Journal of Great Lakes Research 42 (2016) 290–298

Contents lists available at ScienceDirect

Journal of Great Lakes Research

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

Influence of potential fish competitors on Lake Trout trophic ecology in small lakes of the Barrenlands, N.W.T., Canada

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ARTICLE INFO

Article history:
Received 30 November 2014
Accepted 16 July 2015
Available online 1 September 2015

Communicated by Pete Cott

Index words:
Lake Trout
Resource competition
Diet
Stable isotope analysis
Stomach content analysis
Subarctic

ABSTRACT

Local (e.g., habitat compensation activities) and regional (e.g., climate-related range expansion) events that are expected to increase in northern Canada can facilitate movement of fishes into aquatic ecosystems from which they were previously absent. Successful colonization would change fish community structure and potentially alter food web dynamics. We compared the trophic ecology, growth, and body condition of Lake Trout (*Salvelinus namaycush*) in small, tundra lakes that varied in fish community structure to help understand effects of colonization on this key species. Complementary stable isotope and stomach content analyses indicated that Lake Trout foraging differs between lakes with and without multiple large-bodied fishes. In lakes with a single potential competitor, trout consumed primarily pelagic zooplankton, but focused on more littoral resources in the presence of multiple large-bodied fishes. Population trophic niche width and inter-individual variation in Lake Trout diet were larger in lakes with multiple competitors, whereas Lake Trout populations in lakes with only one other large-bodied species were in better body condition. Our findings highlight the potential sensitivity of northern Lake Trout populations to colonizing fish species.

Introduction

Understanding how competing species coexist in a shared environment has long been of interest to ecologists. In theory, coexistence is accomplished through niche differentiation (MacArthur, 1958) via resource partitioning (Schoener, 1986), and has been well-documented within freshwater communities (e.g., Werner and Hall, 1976; Luiselli, 2008). Among fishes, ample literature has identified partitioning of prey resources to be more important than either habitat or time dimensions (see Ross, 1986). Because fish often ingest fewer and/or lower quality prey items in the presence of competitors (Dieterich et al., 2004), outcomes of interspecific competition for prey resources have commonly been documented as declines in growth (e.g., McHugh and Budy, 2006) and condition (e.g., Tonn et al., 1986).

Recent work has focused on direct and indirect trophic interactions between fishes that have come into contact as a result of stocking events (e.g., Eloranta et al., 2015), climate-induced range expansions (e.g., Hayden et al., 2013), or unplanned species invasions (e.g., Sampson et al., 2009). Other mechanisms, such as habitat enhancement activities, can also bring species into contact that did not previously co-occur. In the Northwest Territories (NWT) of Canada, fish habitat compensation projects have been undertaken to offset habitat that was lost due to mining-related activities, and several projects have been designed to increase stream connectivity among lakes with different fish communities (Golder Associates, 2001; Jones et al., 2008; Courtice et al., 2014). Such projects may facilitate colonization of fish species into lakes where they do not currently occur, but where other potential fish competitors are present. Thus, where these projects are successful, the new colonists could alter the trophic niche of resident fish species and overall food web dynamics.

Many lakes in northern Canada are small (mean surface area = 91.4 ha), shallow (mean Z_{max} = 7.4 m), and share similar physical and chemical characteristics (Pienitz et al., 1997). These lakes can often be classified as oligotrophic and contain depauperate assemblages of plankton, macroinvertebrates, and fish (Johnson, 1976; Shortreed and Stockner, 1986; Pienitz et al., 1997). The larger-bodied fishes in these lakes typically include varied combinations of Arctic Grayling (*Thymallus arcticus*), Burbot (*Lota lota*), Cisco (*Coregonus artedii*), Lake Trout (*Salvelinus namaycush*), Lake Whitefish (*Coregonus clupeaformis*), Longnose Sucker (*Catostomus catostomus*), and (*Esox lucius*), with smaller fishes also present (Samarasin et al., 2015). Within the NWT,

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http://dx.doi.org/10.1016/j.jglr.2015.07.014
0380-1330/

adults of the larger-bodied fishes are known to consume similar food resources, including crustaceans, aquatic insects, molluscs, and mites; Arctic Grayling, Burbot, and Lake Trout also consume fishes (Scott and Crossman, 1973). In particular, lake trout is commonly regarded as an opportunistic generalist predator; the preferred diet of adults is generally pelagic forage fish, but in lakes lacking these prey, littoral fishes, benthic invertebrates, and zooplankton make up the diet in variable proportions (Martin, 1966; Pazzia et al., 2002), both within and among Lake Trout populations (Vander Zanden et al., 2000). As large, versatile predators, Lake Trout (and Burbot) has the ability to interact as both predators on, and competitors with, the rest of the fish community (Scott and Crossman, 1973).

A variety of methods are available in ecological research to investigate the trophic niche of organisms. Stomach content analysis (SCA) is a standard tool that can provide detailed information on prey composition, but provides only a 'snapshot' of a consumer's diet at the time of collection. Therefore, methods that infer diet over longer temporal periods complement the information provided by SCA (e.g., Beaudoin et al., 1999). In the last 20 years, stable isotope analysis (SIA) has been increasingly employed in ecological research to understand diets and feeding relationships of consumers (Thompson et al., 2005). SIA of tissues provides a dietary proxy that tracks the flow of elemental isotopes from resources to consumers. In particular, ratios of ^{13}C to ^{12}C and ^{15}N to ^{14}N (measured as $\delta^{13}C$ and $\delta^{15}N$, respectively) are commonly analyzed. Because $\delta^{13}C$ is only slightly enriched between source and consumer, it can provide an indication of the path of energy flow from producer to higher consumers (McCutchan et al., 2003). In freshwater ecosystems, basal resources in the littoral zone can often be differentiated from their pelagic counterparts on the basis of their $\delta^{13}C$ values (Hecky and Hesslein, 1995). In contrast, $\delta^{15}N$ consistently undergoes a step-wise increase between successive trophic levels (McCutchan et al., 2003), and can thus be useful as a trophic-level indicator (Vander Zanden and Rasmussen, 1999). Together, $\delta^{13}C$ and $\delta^{15}N$ reflect the prey materials assimilated by a consumer to indicate its long-term diet and position in a food web; in slow growing fish populations, isotopic turnover can take months to years (Hesslein et al., 1993; Perga and Gerdeaux, 2005).

Traditionally, the results of SIA have been interpreted qualitatively using bi-plots, which present the $\delta^{13}C$ and $\delta^{15}N$ values of individuals (or populations) in isotopic space. Recently, dietary mixing models using Bayesian probability (e.g., Moore and Semmens, 2008) have been developed to estimate relative proportions of organic carbon sources that support a consumer. Linear distance metrics (Layman et al., 2007), originally developed to assess community metrics, have been used successfully at the population level to explore niche width and inter-individual variation in two-dimensional isotopic space (e.g., Swanson et al., 2010).

Comparing the trophic ecology of a widely occurring fishes across lakes that vary in the species of fish that they support can provide a 'natural experiment' on effects of different communities on the trophic niche of the widely occurring species and thus provide insights into effects of colonizing fishes. We studied the trophic ecology, condition, and growth of native Lake Trout in six small lakes of varied fish communities within the Lac de Gras watershed. In three of these lakes, Lake Trout and Burbot are the only large-bodied fishes, whereas the remaining three lakes supported 1–3 additional large-bodied species. We expected that Lake Trout occurring in lakes with multiple large-bodied fishes would consume different prey items than trout coexisting with Burbot only, which could translate into differences in growth and condition. Predicting the effects on native fauna of projects that increase the connectivity of small, tundra lakes is important to fisheries management during this era of increasing development across Canada's northern regions (Schindler, 2001; Gavrilchuk and Lesage, 2014).

Methods

Study area

The study was conducted within the Lac de Gras watershed, Northwest Territories, Canada, ca. 64°28′N, 110°14′W, in a region known as the Barrenlands (Fig. 1). The low topographical relief and glacial history of this area have resulted in an abundance of lakes and streams that cover ca. 21% of the landscape (Jones et al., 2003). The lakes are bordered by sedge tussock, low-tall shrub tundra (Bliss, 1981), and boulders; their littoral zones support low densities of aquatic plants, and are instead dominated by boulders and soft sediments, although small sections of both sand and gravel/cobble substrates can be found. The smaller lakes (ca. <30 ha) are typically ice-free from mid-June to late-October. Sampling conducted on a subset of 10 lakes indicated that they undergo weak thermal stratification by mid-July (M. Hulsman, unpublished data).

Fieldwork was carried out during 2009–2011 in six study lakes that are located within a 7.5 km radius of each other (Fig. 1). All of the lakes are small (mean ± 1 SE; 9.2 ± 2.5 ha) and have moderate maximum depths (9.7 ± 0.9 m); their littoral zones warm to a summer temperature of 15.1 ± 0.1 °C (mean ± 1 SE) (Table 1). All are oligotrophic and share similar pelagic chlorophyll-a levels and chemical characteristics, though two of the lakes (E14 and E17) have elevated levels of total nitrogen due to anthropogenic sources (Table 1). The lakes were designated as either 'Class 1' or 'Class 2', based on the composition of their fish community (Table 2). Class 1 lakes supported Lake Trout and only one other large-bodied fish (Burbot), while Class 2 lakes supported, Burbot, and at least one other large-bodied species (Cisco, Longnose Sucker, and/or Round Whitefish, *Prosopium cylindraceum*). At least one small-bodied species (Lake Chub, *Couesius plumbeus*, Ninespine Stickleback, *Pungitius pungitius*, or Slimy Sculpin, *Cottus cognatus*) was also found in all lakes (Table 2).

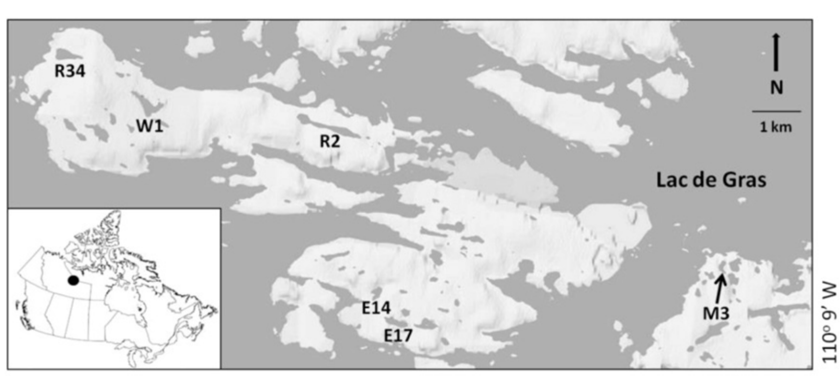

Fig. 1. Map showing locations of the study lakes in the Lac de Gras watershed, Northwest Territories. Inset: Location of the study area in Canada.