International Journal for Parasitology: Parasites and Wildlife 4 (2015) 159–170

Contents lists available at ScienceDirect

International Journal for Parasitology: Parasites and Wildlife

journal homepage: www.elsevier.com/locate/ijppaw

Intestinal coccidiosis of anadromous and landlocked alewives, *Alosa pseudoharengus*, caused by *Goussia ameliae* n. sp. and *G. alosii* n. sp. (Apicomplexa: Eimeriidae)

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ARTICLE INFO

Article history:
Received 9 January 2015
Revised 19 February 2015
Accepted 20 February 2015

Keywords:
Alewives
Alosa pseudoharengus
Coccidia
Goussia

ABSTRACT

Anadromous alewives, *Alosa pseudoharengus*, have experienced significant population level declines caused by factors including habitat destruction. Alewives occur in two different life histories, anadromous and landlocked forms. The landlocked alewife evolved from ancestral anadromous populations, resulting in an exclusively freshwater and phenotypically unique form. The occurrence of parasites in a host is linked to the environment, making alewives an ideal model to compare parasitology within a single species with contrasting life histories. Currently, little information exists on the presence and impacts of parasites in these fish populations; the present study sets out to better understand coccidiosis in the threatened anadromous populations and to understand how coccidian parasites compare in both life history forms. The intestinal coccidian, *Goussia ameliae* n. sp., was described infecting the pyloric cecum of 76% and 86% of young-of-the-year and adult anadromous alewives, respectively, from the Maurice River, New Jersey, USA. The coccidian was found in landlocked alewife populations with a prevalence of 92% and 34% in YOY and adult fish, respectively. An analysis of the small subunit 18S ribosomal RNA gene of *G. ameliae* from both life history forms demonstrated that the coccidian had 100% sequence identity, confirming the same parasite species in both forms. Though genetic analysis demonstrated *G. ameliae* to be identical, some differences were observed in sporulation and morphology of the parasite within the two populations. The sporocysts in anadromous populations were shorter and wider, and sporulation timing differed from that of landlocked fish. These differences may either be attributed to differences in the host type or to the sporulation environment. Lastly, alewives from landlocked populations were frequently co-infected with a second coccidian species in the posterior intestine, which occurred at a lower prevalence. This species, *G. alosii* n. sp., was described based on morphological characters of the sporulated oocysts in fresh parasitological preparations.

1. Introduction

The alewife, *Alosa pseudoharengus*, is an anadromous fish native to the east coast of North America, whose populations have dramatically declined throughout their range. Alewives are a critical component of aquatic and terrestrial ecosystems, being a major source of forage for predatory game fish in freshwater and marine environments, as well as for coastal birds (Hall et al., 2012). They have also been demonstrated to be important agents for nutrient transport in aquatic ecosystems (West et al., 2010). Alewife populations are estimated to have declined by more than 98%, from a maximum catch in 1956 of 16,148 metric tons to a low of 7.5 metric tons in 2006 (Limburg and Waldman, 2009). It is believed that habitat loss caused by damming has been a major factor for the decline of this species, but other factors, including overfishing, pollution, climate change, and increased predation, have also contributed to their declines (Limburg and Waldman, 2009; Hall et al., 2010). In 2006, river herring were identified as a "Species of Concern" (NOAA, 2009), and in 2012, a comprehensive stock assessment by the Atlantic States Marine Fisheries Commission led to a coast-wide closure of commercial and recreational fishing for the two species of river herring, *A. pseudoharengus* and *A. aestivalis* (ASMFC, 2012).

The declines in alewife populations have brought to the forefront a need to better understand the biology of this species. While climate change and habitat loss have had direct impacts on alewife populations, it is also possible that these stressors can have indirect negative impacts to fish by benefiting parasite replication or disease transmission (Marcogliese, 2008). However, little

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http://dx.doi.org/10.1016/j.ijppaw.2015.02.003

information is known about the impacts of infectious diseases, including parasites, in alewives, making it difficult to obtain a full picture of the factors involved in population declines or failed recovery of this species. The negative impacts of diseases and parasites of other clupeid species have been studied in more depth. For example, ichthyophoniasis is a parasitic disease implicated in the mortality of wild Atlantic herring, *Clupea harengus*, and Pacific herring, *C. pallasii* (Rahimian and Thulin, 1996; Marty et al., 1998; Kocan et al., 1999). It has been hypothesized that the failed population recovery of Pacific herring stocks in Alaska following the Exxon Valdez oil spill can be partially attributed to diseases including ichthyophoniasis (Marty et al., 1998; Hershberger et al., 2002).

Coccidians are a group of parasites common in marine fishes, though with little information available on their diversity and impacts on fish populations. Coccidians are apicomplexan parasites that cause intestinal or extraintestinal infections (Dykova and Lom, 2007). Though little is known about the impacts of coccidiosis in fish hosts, it is often assumed that infections cause little disease under natural conditions, unless the host–parasite–environmental balance is disturbed (Davies and Ball, 1993). There have been reports of suspected mortality caused by coccidians in cultured marine fish; *Goussia kuehae* was believed to cause mortality in Asian seabass, *Lates calcarifer*, due to low daily water exchange rates (Gibson-Kueh et al., 2011; Szekely et al., 2013). Additionally, coccidian infections have been suggested to reduce body condition of wild fish. Infections caused by *Goussia* sp. in the liver have been linked to poor body condition in wild blue whiting, *Micromesistius poutassou* (Abollo et al., 2001), and Atlantic herring (Morrison and Hawkins, 1984). In alewives, reports of parasitic infections in general are sparse (Muzzall, 1994). Reports of coccidian infections in clupeid fishes appear to be limited to descriptions of the liver coccidian, *G. clupearum*, and a coccidian in the testis (Morrison and Hawkins, 1984; Morrison and Marryatt, 2012). An intestinal coccidian has been reported within the pyloric ceca of the Pacific herring, *C. pallasi*, by histology, though this species was not fully characterized (Marty et al., 1998). With current information lacking on the parasites of depressed anadromous alewife populations, the intention of the present study was to document and characterize coccidian parasites infecting this species.

A landlocked form of alewife, which spends its entire life in freshwater, has been derived from the ancestral anadromous form (Palkovacs et al., 2008). Anadromous alewives gained entry into lakes through canals or fish transfers, and have adapted to the freshwater environment, thus losing their anadromous life history stage. It is believed that the natural and anthropogenic damming of lake outlets has caused many independent populations of anadromous alewives to diverge into landlocked forms through parallel evolution over the past 300–5,000 years (Palkovacs et al., 2008; Jones et al., 2013). One example of this is in the Laurentian Great Lakes, where alewives were first detected in 1873 and are believed to have been introduced through the Erie Canal and/or through fish transfers. Whichever method of their introduction, massive reproduction and establishment of this species has caused a major shift in the Great Lakes ecosystem (Fuller et al., 2014). Though considered the same species, landlocked and anadromous alewives do not generally cohabitate the same water bodies, thus interbreeding among populations is unlikely (Palkovacs et al., 2008). Divergence of anadromous alewives into a solely freshwater niche led to major phenotypic changes that distinguish the derived landlocked form from the anadromous form, including earlier age and smaller size at maturity, slower adult growth, and reduced fecundity (Gross, 1951; Graham, 1956). Further, Jones et al. (2013) have demonstrated that body form is different in landlocked and anadromous alewives, and is associated with population-level dietary patterns. The fast adaptation and evolution of the alewife to the freshwater environment has been shown to be a result of large regulatory modifications, rather than coding changes (Czesny et al., 2012), and phenotypic changes, such as reduction in gill-raker spacing to adapt to feeding on small plankton found in freshwater, occurred over a short time period (Palkovacs et al., 2014).

The ecology of parasites is directly related to the host environment, and the fast adaptation of the landlocked alewife to a new ecological niche would likely impact the ecology of parasites in this species. Clearly, landlocked alewives have not adjusted to all aspects of life in freshwater lakes, since massive kills have been reported in landlocked alewife populations during the winter months (O'Gorman and Schneider, 1986). Winter mortality is believed to be related to a loss of homeoviscous adaptation (Snyder and Hennessey, 2003) since landlocked alewives cannot escape the coldwater temperatures as effectively as can the anadromous forms in the marine environment. Lepak and Kraft (2008) also propose that in overwintering landlocked populations, a combination of immunosuppression and poor condition leaves fish more vulnerable to disease. The intent of the present study was to identify and compare coccidian parasites in anadromous and landlocked alewife forms.

Anadromous alewives in New Jersey, USA, belong to the mid-Atlantic stock (Palkovacs et al., 2014). They enter streams to spawn in early February, with peak spawning occurring during mid-April through May. The post-spawned adults return to the ocean in mid-June and the hatched larvae remain in freshwater, with emigration of juveniles occurring from July to mid-November (Corbett and Allen, 2012). Based on surveys done in the 1970s, it was concluded that of the 132 spawning runs of alewife and blueback herring, *A. aestivalis*, in the state, nine have already become extinct due to habitat loss and barriers blocking fish passage (Zich, 1978). New Jersey has one of the earliest reported landlocked populations of alewives in Lake Hopatcong, the state's largest lake spanning about 10 km^2 in area, with reports of alewives dating back to 1850 (Gross, 1951). The introduction of alewives in Lake Hopatcong was attributed to the old Morris canal that connected the Delaware River to the lake (Gross, 1951) for means of transporting coal, iron, and zinc across the state. The landlocked alewife population in Lake Hopatcong has been completely isolated from extant anadromous forms since the beginning of the 1900s due to the blockage of canal and river passages to and from the lake. Currently, Lake Hopatcong supports a large population of landlocked alewives, which are the main forage for a variety of game fish. The lake also supports a commercial bait fishery that supplies alewives for fisherman throughout the region. The ecological importance of both anadromous and landlocked populations of alewives in the environment and their importance in supporting large predatory fish led us to better characterize coccidian parasites encountered within this species.

2. Materials and methods

2.1. Fish collection and sampling

2.1.1. Adult anadromous alewives

Adult alewives were collected on April 16, 2014 from the Maurice River, Millville, NJ, during their spawning migration. Samples were collected in conjunction with an annual survey of river herring conducted by the Bureau of Marine Fisheries, N.J. Division of Fish and Wildlife (NJFW) (project led by H. Carberry). Briefly, gill nets were set in the river, left for approximately 1 hour, and checked for river herring. A total of 28 adult alewives (mean fork length = 253 mm, SD = 10.86, n = 28) were collected and kept in a water reservoir until being transported back to shore by boat. The water temperature during fish collection was 13 °C and the salinity ranged from 0 to 0.1 ppt. In the field, fish were euthanized using tricaine methanesulphonate (MS-222) buffered with sodium bicarbonate and