Embryonic exposure to a conspecific alarm cue triggers behavioural plasticity in juvenile rainbow trout

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In fish, the presence of predator cues in the parental or juvenile environment engenders plasticity in the expression of fear-related behaviours. Whether these cues may engender developmental plasticity when they are present in the environment of embryos remains unexplored. Here, we tested in rainbow trout, Oncorhynchus mykiss: (1) whether exposure to alarm cues during embryonic stages engendered developmental plasticity; and (2) whether an abiotic stressor could also orient the behavioural development of fry. We divided fertilized eggs into three groups: a control nonstressed group (Control), a group of embryos exposed to a conspecific alarm pheromone (e.g. predator-related cue stressor, PS), and a group of embryos that were chronically air exposed for 1 min (e.g. abiotic stressor, AS). Stressors were applied once a day, 3 times per week from 19 days postfertilization (dpf) until 52 dpf. Between 57 and 143 dpf, and for each individual, we assessed the propensity to express fear responses in different contexts and learning performances. When exposed to a novel environment or a novel object, PS fish showed significantly less fear-related behaviour, less freezing and higher activity levels than Control fish. PS fish also showed slower acquisition of a learning task than controls. AS fish did not differ from controls in any test situation. Our results show that in ovo exposure to a natural but not an abiotic signal is a prominent inducer of rainbow trout behavioural plasticity across a number of contexts. Our study provides evidence that the expression of neophobia by fish fry may be modulated by the level of risk perceived by embryos in the environment.

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experienced by juveniles. In convict cichlids, *Amatitlania nigrofasciata*, exposure to conspecific alarm cues increases avoidance response to a novel predator odour (Brown, Ferrari, Elvidge, Rammarine, & Chivers, 2013). In the whitetail damselfish, *Pomacentrus chrysurus*, juveniles experienced with predator cues were found to survive better than predator-naive fish (Ferrari, McCormick, Meekan, & Chivers, 2014).

Neophobia (i.e. fear of novel stimuli) is considered to be the first adaptive response when naive prey are exposed to potential predator encounters. More generally, in vertebrates, neophobia is a trait also related to animals’ capacity to adapt to environmental changes or to innovate (Greenberg, 2003). According to the dangerous niche hypothesis, neophobia protects animals from unknown potential dangers, and high-risk environments should favour the expression of this adaptive trait (Greenberg, 2003). In fish, coping styles are well described and proactive individuals are known to be more active and less neophobic (Martins et al., 2011; Sneddon, 2003; Wilson & Stevens, 2005). Here, we tested whether the predation risk perceived by embryos could modulate the propensity to express fear responses towards novelty in juvenile rainbow trout, Oncorhyncus mykiss. For rainbow trout hatchlings, emergence is the time of greatest vulnerability during the early life history. A stressful period when the larva appears from the gravels into the open water, start exogenous feeding, and are confronted with predators. At this stage, learning abilities and any fear-related behaviour, such as fast-start swimming, freezing, hiding and exploring, are essential traits for fry survival. We expected that fry exposed to predator-related cues during embryonic stages would be more cautious with novelty across different contexts. We also tested for a potential effect of predator exposure on learning performances. To test this hypothesis, we compared the behaviour of fry exposed to conspecific alarm cues during embryogenesis to that of nonexposed control fry. To determine whether the effect of the alarm cue is due to a chronic stress exposure or to the nature of the stressor (predator-related cue), we also tested for the effect of a chronic abiotic stressor (air exposure).

In amphibians or fish (wood frog, *Rana sylvatica*: Ferrari & Chivers, 2013; zebrasfish, *Danio rerio*: Speedie & Gerlai, 2008; rainbowfish, *Melanotaenia duboulayi*: Oulton, Haviland, & Brown, 2013; chinook salmon, *Oncorhynchus tschawytscha*: Palm & Powell, 2010; rainbow trout: (Brown & Smith, 1997), individuals facing a predation threat emit chemical alarm signals that warn conspecifics of the danger. The alarm cue is released following skin injuries generally as a result of predator attacks and elicits antipredator behaviour when detected by conspecifics. In rainbowfish, embryos exposed to such cues respond by an increase in heart rate indicating that they are able to detect the threatening value of a signal through the egg membrane (Oulton et al., 2013). In addition, exposure to alarm substance alters physiological development in zebrasfish embryos (Mourabit, Rundle, Spicer, & Sloman, 2010). One would expect that rainbow trout embryos should also perceive these threatening cues since the external egg membrane is highly permeable (Groot & Alderdice, 1985). Moreover, morphological evidence suggests that the olfactory system is functional as early as hatching, and neural responses to chemical stimuli are even induced from 21–22 days postfertilization (Hara & Zielinski, 1989). In amphibians, exposure of eggs and larvae to predators, competitors or abiotic stressors can affect the morphology, behaviour, growth and survival of juveniles (Broomhall, 2004; Pahlka, Laurila, & Merila, 2001; Relyea & Hoveterman, 2003). In fish species, whether the nature (e.g., abiotic or natural) of the stressor applied to embryos has positive or negative effects on adaptive behaviours of juveniles is totally unknown. One study showed that hypoxic stress sustained by brown trout, *Salmo trutta*, embryos from fertilization to the end of embryonic development has long-term effects on the swimming patterns of juveniles, which hence undergo higher mortality by predation (Roussel, 2007). Another study also revealed acquired predator recognition by convict cichlid embryos, which showed reduced activity in response to predator odour (Nelson, Alemadi, & Wisenden, 2013). The effects of embryonic stress, however, remain poorly documented.

In fisheries or in laboratories, fish eggs are subjected to various artificial constraints (transport, sorting) without taking any possible deleterious effects on juveniles’ development into account. Extrinsic stress that results from changes in abiotic factors such as temperature, chemical components or other anthropic factors (e.g., air exposure) are commonly considered to be the most important stressing agent (Lindgren & Laurila, 2005). It is therefore necessary to accurately investigate how behavioural traits may be modulated by early life history through ontogeny. If impaired behaviour consecutive to prenatal stress is now clearly demonstrated in mammals (increased anxiety, reduced stress-coping style, impaired spatial learning and other cognitive deficits; Boersma et al., 2014; Braastad, 1998; Kofman, 2002; Weinstock, 2008; Welberg & Seckl, 2001), such effects of prenatal stress are less obvious in fish. This area of research is particularly relevant in oviparous species since embryos are directly exposed to environmental pressures, unlike mammalian embryos where the effects of the environment mainly occur via maternal effects. Neophobia and learning are of particular interest since these traits may impair the capacity of fish to adapt to husbandry conditions or to novel environments when released in natural conditions for conservation programmes. In this study, we tested whether the predation risk perceived by the embryos (i.e., exposure to conspecific alarm cues) could modulate the propensity to express fear responses towards novelty and learning performances in juvenile rainbow trout. To determine whether the effect of the alarm cue was due to a chronic stress exposure or to the nature of the stressor, we also tested the effect of a chronic abiotic stressor in another experimental group, in which embryos were air exposed.

**METHODS**

**Fertilization and Incubation**

Autumnal rainbow trout (INRA Strains, 30 years of domestication), originated from PEIMA experimental farm (INRA, Sizun, France), were used for these experiments. Oocytes and milt from five females and five males (mean weight: 1.8 kg) were stripped, and eggs from all females were combined, as was milt from all males. Fertilization was performed at 10°C using the medium ActiFish (IMV, L’Aigle, France; 100 ml ActiFish + 400 ml water). Fertilized eggs were divided into one control and two experimental treatment groups as follows: a control group with minimal prenatal stress (Control), a stressed group where eggs were air exposed for 1 min (AS) and a stressed group where eggs were exposed to a conspecific alarm pheromone (PS) (detailed below). Artificial and natural stress procedures were performed once a day at 1200 hours, three times per week from the eyed stage, at 19 days postfertilization (dpf), until yolk sac resorption (52 dpf). In hatcheries, sorting and transport are never practised before the eyed stage. We chose a 5-week exposure window covering the sensitive period when rainbow trout are capable of short-term response to stress with cortisol synthesis, known to occur between 9 days (Auperin & Geslin, 2008) and 14 days (Barry, Malison, Held, & Parrish, 1995) after hatching (33 dpf). Moreover, neural responses to chemical stimuli are induced from 21–22 dpf (Hara & Zielinski, 1989).
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