BRIEF COMMUNICATION

Maternal influence on early lipid content in an introduced partially anadromous population of rainbow trout *Oncorhynchus mykiss*

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ABSTRACT

This study evaluated how the maternal migratory tactic in a partially anadromous population of *Oncorhynchus mykiss* may influence the early energetic status of their offspring. Total lipid content variation (% dry mass) of recently emerged fry caught in the Santa Cruz River, Argentina, was evaluated as a function of their maternal origin (anadromous *v*. resident) and fork length (L_F). Lipid content of fry decreased with L_F and was higher for offspring of anadromous mothers.

Significance Statement

Partial migration is widespread across animal orders and occurs at variable spatio-temporal scales. The study of evolutionary and proximate causes of partial migration has implications for population management and species conservation. The *O. mykiss* population from the Santa Cruz River is the only introduced population that has successfully developed anadromy outside the native range. This recent introduction and evolution of life history strategies is a natural experiment to understand the evolution and persistence of migration.

KEYWORDS

alternative migratory tactics, lipid content, maternal effects, *Oncorhynchus mykiss*, Patagonia,

trout

Rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) is one of several species of salmonids

that displays partial migration; one fraction of the population migrates to the ocean, before

returning to fresh water to spawn (*i.e*., anadromy), while the other completes the whole life

cycle in fresh water (*i.e*., residential; Jonsson and Jonsson, 1993; Sloat and Reeves, 2014;

Kendall *et al.*, 2015). The balance between anadromy and residency in *O. mykiss* is shaped by

interactions among a fish's genotype (Hecht *et al.*, 2015), sex (Rundio *et al.*, 2012),

individual condition (*e.g*., juvenile size, early growth rate, and energy stores; McMillan *et al.*,

2012; Dodson *et al.*, 2013) and environment (Sloat and Reeves, 2014). There is good

evidence of both genetic controls on traits that are associated with life-history adaptation

(*e.g*., growth, metabolism; Hale *et al.*, 2013; Hecht *et al.*, 2015; Elmer, 2016) and the

influence of the environment on an individual´s condition (*e.g*., food supply and water

temperature; Olsson *et al.*, 2006; McMillan *et al.*, 2012). In partially anadromous

populations, there is a strong additional influence associated with maternal investment and

behaviour (*i.e*., maternal effects; Bernardo, 1996). As a result of the marine migration,

anadromous females attain larger size at age and higher growth rates and fecundity (Hendry

& Stearns, 2004), which can result in profound differences in egg provisioning (Einum &

Fleming, 1999) and spawning behaviour (Fleming & Reynolds, 2004) between anadromous

and resident females. Maternal effects might influence juvenile condition (Perry *et al.*, 2005;

Chernoff & Curry, 2007), their physiological pathways (Liberoff *et al.*, 2014) and life-history

adaptation (Zimmerman and Reeves, 2000; Berejikian *et al.*, 2014).

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The Santa Cruz River, Argentina, supports an introduced self-sustaining population of *O. mykiss,* which is the only population known to have developed anadromy outside its native range (Pascual *et al.*, 2001). Introductions of this species in Argentina started in 1904 (Tulian, 1908), but the first validated record of a large *O. mykiss* in the Santa Cruz River was in 1982 (Pascual *et al.*, 2001). Since 1998, this population has been monitored and previous studies indicated that the anadromous and resident forms are now genetically indistinguishable at neutral microsatellite loci (Pascual *et al.*, 2001) and can give rise to either life-history patterns (Riva-Rossi *et al.*, 2007). Previous studies in this system suggest that maternal effects are the main mechanism involved in the perpetuation of anadromy across generations (Liberoff *et al.*, 2014; Liberoff *et al.*, 2015). Offspring of anadromous mothers are more likely to become anadromous because they grow faster and achieve a larger size than resident offspring (Liberoff *et al.*, 2014). In addition, maternal spawning behaviour determines juvenile rearing habitats providing the adequate physical environment for anadromous offspring to achieve larger body sizes and become anadromous (Liberoff *et al.*, 2015).

Since anadromous females attain larger body sizes at age and lay larger eggs than resident females (Einum & Fleming, 1999) it has been suggested that egg provisioning is the main factor leading to body size at age and juvenile growth advantages in the Santa Cruz population. Egg size can be expressed in terms of total lipid content (Leblanc, 2011), which is also a good indicator of fish nutritional status (Sargent *et al.*, 2003). The current study evaluates the variation in lipid content of newly emerged fry from anadromous and resident origins in order to provide further insight into the maternal effects influencing early physiological pathways in *O. mykiss*.

Lipid content of anadromous and resident offspring captured along the Santa Cruz River (Santa Cruz Province, Argentina, total river length *c*. 380 km; Figure 1) were compared. Given that after hatching, lipid reserves from the yolk sac are allocated to meet

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growth demands (Quinn, 2011), the variation in lipid content was evaluated as a function of body size. Young *O. mykiss*, 1 to 3 months old, were captured by electrofishing at three locations in the spring of 2008 and 2009. The location of sampling sites were chosen according to previous surveys and analyses performed on this population, which included gillnet sampling, radio tracking, and electrofishing surveys coupled with sampling of the sport fishery. In addition, a variety of habitats were sampled including main and secondary channels with contrasting physical conditions. Location 1 covered a large spawning area in the middle reach (115 km, stream distance from the ocean) and locations 2 and 3 covered two spawning areas in the upper reach (260–275 km, stream distance from the ocean; Figure 1). In the lower section we did not find fish at the fry stage.

Fish were killed immediately with an overdose of MS-222 and frozen at -20° C until laboratory preparation. Fish were measured (fork length, L_F, to the nearest mm), guts removed and otoliths were dissected. One otolith per individual was used for age estimation and the other was used for maternal origin determination. Age, as days post hatch (dph), was estimated from daily otolith increments (Campana, 1983) and maternal origin was determined combining stable-isotope techniques and otolith microchemistry. The methodology used for age estimation and maternal origin determinations are described in detail in Liberoff *et al.* (2014). Dried whole-body carcasses were ground with mortar and pestle for lipid determinations, where the same fish samples were used to evaluate the influence of the maternal ecotype on juvenile length-at-age variation and their propensity to migrate (Liberoff *et al.* 2014). Lipid content (per cent of dry mass, $M_D\%$) was determined though spectrophotometry based on the Zöllner and Kirsch (1962) method adapted for small aliquots (Honkoop *et al.*, 1999). The working standard was cholesterol. Three replicates were analysed for each individual and results are expressed as the mean value (Supporting Information Table S1).

In total, 101 individuals were analysed, but some otoliths were lost during fish dissection and all three measurements were available from only 70 individuals. Lipid content variation was evaluated as a function of L_F, maternal origin and sampling site by multiple linear regression. The main effect and interaction among variables were evaluated by likelihood-ratio test (LRT). Given a pair of models of different complexity (nested, different number of parameters), which are fitted to the data, LRT allows statistical consideration of whether the data support rejecting the simpler model in favour of the more complex one (Kimura, 1980). Final model residuals were analysed graphically to evaluate assumptions of normality and homogeneity of variance. Model fitting and selection was done in R (www.r-project.org).

Fork length from 24–33 mm and age ranged 25–89 dph (Figure 2). Fry from anadromous and resident origins did not differ in body size at capture ($t_{20.37} = -1.09$, $P > 0.05$) but they differed in age, with resident fry being up to twice as old as anadromous fry ($t_{17.11} = -9.26$, $P < 0.001$; mean $\pm$ 95% CI = 39.29 $\pm$ 1.97 dph, 68.53$\pm$ 6.43 dph for anadromous and resident progeny, respectively) (Figure 2).

Lipid content ranged from 7.77 to 24.56 % dry mass. Lipid content decreased with L_F for both residential and anadromous offspring but regardless of L_F, anadromous offspring displayed higher lipid contents ($F_{2,98} = 38.78$, $P < 0.001$, adjusted $R^2 = 0.43$; Figure 3 and Table 1). Rate of lipid depletion as a function of L_F was the same for progeny of both maternal tactics (*i.e.*, no interaction term; LRT, complex model with interaction term against simpler model, $\chi^2_1 = 0.08$, $P > 0.05$; Figure 3). Lipid content did not differ between collection sites (LRT, complex model with site term against simpler model, $\chi^2_4 = 0.73$, $P > 0.05$).

Similar findings have been reported in other partially anadromous populations of salmonids. In a population of brook trout *Salvelinus fontinalis* (Mitchill 1814), Jardine *et al.* (2008) showed that anadromous offspring displayed higher C:N (a proxy of total lipid

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content) and were longer than resident progeny soon after emergence. In an experimental study with domesticated Arctic charr *Salvelinus alpinus* (L. 1758), Leblanc *et al.* (2016) found that longer embryos originated from larger eggs with more yolk and, thus, more energy. Similar results were found with egg size having a strong effect on offspring body mass and early growth rates in brown trout *Salmo trutta* L. 1758 (Einum & Fleming, 1999) and Atlantic salmon *Salmo salar* L. 1758 (Einum, 2003). In this case study, differences in lipid storage and length at age are probably related to differences in egg size between females from alternative tactics (mean ± 95% CI egg size = 0.12 ± 0.01 g *v.* 0.07 ± 0.02 g for anadromous and resident fish, respectively; Liberoff *et al.*, 2011). Moreover, since resident-maternal-origin fry were older than anadromous offspring, but not larger, they are also likely to display different patterns of energy allocation, using more of their maternal provisioning to reach the same sizes as anadromous offspring. It has been shown that in unfavourable natural conditions, juveniles from larger eggs have survival advantages over conspecifics originating from smaller eggs (Hutchings, 1991; Einum & Fleming, 1999). Given that the Santa Cruz River is an extremely unproductive environment (Miserendino, 2001; Tagliaferro *et al.*, 2013) any early life-history competitive advantage that anadromous-maternal-origin juveniles have over resident-maternal-origin juveniles are likely to carry over into later life stages, and thus are likely to affect the tactic's prevalence across generations.

A great deal of research shows that growth opportunities early in life affect development pathways leading to the expression of alternative migratory tactics (AMT) in salmonids (Metcalfe, 1998; Dodson *et al.*, 2013; Kendall *et al.*, 2015). The specific effect of growth and body size on *O. mykiss* life-history adoption is variable and depends on population, sex and environmental factors (Kendall *et al*., 2015). Some studies suggested a positive relationship between body size and the adoption of anadromy (Satterthwaite *et al.*, 2009; Pavlov *et al.*, 2010; Satterthwaite *et al.*, 2010) as proposed by Liberoff *et al.* (2014) for

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this *O. mykiss* population. The higher nutritional status afforded to anadromous progeny may translate into enhanced growth opportunities, as for ones observed in Liberoff *et al.* (2014). Therefore, the higher nutritional status displayed by anadromous progeny in early stages, coupled with the adequate physical environment determined by maternal spawning site selection (Liberoff *et al.*, 2015), might play an important role in the adoption of the anadromous tactic in this population.

At later stages, lipid content is an important physiological trait associated with life-history adoption in salmonids. There is evidence in *O. mykiss* that fish with higher lipid contents are more prone to become resident (Kendall *et al.*, 2015). McMillan *et al.* (2012) found that regardless of growth, early male maturity was positively correlated with whole-body lipid content 9 months prior to the spawning season. In the Santa Cruz river, migration takes place predominantly at age 2+ years and maturation and spawning in fresh water at age 3+ years (Riva-Rossi, 2004); this suggests that energy reserves for maturing are not met until advanced stages. Liberoff (2013) followed two cohorts of juveniles during the first 2 years of life and did not find bimodal whole-body lipid distributions or differences in whole-body lipid content between smolting and undifferentiated fish in spring prior to migration. These studies suggest that differences observed herein at the fry stage do not carry over into later juvenile stages.

Although the mean lipid content differed between progeny of alternative tactics, both groups showed a wide range of values and, regardless of body size, some fish of anadromous offspring showed low lipid content and *vice versa*. This might be due to individual variation in female attributes. Egg size is strongly related to female age, in general, repeat spawners produce larger eggs than first-time spawners (Kamler, 2005). Given that anadromous females in this river are highly iteroparous (mean number of spawning events 4; Pascual *et al.*, 2001; Riva-Rossi *et al.*, 2007) they show a great phenotypic variation during spawning events [L_F

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380–806 mm, Riva-Rossi (2004); age: 2–9 years, Riva-Rossi *et al.* (2007)] and variation in egg diameter (range: 4.2–6.3 mm, *n* = 44; Sessa, 2013). Therefore, first-time spawners and younger anadromous females might produce eggs with similar sizes to resident females and therefore progeny with similar total lipid contents. If total lipid content has an influence on growth at later stages and on the expression of AMTs, the overlapping lipid content distributions is consistent with the hypothesis that physiological pathways leading to life-history adoption are related to maternal origin; but under certain circumstances they can be reversed and any individual may potentially adopt the anadromous or resident strategy. This is consistent with life-history reversals reported for *O. mykiss* in other populations (Christie *et al.*, 2011; Courter *et al.*, 2013; Sloat and Reeves, 2014) and in this population (Riva-Rossi *et al.*, 2007). Thus, this study provides evidence of maternal effects on early total energy content which, coupled with other factors (rearing environment, heritable growth traits), might play an important role in the adoption and persistence of the anadromous life history.

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TABLE 1 Multiple regression model explaining *Oncorhychus mykiss* lipid content as a function of fork length (L_F) and maternal origin

Variables	Coefficient	SE	95% CI	t	P
Intercept	33.55	4.07	25.47–41.63	8.24	< 0.001
L_F	−0.72	0.14	−1.00 to −0.45	−5.23	< 0.001
Maternal origin (anadromous)	4.73	0.73	3.27–6.18	6.45	< 0.001

Figure 1 Location of study sites 1(O), 2 (●) and 3 (●) sampled along the Santa Cruz River, Argentina

Figure 2 Fork length (L_F) variation as a function of age (days post hatch; dph) and maternal origin (•, anadromous; •, resident) of juvenile *Oncorrhynchus mykiss*.

Figure 3 Lipid content (dry mass; M_D) variation with fork length (L_F) and maternal origin (•, anadromous; •, resident) of juvenile *Oncorrhynchus mykiss*. Multiple regression lines are for anadromous offspring (━) $y = 38.27 – 0.72x$ and resident offspring (━) $y = 33.55 – 0.72x$; $n = 101$.

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$R^2_{adj} = 0.43$

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