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Experimental evidence of population differences in reproductive investment conditional on environmental stochasticity

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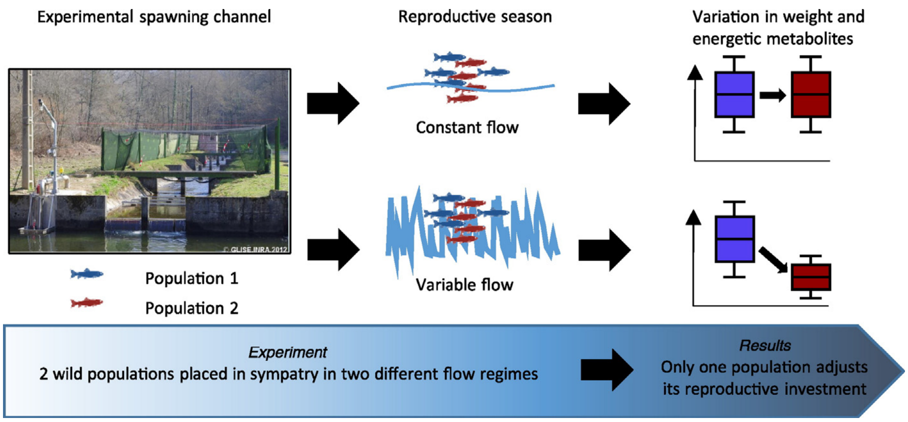
HIGHLIGHTS

- We place two populations of brown trout under contrasting water flow for reproduction.
- Energetic metabolite variation is used as a cue of reproductive investment.
- In constant flow, both populations show the same reproductive investment.
- In variable flow, only one of the populations modifies its reproductive investment.
- Divergent evolution of reproductive investment is expected under hydrological change.

GRAPHICAL ABSTRACT



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ABSTRACT

Environmental stochasticity is expected to shape life histories of species, wherein organisms subjected to strong environmental variation should display adaptive response by being able to tune their reproductive investment. For riverine ecosystems, climate models forecast an increase in the frequency and intensity of extreme events such as floods and droughts. The speed and the mechanisms by which organisms may adapt their reproductive investment are therefore of primary importance to understand how species will cope with such radical environmental changes. In the present study, we sampled spawners from two different populations of wild brown trout, originating from two environments with contrasting levels of flow stochasticity. We placed them in sympatry within an experimental channel during reproductive season. In one modality, water flow was maintained constant, whereas in another modality, water flow was highly variable. Reproductive investment of all individuals was monitored using weight and energetic plasma metabolite variation throughout the reproductive season. Only the populations originating from the most variable environment showed a plastic response to experimental manipulation of water flow, the females being able to reduce their weight variation (from 19.2% to 13.1%) and

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metabolites variations (from 84.2% to 18.6% for triglycerides for instance) under variable flow conditions. These results imply that mechanisms to cope with environmental stochasticity can differ between populations of the same species, where some populations can be plastic whereas other cannot.

1. Introduction

The principle of energy allocation (Fisher, 1930; Williams, 1966) aims at understanding the response of organisms to environmental stochasticity with respect to reproductive success. It states that, to maximize the lifetime reproductive success, reproductive investment should result from a trade-off between current benefits of reproduction, and future opportunities of reproduction, increased by higher survival. Hence, in an environment where annual reproductive success is more variable than annual survival, individuals should invest more on survival, and reduce their reproductive investment (Schaffer, 1974; McNamara and Houston, 1996; Fischer et al., 2011). This concept has been widely applied and demonstrated, with a special regard to age dependent condition (Clutton-Brock et al., 1982). While trans-generational selection is expected to shape such evolutionary optima, it has also been shown that plasticity is possible, and that individuals may adapt to within lifetime changing environment (Bardsen et al., 2010; Bardsen et al., 2014; Kaiser et al., 2014). The use of environmental cues allows for the allocation process to be regulated in an adaptive way: different populations in different environments do not display the same reproductive effort patterns (Tully and Ferrière, 2008; Smallegange, 2011). At the proximal level, this population-dependence in plasticity may be caused by differences in the perception of environmental cues or in the physiological or behavioral response to the cues. At the ultimate level, the difference in the populations' capacity to cope with increased stochasticity will affect their fate in a changing world.

The fact that long term evolutionary processes (selection) and short term adaptive response (plasticity through perception of environmental cues) both contribute to the tuning of reproductive investment is of major interest for forecasting future evolutionary patterns regarding reproductive investment (Crozier and Hutchings, 2014). This question is especially pregnant in the context of rapid climate change which predicts – and verifies (Milly et al., 2002; IPCC, 2013) – increased stochastic climatic events in temperate areas, with increasing occurrence of extreme rainfalls and droughts. This environmental change is especially worrying for aquatic organisms (Fisher et al., 1982; Poff et al., 1997). In particular, salmonid reproduction is highly sensitive to extreme climatic events, as floods can scour and destroy their nests, which are dug in shallow riffle areas, whereas droughts can dry them out (Ottaway et al., 1981; DeVries, 1997; Armstrong et al., 2003; Riedl and Peter, 2013; Gauthey et al., 2015b). Therefore, it seems that salmonid populations should adjust their reproductive investment in function of the degree of environmental stochasticity, although it remains unknown whether reproductive strategies differ in trout populations subjected to contrasting environments.

To analyze this question we performed a manipulative experiment in which brown trout (*Salmo trutta* L.) from two populations naturally subject to different degrees of hydrological variability were kept under either constant or stochastic flow regime. We hypothesized that, within a single reproductive season, the two populations may show different investment strategies when placed in each of these two contrasted regimes. To estimate reproductive investment we measured the variations in plasma metabolites and in weight through the reproductive season, as Gauthey et al. (2015a) recently demonstrated that weight variation is a good proxy of gametic investment, whereas variation of metabolic status indicates investment in reproductive behavioral activity such as intrasexual competition, intersexual preference, and parental care. Building on these recent results, we now therefore investigate how population origin conditions the reproductive investment in relationship to water flow patterns. We then browse the options for the potential evolutionary mechanisms at work and their effect on population dynamics in a changing environment.

2. Material and methods

2.1. Collection and recognition of experimental individuals

We studied the trout populations from River Bastan (France, +43° 16′ 2.51″, −1° 22′ 32.46″) and River Urumea (Spain, +43° 14′ 31.81″, −1° 55′ 28.98″), two rivers with a similar annual mean discharge (ca. 6 $m^3 \cdot s^{-1}$) and located at less than 50 km from each other (Supplementary information S1). They are both located in forest landscapes in a mountainous area. The River Bastan is a snow/rain driven system, whereas the River Urumea is a perennial runoff system (Richter et al., 1998). As a consequence, the River Bastan has a more predictable hydrology than the River Urumea, with mainly less numerous high and low pulse events per year, a lower coefficient of variation of annual discharge, as well as lower coefficients of dispersion for monthly discharge (see Supplementary information S2; Colwell, 1974; Poff and Ward, 1989). Brown trout genitors were sampled by electrofishing in each river and brought back to the INRA Lapitxuri lab (see below) where they were acclimatized in separated tanks — without mixing the populations — during 48 h without food, at a 10 °C temperature. Maturity of fish was diagnosed by palpation through the presence of sperm for males and eggs for females. Only mature fish were selected for the experiment (50 per river). After the acclimatization period fish were individually anesthetized in a small tank using 2-phenoxyethanol with a concentration of 0.3 mL/L. They were then measured (±1 mm), weighed (±1 g), photographed and a 500 μL blood sample was taken. In complement to weight and body size, photography enabled us to recognize fish at the beginning and at the end of the experiment through position and identification of different red and black points that do not change over the reproductive season (Supplementary information S3). This method allowed avoiding the use of visual tag that may affect mating behavior and physiological condition (Barriga et al., 2015).

2.2. Experimental setting

An experiment of semi-natural reproduction was conducted from November 2012 to February 2013 in an experimental channel provided with water derived from the Lapitxuri stream, a tributary to the River Nivelle in south-western France (+43° 16′ 59″, −1° 28′ 54″). The experimental channel is 130 m long, and divided in 13 sections each measuring 10 m long and 2.80 m wide. Variation in flow regime is obtained simultaneously by varying the flow incoming in the experimental channel from the Lapitxuri stream, and by using a water pump to recirculate a fraction of the flow in the channel.

Within the same channel, two separated reaches of 30 m each were constituted to form two distinct environments controlled by different water flow during the entire experiment: constant water flow and stochastic water flow. This single experiment therefore proposes two treatments, although we will hereafter refer to them as experiment B1 (constant environment) and experiment B2 (variable environment). The difference in flow regime between reaches is possible thanks to a derivation of water, wherein the B1 reach gets a stable flow, whereas the B2 reach undergo all the desired flow variations. In experiment B1, water flow was maintained at an intermediate value around 210 $m^3 \cdot h^{-1}$ (SD = 3.4 $m^3 \cdot h^{-1}$). In experiment B2, water flow variations were executed and followed three levels: low water flow (80 $m^3 \cdot h^{-1}$), intermediate water flow (210 $m^3 \cdot h^{-1}$) and high water