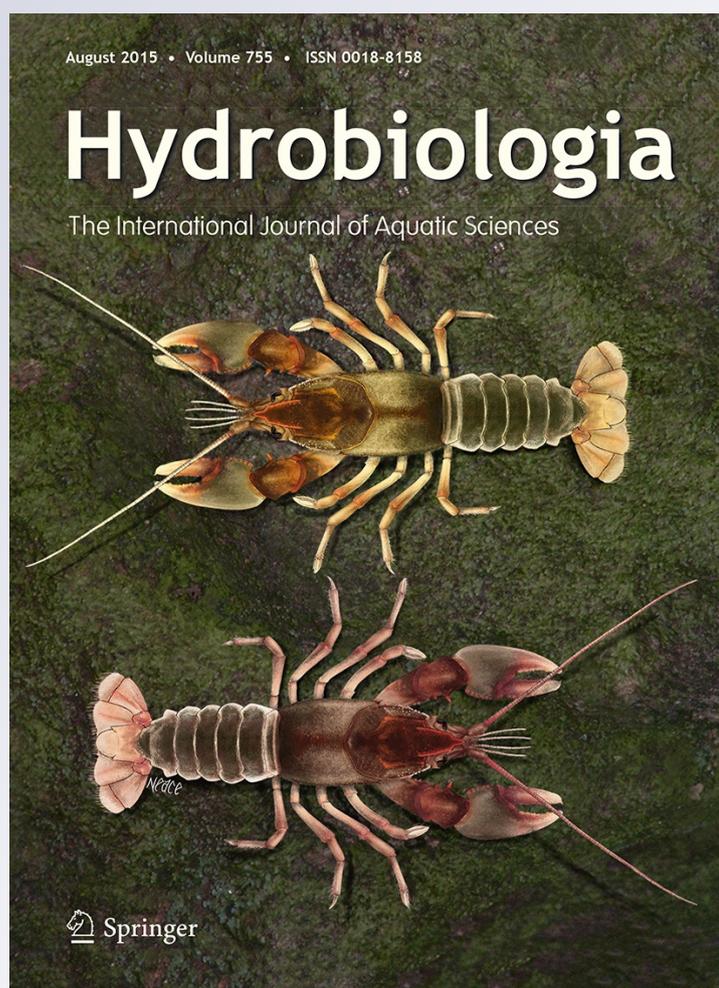
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Dams versus habitat: predicting the effects of dams on habitat supply and juvenile rainbow trout along the Santa Cruz River, Patagonia

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Abstract Because of their remote location and lack of supporting infrastructure, large glacial rivers of southern Patagonia have remained free of dams. But this is bound to change: two dams proposed for the Santa Cruz River would supply 16% of Argentina's hydropower and five dams planned for the Pascua and Baker Rivers could supply over 20% of Chile's hydropower. In this paper, we project the losses of habitat and juvenile *Oncorhynchus mykiss*, a recreationally important species, following the construction of the two dams in the Santa Cruz River. We applied a two-stage fitting approach, using generalized additive models and generalized linear models (GLMs) sequentially to describe habitat-species relationships based on data collected through an intensive field survey of fish and environmental variables along 310 km of river. A simplified GLM trout model based on wetted width, substrate size, and river kilometer was selected which represents the observed geographic distribution very well and with the lowest predictive error. Based on this model, we estimated that habitat supporting 86% of current juvenile trout production will be lost to

flooding by the dams. Our data generate a rare opportunity to perform a dam impact assessment by comparison with potential post-dam conditions.

Keywords *Oncorhynchus mykiss* · Juvenile fish · Habitat variables · Species-habitat models · Dams · Patagonia · Argentina

Introduction

Dams have become common human-made structures in rivers around the world. More than 45,000 large projects (height of at least 15 m from the foundation or a reservoir volume of more than 3 million m³) and an exponentially larger number of small projects have been constructed, covering two-thirds of the world's major rivers (World Commission on Dams, 2000; McAllister et al., 2001). Dams have multiple purposes, including providing water for agriculture, domestic, or industrial use, as well as hydropower generation and flood control. However, dams also alter flow regimes and divert flows which affect existing water rights and access to water with significant impacts on the environment and human livelihoods. Dams have led in many cases to irreversible loss of species and habitat (Graf, 1999; World Commission on Dams, 2000; Ligon et al., 2012), irreversible changes in riparian vegetation, and damage to fish populations (Poff, 1997). Fish are affected by the disruption of cues to the spawning cycle, by loss of habitat, by proliferation of non-native

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species that benefit from regulated flow, and by simple blockage of passage. The effects of dams on salmonids, which are highly mobile species that make extensive use of watershed throughout their life cycle, have been extensively studied and documented (Collins, 1976; Angilletta Jr. et al., 2008; WSC, 2009). Commonly, studies examining the impacts of dams on ecological communities have concentrated on the effects downstream of impoundments. However, some of the most profound impacts can occur a long distance downstream from the impoundment through, (i) altered flow and high evapotranspiration leading to increased salinity, (ii) alterations to physical habitat, and (iii) reduced silt and nutrient transport (Louca et al., 2009).

Despite of the ecological importance of such changes produced by dams, little consideration has been given to determining the relationships between characteristics of the habitat and fish abundance in rivers of semi-arid regions. Such knowledge is fundamental for the provision of advice as to the likely impacts of impoundments and how to ameliorate such effects. Whereas the typical prescription for dam environmental impact assessments recommends collecting pre and post-dam data on resources and users throughout the catchment (Word Commission on Dams, 2000), the fact is that this is seldom done. Lack of pre-dam data coupled with a general disregard for anticipating and avoiding impacts of dams has resulted in poor-quality predictions of their effects and very limited success with efforts to counter the ecosystem impacts typically produced by dams (McAllister et al., 2001).

In this paper, we report on baseline information and projected losses by the construction of two large dams of exotic rainbow trout (*Oncorhynchus mykiss*) in one of the last free-flowing rivers in Patagonia, the Santa Cruz River. We developed and applied a systematic survey approach that provides a useful and valuable tool for generating pre-dam data and for predicting fish responses to changes in habitat in large rivers in Patagonia, which pose difficulties in sampling due to their scale, remote location, and extreme weather conditions.

The Santa Cruz is one of three large rivers that have their headwaters in the Patagonian Ice Fields (PIFs) in the Andes Mountains of Chile and Argentina. The other two are the Baker and Pascua Rivers in Chile. Together with the Rio Negro of Argentina, these three rivers constitute the four largest rivers of Patagonia in terms of discharge (Tagliaferro et al., 2013). The three

PIF rivers have distinctive characteristics differentiating them from other rivers of Patagonia (Tagliaferro et al., 2013), as well as from most large rivers in temperate ecoregions of the world (Milner & Petts, 1994; Carrasco et al., 2002). A discharge strongly dominated by ice melt provides them with (Tagliaferro et al., 2013) (a) a distinct seasonal cycle with peaks and low flows delayed by as much as 6 months with respect to rivers dominated by snow melt and rainfall, (b) an extremely stable discharge with much lower variability than other rivers, both within and among years, and (c) a high glacial sediment load. Because of their remote location and the lack of supporting infrastructure, these three rivers have remained free of dams. Two dams proposed for the Santa Cruz River are projected to supply 16% of Argentina's hydropower (Quiroga, 2008) and a series of five dams to be built in the Pascua and Baker rivers are expected to supply over 20% of Chile's hydropower (Endesa, 2006).

The two hydroelectric projects in the Santa Cruz River will dam up 197 km (52%) of main stem river, leaving only a lower stretch of 185 km (48%) of the current length of regulated river. Projected losses in terms of macroinvertebrates and native fish as a result of the two dams are large (Tagliaferro et al., 2013, 2014). Rainbow trout were introduced in the river between 1908 and 1910 (Pascual et al., 2001; Riva Rossi et al., 2003).

The Santa Cruz river is the one of the rare examples outside the species' native range where introduced rainbow trout are known to have recreated a polymorphic behavior displaying both anadromous—ocean migrating—and non-anadromous lifestyles, with anadromous fish sustaining a unique and valuable fishery (Pascual et al., 2001). The introduction of rainbow trout into the Santa Cruz River, and in Patagonia in general, has created a complex trade-off between development and conservation. It became a highly valued species, used for both food and recreation, but it also has posed serious threats to native fish fauna by means of changes in the distribution and diet overlap with native galaxiids, implying intense prey competition (Tagliaferro et al., 2014b). Thus, a bitter debate has been brewing between those promoting economic development through recreational fisheries and those concerned with the effects of trout on environmental integrity (Pascual et al., 2009). Traditionally, conservation goals have been aimed at protecting endemic native species and

“pristine” ecosystems and their putative integrity and stability (Forum, 2004). However, in the last few years, scientists and managers have just started recognizing the potential desirable effects and conservation benefits of non-native salmonids on recipient ecosystems. For example, introduced rainbow trout provide numerous ecosystem services, including cultural (recreation), provisioning (food and commercial harvest), and a source of a nutritional resource for other species, marine-derived nutrients, and energy to freshwater habitats (Bottom et al., 2009). Because the environmental tolerance of rainbow trout is relatively narrow and habitat requirements at each life stage are very specific (e.g., Tagliaferro et al., 2013; Liberoff et al., 2014), it constitutes a sensitive indicator of water quality and habitat integrity. Thus, a novel approach and a different value system that take into account the ecosystem function provided by this non-native species (Schlaepfer et al., 2011) may be required to manage this and other ecosystems in Patagonia where non-native salmonids are firmly established.

The main objective of this paper is to provide a river wide inventory of juvenile rainbow trout in the main stem Santa Cruz River in the face of dam construction. In order to do this we (1) conducted an intensive field survey in 2010 along 310 km of the main stem Santa Cruz River, (2) built a habitat-based model of the distribution of juvenile rainbow trout, (3) fit the model to the survey data applying a two-stage model fitting approach based on generalized additive models (GAMs) and generalized linear models (GLMs), (4) used the model selection procedure to identify significant habitat variables and to determine the specific shape of the habitat-abundance relationship, and finally, (5) used our selected model to map the geographic distribution of juvenile trout and to estimate the expected losses by dam construction (i.e., the fraction of the population of juveniles inhabiting the upper section, where lotic spawning and juvenile rearing habitat will be obliterated).

Materials and methods

Study area and sampling procedures

The Santa Cruz River (50°S; 70°W) runs for 382 km across the Patagonian plateau to drain in the Atlantic Ocean (Fig. 1b, c). The upper Santa Cruz basin is

dominated by two large glacial-fed lakes, Viedma and Argentino, which form the Santa Cruz River. Land-locked populations of rainbow trout inhabit many of the second- to third-order tributaries that feed the head lakes. On the other hand, few springs and small tributaries enter the main stem river, none of them significant from the point of view of their trout populations. We restricted our analysis to the main stem river, which is the domain of the anadromous rainbow trout, as revealed by telemetry studies, and of the resident fish to which they are most closely related (Riva Rossi et al., 2003).

Average flow of the Santa Cruz river is $691 \text{ m}^3 \text{ s}^{-1}$, with an average minimum of $278.1 \text{ m}^3 \text{ s}^{-1}$ (September) and an average maximum of $1,278 \text{ m}^3 \text{ s}^{-1}$ (March). Annual mean water temperature is 9°C with maxima registered in January (15°C) and minima in July (3°C). The Santa Cruz main stem river has a regular gradient (mean slope 0.6 m km^{-1}), without a clear differentiation in sections or reaches (Tagliaferro et al., 2013). The locations of the two proposed dams are at river 132 km downstream of the lake (Cóndor Cliff, 50.206°S , 70.785°W) and river 197 km (Barrancosa, 50.185°S , 70.177°W). Together they will dam up 197 km of river, reducing the unregulated length of river to 49% of pre-dam conditions (lower stretch, Fig. 1c).

We conducted an intensive field survey of the main stem Santa Cruz River during September 20–29, 2010 (month of minimum discharge). Two crews navigated the main stem river downstream, one taking continuous measurements of depths and river widths and the other making stops for stream habitat measurements and biological samples. A total of 52 sites located at regular 6 km intervals (hereafter referred to as “segments”) were sampled along the 310 river km (Fig. 1c). The uppermost site was located at Charles Fuhr (10 km downstream from Lake Argentino) and the lowermost site was located close to the estuary, at the town of Piedra Buena (318 km from the lake). We designed this one-time whole-river sampling scheme to generate a detailed geographic inventory of the river habitats and their biological communities, to complement data collected during eight sampling campaigns of detailed local and seasonal surveys performed between 2008 and 2010 which included river physical characteristics, invertebrates, and fish at sites along the river. Those surveys indicated that seasonal and inter-annual variation in community structure was low and

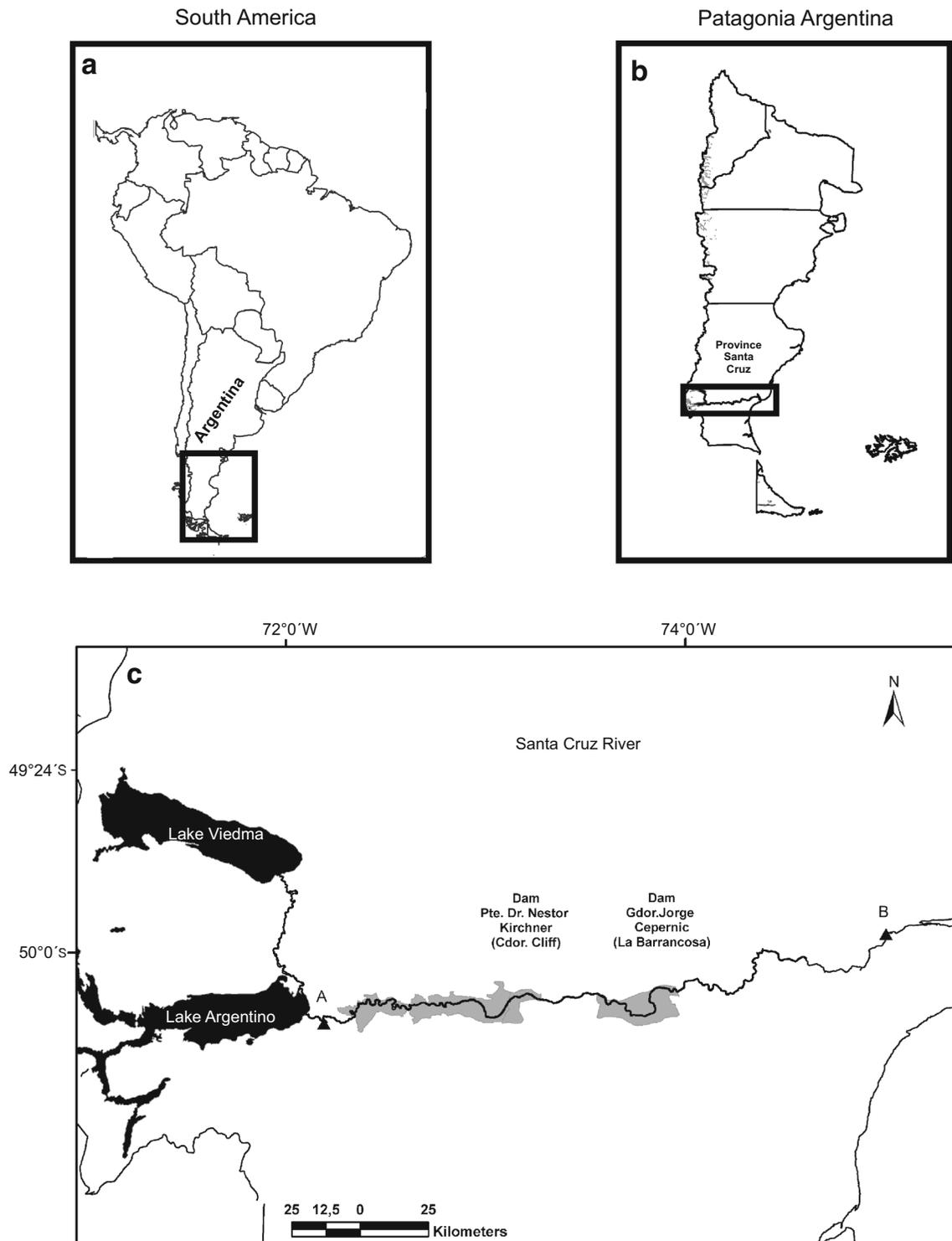


Fig. 1 a Location of Argentina in South America. b Location of the Patagonia Argentina and Santa Cruz River. c Santa Cruz Rivers. Points A and B represent the first and last sites sampled

during September 2010. *Arrows* indicate the location of the two dams, and *gray areas* indicate the area to be inundated by proposed dam construction

we were thus confident that a better baseline could be obtained by a geographically detailed one-time, intensive sample.

A total of 15 habitat variables were measured at each of the 52 sites along the river (Table 1), including water characteristics and river morphology, dissolved solids and organic matter, and macroinvertebrate abundance. Site positions were obtained with a GPS (Oregon 550 Garmin). Macro-scale variables of the river (i.e., bankfull width, wetted width, and channel depth) were measured either continuously or every 300 m. Wetted and bankfull widths were measured using a laser distance meter (TruPulse 200). Depths across the river were recorded with a Lowrance LCX-15MT echosounder mounted on a boat that navigated downstream in a zig-zag pattern, to make sure that the thalweg was regularly crossed.

Local variables, within a 15 m radius from the sampling point (e.g., dissolved oxygen, depth, current speed, substrate size), were measured in situ at each of the 52 sites following Gordon et al. (2004). Mean local depth was calculated from three measurements within the sampling area. Surface current speed was obtained by timing a half-submerged plastic filled cup over a distance of 5 m at each sampling site. Water temperature, conductivity, and dissolved oxygen were measured using an YSI 85 multi-parameter probe (YSI Co). Substrate size composition was estimated following the Wolman Pebble count procedure (Wolman, 1954), by walking upstream along a zig-zag line across

a working area of 100 m long and 2–5 m wide and measuring the width of 100 pieces randomly chosen. Water samples of 500 ml were collected below the surface, filtered using a 47 mm diameter GF/F Munktell filter, and preserved at -10°C to estimate total suspended solids. In the lab, samples were dried at 60°C for 24 h, weighed, and burned at 500°C for 4 h to assess suspended organic and inorganic matter. Macroinvertebrate samples were taken at each of the 52 sites with a kick-net of 450 μm mesh size, 0.25 m^2 area. For details on processing and specific results see Tagliaferro et al. (2013). In this paper, we used the total number of individuals recorded in each of the 52 sites. For each of the 52 sites, we defined a buffer area of 300 m radius, then the maximum channel depth of all field measurements within the buffer area was assigned to each site (maximum depth). The slope and sinuosity at each of the 52 sites were calculated considering the previously defined segments (6 km length). The slope was calculated for each segment from a 90 m digital elevation model (<http://srtm.csi.cgiar.org/>), and the sinuosity was calculated as the geographic distance between the two extreme points of the segment divided by the segment length.

We captured fish in each of the 52 sites using a standard single-pass electrofishing procedure (Smith-Root LR-24 electrofisher; freq. 90 Hz; pulse width 3 ms). At each site, a 100 m transect was sampled following a zig-zag track from the littoral zone to a depth of 0.7 m. To standardize the sampling process as

Table 1 Summary of physical and chemical and habitat variables measured at the 52 sampling sites of the Santa Cruz river

Variable	Abbreviation	Mean	SD	Range
Mean local depth (m)	md	0.29	0.15	0.07–0.81
Mean local water velocity (m s^{-1})	mv	0.29	0.24	0–0.89
Water temperature ($^{\circ}\text{C}$)	temp	6.87	1.44	4.7–11.0
Conductivity ($\mu\text{S cm}^{-1}$)	cond	26.80	2.97	14.3–35.0
Dissolved oxygen (mg l^{-1})	DO	12.32	0.69	10.64–15.43
Substrate size (mm)	sz	78.13	25.50	15.5–147.5
Suspended inorganic matter (mg l^{-1})	IM	22.22	18.97	5.2–117.0
Suspended organic matter (mg l^{-1})	OM	3.09	2.23	0.6–12.8
Wetted width (m)	ww	139.44	34.14	80–216
Bankfull width (m)	bw	188.59	40.045	110–281
Distance from lake along river (km)	rkm	162.80	90.921	9.8–315.8
Slope (m km^{-1})	slp	0.6	0.2	0.1–0.9
Max channel depth (m)	mcd	5.660	2.945	2.3–19.8
Sinuosity	sin	1.3	0.2	1.1–2.0
Macroinvertebrates abundance (num)	mab	86.769	97.006	1–514

Abbreviation refers to the names of the variables as they appear in the GLM models

SD standard deviation

much as possible, in sites on river bends, we always choose the lower gradient, inside bank to conduct the electrofishing. As the main stem Santa Cruz River is relatively homogenous with respect to physical habitat, we found locations suitable for electrofishing in each of the 52 sites. Fish were euthanized with an overdose of MS222 and stored in a portable freezer at -18°C . In the laboratory, all fish were counted, length-measured measured with a digital caliper to the nearest 0.01 mm, and weighed on a Mettler PC 440 Delta Range balance (0.003 g nearest unit). In this paper, we report on catches of juvenile rainbow trout. See Tagliaferro et al. (2014a) for a report of the native fish *Galaxias maculatus*.

Data analysis

We used the number of juvenile rainbow trout collected in each of the 52 sites along the river as an index of relative abundance (from now on “abundance”). We examined the length distribution of all captured fish to assign them their stage and age. We then inspected the distribution of each of the 15 habitat variables and search for correlations between pairs of variables. This analysis allowed us to identify spatial patterns in habitat distribution and identify variables that because of collinearity could be deemed spurious in our trout-habitat relationships and, therefore, be considered as variables to be dropped from models.

We used regression techniques, which are widely used to model the abundance of fish as a function of environmental data (Fausch et al., 2001; Guisan et al., 2002). Abundance data typically show a non-linear response to explanatory variables and non-normal errors, and thus violate assumptions of traditional linear regression models. GAM and GLMs are more flexible statistical tools that allow for nonlinearity and non-constant variance structures in the data (Hastie & Tibshirani, 1990). Both GLMs and GAMs use a link function that transforms the non-linear mean of the response variable into a linear predictor. While GLMs use a parametric model to portray the non-linear mean responses in the data, GAMs use a non-parametric smoother, making them a flexible tool for exploring the shape of the response variable. GAMs allow identification of the general shape of the response variable for each explanatory variable, whereas GLMs provide a more direct and robust technique to evaluate the goodness-of-fit and to interpret the results (Guisan

& Zimmermann, 2000). To take advantage of the strength of each technique, we used a two-stage model fitting approach, similar to that used by Franklin (1998) and Lancelotti et al. (2010) based on combining GAMs and GLMs, both assuming a scaled Poisson distribution with a log-link function. This model structure provides a good description of the error structure of discrete variables (i.e., number of fish) when there is variance overdispersion (variance larger than the mean). All statistical analyses were conducted using the R software (R Development Core Team, 2008), applying different packages for specific analyses (see below).

First, non-parametric GAMs were fitted to explore the response (relative abundance) of juvenile rainbow trout to the predictor variables, applying the smoothing spline function (Hastie & Tibshirani, 1990; Hedger et al., 2005; McMillan et al., 2013). The objective of this step was twofold: identifying those variables among the 15 predictors to which the abundance of trout was more strongly related, and identifying the shape of the response to specific predictors. In this step, we fitted more than 96 alternative models incorporating five different variables at a time and in different combinations until we identified a set of variables that trout abundance was consistently and significantly related to. Then GLMs were used to reproduce the identified shapes with adequate parametric terms in the model for the subset of the best predictor variables as indicated by the GAMs, and for a further evaluation of significant variables. To obtain the minimal adequate model (i.e., a model in which all terms are significant for each data set), we fitted all possible models using the “dredge” function within “MuMIn” package (Barton, 2013). Also a backward fitting procedure was followed, dropping variables one at a time starting from the saturated model. Significance tests for individual predictor variables were conducted as a mean of model comparison based on F-tests. All statistical analyses were conducted with R software (R Development Core Team, 2008). Model fitting and deviance analyses were conducted with the package “mgcv” (Wood, 2014).

For GLMs, we included second-order polynomial functions to accommodate non-linearities in the response variable observed in GAMs analyses (Franklin, 1998). A first round of modeling showed that some habitat attributes appeared to be significantly associated to high trout abundance in the upper river (e.g.,

wetted width or substrate size) but not in the lower river. This inconsistency was readily solved when river kilometer (rkm) was introduced in the model, hinting at the existence of different domains within the river, where different habitat-trout relationships might apply. We investigated the existence and location of these domains by exploring different shapes for the effect of rkm on trout abundance. After fitting the GAMs, it was apparent that the response function of trout to rkm might be better represented by a segmented linear regression (or piecewise regression), i.e., two segments, each one with its own slope, connected by a point whose value is known as breakpoint (Muggeo, 2008). The algorithm used to find the value of this point is an iterative procedure that requires only the starting values for the breakpoint of the variable of interest (Muggeo, 2013). We followed the methodology suggested by Muggeo (2013), which proposes a readjustment of the selected model. This specific analysis was conducted using the package “segmented” (Muggeo, 2013).

The model selection process to obtain the minimal adequate GLM was based on two combined criteria. As with the GAM model selection, we first conducted *F*-tests to find the set of significant independent variables that best explained the abundance of trout at

each site along the riverscape. Since prediction was the goal, we then used a goodness-of-fit criterion that depends on the error of prediction to select the best fitting model among the candidate GLM models. Such a measure is provided by “one item out” cross-validations, similar to that proposed by Linhart & Zucchini (1986) and Efron & Tibshirani (1993). A prediction for each of the *n* observed abundances is obtained from the linear data fitted to the remaining points, and the proportional distance between the prediction and the observed abundance, for example, is used as a prediction error for that observation. Let Y_i be an observation and let \hat{Y}_i be the estimated value when the point *i* is excluded. The percentage error for the *i*th observation is

$$E_i = \left| \frac{Y_i - \hat{Y}_i}{Y_i} \right| \times 100.$$

The median or the percentiles of the *n* estimates of error (E_i 's) provide measures of the prediction error associated to each a particular model.

In our case, for each one of the 52 sites, a prediction of the trout abundance was obtained from the model fitted to the data for the remaining sites (excluding the data for the one site). The distribution of deviations

Table 2 Summary of alternative models (GLMs) of trout-juvenile abundance fitted with habitat variables

Models GLMs	Dev	Df	P value	% Prediction error	
				Median abundance	90% percentile
M1 aom ~ poly (ww,2) + poly (sz,2) + poly (rkm,2) + poly (mab,2)	327.32	43		62.64	307.35
M2 aom ~ poly (ww,2) + poly (sz,2) + poly (rkm,2) + mab	334.11	44	0.35	56.95	298.7
M3 aom ~ poly (ww,2) + poly (sz,2) + poly (rkm,2)	358.57	45	0.08	63.74	321.8
M4 aom ~ poly (ww,2) + poly(mab,2) + poly(rkm,2)	427.88	45	0.01	71.07	227.93
M5 aom ~ poly (sz,2) + poly(mab,2) + poly(rkm,2)	421.81	45	0.01	70.04	322.03
M6 aom ~ poly (sz,2) + poly(rkm,2)	469.99	47	0.03	68.72	352.6
M7 aom ~ poly (sz,2) + poly(rkm,2)	517.94	47	0.01	76.05	324.23
M8 aom ~ 1				69.56	1,258.82
M9 aom ~ poly (ww,2) + poly (sz,2) + segmented(rkm,2)	334.1	43	0.02	51.15	349.65

The relative abundance of *O. mykiss* (aom) was fitted with four environmental variables ww (wetted width), sz (substrate size), rkm (river kilometer), and mab (macro invertebrates abundance). The prefix “poly” preceding terms in the models refers to second-order polynomial functions used to accommodate non-linearities in the response variable. Model nine (M9) include the function “segmented” used to accommodate the functional response of fish abundance to river kilometer, which has a different slope downstream and upstream to the kilometer 153.8 (see “Results”). The analyses were conducted with a quasi-Poisson family distribution, with an over dispersion factor of $\varphi = 7.6$. *Dev* and *Df* correspond to the residual deviance, and degree of freedom respectively. The median absolute error and 90% percentile prediction errors (last two columns) were estimated with a leave-one-out cross-validation analysis for each alternative model. In bold the selected model

between observed and predictive values provides a portrayal of predictive errors and a specific quantile from this distribution, an overall measure of predictive error. Table 2 provides these statistics for each model of relative abundance of the juvenile's trout.

Results

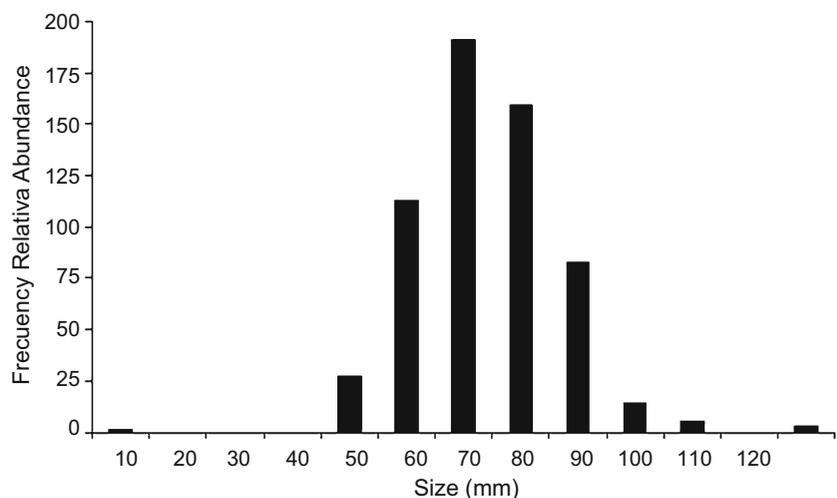
A total of 571 rainbow trout were caught at 45 of the 52 sites sampled. The fish had a mean length of 69 mm (range 50–110 mm, Fig. 2), a size that corresponds to 0+ fish, determined by scale analysis (Liberoff et al., 2014). The hatching of rainbow trout in the Santa Cruz River occurs between November and January so, on average these fish were 9 month of age. The abundance of rainbow trout was not homogeneous along the river (Fig. 3c), but had maximum values in the mid-section of the river, between rkm 100 and 200 (measured from the lake to the mouth), with peak abundance at rkm 160. The abundances were lower and variable in the upper 100 km section of the river and much lower in the lower 100 km section of the river (Fig. 3c).

Before proceeding with modeling trout abundance as a function of habitat variables, we did some exploratory data analysis of the habitat attributes themselves along the river, and correlations among pairs of variables. As expected, bankfull width and wetted width, two alternative attributes related to the shape of the channel, had a strong correlation ($r^2 = 0.7$). We chose to keep only wetted width,

which emerged as the most significant explanatory variable in our models (see below). Also, our records of water temperature showed an increasing trend with rkm ($r^2 = 0.9$). The survey was conducted moving downstream, on 10 consecutive days, a period in which we experienced unusually warm and windless weather for the season. We suspected that the increasing water temperature was associated to this warming trend rather than to a geographic arrangement. Such relationship between air and stream temperature was also recorded by Bartholow's (1989) from hundreds of locations throughout the West of North America, who concluded that air temperature over the stream was the most influential factor for warming the streams. To support this, a geographic pattern in temperature in any of 8 previous surveys conducted between 2008 and 2011 was not found, which albeit not being as systematic in their geographic coverage, did cover sites in different sections of the main stem river. We, therefore, decided to drop temperature from the analysis, keeping only rkm in our model explorations.

As a sample of the larger database, Fig. 3 shows a subset of variables that, after model selection procedures (see below), ended up being good predictors of trout abundance. Substrate size had significant variability among sites, around an overall dome-shape pattern, with maximum values at mid-stream locations (Fig. 3f). Wetted width also had significant variability and an inverse shape, with lower overall values at midstream locations. In fact, substrate size and wetted width were negatively

Fig. 2 Size frequency of juvenile rainbow trout caught at 45 of the 52 sampling sites of the Santa Cruz river ($n = 571$)



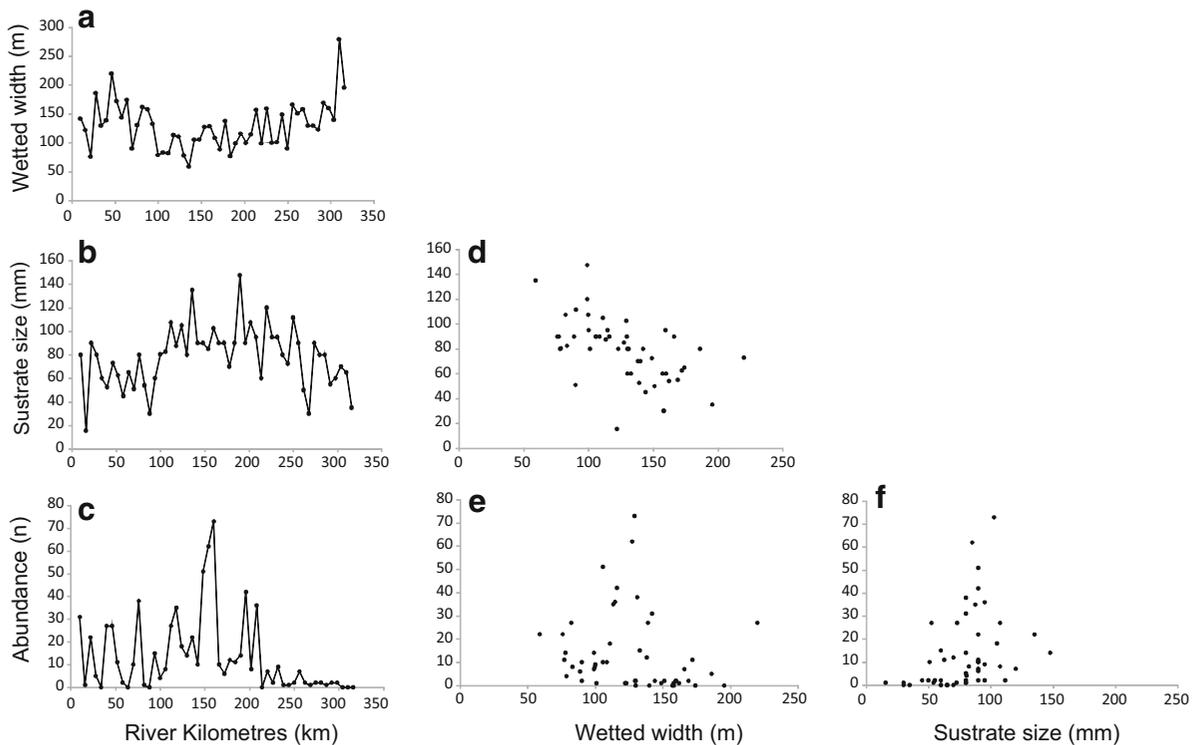


Fig. 3 Habitat variables (wetted width and substrate size) and juvenile rainbow trout abundance along the river (*left panels*) and X–Y plots of pairwise combinations of these three variables.

correlated ($r^2 = 0.5$; Fig. 3e). Trout abundance appeared to be maximal for intermediate values of both variables, something that was further analyzed with our GAMs and GLMs multivariate models.

After removing temperature, the fit of GAMs with the remaining 14 habitat variables (96 alternative models, five different variables at a time and in different combinations) allowed us to identify a set of four variables that trout abundance was consistently and significantly related to (Fig. 4) wetted width, substrate size, rkm, and macroinvertebrate abundance. All other variables were systematically discarded in all specific backward stepwise model evaluations. The robustness of this basic model was further evaluated by 10 separate tests by incorporating each of the 10 remaining variables one at a time. The fit of the GAMs also indicated the particular shape of the partial response of trout abundance to each of these four variables (Fig. 4). All responses were non-linear. The response to wetted width was clearly dome shaped, with a maximum at intermediate values. The response to substrate size was also dome shaped, but with a

In all graphs, points correspond to sampling sites ($n = 52$). River kilometers (rkm) is the distance from the Argentino Lake downstream to the mouth

maximum close to maximum recorded values of substrate size. The response to rkm is decreasing, with potential maximum upstream and declining abundances toward the estuary. The response to macroinvertebrate abundance is more complex, with an apparent overall increasing response for higher macroinvertebrate abundances.

A first round of model selection by fitting the GLMs to trout abundance as a function of the four candidate variables above (Table 2) allowed us to discard macroinvertebrate abundance (P value = 0.35), while supporting the significance of the other three variables to explain trout abundance. Also, it supported the use of quadratic, dome-shape functions to represent the responses of trout to these three variables (Fig. 5; model 3 in Table 2). A second round of model evaluations allowed us to test and select an alternative model for the response to rkm applying a segmented linear function by piecewise regression (Table 2, model 9; Fig. 5). This model indicates that the best response of trout to distance along the river consists of a homogeneous response (slope = 0) up to

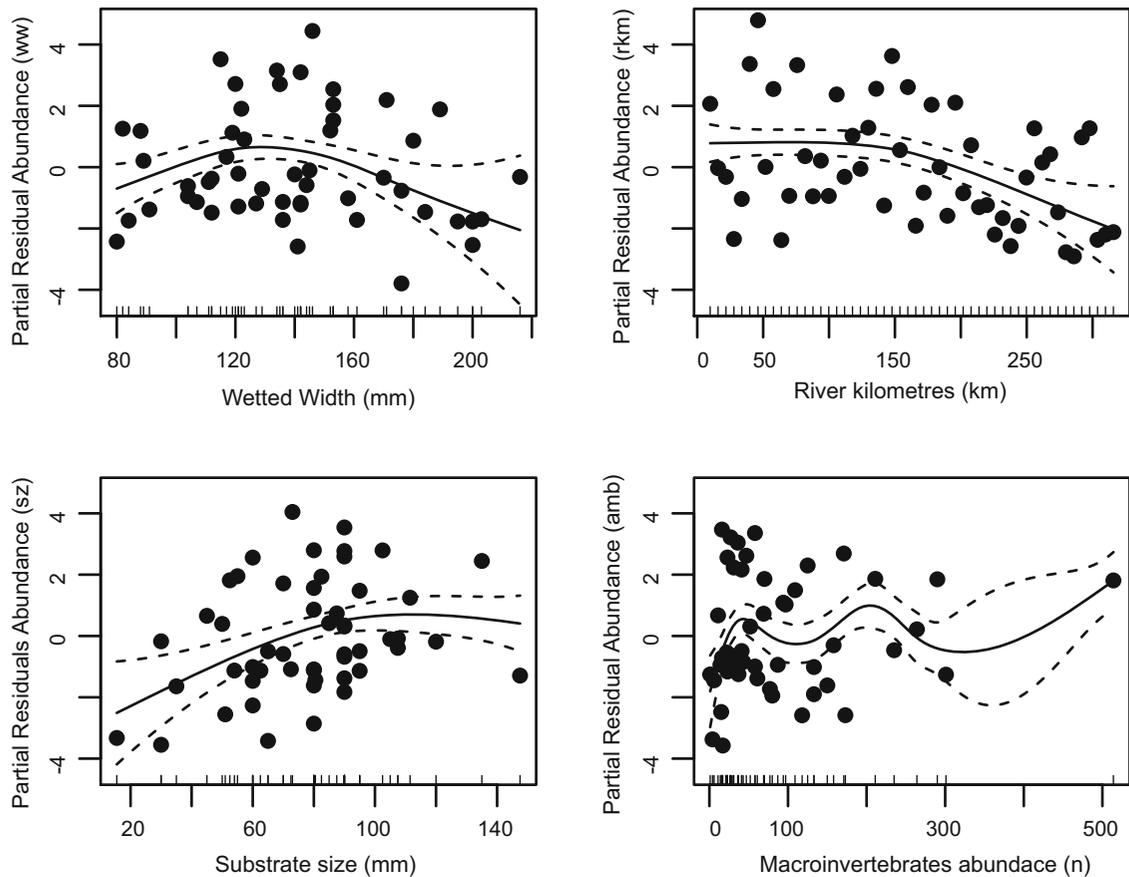


Fig. 4 Partial residuals of trout relative abundance against four significant explanatory variables based on GAMs. *Solid and dotted lines* represent the fitted values and 95% confidence interval, respectively

rkm 153.8 (breakpoint, SE 7.04), and a strongly declining response from that point and downstream toward the estuary. This model, with quadratic response to wetted width and substrate size and a segmented linear function with rkm (model 9 in Table 2), was considered the overall best model because it had a lower value of the over dispersion parameter (6.7 as compared to 8.7 in the previous best model), the smallest deviance, and the lowest median absolute error predictions. This model was able to fit the distribution of juvenile trout along the river well (Fig. 6), including the general differences between river sections: upper (intermediate abundances), middle (highest abundances), and lower (lowest abundances). The model is also able to capture local differences in abundances well, such as the two maximal abundances in the middle section and other specific high and low abundances in the other sections. The model is also favorably judged in terms of its

depiction of cumulative abundances (Fig. 7a). It is able to capture the general shape of the distribution as well as particular transitions associated to high abundance sectors. However, the model underestimates abundance of juvenile rainbow trout when the abundance is greater than 20 individuals. According to this model (model 9), 86% of the juvenile trout are produced in the upper half section of the river (51% to be inundated by the dams (Figs. 1, 7a) and a high concentration of fish (50% of the juvenile production of the river) occurs in the 70 km section in between the two dams to flooded by the lower dam (Table 3).

Discussion

Most studies of juvenile salmonid habitat preferences have been conducted in small, wadeable streams, with habitat structures typically characterized by pool-run-

Fig. 5 Fitted polynomials estimated by GLM for three explanatory variables of juvenile rainbow trout abundance in the Santa Cruz river, and the piecewise fit to river km (*lower right panel*). The *dotted lines* represent pointwise 2 SE curves, and points are partial residuals. Each point corresponds to one of the 52 surveyed sites

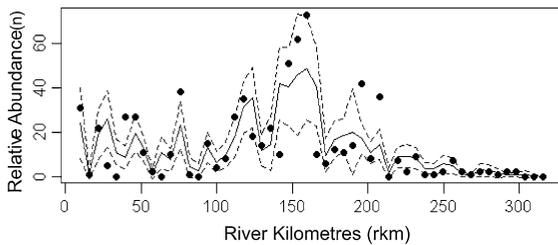
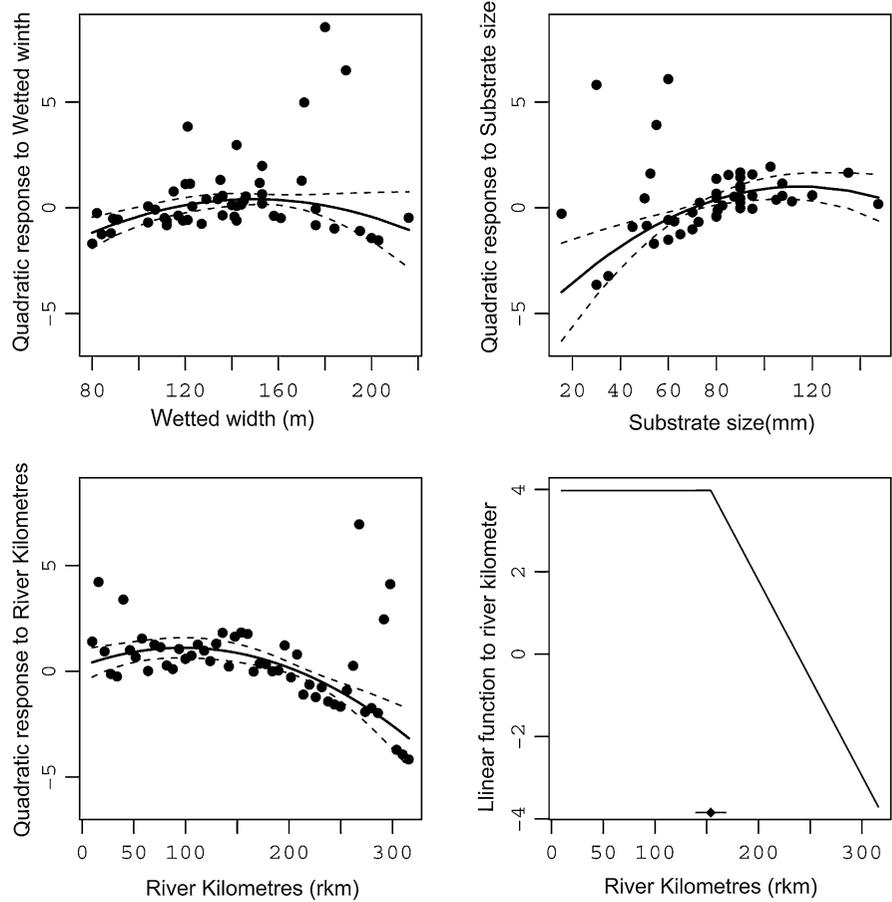


Fig. 6 Relative abundance of juvenile rainbow trout along the Santa Cruz River (*dots*), fitted top GLM model (M9; *solid line*), and confidence intervals (*broken lines*)

riffle sequences (Bisson et al., 1988; Milner et al., 1993) and focusing on local variables, such as temperature, cover, and current velocity (Jowett, 1990; Milner et al., 1993; Inoue et al., 1997). Meanwhile, few studies have been conducted in large rivers, mainly because of the intrinsic difficulties of generating a representative sampling scheme in large systems (Murphy et al., 1989; Mäki-Petäys et al., 1997).

We were able to conduct an assessment of fish and habitat of an extended portion of a large river, through a systematic field survey considering variables measured at different scales, measured through a combination of instrumental methods, and with a calibrated model of predictive value as the final product. Our work was in part facilitated by the general homogeneity of the Santa Cruz River, which has been previously recognized by Tagliaferro et al. (2013, 2014a), when reporting data on macroinvertebrates and native fish. The Santa Cruz has no second- or third-order tributaries, where the highest abundance of juvenile salmonids is found in other rivers around the world (Murphy et al., 1989; Boughton et al., 2009). The main stem itself is largely homogeneous, without a clear division in subsections or reaches, as opposed to most of the rivers, where studies of salmonid habitat have been carried out (Heggnes, 1990; Kocik & Ferreri, 1998).

Fig. 7 a Cumulative frequency of juvenile *O. mykiss* abundance along the river according to the observations (gray diamonds) and the model (solid line), and proposed position of dams (vertical dotted lines). The bars show the cumulative juvenile trout abundance for each of the river sections delimited by dams (Fig. 1c): above Condor Cliff, in between two dams, and below Barrancosa dam. The open circles indicate spawning positions of radiotracked adult fish (Riva Rossi et al., 2003). **b** Plot of observed versus predicted abundances of the juveniles rainbow trout

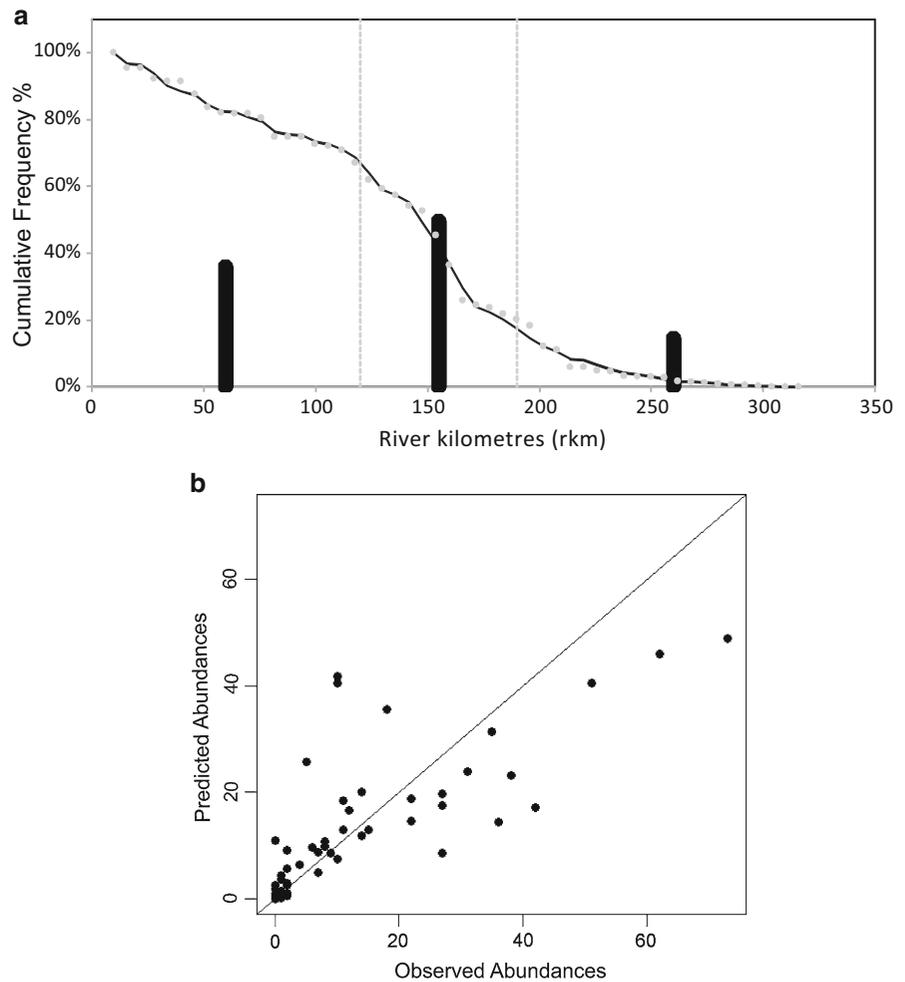


Table 3 Summary of the selected model (M9, Table 2)

	Estimate	SE	<i>t</i> value	(<i>Pr</i> > <i>t</i>)
Intercept	3.97	0.83	4.7	2.41e−05
poly (ww.2) 1	0.39	1.43	0.2	0.78
poly (ww.2) 2	−3.12	1.2	−2.5	0.01*
poly (sz.2) 1	5.27	1.69	3.1	0.003**
poly (sz.2) 2	−2.69	1.15	−2.3	0.02*
poly (rkm.2) 1	10.54	7.02	1.5	0.14
poly(rkm.2) 2	4.12	3.44	1.1	0.23
U1.k	−0.04	0.01	−2.66	NA

Column Estimate refers to the estimated value for each model parameter

Bold values represent the selected model with the lowest prediction error which was applied to the segmented function

Our model selection procedure led us to a simple and biologically meaningful model to explain juvenile trout relative abundance based on three predictor variables: wetted width, substrate size, and rkm. Changes in wetted width throughout the river are related to some extent to the cross-section of the channel and, therefore, to hydrologic characteristics, such as water velocity, turbulence, etc., which, in turn, affect the size of substrate particles. Wetted width and substrate size are negatively correlated, indicating that wider sections of the river, where water speed is lower, had smaller substrate particles than narrower sections, with faster current and larger substrate particle size. The quadratic relationship of juvenile relative abundance with each of these two variables indicates that

juvenile trout in the Santa Cruz select sites with intermediate wetted widths and intermediate substrate size (80–216 m, 15.5–147.5 mm, respectively).

But juvenile abundance along the river is not related to these two habitat variables alone. River kilometer, a variable related to the relative location along the river, needs to be included in the model to explain the overall pattern of juvenile trout abundance. The segmented linear function selected indicates that there are two different domains in the river, with trout responding homogeneously to habitat conditions in the upper half of the river, but declining in the lower sections for reasons unaccounted for by the habitat variables we recorded. This pattern could therefore emerge as a result of habitat differences between these two sections that are not captured by our set of 15 variables. An alternative explanation is that the pattern is related to the distribution of spawning adults which, in the end, will determine the distribution of their offspring. In the Santa Cruz River, a radiotracking program in which 22 adult rainbow trout were followed throughout the spawning migration (M. Garcia Asorey, unpublished data; Riva Rossi et al., 2003) indicated that 60% of those fish migrated to spawn in upstream locations (estimated spawning locations shown in Fig. 7). Liberoff et al. (2014) found that the distribution of YOY rainbow trout along the Santa Cruz River is strongly influenced by spawning activity. Our data and models with a distribution of juveniles biased toward upper locations as depicted by our segmented regression model, support the observations that rainbow trout/steelhead spawn primarily in the upper section.

This is one of the few studies using a riverscape approach to describe spatially continuous fish abundance and habitat relationships before the construction of the dams (Fausch et al., 2002; Torgersen et al., 2006). The application of this approach provided a spatially comprehensive view of an exotic trout population along the Santa Cruz River, a semi-pristine basin, allowed characterization of the physical habitat conditions from the headwaters to the river mouth, and identified some of physical drivers regulating trout distribution and abundance. Previous studies using the riverscape approach have shown similar patterns in the distribution of juvenile salmonids. For instance, Brenkman et al. (2012) used a linear model to estimate the relationship between salmonid species density and 11 stream habitat characteristics in the Elwha River,

Washington, USA and found the density of juvenile trout was positively associated with substrate size but negatively associated with the position of trout along the river, with the highest abundance of trout located in the lower section of the river, downstream of the Elwha Dam. Therefore, they concluded that trout abundance was most strongly influenced by the presence of the two dams blocking the river corridor at rkm 7.5, than by other natural physical factors. Roni et al. (2012) used multiple regression models to examine the relationship between habitat variables and growth, survival, and emigration in juvenile Coho salmon also in two small western Washington rivers, finding that rkm correlated both positively and negatively with juvenile densities. In another study, McMillan et al. (2013) used GAMs to examine the correlation between juvenile salmonid density and five stream habitat variables in the Calawah River, Washington. They found a negative association between densities of age-0 steelhead and wetted width (contrary to our results); however, the variable accounting for location of the habitat within a stream was more important than the habitat variables, a pattern similar to what we found in the Santa Cruz River. These authors also suggest that distributions and abundance of young-of-the-year juveniles might reflect differences in the abundance and location of spawning adults. Consistent with this finding, and our results, many studies have documented high juvenile density areas occurring in the proximity of spawning areas (Murphy et al., 1989; Foldvik et al., 2010; Flitcroft et al., 2014). Differences and similarities among these and our study, and in particular the overall importance of river location for explaining abundance patterns, highlight the potential limitations to extrapolating fish–habitat relationship models to broader areas or to streams other than those in which the data were collected (McMillan et al., 2013).

All in all, our riverscape approach provided a baseline inventory for juvenile trout along the river and in relation to proposed dam sites. Most of the juvenile trout (86%) and (60%) spawning sites of adults breeding are found in areas that will be flooded by the dams, and thus, access to the ocean will be cut-off. As a result, the impact of this project on Santa Cruz steelhead trout will be extremely severe. Because the whole upper section will be flooded and no spawning areas will remain above the two dams, passage systems, which may work for

other species in the watershed (e.g., Chinook salmon, Ciancio et al., 2005) may prove superfluous for this species.

One aspect that we did not take into account in our model was density dependence. Density-dependence processes during early fluvial stages are known to play a dominant role in the regulation of abundance in salmonid populations (Milner et al., 2003; Quinn, 2005), particularly in rivers such as the Santa Cruz with highly stable hydrological conditions (Armstrong et al., 2003; Milner et al., 2003; Einum, 2005). Various analyses of the dynamics of anadromous salmonid populations, based on modeling the specific density dependent and independent processes along their complex life cycle (Scheuerell et al., 2006), point at the dominant importance of river habitat and early stages in determining overall population size (Scheuerell et al., 2006; Honea et al., 2009). Based on all this evidence, we believe that the juveniles analyzed in our study had gone through high mortality processes associated with early stages (e.g., eggs and fry) and major demographic bottlenecks.

Some factors may in part compensate for those losses. For instance, changes in behavior by spawners in response to the dams may increase the relative production of the lower section. Likewise, improvements in water quality, food availability, or habitat conditions for juvenile production as a result of water regulation in dams may also increase the production of juveniles in the lower section. But water regulation may also reduce the production of juvenile trout or may even affect the rate of smoltification leading to the anadromous lifestyle (Angilletta Jr. et al., 2008). In any event, projecting the specific impacts of water regulation on trout behavior, survival, growth, or smoltification as they impact on juvenile production and the size of the adult anadromous population is a very uncertain task. Brenkman et al. (2012) postulates that dams have generated a decrease in the population size of salmonids in rivers of the United States and changed evolutionary trajectories of life-history strategies and fish migration patterns that are altered within rivers because the rivers have disrupted hydrological connectivity.

From a social point of view, the alterations produced by dams change the scheme of resource use, frequently entailing a reallocation of benefits from local riparian users to new groups of beneficiaries at a regional or national level (Word Commission on Dams, 2000).

Whereas the benefits for new beneficiaries are usually readily measured and judged in terms of dollars, kilowatts, or hectares under irrigation, the losses for riparian users typically go untested. For example, if the production of trout in the section below dams was to remain unaffected by the dams, the population is bound to be reduced to a fraction of its current size, strongly affecting riparian users of the steelhead trout as a source of recreation or income. In this context, the consequences of this project on Santa Cruz steelhead trout are the alteration of the primary habitat of the juvenile trout and the reductions of spawning areas.

Our data and models provide the building blocks for an impact assessment on the main recreational fishing activity in the watershed, and our results generate a rare opportunity to fulfill the prescription for dam environmental impact assessments based on collecting pre and post-dam data on resources and users throughout the catchment.

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