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Review

The physiology and toxicology of salmonid eggs and larvae in relation to water quality criteria

Roderick Nigel Finn *

Department of Biology, University of Bergen, Allégaten 41, N-5020 Bergen, Norway

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Abstract

The purpose of this review is to collate physiological knowledge on salmonid eggs and larvae in relation to water quality criteria. Salmonid genera reviewed include *Coregonus*, *Thymallus*, *Salvelinus*, *Salmo*, and *Oncorhynchus* spp. When physiological data for salmonids are lacking, the zebrafish and medaka models are included. The primary focus is on the underlying mechanisms involved in the hydro-mineral, thermal, and respiratory biology with an extended section on the xenobiotic toxicology of the early stages. Past and present data reveal that the eggs of salmonids are among the largest shed by any broadcast spawning teleost. Once ovulated, the physicochemical properties of the ovarian fluid provide temporary protection from external perturbations and maintain the eggs in good physiological condition until spawning. Following fertilisation and during early development the major structures protecting the embryo from poor water quality are the vitelline membrane, the enveloping layer and the chorion. The vitelline membrane is one of the least permeable membranes known, while the semi-permeable chorion provides both physical and chemical defense against metals, pathogens, and xenobiotic chemicals. In part these structures explain the lower sensitivity of the eggs to chemical imbalance compared to the larvae, however the lower metabolic rate and the chronology of gene expression and translational control suggest that developmental competence also plays a decisive role. In addition, maternal effect genes provide a defense potential until the mid-blastula transition. The transition between maternal effect genes and zygotic genes is a critical period for the embryo. The perivitelline fluids are an important trap for cations, but are also the major barrier to diffusion of gases and solutes. Acidic environmental pH interferes with acid–base and hydromineral balance but also increases the risk of aluminium and heavy metal intoxication. These risks are ameliorated somewhat by the presence of ambient humic acid. High temperatures during development may be teratogenic, cause sexual bias, or long-term effects on muscle cellularity. Xenobiotics cause inhibition of neural acetylcholine esterase and carboxylases and disrupt the normal signalling pathways of hormones by binding to relevant receptors and mimicking their actions. A complex suite of genes is activated in response to environmental or parentally transmitted xenobiotics. The primary defense mechanism in embryos involves resistance to uptake but later biotransformation via the aryl hydrocarbon receptor (AHR)-mediated activation of members of the cytochrome mixed-function mono-oxygenase superfamily (CYP1A, CYP2B, and CYP3A) and subsequent glucuronidation or glutathionation. Due to the number of duplicate or triplicate genes coding for intermediates in the signalling pathways, and cross-talk between nuclear orphan receptors and steroid hormone receptors, a large number of complications arise in response to xenobiotic intoxicaton. One such syndrome, known as blue-sac disease causes an anaphylactoid response in hatched larvae due to increased permeability in the vascular endothelium that coincides with AHR-mediated CYP induction. Early embryos also respond to such xenobiotic insults, but apparently have an immature translational control for expression of CYP proteins, which coincides with a lack of excretory organs necessary for the end-point of biotransformation. Other syndromes (M74 and Cayuga) are now associated with thiamine deficiency. Where possible guidelines for water quality criteria are suggested.
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* Tel.: +47 55583595; fax: +47 55589667.
E-mail address: nigel.finn@bio.uib.no.

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Contents

1. Introduction

Salmonidae are indigenous to the temperate or cool northern hemispheric regions of Eurasia and North America, with several species now introduced to the southern hemisphere. Their representatives rank among the most prized of sportfish, and are equally valued in the commercial fisheries and aquaculture arenas. Many are diadromous, leaving the oceans to re-enter their natal rivers or streams in autumn or spring to lay eggs. Some species, including members of each genera, spend their entire life cycles in freshwater, but may still undertake a spawning migration. These latter species are classified as potamodromous, while the former are known as anadromous (McDowell, 1992). Dependent upon the species, the pre-spawning residence within the respective freshwater systems varies from days to months in anadromous forms, and years for the potamodromous forms.

The eggs are laid within the hyporheic zone of the indigenous watersheds and remain dependent upon the quality of the percolating water until emergence. Following hatch, the yolk-sac larvae are motile, but essentially passive recipients of the prevailing water conditions (Armstrong and Nislow, 2006). The importance of the hyporheic zone for the differential retention of conservative and reactive solutes (Johansson et al., 2001; Jonsson, 2003) or residence times of harmful substances such as crude oil and silt are beginning to be appreciated (Heintz et al., 2000; Massa et al., 2000; Malcolm et al., 2003; Meyer, 2003; Short et al., 2003; Carls et al., 2004; Gottesfeld et al., 2004; Groves and Chandler, 2005). Of particular note are the great number of human activities that may potentially impact this ecotone (Hancock, 2002; Jonsson and Wörman, 2005; McMichael et al., 2005). The anthropogenic impact may also be indirect due to mass transfer of bioaccumulated contaminants that are released from the carcasses of semelparous species following their spawning migration (Debruyn et al., 2004; O'Toole et al., 2006).

The typical oligotrophic nature of the freshwater habitats of Salmonidae renders them highly sensitive to anthropogenic effects and climate change (Mote et al., 2003). Recent biotest assays and statistical models continue to demonstrate that sub-optimal habitat conditions are the most important and ubiquitous stress factor for salmonids in European rivers (Dumas and Darolles, 1999; Luckenbach et al., 2003; Borsuk et al., 2006). In the context of conservation physiology (Wilkelski and Cooke, 2006) this review aims to highlight physiological processes in salmonid eggs and yolk sac larvae that are sensitive to perturbations in their aquatic environment.

2. Ovarian fluid

The eggs of salmonids arise from the synchronous development of oocytes under the control of pituital and follicular steroids. At the end of the vitellogenic phase maturing oocytes break free of their follicles, and the ovarian wall ruptures. The newly ovulated eggs rest within the protection of the isosmotic fluid of the maternal peritoneal cavity prior to ejection at spawning. The fluid variously called ascites, ovarian-, peritoneal- or coelomic-fluid originates from the coelomic epithelium and mesovarium (Matsubara et al., 1985) and can account for up to 10–30% of the total egg volume (Lahnsteiner, 2002). The complex properties of the fluid, which in salmonids includes a high Na^+, protein, triglyceride, and pH, have been shown to be related to egg quality and delayed over-ripening (Lahnsteiner et al., 1999; Lahnsteiner, 2000, 2002; Wendling et al., 2000; Aegerter and Jalabert, 2004; Rime et al., 2004). This latter property has been used to prolong over-ripening in other species such as zebrafish (Corley-Smith et al., 1995). The effects of the fluid as a pheromone have been studied (Olsén et al., 2001, 2002) and it is a well-known diluent for sperm motility and fertilisation success (Turner and Montgomerie, 2002; Alavi and Cosson, 2005, 2006). Considering the importance of the fluid properties for gamete physiology, it is surprising to find very little information concerning the effects of water quality on its consistency and secretion. Exposure to different environmental factors, including ammonia, urea and xenestrogens has been demonstrated to alter the composition of the fluid in a marine teleost, *Zoarces viviparus* (Korsgaard et al., 2002; Rasmussen et al., 2002). This is most certainly an area for further investigation in salmonids which, depending upon ambient temperature, can retain their eggs in the ovarian fluid for days prior to oviposition.

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