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Ontogenic changes in the osmoregulatory capacity of the Nile tilapia *Oreochromis niloticus* and implications for aquaculture

S. Fridman [a,*], J.E. Bron [a], K.J. Rana [b]

[a] *Institute of Aquaculture, University of Stirling, Scotland, United Kingdom*
[b] *Aquaculture Division, University of Stellenbosch, South Africa*

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ABSTRACT

The Nile tilapia, one of the most extensively cultured tropical freshwater species, offers considerable potential for culture in low-salinity water. The ontogeny of osmoregulation in the Nile tilapia was studied from spawning to yolk-sac absorption after exposure to different experimental conditions ranging from freshwater to 25 ppt. Eggs were able to withstand elevated rearing salinities up to 20 ppt, but transfer to 25 ppt induced 100% mortality by 48 h post-fertilization. Across all stages, embryos and larvae hyper-regulated at lower salinities and hypo-regulated at higher salinities. Osmoregulatory capacity increased during development and from 2 days post-hatch onwards remained constant until yolk-sac absorption. Adjustments of larval osmolality following abrupt transfer from freshwater to experimental salinities (12.5 and 20 ppt), followed a pattern of crisis and regulation, with values for larvae stabilising at *c.* 48 h post-transfer for all treatments, regardless of age at time of transfer. Age at transfer to experimental salinities (7.5–20 ppt) had a significant positive effect on larval ability to osmoregulate, with larvae transferred at 8 days post-hatch maintaining more constant whole-body osmolality over the experimental salinities tested than larvae at hatch. Concomitantly, survival following transfer to experimental salinities increased with age. There was a significant effect (GLM; $p<0.05$) of the salinity of incubation and rearing on the incidence of gross larval malformation that was seen to decline over the developmental period studied.

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1. Introduction

In recent times, diminishing freshwater resources resulting from rapidly increasing urban, industrial and agricultural water use and from the impact of climate changes, have prompted an urgent need to manage freshwater, brackish water and marine environments more efficiently. Under these conditions, diversification of aquacultural practices, either by the introduction of new candidate species or by the adaptation of culture methods for existing species is vital at a time when innovation and adaptability of the aquaculture industry is fundamental to the maintenance of its sustainability. The Nile tilapia (*Oreochromis niloticus*, *niloticus* L.), whose culture now extends well beyond its natural range, dominates tilapia aquaculture because of its adaptability and fast growth rate. Although not considered to be amongst the most salinity-tolerant of the cultured tilapia species, the Nile tilapia still offers considerable potential for culture in low-salinity water (Fridman et al., 2012; Suresh and Lin, 1992).

It is well established that measurement of blood or body fluid osmolality in teleosts provides a route for the evaluation of osmoregulatory status and the ability to withstand osmotic stress (Alderdice, 1988). Salinity is known to exert selective pressure on studied fish developmental stages, influencing reproduction, dispersal and larval recruitment in marine, coastal and estuarine habitats (Anger, 2003). Improved knowledge of the limits of salinity tolerance of the Nile tilapia during the sensitive early life stages and concerning the ability to predict responses of critical life-history stages to environmental change could prove invaluable in improving larval rearing techniques and extend the scope of this globally important fish species, allowing an expansion of culture area where fresh water is limiting. Recent reports on ontogenic changes in osmoregulatory capacity during early life stages have been mainly confined to marine teleost species in an attempt to explain species and developmental stage-specific distribution *i.e.* turbot (*Scophthalmus maximus*) (Brown and Tytler, 1993), chum salmon (*Oncorhynchus keta*) (Kaneko et al., 1995), sea bass (*Dicentrarchus labrax*) (Varsamos et al., 2001), Japanese eel (*Anquilla japonica*) (Okamoto et al., 2009; Unuma et al., 2005), Mozambique tilapia (*Oreochromis mossambicus*) (Yanagie et al., 2009) and the gilt-head sea bream (*Sparus aurata*) (Bodinier et al., 2010).

In the present study, the responses to and physiological effects of osmotic challenge during ontogeny in the Nile tilapia were assessed through the measurement of embryo and larval osmolality and osmoregulatory capacity. In addition, the short-term osmoregulatory responses of yolk-sac larvae to abrupt transfer to a range of salinities (7.5–25 ppt) in terms of osmoregulatory capacity, survival and the

* Corresponding author: Tel.: +44 1786 467874; fax: +44 1786 472133.
E-mail address: scf1@stir.ac.uk (S. Fridman).

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related incidence of deformity were investigated. This is the first study to give a complete picture of the ontogeny of osmoregulatory ability over a range of salinities during successive early life stages in the euryhaline Nile tilapia and provides valuable insights into ontogenic variations in the capacity of this species to hyper- and hypo-regulate over a range of salinities.

2. Materials and methods

2.1. Egg supply, preparation of media and rearing systems

All eggs were obtained from Nile tilapia breeding populations held at the Tropical Aquarium, Institute of Aquaculture, University of Stirling, UK. Broodstock were maintained individually in partitioned 200 l freshwater aquaria with re-circulated, pre-conditioned freshwater (local tap water aerated and heated to 28 ± 1 °C for 24 h prior to use) and fed on artificial pellets (#5 trout pellet, Trouw Aquaculture Limited, Skretting, UK). The light regime was maintained at a 12:12 h light:dark period. Eggs were obtained from ripe females by manually stripping eggs from a ripe female into a Petri dish followed by the addition of freshly-stripped milt from two males per female. After 1–2 min fertilization, water was added and eggs were placed in their respective incubation unit and designated as a batch.

Independent test incubation units each comprised a 20 l plastic aquarium with an attached Eheim pump (Series 94051) supplying 6 × 1 L plastic bottles using down-welling flow (Rana, 1988). Temperature in the incubation units was maintained at 28 ± 1 °C using individual 300 W thermostatically controlled heaters (Visi-therm, Aquarium-systems, Mentor, Ohio, USA). The experimental salinities were prepared using conditioned water (tap water aerated and heated to 28 ± 1 °C for 24 h prior to use) and commercial salt (Tropic Marin, Aquarientechnic, D-36367, Germany) and salinity was measured using a salinity refractometer (Instant Ocean Hydrometer, Marineland Labs., USA) accurate to 1 ppt. About 10% of water was replaced daily in the incubation aquaria to compensate for evaporation and salinity was adjusted accordingly. Dead eggs and larvae were removed daily to prevent fungal infection. The light regime was maintained as for broodstock.

2.2. Ontogenic profile of osmoregulatory capacity

In the first experiment, ovarian fluid and pre-fertilized eggs were initially sampled for osmolality. Eggs were then fertilized in freshwater and transferred at 3–4 hours (h) post-fertilization to the experimental salinities *i.e.* 7.5, 12.5, 17.5, 20 and 25 ppt. Control eggs remained in freshwater. Sampling was initially performed at time of transfer and subsequently at developmental points during embryogenesis *i.e.* gastrula (*c.* 24 h post-fertilization) and completion of segmentation period (*c.* 48 h post-fertilization) and then at hatch, 2, 4 and 6 days post-hatch and finally at yolk-sac absorption. Triplicate experiments were conducted using three different batches of eggs, with each batch sub-divided between three replicate round-bottomed incubators within each incubation unit. A pooled sample of 30 embryos or newly hatched yolk-sac larvae (10 from each replicate) was collected at each sampling point, rinsed in distilled water (DW), blotted dry and immediately frozen at −70 °C.

The small size of Nile tilapia embryos and yolk-sac larvae prevented efficient collection of blood or specific body fluids for osmolality measurements therefore whole-body measurements were used for osmolality measurements. This approach was validated by initial experiments that measured the effect of yolk materials on osmolality values in which the osmolalities of larval body regions were measured and no significant differences were found between them. Pools of whole larvae were thawed on ice, homogenised with a motorised Teflon pestle (Pellet Pestle® Motor, Kontes) and the homogenate centrifuged at 10 °C for 10 min at 14 000 g (Eppendorf centrifuge, 5417R). The supernatant overlying the pellet was carefully removed into a single well of a 96-well plate and thoroughly mixed with a pipette to ensure homogeneity of each sample. Osmolality was determined using an Advanced 3MO Plus MicroOsmometer (Advanced Instruments, MA, USA.) using three replicates of 20 µl aliquots of supernatant from each pool and the accuracy of the machine was regularly checked against calibration standards of 50 and 850 mOsm kg^{-1} and osmolality was expressed as whole body osmolality (mOsmol kg^{-1}).

2.3. Acclimation time

In the second experiment, the acclimation time of yolk-sac larvae at hatch, 3 and 6 days post-hatch to abrupt salinity challenge was assessed to determine the time necessary for whole-body osmolality to reach a steady-state after abrupt transfer from the rearing medium (freshwater) to two experimental salinities (12.5 and 20 ppt). Triplicate experiments were conducted using three different batches of eggs. Pooled samples, consisting of 30 whole yolk-sac larvae collected at 1.5, 3, 6, 12, 24, 48 and 72 h post-transfer, were rinsed in distilled water (DW), blotted dry and immediately frozen at −70 °C. Whole body osmolality (mOsmol kg^{-1}) was determined as described above.

2.4. Osmoregulation and survival following abrupt salinity challenge

In a third experiment, healthy yolk-sac larvae were transferred directly from freshwater to 7.5, 12.5, 17.5 or 25 ppt at hatch, 2, 4, 6 and 8 days post-hatch. Larvae were exposed to their experimental salinity for 48 h prior to sampling. Control larvae remained in freshwater. Triplicate experiments were conducted using three different batches of eggs. Pooled samples, consisting of 30 whole yolk-sac larvae (10 from each replicate) were rinsed in distilled water (DW), blotted dry and immediately frozen at −70 °C. Whole body osmolality (mOsmol kg^{-1}) was determined as described above.

2.5. Larval malformation

Thirty newly-hatched yolk-sac larvae from each of the three batches from the first experiment were selected at random from freshwater, 12.5 and 20 ppt and were examined under a dissecting microscope in order to observe incidence and type of malformations. Thereafter, thirty live yolk-sac larvae were selected at regular time points during yolk-sac absorption *i.e.* 2, 4, 6 days post-hatch and complete yolk-sac absorption and malformations were assessed as before. The percentage of abnormality was calculated, based on the numbers of normal and malformed larvae as follows: percentage of malformed larvae (%) = 100 × number of malformed larvae/number of normal larvae.

2.6. Statistics

Statistical analyses were carried out with Minitab 16 using a General Linear Model (GLM) or with Tukey's *post-hoc* pair-wise comparisons ($p<0.05$). Homogeneity of variance was tested using Levene's test and normality was tested using the Anderson–Darling test. Where data failed assumptions, they were transformed using an appropriate transformation. All percentage data were normalised by arcsine-root transformation prior to statistical analyses and data are presented as back-transformed mean and upper and lower 95% confidence limits. Significance was accepted when $\rho<0.05$ and results were expressed as mean ± S.E.

3. Results

3.1. Ontogenic profile of osmoregulatory capacity

Osmolality of unfertilized eggs (358.2 ± 4.95 mOsmol kg^{-1}) was similar to that of ovarian fluid (370.7 ± 2.30 mOsmol kg^{-1}) but was seen to

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