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Notes

Sexual maturation in stream residents from migratory populations of brook trout inhabiting Lake Superior tributaries

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ABSTRACT

There is mounting evidence that populations of brook trout (*Salvelinus fontinalis*) inhabiting bays and tributaries along the north shore of Lake Superior exhibit partial migration. In this system some fish originate in tributaries and move into the lake for much of the year, grow large and migrate back into tributaries to spawn, whilst other smaller fish reside in tributaries and grow slowly. This study determined whether the stream dwelling brook trout reach sexual maturity in the stream habitats, a criterion needed to distinguish partial migration from other forms of migration that could maintain divergent forms and life histories of brook trout. Maturational development was determined for fish collected in July and August. Sampling these populations during fall spawning was not permitted due to conservation concerns. Male and females sampled from tributaries displayed $\delta^{13}C$ signatures and growth histories characteristic of stream residency. Assessment of maturational development suggested that 33% of females would have been expected to spawn in the fall of that year. Our findings demonstrate that a portion of fish residing in tributaries reach sexual maturity without adopting summer residency in the lake providing evidence for partial migration over other forms of migration. Improved understanding of the variation in migratory behaviour in these brook trout populations will contribute to their conservation and management in the face of lake-wide declines of the migrant fish.

Introduction

Brook trout (*Salvelinus fontinalis*) in Lake Superior and tributary streams display complex variation in migratory behaviour and habitat use. These include larger fish that originate in tributaries, reside in the lake for most of the year, and migrate back into tributaries to spawn in the fall (lake form) and smaller fish that reside in tributaries (stream resident form) (Huckins et al., 2008; Newman and Dubois, 1997). The lake form is the focus of conservation concern (Newman and Dubois, 1997). There is bi-national interest in conserving the remaining populations and restoring populations in tributaries believed to have produced the lake form in the past (Horns et al., 2003; Newman and Dubois, 1997; Schreiner et al., 2008). Declines in the distribution and abundance of the lake form occurred prior to biological investigation of their life history and migratory behaviour, and a better understanding of the ecology of these populations has been identified as a research need (Newman and Dubois, 1997; Schreiner et al., 2008).

Partial migration describes instances where some individuals from a population complete their life cycle in their natal habitat (residents) whilst others migrate to a different habitat to rear and later return to their natal habitat to breed (migrants). Recent reviews have stressed that partial migration in fishes could be more widespread than previously appreciated (Kerr et al., 2009; Chapman et al., 2011, 2012a). Partial migration is reported most often for populations where adults spawn in a tributary and some progeny migrate to a lake or marine coast and back over their lifetime, whilst other progeny complete their life cycle in the natal tributary (Jonsson and Jonsson, 1993; Stolarski and Hartman, 2010). These differences in migratory behaviour are often linked to differences in life history (Ridgway, 2008) and in population dynamics and persistence (Velez-Espino et al., 2013). Partial migration is typically inferred from observations of morphologically divergent fish occupying different habitats at one time of the year and the same habitat at another time of the year, usually during spawning (Chapman et al., 2012b). Migratory behaviour is often inferred from habitat use and morphology because individuals are often hard to track over their lifetimes (Baker, 1978).

Phenotypic variation amongst individuals occupying different habitats and coexisting in a common geographical area can reflect one of at least four migratory systems (numbered hypotheses; H1 to H4 in Fig. 1): juvenile and adult life stages in a population where all individuals migrate, with younger juveniles residing in the natal habitat and older juveniles and adults residing in a new habitat (migration, H1; Waples et al., 2001), members of sub-cohorts that differ in the age at which individuals migrate from the natal habitat (staggered migration, H2; Metcalfe, 1998; Metcalfe et al., 1989; Utrilla and Lobón-Cerviá,

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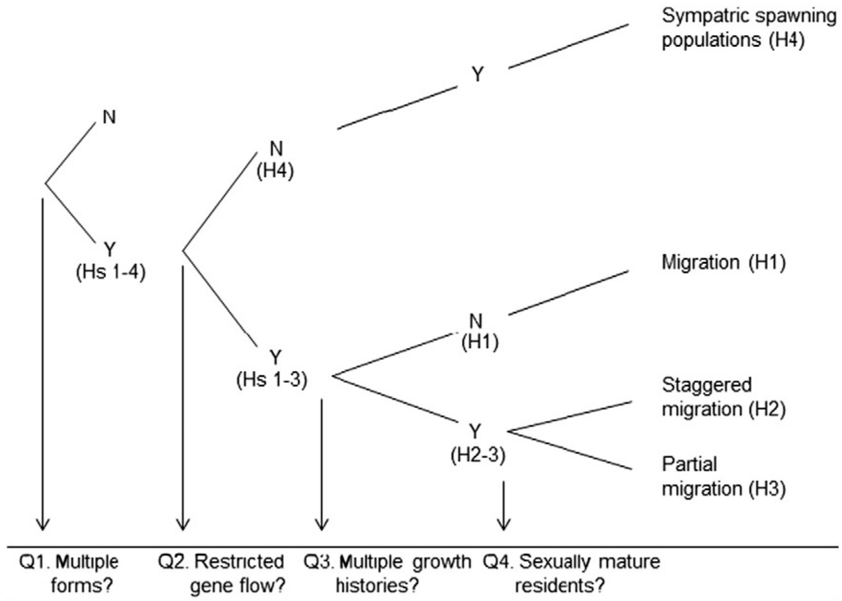

Fig. 1. A decision tree for distinguishing amongst four alternative migratory systems (hypotheses H1 to H4) consistent with the observation of individuals differing in body size and shape occupying different habitats during the non-breeding season and the same habitat during the spawning season. The hypotheses can be distinguished by evaluating four questions (Qs) one of which, Q4, is tested here by determining whether individuals residing in the spawning habitat (natal streams) reach sexual maturity.

1999), a combination of resident and migratory individuals within a single population (partial migration, H3; Doucett et al., 1999; Forseth et al., 1999; Kerr et al., 2009) or sympatric populations differing in migratory behaviour (resident versus migratory) (H4; Fraser and Bernatchez, 2005; Jones et al., 1997). This set of hypotheses encompasses the diversity of known migratory patterns for fishes. Distinguishing amongst the hypotheses can narrow the possibilities and, if no hypothesis is supported, reveal new migratory patterns.

The hypotheses can be distinguished by addressing four questions (Q1 to Q4 in Fig. 1). Testing for the occurrence of distinct forms (Q1) is a step towards characterizing the nature of the phenotypic variation. Testing for restricted gene flow between forms (Q2) distinguishes hypotheses involving phenotypic differentiation within a single population from those involving sympatric populations or newly evolving species (D'Amelio and Wilson, 2008; Magnan et al., 2002). Testing for multiple distinct growth histories (Q3) distinguishes hypotheses where different forms represent juvenile and adult life stages from a migratory population with a common growth history (e.g. migration) from those where different forms represent distinct growth phenotypes (e.g. partial migration). Testing for resident individuals reaching sexual maturity in their natal habitat (Q4) further distinguishes hypotheses where juvenile and adult life stages occupy different habitats from hypotheses that involve multiple distinct phenotypes.

We determined whether brook trout inhabiting tributaries along the north shore of Lake Superior and its tributary streams mature whilst residing in tributaries (Q4) by sampling individuals from populations displaying phenotypic variation in migratory behaviour. By definition, partial migration requires that at least some animals from the population reach sexual maturity whilst remaining in the habitat where breeding takes place (Fig. 1). For fishes, this question is rarely tested (Robillard, 2012), but its evaluation is necessary to distinguish partial migration (H3) from migration (H1) and staggered migration (H2). Testing it ensures that fish residing in the natal habitat are not juveniles that have yet to migrate. We focused on brook trout from the Nipigon Bay area of Lake Superior because establishing whether some individuals reach sexual maturity whilst residing in tributary streams is an outstanding question, important for delineating the migratory behaviour of these populations. Brook trout sampled from the lake and streams differ markedly in habitat use and trophic ecology (Q1; Robillard et al., 2011b), arise from a common population (Q2; D'Amelio and Wilson, 2008), and display different growth histories and lifespans (Q3; Robillard et al., 2011a) with juvenile-sized fish leaving the stream to feed in the lake (Coppaway, 2011) and large fish from the lake returning to tributaries at the time of spawning (Mucha and Mackereth, 2008).

We first analyzed stable isotopes and growth histories to identify a set of fish that were stream resident for the summer. This step was taken because approximately 8% of brook trout sampled in these streams make periodic foraging forays into the lake and were likely fish adopting the lake-dwelling life history (Coppaway, 2011). We then visually assessed the maturational development of males and females, and measured egg diameter of maturing females to assess whether they would spawn in the coming autumn.

Methods

Study area

This research was conducted in Nipigon Bay, Lake Superior, Ontario (48°55′29″ N, 87°51′10″ W); an area in Lake Superior where large brook trout are still observed in the lake and tributaries. Nipigon Bay is the most northerly portion of Lake Superior (Fig. 2). It is shallow, productive, and nearly enclosed by a peninsula and several islands.

The study area included eight streams located between Nipigon and Rossport, Ontario: Stillwater Creek, Dublin Creek, MacInnes Creek, Cypress River, Little Cypress River, Little Gravel River, Nishin Creek and McLeans Creek (Fig. 1). Catchment sizes range from 6.7 to 160.9 km^2. Development in these watersheds is minimal. The streams are high gradient, low productivity systems lacking in-stream cover and deep pools. Stream discharges drop considerably in summer, with rapid increases in discharge following heavy rains. Seven of eight streams have an impassable waterfall or perched culvert within 2 km of Lake Superior; but there is no such impassable barrier on MacInnes Creek. Brook trout occurred in all study streams. Non-native rainbow trout (*Oncorhynchus mykiss*), coho (*Oncorhynchus kisutch*), Chinook (*Oncorhynchus tshawytscha*) and pink salmon (*Oncorhynchus gorbuscha*), and several species of native cyprinids, catostomids, gasterosteids and cottids, also occurred in the streams.