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Life-history variation among four shallow-water morphotypes of lake trout from Great Bear Lake, Canada

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ABSTRACT

Phenotypic variation within populations is common in many salmonids, especially when inhabiting northern postglacial systems. We compared life-history traits among four lake trout morphs co-existing in the shallow-waters of Great Bear Lake (Northwest Territories, Canada). Adult growth rate, age- and size-at-maturity, and survival differed among morphs, consistent with their degree of foraging specialization and predictions from foraging theory, e.g., reduced somatic growth and higher reproductive investment in the generalist morph, high growth throughout life in the piscivorous morph, and intermediate life-histories in the more benthic- and pelagic-oriented morphs. Fecundity and egg size also varied among morphs. However unexpected findings also arose, such as comparable immature growth rates among morphs. Other traits, such as a high proportion of resting individuals among all morphs, suggest life-history adaptations to northern latitudes. Longer resting periods are likely needed to obtain enough energy for reproduction, and may also allow greater investment in post-maturation growth. Overall, lake trout from Great Bear Lake demonstrated remarkable longevity and exceptional asymptotic sizes, even for a northern freshwater ecosystem. Our study provides new insights into life-history evolution among lake trout morphs that use different food sources and habitats. In addition, it contributes to our understanding of this complex aquatic ecosystem, which exhibits one of the highest known levels of intraspecific diversity among freshwater fish.

Introduction

Numerous salmonid species are widely distributed in North America and occupy a diversity of aquatic habitats (Behnke, 2002). Natural environmental gradients found in aquatic habitats, especially in lacustrine systems (e.g., pelagic vs. littoral, shallow vs. deep water), significantly influence phenotypic characteristics in salmonids (Robinson and Parson, 2002; Goetz et al., 2011). For many salmonids, intraspecific variation in resource use, both among and within populations, is common. Within a given aquatic ecosystem, such variation can take the form of resource polymorphism or continuous niche variation (individual specialisation) (Bolnick et al., 2003; Morbey et al., 2006).

Salmonid species can also show intraspecific differences in life-history traits, often linked to polymorphism and resource use variation (e.g., Jonsson and Jonsson, 2001; Parra et al., 2009; Chavarie et al., 2010). Regardless of whether these differences originate from genetic and/or phenotypic divergence (Panfili et al., 2004), they can have population-level consequences, particularly when body size is involved (Baglinière and Maisse, 2002; Nicola and Almodóvar, 2004; Quince et al., 2008a). For example, individual growth rate, can play a pivotal role in shaping other life-history traits (e.g., survival, longevity and reproduction) that can influence population-level processes (Rikardsen and Elliot, 2000; Loewen et al., 2010; Sogard et al., 2012).

Lake trout, *Salvelinus namaycush*, has a widespread distribution in northern North America, where it is a dominant predator within lakes (Martin and Olver, 1980; Behnke, 2002). Among species of *Salvelinus*, lake trout is generally considered to display limited resource polymorphism (e.g., Snorrason and Skúlason, 2004; Hansen et al., 2012), but recent studies have demonstrated remarkable morphological diversity (Muir et al., 2015). In the Laurentian Great Lakes and other large, deep lakes, lake trout morphs specialize between shallow and deep water habitats and exhibit associated differences in body shape, life-history, lipids and buoyancy, trophic levels, and/or genetics (Moore and Bronte, 2001; Zimmerman et al., 2006, 2007, 2009; Goetz et al., 2010; Hansen et al., 2012; Muir et al., 2014).

Recent studies of lake trout from Great Bear Lake, NWT, Canada, have established extensive polymorphism, independent of depth

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differentiation (Blackie et al., 2003; Alfonso, 2004; Chavarie et al., 2013, 2014a,b). Instead, lake trout morphotypes within shallow waters are associated with a benthic–pelagic gradient, combined with differential resource use (e.g., picivores vs. insectivores) (Chavarie et al., 2014b). This polymorphism offers the opportunity to examine predictions from resource polymorphism theory and consequent variation in life-history (Fraser et al., 2008). A combination of related traits associated with resource partitioning can result in a coordinated life-history strategy within a group of similarly specialized individuals. For example, piscivorous Arctic char (*Salvelinus alpinus)* exhibit a larger size at maturity, delayed maturity, low reproductive investment upon maturation, and longer life span; conversely, insectivorous char with slow growth rates typically display the opposite suite of life-history traits (Nordeng, 1983; Jonsson and Jonsson, 2001).

The aim of this study is to compare life-history tactics among the four shallow-water morphs from Great Bear Lake, to improve our understanding of this case of sympatric intraspecific diversity. To examine life-history differences among morphs, we compared age, growth, maturity, and reproductive output. Variation (or lack thereof) in life-history patterns among morphs is then discussed in the framework of ecological opportunities and niche space.

Materials and methods

Study system

Great Bear Lake (Fig. 1A) is one of the largest and deepest freshwater systems in North America, with a surface area of 31 790 km^2 and a maximum depth of 446 m (MacDonald et al., 2004). Located in northeastern Northwest Territories, 250 km south of the Arctic Ocean, its limnological features are similar to other Arctic freshwater systems associated with low productivity (Johnson, 1975). This post-glacial lake has remained relatively isolated and is lightly exploited by a small, subsistence fishery that supports a Dene community (Déline), and by a fly-in sport fishing lodge.

Several salmonids in the lake, including lake trout, cisco (*Coregonus artedi*), and lake whitefish (*Coregonus clupeaformis*), are characterized by considerable intra-specific diversity (Chavarie et al., 2013, 2014a; Howland et al., 2013; and L. Chavarie, *pers. obs.*). In lake trout, polymorphism includes four morphs that co-exist in the shallow-water (≤30 m) zone (Chavarie et al., 2013). There is a generalist morph, with a smaller head and intermediate fins (Morph 1), a piscivorous morph with the largest head and jaws but smallest fins (Morph 2), a benthic morph with the longest fins and a robust body shape (Morph 3), and a pelagic morph with a thick curved lower jaw and the smallest caudal peduncle (Morph 4) (Chavarie et al., 2013, 2014a) (Fig. 1B). Great Bear Lake is divided into five "arms" (Keith, McVicar, McTavish, Dease, and Smith), and additional morphological differentiation in body shape was demonstrated within morphs among arms (Chavarie et al., 2014a).

Data collection

For this study, fish were caught at depths ≤30 m using paired bottom sets of a 14-cm and a multi-mesh (3.8–14 cm stretch mesh) gill net, with each set soaked for approximately 24 h, during July and August, 2002–2011. Sampling of the 902 adult lake trout used in this study occurred in all five arms, usually one arm per year: Dease (2005 and 2010), McVicar (2003 and 2008), Keith (2002–2004, 2006, 2007, and 2010), McTavish (2009) and Smith (2006 and 2011). We obtained lateral, full-body, digital images of each fish, and assigned each fish to a morph using a multivariate assignment method based on body and head shape, and linear measurements (see Chavarie et al., 2014a). Measurements of characteristics and tissues/structures related to life history were sampled, including fork length, somatic weight, sex, reproduction state (current year spawner or resting), gonad weight, ovaries of female current year spawners, and sagittal otoliths. Following the reproductive states and descriptions used for other northern iteroparous salmonids (Bond and Erickson, 1985; Howland, 1997), current year spawners included all individuals expected to spawn in the fall of the year in which they were collected. These individuals were distinguished as having gonads that were fully developed and enlarged (females with eggs at or near full size and ovaries filling body cavity, males with large lobate testes of white to purplish in color), whereas resting individuals were defined as adults that were recovering from a previous spawning event and were discerned as follows: females with ovaries that fill ≤50% of body cavity and contained small seed eggs, occasional atretic

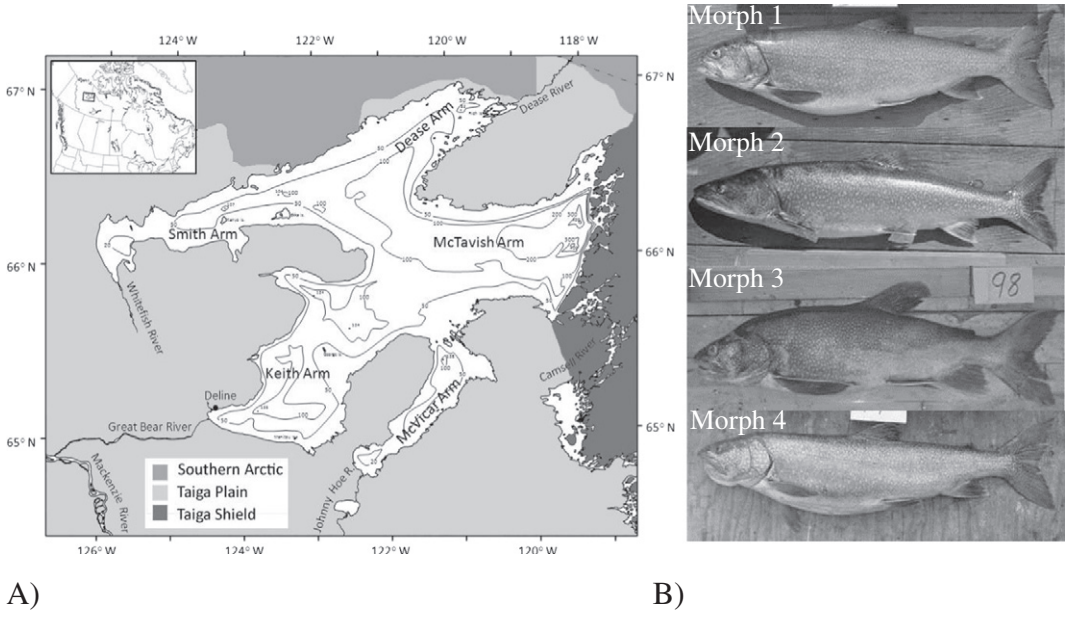

Fig. 1. A) Map of Great Bear Lake, Northwest Territories, Canada, adapted from Johnson (1975) and Chavarie et al. (2014a, 2014b), indicating general bathymetry, the terrestrial ecozones adjacent to the lake, and its major rivers. Insert: location of study area within Canada. B) The four shallow-water morphotypes of Lake Trout from Great Bear Lake: the generalist, the piscivore, the benthic, and the pelagic, Morphs 1–4, respectively.