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## Life history variation within and among naturalized rainbow trout populations of the Laurentian Great Lakes

T.A. Johnston<sup>a,\*</sup>, M.C. Prévost<sup>b</sup>, L.C. Haslam<sup>a</sup>, P.A. Addison<sup>c</sup>

<sup>a</sup> Ontario Ministry of Natural Resources and Forestry, Aquatic Research and Monitoring Section, Cooperative Freshwater Ecology Unit, Laurentian University, Sudbury, ON, P3E 2C6, Canada

<sup>b</sup> Department of Biology, Laurentian University, Sudbury, ON, P3E 2C6, Canada

<sup>c</sup> Ontario Ministry of Natural Resources and Forestry, Northwest Science and Information Section, Thunder Bay, ON, P7E 6S8, Canada

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### ABSTRACT

We examined naturalized rainbow trout spawning stocks from across the Great Lakes to determine: i) how reproductive characteristics among adults within populations vary with sex, ontogeny and energetic status, and ii) if variations in growth and reproductive characteristics among populations reflect differences in the environments they inhabit. Females in spawning runs tended to be larger and older than males, but growth rates were similar between sexes. As predicted, females had larger and more lipid-rich gonads and livers, and lower somatic condition and muscle lipid concentrations than males. Within populations, gonad size, fecundity, and egg size were related primarily to body size, and secondarily to indices of adult condition. Gonadosomatic index (GSI) increased with body size in females and declined with body size in males. Egg size increased with female size and declined with liver size and/or lipid content, whereas relative fecundity showed opposite trends. In contrast, egg lipid content appeared to be more strongly related to liver size and lipid content (positive effects) than to female size. Among populations, growth rate and muscle lipid concentration declined from south to north, but contrary to predictions, none of the reproductive traits examined showed strong covariation with environmental gradients. Growth, energetic status, and reproductive investment of Great Lakes naturalized rainbow trout vary both within and among populations, but localized adaptation to environmental conditions appears to be subtle.

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### Introduction

Diversity in life histories arises from both genetic variation and environmentally driven phenotypic plasticity, and appears at the intra-specific, as well as interspecific levels. Understanding the patterns, causes and consequences of life history variation is a central theme in evolutionary research (Stearns, 1992; Roff, 2002). It is also of interest from a resource management perspective because of the influence of life history traits on population regulation and, in particular, on the response of populations to exploitation (Jennings et al., 1998; Winemiller, 2005). Fishes, in particular, are an excellent group for studies of life history variation because of their wide diversity of reproductive strategies (Winemiller and Rose, 1992; Matthews, 1998; Mims et al., 2010). Much of this diversity is at the interspecific level due to genetic variation associated with different phylogenetic histories. However, intraspecific life history variation in fishes can be substantial and evident at a variety of spatial and temporal scales.

Within fish populations, life history traits may vary with the age and size of an individual (ontogenetic effects), particularly for iteroparous species. Given the trade-off that must be made between current and

future reproductive effort in iteroparous organisms, life history theory predicts that reproductive investment should increase with age as the probability of future reproduction diminishes (terminal investment hypothesis) (Williams, 1966; Pianka and Parker, 1975; Clutton-Brock, 1984). Absolute measures of reproductive effort (e.g., gonad size, fecundity) tend to show the most pronounced and consistent relationships with adult size and age, but the size or quality of offspring produced may also exhibit distinct ontogenetic trends (Kamler, 2005). In addition to this ontogenetic pattern, some of the observed variation among individuals would be expected to follow from short-term variation in their energetic and nutritional status (Marshall et al., 1999), though evidence for this at the level of individual fish remains limited (Lambert et al., 2000; Moles et al., 2008; Muir et al., 2014).

At a broader scale, variation in environmental conditions, both abiotic and biotic, may lead to divergence in life history traits among populations or stocks across species' ranges. Growth rates of fish vary with climatic conditions and the productivity of waterbodies (Hyatt et al., 2004; Blanck and Lamouroux, 2007; Blair et al., 2013) and are linked to various life history traits (Dmitriew, 2011). More rapid growth is often associated with earlier maturation (Beauchamp et al., 2004), shorter lifespan (Craig, 1985; Munch and Salinas, 2009), and possibly increases in annual reproductive effort (Healey, 1978, 1980; Brodeur et al., 2001). In addition, the environmental conditions that females experience as juveniles may

\* Corresponding author. Tel.: +1 705 671 3828.

E-mail address: [tjohnston@laurentian.ca](mailto:tjohnston@laurentian.ca) (T.A. Johnston).

influence how as adults they allocate their reproductive effort between quantity and quality of offspring (Jonsson et al., 1996; Taborsky, 2006; Burton et al., 2013b).

Salmonid fishes (family Salmonidae) display a wide range of life history strategies and have been widely used as models in life history research (Hendry and Stearns, 2004). The group contains both semelparous and iteroparous species, and covers a wide range of age-at-maturity, longevity, and spawning behavior. There is good evidence that life histories of some salmonids may evolve rapidly following their introduction to new habitats (Kinnison et al., 1998; Hendry et al., 2000). Rainbow trout (*Oncorhynchus mykiss*) populations of the Laurentian Great Lakes present an interesting case for studying intraspecific variation and diversification of life histories. The rainbow trout is an iteroparous salmonid native to western North America that has been widely introduced to freshwater systems around the world (Crawford and Muir, 2008). Introductions into the Laurentian Great Lakes began in the late 1800s, and this was followed by many subsequent stocking events throughout the system (MacCrimmon and Gots, 1972; Crawford, 2001). Naturalized populations are now established in all of the Great Lakes where they have adopted a potamodromous life history; adults live in the upper pelagic zone of the lakes (Negus and Hoffman, 2013) and spawn in inflowing tributaries that serve as juvenile habitat for the first 1 to 3 years of life (MacCrimmon and Gots, 1972). Because the rainbow trout range in the Laurentian Great Lakes covers a broad geographic area that includes a diversity of climatic and habitat conditions, it is likely that these naturalized populations exhibit phenotypic differences (Biette et al., 1981), possibly in response to the environment, and possibly due to genetic divergence (local adaptation and/or drift). This could have implications for how these populations are managed.

Our objective was to determine how selected life history traits varied in rainbow trout of the Laurentian Great Lakes. We sampled multiple spawning stocks across the basin and examined both fine-scale variation (among individuals within populations) to assess sexual, ontogenetic and condition effects, and broad-scale variation (among populations) to assess potential local adaptation to environmental conditions. Variation in both sexes was considered, but our emphasis was on female traits, particularly on variation in egg quality. We hypothesized that rainbow trout reproductive effort within populations would vary with ontogeny, as well as with adult body condition, and that growth and reproductive traits of stocks would vary geographically along climatic and waterbody productivity gradients. We predicted that: i) females would exhibit greater reproductive investment, and consequently, reduced body condition relative to males; ii) gonad size, fecundity, and egg quality would all increase with adult size and/or age, consistent with the terminal investment hypothesis, as well as with adult body condition; iii) adult growth rate would decline from south to north across the Great Lakes because of declining temperature and waterbody productivity, and that this would be accompanied by a declining trend in total reproductive effort, reflected in gonad size and fecundity; and iv) spawning stocks utilizing lower productivity tributaries would produce larger eggs to enhance offspring survival. It was hoped that results of this research would both improve our understanding of the life history and reproductive ecology of a naturalized salmonid, and support management decisions for an important Great Lakes fishery.

## Materials and methods

### Field sampling

Field sampling was carried out on known spawning tributaries around the Laurentian Great Lakes in the spring from 2005 to 2007. Fish were captured by angling in most cases, but were dip-netted from fish passage-ways on several tributaries. Our fish processing followed both non-lethal and lethal sampling protocols. Non-lethal sampling effort was more extensive ( $n = 17$  tributaries), extended throughout the spawning season, and gathered information on adult

size, age and egg quality. Lethal sampling effort was restricted to fewer sites ( $n = 8$  tributaries), was carried out in the immediate pre-spawn period, and yielded a wider variety of adult trait data, including otolith age determinations that could be compared with the more commonly determined scale ages. Our focus was on wild, naturalized fish and we haphazardly selected tributaries that were known to have high proportions of naturally produced adults returning to spawn, primarily on the Canadian side of the Great Lakes. However, adults of domestic or hatchery origin were also present in some tributaries. Fish that appeared to have a high body depth to length ratio, relatively shorter pectoral and pelvic fins, and / or exhibited signs of fin or snout erosion (generally acquired from captive rearing at high density) were categorized as domestic (Pulcini et al., 2013; Johnston and Wilson, 2015), and fish with distinct fin clips were categorized as stocked fish of hatchery origin. Adults categorized as domestic or stocked were processed similarly to the wild fish but were excluded from our analyses in the current study.

Non-lethal fish processing proceeded as follows. Sex and maturity state of each fish were determined by examining external features (kype on mature males, distended abdomen on gravid females) and by gently stroking the sides of the fish to detect semen, ova or ovarian fluid. For ovulated females, a sample of ripe ova (~20 mL) was collected and placed in a small plastic bag. For each fish, we measured from the tip of the snout to the fork of the tail (fork length, FL,  $\pm 10$  mm), removed a scale sample (~10) from the mid-body region above the lateral line, and removed two pieces of caudal fin tissue using a paper hole punch (each ~5 mm diameter) for a concurrent study on rainbow trout genetics (P.A. Addison, unpublished data). Fish were immediately released following processing. Fish identified as recaptures in the same sampling year (tissue sample holes on caudal fin) were immediately released without processing. Ova samples were held on wet ice and transported to the laboratory where they were weighed ( $\pm 0.1$  g wet) then frozen at  $-20$  °C. In addition to the wild Great Lakes stocks, we also obtained body size data and ova and scale samples from females of three other stocks: i) a native, landlocked, slow-growing stock; ii) a native, anadromous, fast-growing stock; and iii) a captive reared broodstock. The two native stocks were from British Columbia, Canada, and were sampled to provide native population reference points for comparison with the naturalized Great Lakes stocks. The captive broodstock (Tarentorus Fish Culture Station, Sault Ste. Marie, ON) was descended from one of the naturalized stocks sampled as part of this study (Ganaraska River, Lake Ontario) and was sampled to assess the short-term effects of captive-rearing on growth and egg size.

Lethal fish processing proceeded as follows. We attempted to select equal numbers and a wide size range of both sexes at each site. All selected females were unovulated (i.e., eggs not free-flowing) and all selected males were ripe (i.e., semen free-flowing) at the time of capture. Selected fish were killed by a sharp blow to the top of the head, packed on wet ice and transported to the laboratory for further processing within 24 h. Each individual was weighed (total mass,  $\pm 10$  g wet) and measured from the tip of the snout to the fork of the caudal fin (fork length, FL,  $\pm 1$  mm). All soft tissue samples subsequently removed were stored in small plastic bags at  $-20$  °C. For each male, testes were removed, weighed ( $\pm 0.1$  g wet), and frozen. For each female, ovaries were removed and weighed whole ( $\pm 1$  g wet), then a subsample of ovary was removed from the mid-region, weighed ( $\pm 0.1$  g), and frozen. For both sexes, the carcass was weighed without gonads (somatic mass,  $\pm 10$  g wet) then the liver was removed, weighed ( $\pm 0.1$  g wet), and frozen. The carcass was weighed a final time following the removal of all remaining viscera posterior to the pericardial cavity (eviscerated mass,  $\pm 10$  g wet), and a sample (~30 g wet) of skinless, axial muscle was removed adjacent to the dorsal fin and above the lateral line, weighed ( $\pm 0.1$  g wet), and frozen. Both sagittal otoliths were removed, rubbed clean, placed into a 1.5 mL plastic tube and allowed to air dry, and a scale sample (~10) was removed from the mid-body region above the lateral line, stored in a paper envelope and allowed to air dry.

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