Ghoti papers

Ghoti aims to serve as a forum for stimulating and pertinent ideas. Ghoti publishes succinct commentary and opinion that addresses important areas in fish and fisheries science. Ghoti contributions will be innovative and have a perspective that may lead to fresh and productive insight of concepts, issues and research agendas. All Ghoti contributions will be selected by the editors and peer reviewed.

Etymology of Ghoti

George Bernard Shaw (1856–1950), polymath, playwright, Nobel prize winner, and the most prolific letter writer in history, was an advocate of English spelling reform. He was reportedly fond of pointing out its absurdities by proving that ‘fish’ could be spelt ‘ghoti’. That is ‘gh’ as in ‘rough’, ‘o’ as in ‘women’ and ‘ti’ as in palatial.

If Arctic charr *Salvelinus alpinus* is ‘the most diverse vertebrate’, what is the lake charr *Salvelinus namaycush*?

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Abstract

Teleost fishes are prominent vertebrate models of evolution, illustrated among old-world radiations by the Cichlidae of East African Great Lakes and new-world radiations by the circumpolar Arctic charr *Salvelinus alpinus*. Herein, we describe variation in lake charr *S. namaycush* morphology, life history, physiology and ecology, as another example of radiation. The lake charr is restricted to northern North America, where it originated from glacial refugia and diversified in large lakes. Shallow and deepwater morphs arose in multiple lakes, with a large-bodied shallow-water ‘lean’ morph in shallow inshore depths, a small-bodied mid-water ‘humper’ morph on offshore shoals or banks, a robust, large-bodied moderate to deep-water ‘redfin’ morph and a large-bodied deep-water ‘siscowet’ morph at depths > 100 m. Eye position, gape size, and gillraker length and spacing adapted for feeding on different-sized prey, with piscivorous morphs (leans, siscowets and presumably redfins) reaching larger asymptotic size than invertivorous morphs (humpers). Lean morphs are light in colour, whereas deepwater morphs are drab.

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Lake charr: a diverse evolutionary model  A M Muir et al.

and dark, although the pattern is reversed in dark tannic lakes. Morphs shift from benthic to pelagic feeding at a length of 400–490 mm. Phenotypic differences in locomotion, buoyancy and lipid metabolism evolved into different mechanisms for buoyancy regulation, with lean morphs relying on hydrodynamic lift and siscowet morphs relying on hydrostatic lift. We suggest that the Salvelinus genus, rather than the species S. alpinus, is a diverse genus that should be the subject of comparative studies of processes causing divergence and adaptation among member species that may lead to a more complete evolutionary conceptual model.

**Keywords**  Adaptive radiation, evolution, lake trout, phenotypic diversity, resource polymorphism, speciation

**Introduction**

Teleost fishes are prominent among vertebrates as models of evolution (Skulason and Smith 1995; Schluter 1996). Old- and new-world teleosts have repeatedly, and in parallel, undergone adaptive radiations, defined by Simpson (1953) as ‘more or less simultaneous divergence of numerous lines from much the same adaptive type into different, also diverging adaptive zones’. A recent conceptualization of adaptive radiations theorizes that ecological opportunity caused by key innovations, colonization of novel habitats or extinction of an antagonist leads to release from natural selection and subsequent ecological release. This process results in morphological and ecological diversification that includes, among other things, increased trait variation, increased population size and broadened niche use, yielding subsequent local adaptations (Yoder et al. 2010). The theory of resource polymorphism explains how habitat and trophic partitioning, and divergence of sympatric phenotypes best adapted to use those resources generates conditions for adaptive radiation (Skulason and Smith 1995). Adapted phenotypes confer reproductive fitness. Frequency-dependent and disruptive selection for adapted phenotypes, in concert with reduced gene flow among locally adapted populations, permits the accumulation of genetic differences to maintain radiations through time (Harmon et al. 2010). Reduced intraspecific competition and availability of novel resources are therefore primary forces generating variation for speciation (hereafter referred to as diversity: Skulason and Smith 1995; Schluter 1996; Harmon et al. 2010).

Genetic differences accumulate at geological time scales; therefore, many old-world radiations have progressed further towards stable endpoints (i.e. speciation) compared to new-world radiations. Among fishes, one of the most prominent old-world radiations is the Cichlidae of the East African Great Lakes (Clubaut et al. 2007). These fishes have undergone tremendous diversification in food and habitat use to establish ‘species flocks’ with more than 300 endemic species in some lakes (Meyer 1987). By contrast, geologically young lakes (i.e. ~10 000 years BP) in recently glaciated regions have had less time for selection to act upon colonists. Geologically, young systems are therefore species depauperate, often having fewer than 20 species. Glacial activity, isostatic rebound and volcanism have created complex deep- and shallow-water habitats for fishes colonizing on receding glacial fronts. In these systems, novel, unoccupied habitats provide ecological opportunity for colonizers. Distance among habitats in large lakes (i.e. >2000 km²) and habitat complexity in both large and small lakes in association with divergent reproductive behaviours can function as sympatric isolating barriers to gene flow (Muir et al. 2012). Within post-glacial lake ecosystems, freshwater fishes, including the Salvelinus charrs (family Salmonidae), have commonly diverged to occupy profundal, littoral and pelagic habitats, while partitioning invertebrate and fish prey resources within those habitats (Berg 1948; Hubbs and Lagler 1949; Snorrason et al. 1994; Zimmermann et al. 2006; Klemetsen 2010; Chavarie et al. 2013; Muir et al. 2014).

The Arctic charr Salvelinus alpinus (Linnaeus, 1758) has shown prominent adaptive radiations across its circumpolar range (reviewed by Jonsson and Jonsson 2001; Klemetsen 2010). For example, Thingvallavatn, Iceland contains four morphs – large and small benthic morphs and planktivorous and piscivorous pelagic morphs – that differ in morphology, food habits and spawning time
(Snorrason et al. 1994; Skúlason et al. 1999; Kappalova et al. 2011). The lake charr Salvelinus namaycush (Walbaum, 1792; called lake trout in North America) of North America shows phenotypic, life history, physiological and ecological diversity comparable to its sister taxa the Arctic charr, but this diversity is less well studied and existing knowledge has not been systematically reviewed and synthesized. Diversity within the lake charr is therefore under-appreciated. Herein, we challenge the notion that S. alpinus could be the most diverse vertebrate (sensu Klemetsen 2010, 2013) and offer that Salvelinus is a diverse genus, whose member species have undergone rapid evolution via adaptive radiations to occupy deep- and shallow-water niches in recently glaciated regions. Our objectives are to survey morphological, life history, physiological and ecological variation within S. namaycush across its range and to place that diversity within the global context of biodiversity. We intend to stimulate new multidisciplinary international research to further understanding of evolutionary processes. In addition, showing that variation in S. namaycush is comparable to S. alpinus may facilitate comparative and integrative studies. Focusing such research on regions of distributional overlap could be particularly informative.

**Distribution of variation**

The lake charr is restricted in distribution to northern North America (Fig. 1). The current distribution is thought to originate from four main southern and one northern Wisconsinan glacial refugia (Bailey and Smith 1981; Crossman and McAllister 1986; Wilson and Hebert 1998; Wilson and Mandrak 2004). Most documented examples of lake charr diversity are restricted to within the maximum margin of the Laurentide ice sheet extending south of the Laurentian Great Lakes in the southeast to the Arctic islands in the northwest, west to the continental divide and east to the continental margin (Fig. 1). In contrast to S. alpinus, which has readily radiated in many small post-glacial lakes (i.e. <100 km²) throughout the holarctic (Snorrason et al. 1994; Klemetsen 2010), with one exception discussed below, all documented examples of lake charr diversity occur within the largest lakes of North America (i.e. >2000 km²; Table 1; Lawrie and Rahrer 1973; Goodier 1981; Blackie et al. 2003; Zimmerman et al. 2006, 2007; Chavarie et al. 2013; Muir et al. 2014).

**Phenotype**

**Morphology**

In general, shallow and deepwater lake charr morph pairs have arisen multiple times across the range (Fig. 2). In all lakes, a single shallow-water ‘lean’ morph occurs, with the exception of Great Bear Lake, and historically Lake Superior, where multiple shallow-water morphs occur (occurred). Lean refers to the slender, streamlined body shape and low body lipid content of this morph. The number of deepwater morphs ranges from one (e.g. Lake Mistassini) to three or more (e.g. Lake

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**Figure 1** (a) Lake charr distribution, and (b) maximum extent of the Laurentide ice sheet (10 000 years BP), and locations of refugia along the Wisconsinan glacial margin (adapted from Wilson and Mandrak 2004; Dyke 2004).
In addition, two common deep-water morphs occur across the range. The first common deepwater morph is a 'humper', which in Lake Superior, occupies offshore, mid-water shoals or banks and is small in body size (typically <500 mm) with a small head, narrow peduncle, moderately large eye situated dorsally on the head and short paired fins. The second common deep-water morph is a 'siscowet', which in Lake Superior occupy waters >100 m and has a moderate-sized head with a characteristic sloping snout in front of the moderately large eye (Peck 1975; Burnham-Curtis and Bronte 1993; Moore and Bronte 2001; Bronte et al. 2003; Muir et al. 2014). The name siscowet is aboriginal Ojibwe and refers to the high body fat content of this morph. A 'redfin' morph also occurs in Lake Superior (Muir et al. 2014) and possibly Great Bear Lake (Chavarie et al. 2013). The redfin is robust in body size, has a relatively large head, long deep peduncle and especially large fins (Muir et al. 2014). Common-garden experiments demonstrated that variation in body condition, morphology and body lipid concentration between Lake Superior lean and siscowet lake charr persists under identical laboratory environmental conditions, thereby demonstrating a genetic, rather than an environmentally driven plastic, mechanism for generating phenotypic variation (Goetz et al. 2010).

Great Bear Lake are particularly interesting because the pattern of diversity differs from that currently observed in other lakes. Great Bear Lake contains as many as four shallow-water lake charr morphs (Blackie et al. 2003; Alfonso 2004; Chavarie et al. 2013) and appears to be the only lake experiencing a radiation that does not involve a deepwater morph. Lack of a deepwater morph could be explained by the lake's cold isothermal conditions, low productivity and hyperoligotrophy, especially in offshore waters (Miller 1947). The Great Bear Lake ecosystem appears compressed into the more productive nearshore areas within bays due to its limnology, whereas offshore waters are relatively devoid of energy and nutrients (see references in Muir et al. 2013a,b). Great Bear Lake is considered a model for understanding the historical shallow-water lake charr community of Lake Superior, where up to 10 lake charr morphs, several that lived in shallow water, occurred (Goodier 1981).

Diverse lake charr populations in large lakes contrast with the apparent lack of differentiation among lake charr populations in thousands of small Precambrian Shield Lakes (Wilson and Mandrak 2004). The major difference between large and small lakes is a lack of deep (i.e. >100 m) water in most small lakes (Table 1). Great Slave Lake contains lean- and siscowet-like

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**Table 1** Physical attributes of lakes containing multiple lake charr morphs.

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Great Bear</th>
<th>Great Slave</th>
<th>Mistassini</th>
<th>Superior</th>
<th>Rush</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latitude (°N)</td>
<td>65° 55'</td>
<td>61° 40'</td>
<td>50° 58'</td>
<td>47° 43'</td>
<td>46° 53'</td>
</tr>
<tr>
<td>Longitude (°W)</td>
<td>120° 49'</td>
<td>113° 16'</td>
<td>73° 37'</td>
<td>86° 36'</td>
<td>87° 55'</td>
</tr>
<tr>
<td>Surface area (km²)</td>
<td>31 153</td>
<td>27 200</td>
<td>2335</td>
<td>82 100</td>
<td>1.3²</td>
</tr>
<tr>
<td>Mean depth (m)</td>
<td>71.7</td>
<td>41</td>
<td>64</td>
<td>147</td>
<td>25²</td>
</tr>
<tr>
<td>Maximum depth (m)</td>
<td>446</td>
<td>614</td>
<td>183</td>
<td>406</td>
<td>83²</td>
</tr>
<tr>
<td>Volume (km³)</td>
<td>2236</td>
<td>1580</td>
<td>150</td>
<td>12 000</td>
<td>0.03²</td>
</tr>
<tr>
<td>Shoreline length (km)</td>
<td>2719</td>
<td>3057</td>
<td>461¹</td>
<td>2783</td>
<td>8.8²</td>
</tr>
<tr>
<td>Surface elevation (m)</td>
<td>186</td>
<td>156</td>
<td>372</td>
<td>183.5</td>
<td>195</td>
</tr>
<tr>
<td>Trophic state</td>
<td>Oligotrophic</td>
<td>Oligotrophic</td>
<td>Oligotrophic</td>
<td>Oligotrophic</td>
<td>Mesotrophic</td>
</tr>
<tr>
<td>Number of fish species</td>
<td>15</td>
<td>21</td>
<td>12</td>
<td>87</td>
<td>17</td>
</tr>
</tbody>
</table>

Unless otherwise indicated, data from Kalff (2002).
¹Johnson (1975).
²Hebert (2007).
⁵United States Environmental Protection Agency and Government of Canada (2002).
⁶Christy (1929).
⁷ESRI 'dtt_wat' series, Redlands, CA, USA.
⁸A. M. Muir and C. C. Krueger, unpublished data.
⁹Estimate (excluding islands) generated by AMM using measurement tool in Google Earth 03 Dec 2014.
Lake charr morphs (Zimmerman et al. 2006; Zimmerman and Krueger 2009); Lake Mistassini, Quebec contains lean and humper morphs (Zimmerman et al. 2007); and Atlin Lake, Yukon, Canada contains two phenotypes that differed primarily in head shape, body depth and fin position (Northrup et al. 2010). Rush Lake, Michigan, is a sole documented exception to the observation that lake charr diversity occurs only in large lakes. Rush Lake is a 1.3 km² post-glacial lake on the southern shore of Lake Superior (Hubbs 1929), which has one small, 80-m pocket of deep water. A shallow-water lean lake charr was described by Hubbs (1929) as similar to those inhabiting the nearshore waters of Lake Superior. A deepwater morph was also described Salvelinus namaycush huronicus [genus formerly Cristivomer; Holotype: UMMZ 81618; Paratypes: UMMZ 80510-80514 (5), 80518 (1); hereafter huronicus]. This fish was dark black and bronze in colour, had a broadly U-shaped snout observed from the dorsal aspect, a small mouth, reached a small maximum adult size (<1 kg), matured at a small size (i.e. ~300 mm; young age inferred) and spawned during August as opposed to October–November when the lean morph spawns (Hubbs 1929, 1930).

Adaptive traits
Lake Superior humper and siscowet morphs have large eyes that are positioned high on the head, an arrangement that provides improved binocular and low-light vision (van der Meer and Anker 1984; Bond 1996). Siscowet live in deep water (>100 m) and move off the bottom at night to prey on vertically migrating ciscoes (Salmoniformes: Coregonidae; Hrabik et al. 2006). Humper also live in deep water and are thought to feed on small food items, such as Mysis diluviana, deepwater sculpin Myxocephalus thompsoni, zooplankton and insect larvae, such as Chironomidae spp., but diet data for this morph are limited (Peck 1975). Large eyes positioned high on the head could be adaptive for feeding from below on Mysis (humper) and ciscoes (siscowet) either at night or on...
bottom in deep habitats with little light penetration. By contrast, leans have relatively small eyes that are positioned low on the side of head providing a wide lateral field of view, which is adaptive for daytime predation on pelagic fishes (Bond 1996).

Head and thereby gape size, as well as gillraker length and spacing, limit the type and size of prey that can be consumed and retained (Keast and Webb 1966). Piscivores, such as lean and siscowet lake charr, have large heads and mouths (i.e. absolute size rather than relative to body size), whereas humper lake charr, which are thought to feed on smaller prey, have smaller heads and gapes. Gillrakers form the branchial sieve, which filters and retains food particles in the buccal cavity. Large piscivorous lake charr in Great Bear Lake (i.e. lean morph) have much reduced, almost non-functional gillrakers compared to the small insectivore morph, which has numerous long gillrakers (A. M. Muir, unpublished data).

Body coloration
Lean lake charr morphs tend to be silvery and light overall with a white ventral aspect, which has no vermiculation; a pattern cryptic under variable light conditions for pelagic predators (Endler 1978; see Fig. 2). By contrast, deepwater morphs tend to vary; they can be drab, dark, or alternatively, bright red, orange and yellow (n.b., these colour wavelengths are absorbed from water by 10 m depth). The typical coloration pattern is reversed in Lake Mistassini, where the deep-water (>50-m depth) humper-like morph is light and silvery, compared to the shallow-water form, which is nearly black (Fig 2; Zimmerman et al. 2007). This reversal could be because the water of Lake Mistissini is dark, almost black, due to high tannin content. By contrast, lake charr in the south arm of Atlin Lake, BC are locally known as the ‘glacial’ variety (Northrup et al. 2010). These fish are bright silver in colour likely due to high glacial meltwater turbidity influx in the south arm of the lake, whereas, lake charr in other portions of the lake not influenced by glacial silts are strikingly darker in appearance (Northrup et al. 2010). Sexual differences in body coloration associated with spawning occur in Great Bear Lake insectivorous char where males develop distinct nuptial coloration and tubercles in some populations (Muir et al. 2012).

Life history
Growth
Lake charr morphs grow to different asymptotic lengths (L_{inf}) within lakes. Piscivorous morphs (leans and siscowets) generally reach larger asymptotic size than invertivorous morphs (humpers). For example, lean morphs grew to longer asymptotic length than humper morphs in both Lake Mistassini (Hansen et al. 2012) and Rush Lake (M. J. Hansen, unpublished data; Fig. 3). Further, humper and lean morphs grew to nearly identical asymptotic lengths in these two lakes, and humper morphs in these two lakes grew to a similar asymptotic length as the humper morph at Isle Royale, Lake Superior (Burnham-Curtis and Bronte 1996; Fig. 3). In contrast, the rate at which humper morphs grew to their asymptotic length (K) was much faster at Isle Royale, Lake Superior than in either Lake Mistassini or Rush Lake (Fig. 3). Siscowet morphs grew similarly at Big Reef, Lake Superior and in Great Slave Lake.
The siscowet of Lake Superior were known to lake charr from the Laurentian Great Lakes that around 430 mm length (Van Oosten and Deason 1938; Dryer et al. 1965; Fisher and Swanson 1996). Consistent with these observations, stable carbon and nitrogen isotopes suggested that lean and siscowet-like lake charr morphs from Great Slave Lake also shifted from benthic to pelagic feeding as body size increased (i.e. ~430 mm standard length \( L_s \); Zimmerman et al. 2009). On the basis of these data, Zimmerman et al. (2009) suggested that small (i.e. juvenile) lean and siscowet lake charr partition benthic resources within deepwater habitats, and that around 430 mm \( L_s \) rapid morphological and buoyancy diversification accompanies a shift from benthic to pelagic feeding. Lean lake charr transition to pelagic feeding by moving to shallow depths (i.e. <100 m), whereas siscowet transition to primarily pelagic feeding over the same deepwater (although horizontal movements for shallow-water foraging also likely occur), while undergoing pronounced changes in lipid metabolism and mid-body profile (Zimmerman et al. 2009) to facilitate vertical migration (Hrabik et al. 2006).

Buoyancy
Phenotypic differences associated with locomotion and buoyancy control in concert with differences in lipid metabolism among lake charr morphs support the hypothesis that lake charr have evolved two different mechanisms for buoyancy regulation – hydrodynamic and hydrostatic lift (sensu Eshenroder et al. 1999). Lean lake charr likely rely more on hydrodynamic lift via sustained swimming and a greater reliance on the swim bladder to maintain neutral buoyancy. Relative to other Lake Superior morphs, lean lake charr were more adapted to pelagic swimming by having low buoyancy (i.e. low body lipid content), shorter paired fins, a more streamlined body shape and a long, narrow caudal peduncle (Webb 1984; Bond 1996; Muir et al. 2014). By contrast, Lake Superior siscowet are highly buoyant (i.e. high body lipid content), have long paired fins, and thick and short caudal peduncles, which suggests that they rely more on hydrostatic lift to maintain buoyancy and move vertically in the water column than lean lake charr (Muir et al. 2014). The siscowets’ thick caudal peduncle and relatively large paired fins are adaptive for beat-and-glide locomotion, for slowing descent due to hydrostatic pressure when foraging in pelagia, and for manoeuvring over rocky substrate when foraging near bottom (Webb 1984).

Ontogeny
Lake charr from the Laurentian Great Lakes undergo an ontogenetic shift from benthic to pelagic feeding at a length of 400–490 mm (Van Oosten and Deason 1938; Dryer et al. 1965; Fisher and Swanson 1996). Recent transcriptomic analysis of hepatic gene frequencies and expression (qPCR) between Lake Superior siscowet and lean morphs indicated differential expression of gene groups involved in lipid synthesis, metabolism and transport (i.e. acyl-CoA desaturase, acyl-CoA binding protein, peroxisome proliferator-activated receptor gamma and apolipoproteins; Goetz et al. 2010). Genetic differences in lipid metabolism between lean and siscowet morphs support the hypothesis that selection for deep-water adaptations has been strong and provides the first empirical evidence of reproductive isolation among lake charr morphs.

Physiology
Lipid metabolism
The siscowet of Lake Superior were known to native peoples and early voyageurs as morphologically distinct and highly lipid rich in comparison with the lean morph (Agassiz 1850; Roosevelt 1865; Thurston 1962). Recent transcriptomic analysis of hepatic gene frequencies and expression (qPCR) between Lake Superior siscowet and lean morphs indicated differential expression of gene groups involved in lipid synthesis, metabolism and transport (i.e. acyl-CoA desaturase, acyl-CoA binding protein, peroxisome proliferator-activated receptor gamma and apolipoproteins; Goetz et al. 2010). Genetic differences in lipid metabolism between lean and siscowet morphs support the hypothesis that selection for deep-water adaptations has been strong and provides the first empirical evidence of reproductive isolation among lake charr morphs.

Anadromy
Lake charr have retained some osmoregulatory capacity common to the anadromous or semi-anadromous charrs S. alpinus and S. fontinalis. Freshwater resident and marine migrant lake charr life history types occur in the Canadian Arctic (Lindsey 1964). Otolith microchemistry revealed that 27% of lake charr >13 years age from four Arctic lakes made annual marine feeding migrations (Swanson et al. 2010, 2011). Marine-derived carbon represented 60–66% of migrants diet, and they had significantly higher C/N, fed at a higher trophic level and were in better physiological condition than freshwater residents (Swanson et al. 2010). An ability to tolerate low salinity (6–9‰), common in the Arctic Ocean, raises several questions about zoogeography of the species with respect to other charrs and provides some understanding of potential colonization pathways (Lindsey 1964). For example, why are lake charr restricted in distribution to North America
and what mechanisms minimize the zone of distributional overlap between *S. alpinus* and *S. namaycush*?

**Ecology**

**Trophic niche**

Prey is the primary niche axis thought to generate and maintain lake charr diversity. Understanding trophic niche partitioning among lake charr morphs is challenging because lakes at the southern extent of the distribution have been considerably altered by non-native prey introductions and losses of lake charr diversity (Goodier 1981; Mills et al. 1993; Ricciardi 2001; Guinand et al. 2003, 2012). Historical trophic data are from gut contents, which limit spatio-temporal resolution of food habits. For example, comparisons of Lake Superior lean and siscowet diets revealed only minor differences (Dryer et al. 1965; Fisher and Swanson 1996). However, other studies with large sample sizes (~7000 individuals) found seasonal differences in diet among morphs and also that inshore leans primarily ate non-native rainbow smelt *Osmorus mordax* (71% by weight), while their offshore conspecifics ate primarily coregonines (75% by weight; Conner et al. 1993). Offshore lake charr also ate more *Mysis* and sculpins (*Cottidae* spp. and *Myoxocephalus thompsonii*) than inshore lake charr. Similarly, on the basis of 16 073 lean and 1334 siscowet stomachs collected from Lake Superior during 1986–2001, siscowet diets averaged by number 29% rainbow smelt, 27% coregonines, 22% sculpin (*Myoxocephalus thompsonii, Cottus cognatus* and *C. ricei*) and 11% stickleback (*Pungitius pungitius* and *Gasterosteus aculeatus*), whereas lean lake charr diets were dominated by rainbow smelt (80%), with fewer coregonines (9%), sculpin (4%) and stickleback (3%; Ray et al. 2007; N.B., that this study only examined prey fishes consumed by lake charr and omitted other prey items).

Lean and siscowet-like lake charr in Great Slave Lake partitioned trophic resources within benthic (small charr) and pelagic (large charr) habitats, consistent with ontogenetic diet shifts (Zimmerman et al. 2009). All Great Slave Lake morphs were piscivores, but sculpin (*Myoxocephalus thompsonii, Cottus cognatus*) were the predominant summer prey for a group of putative humpers (Zimmerman et al. 2009). Piscivorous lake charr in Great Bear Lake fed almost exclusively on fishes, including *Coregonus artedi, Pungitius pungitius, S. namaycush* and *Myoxocephalus quadricornis*, while invertivores primarily fed on Trichoptera and Diptera (primarily Chironomidae larvae; Blackie et al. 2003). The invertivorous morph identified by Blackie et al. (2003) was also observed eating lake charr eggs and a vole (*Microtus sp.*) during a time when the piscivorous morph was spawning (A. M. Muir and C. C. Krueger, personal observation).

In contrast to gut contents, which provide a point estimate, stable carbon and nitrogen isotopes provide an integrated signature of trophic resource use over longer time periods in the life history of the animal. Isotopes revealed greater trophic separation among morphs than diet analyses. For example, western Lake Superior siscowet were the top predator in the food web (\(\delta^{14}N = 11.69 \pm 0.18\)) and had a more diverse diet than lean lake charr (\(\delta^{12}C = 9.59 \pm 0.17\); Harvey and Kitchell 2000). Siscowet also derived a greater proportion of their nutrition from offshore pelagic prey (\(\delta^{13}C = -27.40 \pm 0.21\)), such as blounder *Coregonus hoyi* and kiyi *Coregonus kiyi*, than lean lake charr, which relied more on nearshore resources (\(\delta^{13}C = -25.08 \pm 0.21\)), such as cisco *Coregonus artedi* and slimy sculpin (Harvey and Kitchell 2000). Siscowet diet was more diverse than lean lake charr diet, and diet overlap was low (data summarized by Kitchell et al. 2000), to provide further evidence of niche partitioning between these two morphs (Bronte et al. 2003).

**Physical habitat**

Water depth is the second primary niche axis thought to generate and maintain lake charr diversity. In contrast to the Arctic charr, which has readily radiated into benthic and pelagic morphs in many small post-glacial lakes throughout the holarctic (Snorrason et al. 1994; Klemetsen et al. 2010), with one exception described herein, all documented examples of lake charr diversity occur within the largest lakes of North American (i.e. >300 km²; Goodier 1981; Blackie et al. 2003; Zimmerman et al. 2006, 2007; Northrup et al. 2010; Chavarie et al. 2013; Muir et al. 2014). Of 1781 boreal shield lake charr lakes surveyed in the Province of Ontario, Canada, only 25 have a maximum depth greater than 83 m and no lakes apparently contain multiple lake charr morphs (Carl et al. 1990). Ample deepwater (i.e. >100 m)
habitats provide ecological opportunity in large lakes. For example, Lake Superior has a maximum depth of 407 m, and approximately 80% of its waters are greater than 50 m deep (Eshenroder and Lantry 2012). The deepwater pelagic zone extends from approximately the 80 m water depth (Horns et al. 2003) up to the thermocline, excluding the hypolimnetic epibenthic and warmer epilimnetic waters above the thermocline (Eshenroder and Lantry 2012). The physical characteristics of these water masses provide contrasting shallow- and deepwater epilimnetic, deepwater hypolimnetic and deepwater pelagic habitats, each with divergent selection pressures (Muir et al. 2014).

Unlike other salmonines, lake charr typically spawn in lakes (reviewed by Muir et al. 2012), although an adfluvial life history type occurs in a few Lake Superior tributaries (Loftus 1958) and likely elsewhere in the northern part of the distribution. Spawning habitat has been generally described, but only for the lean morph (Martin 1957; Martin and Olver 1980; Wagner 1982; Gunn and Keller 1984; Edsall et al. 1989, 1992; Marsden et al. 1995). Lake charr may spawn primarily on glacially derived bedforms in the Laurentian Great Lakes (Riley et al. 2014) and in both deep and shallow water (Janssen et al. 2007), but how morphs partition this spawning habitat and how it provides an isolating mechanism to gene flow is unknown.

Reproduction

Although phenotypic, ecological and genetic differences suggest lake charr diversity is not merely an expression of plasticity, evidence of reproductive isolation among morphs is sparse. Triggers to spawning, mate selection and spawning habitat selection are largely unknown (reviewed by Muir et al. 2012). A single study of seasonal changes in gonadosomatic index and hormone levels showed that lean and siscowet morphs from two areas of southern Lake Superior underwent concurrent gonadal maturation during October, thereby suggesting that timing of gonad maturation may not be a mechanism for reproductive isolation (Goetz et al. 2011). In general, lake charr are thought to spawn between September and November (Scott and Crossman 1973). However, Eschmeyer (1955) and Bronte (1993) reported mature, ripe female siscowets during spring (July and April, respectively) in Lake Superior. Humper lake charr around Isle Royale, Lake Superior have also been observed in spawning condition during June (Eschmeyer 1955), August (Burnham-Curtis and Bronte 1996) and mid-September (Rahrer 1965). Mature, ripe and spent redfin lake charr were caught during August 2013 on Superior Shoal, Lake Superior (Co-authors, unpublished data; this same population was referred to by Rahrer 1965 as humper-like). Similarly, a siscowet-like morph in Great Slave Lake appears to spawn at least 2 weeks earlier than the lean morph (C. C. Krueger, unpublished data). In Great Bear Lake, the invertivores described by Blackie et al. (2003) tend to spawn as much as three weeks prior to the piscivorous morph (A. M. Muir and C. C. Krueger, unpublished data).

Discussion

On the basis of data reviewed herein, we suggest that S. namaycush is as diverse as S. alpinus. We also know that brook charr S. fontinalis show divergent adfluvial and riverine life histories in the Laurentian Great Lakes (Robillard et al. 2011), and anadromy along the east coast of North America (Curry et al. 2010). On the basis of our synthesis, we offer a modification to Klemetsen’s (2013) finding that Arctic charr could be the most variable vertebrate – that is – Salvelinus is a diverse genus, whose member species commonly and repeatedly undergo parallel rapid evolution via adaptive radiations. Both S. namaycush and alpinus show parallel pelagic and benthic adaptations (data summarized by Klemetsen 2010, 2013; and herein), genetically based differences in morphology (Skulason et al. 1996; Goetz et al. 2010), exceptional phenotypic variation (Sandlund et al. 1992), differential trophic resource use (Snorrason et al. 1994; Harvey and Kitchell 2000; Blackie et al. 2003), reproductive isolation via spatial and temporal differences in spawning time (Skulason et al. 1989; Bronte 1993) and alternative life histories (Skulason et al. 1996; Hansen et al. 2012).

Recognizing Salvelinus as a diverse genus will facilitate comparative studies of processes generating divergence and adaptation among member species that may lead to a more complete evolutionary conceptual model. Placing these patterns of diversity within the hierarchy observed in Teleostei and the chronology of divergence and adaptive events will further refine this model. Among new-world fishes, the threespine stickleback Gasterosteus aculeatus of British Columbia (Peichel et al.
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2001; Meyer 2002; Hohenlohe et al. 2010) has repeatedly and independently evolved distinct limnetic and benthic morphs from marine ancestors that colonized post-glacial coastal lakes. Similarly, European and North American coregonines – both the whitefishes Coregonus lavaretus and clupeaformis and ciscos – have evolved into species flocks containing pelagic, limnetic and dwarf forms throughout the holarctic (Koelz 1929; Berg 1948; Svardson 1979; Bernatchez and Dodson 1990; Bernatchez et al. 1996; Muir et al. 2013b). How do patterns of diversity and processes generating and maintaining that diversity compare among Teleostei and how do they relate to the remarkable explosion of diversity seen within the old-world Cichlidae?

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