Global Journal of Fisheries Science
Volume 8(4), pages 92-97, August 2026
Article Number: 2C8F07461
ISSN: 2782-750X
https://doi.org/10.31248/GJFS2026.111
https://integrityresjournals.org/journal/GJFS
Full Length Research

Ammonia levels during walleye (*Sander vitreus*) egg development

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Received Date: 06 July 2026 | Accepted Date: 10 August 2026 | Published Date: 30 August 2026

ABSTRACT: This study documented ammonia levels in walleye (*Sander vitreus*) eggs shortly after fertilization until hatch. Walleye eggs from Merritt Reservoir, Nebraska, USA were incubated at 16℃ in 9.5-cm diameter Petri dishes containing 30 mL of well water with a pH of 7.6 and alkalinity (as $CaCO_3$) of 210 mg/L. Ten dishes were used, with each containing 20 randomly selected viable eggs. Daily ammonia levels varied significantly throughout development. Mean ammonia levels were less than 0.100 mg/L/egg for the first nine days of incubation, significantly increased to 0.130 mg/L/egg on day 10 when hatching began, and significantly increased again to the highest level of 0.238 mg/L/egg on day 11 during peak hatching. Ammonia then significantly dropped to 0.19 mg/L/egg when hatching ceased on day 13. The results from this, the first study to document ammonia concentrations during walleye egg development, have practical implications for fish rearing, particularly with walleye eggs incubated in recirculating aquaculture systems.

Keywords: Ammonia, egg, hatch, *Sander vitreus*, walleye.

INTRODUCTION

Walleye (*Sander vitreus*) are one of the most recreationally important sportfish in North America (Goeman, 2002). Their native range spans much of North America, from northern Canada to the central United States (Johnston *et al*., 2012). Many walleye fisheries are sustained by hatchery rearing and stocking because of overexploitation and a lack of natural reproduction (Johnson, 1961; Sullivan, 2003; Hansen *et al*., 2015; Shaw *et al*., 2018; Raabe *et al*., 2020). It has been estimated that approximately one billion hatchery-reared walleye fry and juveniles are stocked annually (Fenton *et al*., 1996; Kerr, 2008, 2011; Halverson, 2008).

After the artificial spawning of wild walleye broodstock (Gonsorowski *et al*., 2024), fertilized eggs are typically incubated in flow-through upwelling jar incubators (Soupir and Barnes, 2006; Summerfelt and Johnson, 2015; Voorhees and Barnes, 2024). Shortly after hatch, walleye fry are either directly stocked into recreational fishing waters or reared to a larger size for stocking later (Czesny *et al*., 2005; Zebro *et al*., 2025). Because traditional flow-through incubation systems are continually flushing water through the jars containing walleye eggs, accumulation of metabolic waste, such as ammonia, is typically not an issue. However, with the advent of recirculating aquaculture systems (RAS), potential changes in water quality need to be considered during system design and operation (Ebeling and Timmons, 2012; Balami, 2021; Johnson *et al*., 2021).

In general, ammonia in fish eggs originates from embryo catabolism of the yolk protein for energy (Wright and Fyhn, 2001; Essex-Fraser *et al*., 2005; Zimmer *et al*., 2017). Ammonia levels gradually increase throughout larval development (Rice and Stokes, 1974; Davenport *et al*., 1983). Peak levels occur within the egg just prior to hatch because of the limited excretion capability of underdeveloped gills and the barrier to diffusion created by the chorionic membrane and perivitelline fluid (Rice and Stokes, 1974; Wright and Fyhn, 2001; Essex-Fraser *et al*., 2005; Zimmer *et al*., 2017; Qi *et al*., 2025). To detoxify ammonia prior to hatch and active excretion, fish embryos enzymatically convert it to glutamine (Essex-Fraser *et al*., 2005). Coinciding with gill maturation and the switch to branchial excretion after hatch, a rapid increase in ammonia efflux occurs (Zimmer and Wood, 2016).

Ammonia levels during egg development have been documented for very few fish species, including only rainbow trout (*Oncorhynchus mykiss*; Rice and Stokes, 1974), cod (*Gadus morhua*; Davenport *et al*., 1983), plaice (*Pleuronectes platessa*; Davenport *et al*., 1983), and lumpfish (*Cyclopterus lumpus*; Davenport *et al*., 1983). Ammonia toxicity in walleye eggs and larval stages is unknown. With walleye eggs currently being incubated within RAS in both the state of Iowa (USA) and South Dakota (USA), there is an urgent need to understand ammonia production during embryonic walleye development. Thus, the objective of this study was to document the ammonia released by walleye eggs during incubation until hatch.

MATERIALS AND METHODS

On 1 May 2024, feral broodstock walleye were netted from Merritt Reservoir, Nebraska, USA, and artificially spawned. The fertilized eggs were pooled from multiple individual spawns and transported approximately four hours to McNenny State Fish Hatchery, rural Spearfish, South Dakota, USA. At the hatchery, 20 viable eggs were randomly selected, placed into one of 10 9.5-cm diameter plastic Petri dishes containing 30 mL of well water (total hardness as $CaCO_3$ = 360 mg/L, alkalinity as $CaCO_3$ = 210 mg/L, pH = 7.6, total dissolved solids = 390 mg/L). The dishes with eggs were placed into a refrigeration unit (Wine Enthusiasts Model 268 78 28 01, Valhalla, New York, USA) and incubated at 16℃ based on the techniques described by Voorhees and Barnes (2024). Water in the Petri dishes was exchanged daily using a 10-mL pipette to both extract water from the dish and then subsequently refill the dish with fresh water. To shield the incubating eggs from light, black corrugated plastic was placed on top of the Petri dishes. Black plastic was also placed underneath the dish to make the eggs easier to see. The plastic on top of the Petri dishes was removed during water exchanges and removal of dead eggs and dead fry. Dead eggs, indicated by coloration changing to white because of yolk coagulation (Piper *et al*. 1982), and dead fry were removed and counted at the same time as water exchanges.

Immediately prior to water exchange, ammonia levels in each dish were measured daily using spectrophotometric methods (Ammonia TNT 830, DR3900 Benchtop Spectrophotometer; HACH, Loveland, Colorado, USA). The daily total ammonia measured was divided by the number of eggs in the Petri dish to obtain the ammonia released by each egg.

Data were analyzed by one-way analysis of variance (ANOVA) using the SPSS statistical program (24.0, IBM, Armonk, New York, USA). A Tukey HSD Post Hoc Test was used for pairwise comparisons. Significance was predetermined at $p < 0.05$. The experimental unit was the Petri dish.

RESULTS AND DISCUSSION

Daily ammonia levels varied significantly throughout development ($p < 0.001$; Table 1). Mean ammonia levels were less than 0.100 mg/L/egg for the first nine days of incubation, significantly increased to 0.130 mg/L/egg on day 10 when hatching began, and significantly increased again to the highest level of 0.238 mg/L/egg on day 11 during the peak of hatching (Figure 1). Ammonia then significantly dropped to 0.19 mg/L/egg when hatching ceased on day 13.

The results of this, the first study to document ammonia levels during walleye egg development to hatch, are similar to those reported previously for other fish species. Rice and Stokes (1974) observed a similar pattern during the development of rainbow trout, with relatively low levels during initial development followed by a sharp increase at hatch. Similarly, Davenport *et al*. (1983) reported a 12-fold increase in ammonia levels at hatch in cod. Plaice followed a similar pattern, although at lower levels than cod (Davenport *et al*., 1983). However, ammonia levels from lumpfish eggs were the highest shortly after fertilization, decreased the next few days, and then rose slightly at hatch, which Davenport *et al*. (1983) attributed to the breakdown of a sticky layer.

The large increase in ammonia levels at hatch observed in this study is likely because of the low permeability of the vitelline and chorionic membranes, which limit ammonia diffusion (Rice and Stokes, 1974; Wright and Fyhn, 2001; Essex-Fraser *et al*., 2005; Zimmer *et al*., 2017; Qi *et al*., 2025). Ammonia accumulates within the egg during development because of embryo catabolism of the yolk protein for energy (Wright and Fyhn, 2001; Essex-Fraser *et al*., 2005; Zimmer *et al*., 2017) and is released upon hatch (Rice and Stokes, 1974; Davenport *et al*., 1983). While walleye eggs have an external sticky layer like that of lumpfish (Krise *et al*., 1986), it is removed during artificial spawning to facilitate hatchery rearing. This study used artificially-spawned eggs where the sticky layer had been removed, removing any potential influence of the decomposition of the sticky layer on ammonia levels (Davenport *et al*., 1983).

The toxicity of the ammonia levels on walleye eggs at hatch observed in this study is unknown. However, the peak ammonia level of 0.130 mg/L/egg observed prior to hatch was relatively low compared to the peak level during hatch of 0.238 mg/L/egg, and was likely not problematic. Voorhees and Barnes (2023) successfully incubated walleye eggs to hatch in Petri dishes under a variety of conditions, with maximum loadings prior to the eyed stage of development of 20 eggs/dish without any water changes to 40 eggs/dish with water changed every-other-day. Egg ammonia toxicity varies substantially among fish species

Table 1. Mean (SE) of ammonia (mg/L) per walleye egg. Means with different letters are significantly different (p<0.001).

Day	Ammonia	n
1	0.008 (0.001) w	10
2	0.006 (0.001) w	10
4	0.007 (0.002) w	10
5	0.010 (0.002) w	10
7	0.012 (0.002) w	10
8	0.026 (0.005) w	10
9	0.044 (0.008) w	10
10	0.128 (0.011) x	10
11	0.238 (0.019) y	8
12	0.210 (0.001) zy	2
13	0.189 (0.000) y	2

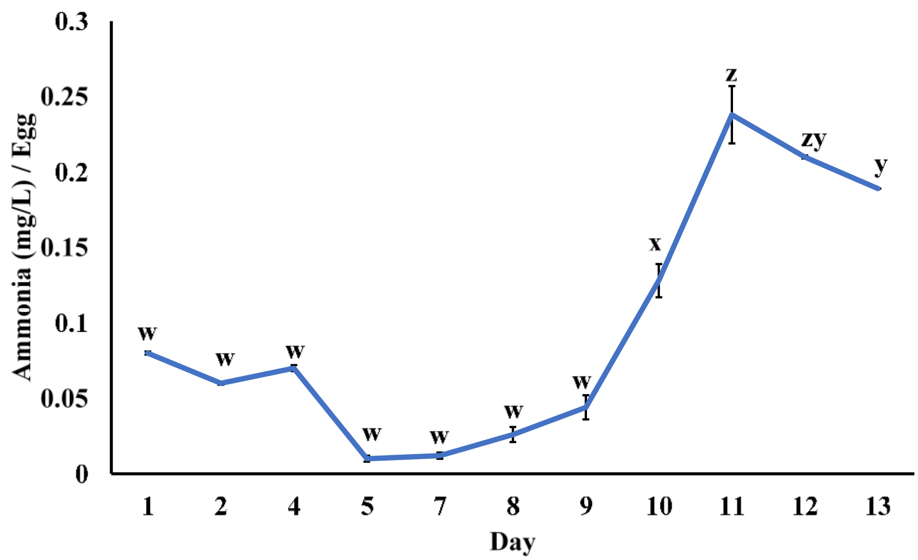

Figure 1. Ammonia per egg with standard error of walleye eggs over the incubation period in Petri dishes. Different letters indicate significant differences (p < 0.001).

(Burkhalter and Kaya, 1977; Chen *et al*., 2013; Wang *et al*., 2015; El-Greisy and Ahmed, 2016). Of course, it is not total ammonia that is of importance. Un-ionized ammonia is toxic to eggs and newly-hatched fry of a number of fish species at relatively low levels, while ionized ammonia is relatively harmless (Thurston and Russo, 1983; Vosylienė and Kazlauskienė, 2004; Brinkman *et al*., 2009; Chen *et al*., 2013; Wang *et al*., 2015; El-Greisy and Ahmed, 2016; Qi *et al*., 2025). The ionization of ammonia is affected by pH and temperature, with higher pH and warmer water temperatures increasing toxicity (Ip *et al*., 2001; Wurts, 2003; Merck, 2026). Other factors, such as oxygen deficiency, carbon dioxide levels, and physical stress, can also influence ammonia toxicity (Burkhalter and Kaya, 1977; Francis-Floyd *et al*., 2009).

Information on walleye egg and newly hatched fry ammonia toxicity is particularly needed if walleye eggs are incubated in recirculating aquaculture systems. Such toxicity information could be combined with the walleye egg ammonia values observed in this study to engineer appropriately-sized ammonia-detoxifying biofilters (Malone and Pfeiffer, 2006; Greensword and Malone, 2023).

It is possible that the results of this study may be strain- and egg-size specific. Only eggs obtained from walleye spawned at one lake (Merritt Reservoir, Nebraska) were used. There are numerous strains, subpopulations, or races of walleye (Colby and Nepszy, 1981; Galarowicz and Wahl, 2003), which could potentially influence ammonia metabolism. This study also used relatively large walleye eggs. Egg size varies among walleye populations, largely because of the size of the spawning female (Wolfert, 1969; Serns, 1982; Baccante and Colby, 1996; Malison and Held, 1996; Moles *et al*., 2011; Feiner *et al*., 2019; Gonsorowski *et al*., 2024). Different size eggs would likely produce different amounts of ammonia, although the relative differences are unknown. Lastly, the results of this study occurred at an incubation temperature of 16℃. Higher or lower temperatures would likely influence embryonic metabolic rates (Eme *et al*., 2015; Summerfelt and Johnson, 2015) and subsequent ammonia production.

In conclusion, this study, the first to document ammonia concentrations during walleye egg development, documents relatively stable levels during most of egg incubation with a large increase at hatch. This basic information has practical implications for fish rearing, particularly with those systems recirculating water during walleye egg incubation. Biofiltration, if desired, can be appropriately sized. In addition, dilution by adding water to a recirculating aquaculture system – in essence making it a partial-recirculating aquaculture system – can also occur to decrease peak ammonia levels during hatch. Additional research is needed to determine ammonia toxicity during egg incubation of walleyes and other fish species, as well as just actual ammonia output by eggs from a number of other cultured fish species.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest regarding the publication of this paper.

ACKNOWLEDGEMENTS

Thanks to the incredible Nebraska fisheries crew who assisted with egg procurement and to Kali Roduner for her assistance in data collection.

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