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# Resource partitioning among top-level piscivores in a sub-Arctic lake during thermal stratification

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ABSTRACT

In systems with multiple piscivores, co-occurrence is dependent on resource partitioning. This is pronounced in oligotrophic northern lakes, which have simple food webs and short open-water seasons. We used acoustic telemetry and stable isotopes to quantify habitat and dietary partitioning during thermal stratification among three piscivores that commonly co-occur in Canadian sub-Arctic lakes—burbot (Lota lota), lake trout (Salvelinus namaycush), and northern pike (Esox lucius). Spatial core areas and core habitat niches (space and depth) did not significantly overlap among species. Although burbot and lake trout occupied similar mean daily depths (16.2 m and 13.4 m, respectively), and water temperatures (5.4 °C and 6.9 °C, respectively), they were spatially segregated. Burbot were closely associated with the lake bottom on steep drop-offs between the offshore and nearshore zone with moderate substrate complexity, whereas lake trout were located over deep offshore basins and suspended above the lake bottom. Northern pike occupied shallow depths (5.3 m) and warmer water (16.5 °C) within the nearshore region and were closely associated with bottom substrate of highest complexity. Some significant overlap among spatial home ranges and broad habitat niches indicated that these species interact. However, dietary niches did not significantly overlap at either the core or broad levels, suggesting that species were utilizing spatially diverse food sources. Our results highlight the importance of including depth and space when quantifying resource partitioning among fishes and provide insight into the mechanisms that promote piscivore co-occurrence in northern lakes.



## Introduction

Understanding patterns of resource partitioning among co-occurring species provides insights into processes that allow community co-existence. In aquatic ecosystems, segregation of food resources is often viewed as the principal mechanism of resource partitioning (Ross, 1986). However, in ectotherms such as fish, interactions between a species' physiology and the environment can also influence resource partitioning (Huey, 1991; Stevenson, 1985). Temperate freshwater fishes are classified into three thermal guilds, eurytherms (warm water), mesotherms (cool water), and stenotherms (cold water), which correspond to physiological optimal temperatures for growth (Magnuson et al., 1979). As a result, the distributions of fishes within aquatic ecosystems are often directed by thermal conditions of the water body they occupy (Magnuson et al., 1979). Habitat segregation of fishes differing in thermal niche is often observed in lakes that undergo thermal stratification. The existence of a metalimnion plays an important role as it forms a physical barrier to chemical exchange (e.g., renewal of hypolimnetic oxygen), as well as a biological barrier to fish species that cannot tolerate warm water temperatures (Wetzel, 2001). In sub-Arctic regions, thermal stratification occurs during summer months, when lake production and fish growth is greatest (Hurst and Conover, 2003; Wetzel, 2001). Although summer in sub-Arctic regions is short, it represents a critical period for fishes to obtain energy for the development of gonads, somatic growth, and lipid storage to endure long, unproductive winters (Shuter et al., 2012).

Sub-Arctic regions are expected to undergo major physical and biological changes resulting from climate change and a rapidly expanding natural resource sector (Cott et al., 2015a; IPCC, 2013; Lemly, 1994; Prowse et al., 2006). Climate change is predicted to result in warmer annual air temperatures and extend the period of thermal stratification, and thereby potentially reduce preferred habitat for native cold water fishes (Reist et al., 2006). Consequently, warmer air temperatures will also develop suitable thermal habitat in northern lakes to support warm water fishes, such as smallmouth bass (*Micropterus dolomieu*), which can alter the habitat use and prey community of native fish populations (Sharma et al., 2007; Vander Zanden et al., 1999). Additionally, habitat alteration from natural resource extraction may lower the quality of nearshore habitat, and indirectly increase exploitation by providing access to pristine lakes (Cott et al., 2015a; Lemly, 1994; Schindler and Lee, 2010). Consequently, these potential changes to sub-Arctic

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lakes could alter interspecific interactions and lead to shifts in community dynamics.

Top-level piscivores are often highly mobile, allowing them to feed on a wide range of prey in disparate habitat types (e.g., nearshore–offshore regions; McCann et al., 2005; Schindler and Scheuerell, 2002). As such, piscivores have the potential for substantial habitat and dietary overlap with co-occurring species, including other piscivores. Quantifying the degree of resource partitioning among piscivores in sub-Arctic lakes can identify key bioenergetic pathways that enable the co-occurrence of otherwise trophically similar species (Cooke and Suski, 2008). Lake trout (*Salvelinus namaycush*), northern pike (*Esox lucius*), and burbot (*Lota lota*) are three piscivores that commonly co-occur in freshwater lakes of the Canadian sub-Arctic (Cott et al., 2011). Lake trout is stenothermic, but typically lives in pelagic habitats and is described as an opportunistic generalist predator, which as adults preferentially feed on pelagic forage fish (Martin and Olver, 1980; VanderZanden and Rasmussen, 1996). Northern pike is a mesotherm, and can be generally described as an opportunistic visual ambush predator associated with littoral habitat structure such as vegetation (Casselman and Lewis, 1996; Scott and Crossman, 1973). Burbot is also a stenotherm that is almost exclusively piscivorous and is associated with benthic habitats (Amundsen et al., 2003). Building on results of a previous study that found burbot, lake trout, and northern pike differ in mean food web position during the open-water season in sub-Arctic lakes (Cott et al., 2011), we sought to determine whether this dietary niche partitioning was a function of differences in habitat use, or differences in prey selection within common habitats. We predicted that habitat and dietary niches would follow a similar pattern, whereby each species would utilize spatially distinct food sources.

To address our research questions, we combined two commonly used methods to study resource partitioning in aquatic ecosystems: 1) high-resolution passive acoustic telemetry, used to quantify the horizontal (spatial) and vertical (depth) distributions of each piscivorous fish species and, 2) stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), used to quantify dietary niche partitioning. This research will add to the limited studies (see Cunjak et al., 2005; Matich and Heithaus, 2014; Speed et al., 2011) that have corroborated multi-species results of telemetry and stable isotope analysis (SIA) in a similar framework to examine how habitat and dietary partitioning relate in aquatic ecosystems.

## Methods

### *Study site*

The study took place at Alexie Lake (62°40′36.59″ N, 114° 4′22.76″ W), a scientific research lake closed to the public, located approximately 30 km north east of Yellowknife, Northwest Territories (NT), Canada (Fig. 1). Alexie Lake is a medium-sized (402 ha, maximum depth 32 m), oligotrophic lake that undergoes thermal stratification during summer months (Healey and Woodall, 1973). In addition to the three top-level piscivores — burbot, lake trout, and northern pike — the fish community is composed of lake whitefish (*Coregonus clupeaformis*), cisco (*Coregonus artedi*), lake chub (*Couesius plumbeus*), ninespine stickleback (*Pungitius pungitius*), trout-perch (*Percopsis omiscomaycus*), slimy sculpin (*Cottus cognatus*), spoonhead sculpin (*Cottus ricie*), and deepwater sculpin (*Myoxocephalus thompsoni*) (Cott et al., 2011). The lake also contains the opossum shrimp, *Mysis diluvania*.

### *Lake water temperature and dissolved oxygen*

Lake water temperatures were recorded 5 July–12 September, 2012 using a string of data loggers (HOBO Pendant Temp/Light, 64 k model UA-002-64, Onset Computer Co., Cape Cod, MA) installed over the

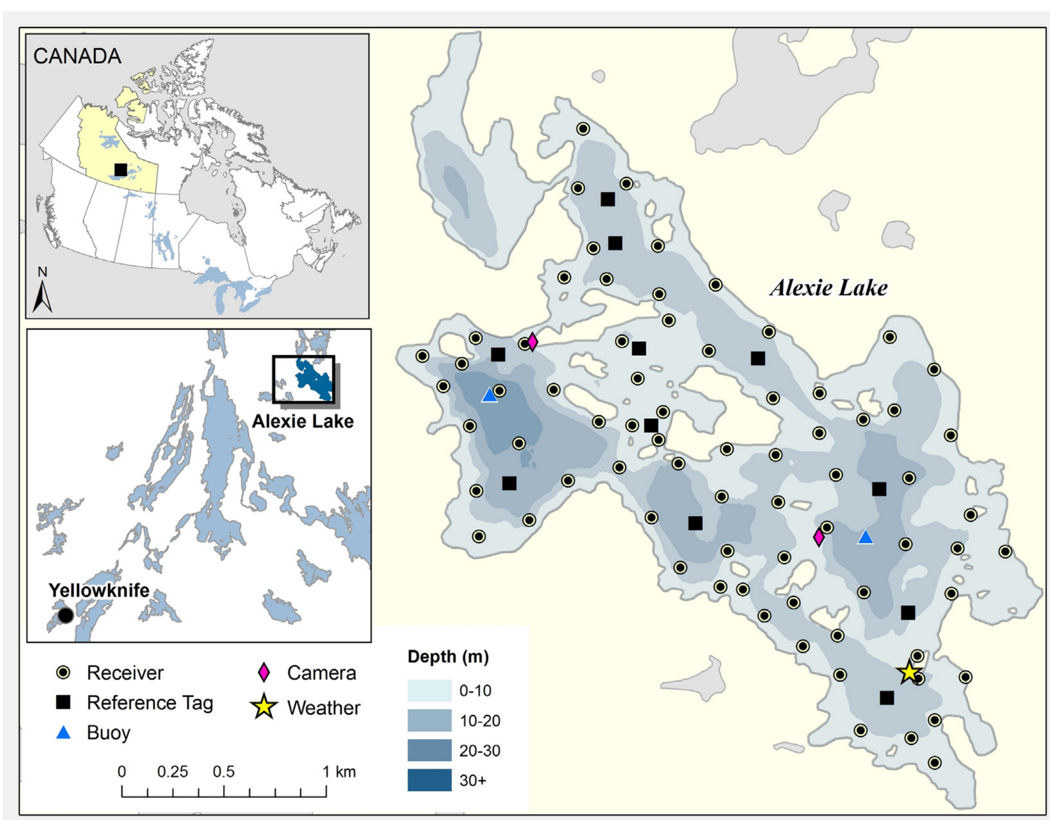


**Fig. 1.** Location of Alexie Lake, NWT, Canada (inset). The map of Alexie Lake, includes the locations of 72 telemetry receivers and corresponding co-located sync tags (circles), acoustic reference tags (squares), center buoys to which temperature and light loggers were attached (triangles), ice-monitoring cameras (diamonds), and the weather station used to monitor air temperature and wind direction and speed (star). Depth contours are every 10 m.

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