The Arctic char (Salvelinus alpinus) "complex" in North America revisited

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CHARR II

Review Paper

The Arctic char (*Salvelinus alpinus*) "complex" in North America revisited

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Abstract The Arctic char (*Salvelinus alpinus*) species "complex" has fascinated biologists for decades particularly with respect to how many species there are and their geographic distributions. I review recent research on the species complex, focussing on biodiversity within northwestern North America, which indicates (i) what was once considered a single taxon consists of three taxa: *S. alpinus* (Arctic char), *S. malma* (Dolly Varden), and *S. confluentus* (bull trout), (ii) morphological and genetic data indicate that *S. alpinus* and *S. malma*, and *S. malma* and *S. confluentus* exist as distinct biological species in sympatry, (iii) sympatric forms of *S. alpinus* exist in Alaska as in other areas of the Holarctic, (iv) Dolly Varden comprises two well-differentiated subspecies, *S. m. malma* and *S. m. lordi*, in the eastern Pacific and the northwestern Canadian Arctic that meet at a contact zone on the southern edge of the Alaska Peninsula, and (v) Dolly Varden and bull trout consist of several population assemblages that have legal status as distinct conservation units under US and Canadian law. This research has significantly revised what constitutes the *S. alpinus* species "complex", provided insights into the ecology and genetics of co-existence, and promoted conservation assessment that better represents biodiversity within *Salvelinus*. A geographically and genetically comprehensive analysis of relationships among putative taxa of Pan-Pacific *Salvelinus* is still required to better quantify the number of taxa and their origins.

Keywords Dolly Varden · Arctic char · Bull trout · Geographic distribution · Taxonomy · Conservation

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Introduction

In 1961, McPhail summarized the taxonomic complexity of northwestern North America chars (*Salvelinus*) which included an array of morphological types within the Arctic char (*Salvelinus alpinus*) "complex" and he stated that it consisted of an "undetermined number of species". In particular, McPhail's (1961) study strove to understand the systematic status of Dolly Varden char (*S. malma*) as it related to one or more other taxa within *S. alpinus*, yet it was even more complicated than he envisioned. The immense phenotypic complexity and its implications for systematics and taxonomy within the Arctic char group are intriguing (Klemetsen, 2013), but they are also part of a more general phenomenon of "species complexes"

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in several north temperate fishes (McPhail, 1966; Hagen & McPhail, 1970; Behnke, 1972; Taylor, 1999).

Since McPhail's (1961) study, considerable research has been conducted on the evolutionary relationships between and within *S. alpinus* and *S. malma* that have led to some clarification of the taxonomic status, composition, and relationships within the original *S. alpinus* complex, particularly on what forms are outside, but related to, the *S. alpinus* complex sensu stricto. Many of the studies, however, have also raised new questions. In this brief review, I summarize the major results and identify new questions. This review focusses on northwestern North America and principally on distinctions and relationships among named taxa and not a second aspect of complexity within the *S. alpinus* complex, i.e. that of myriad forms of sympatric populations some of which have been given taxonomic designations. An extensive literature already exists for char in eastern North America and Eurasia in terms of taxonomy, phylogeography, and sympatric populations within *S. alpinus* senu lato (e.g. Nordeng, 1983; Jonsson & Jonsson, 1991; Savvaitova, 1995; Kottelat & Freyhof, 2007; Klemetsen, 2013; Reist et al., 2013).

Species identity

In McPhail's (1961) study, the morphological data led him to conclude that there were at least two species of char within the Arctic char group (Dolly Varden and Arctic char), each with three morphological types that were strongly patterned geographically. Within *S. malma*, there was a form found south of the Alaska Peninsula ("southern Dolly Varden"), a form found north of the Alaska Peninsula and eastward to the Mackenzie River ("northern Dolly Varden"), and possibly an interior Alaskan form. Within *S. alpinus*, there was a Bering Sea-western Arctic form, an eastern form distributed east of the Mackenzie River, and a Bristol Bay-Gulf of Alaska form. Both the species and forms within species were defined largely by differences in numbers of gill rakers, vertebrae, and pyloric caeca (McPhail, 1961; Reist et al., 1997). McPhail (1961) also studied morphology and char within a few Alaskan lakes and demonstrated that in all areas there were two discrete forms of char living in sympatry. In comparison with reference samples from other areas, McPhail (1961) concluded that one form resembled Arctic char and the other resembled Dolly Varden. McPhail's (1961) analysis, therefore, was the first "acid test" of the distinct biological species status of the two chars using morphological data (Avise, 1994)—they existed as discrete units in sympatry (see also DeLacy & Morton, 1943). A few samples from Hansen Creek in Lake Aleknagik (Bristol Bay), however, did not fall neatly into either Arctic char or Dolly Varden. McPhail (1961) suggested that these individuals might represent interspecific hybrids, although he concluded that these fish were "a form" of *S. malma* rather than hybrids. Further, Gharrett et al. (1991) conducted an allozyme study of sympatric Arctic char and Dolly Varden in the Karluk River system and demonstrated significant, and sometimes striking, differences between the two char at several loci strongly supporting their status as distinct biological species.

The work of McPhail (1961) was followed up by a series of investigations (e.g. McCart, 1980; Morrow, 1980; Reist et al., 1997) that better defined the geographic distributions of the two chars, particularly with respect to the "Bering Sea-Western Arctic" form of *S. alpinus* proposed by McPhail (1961). Taken together, these works, and especially that of Reist et al. (1997), established the currently accepted distributions of *S. malma* and *S. alpinus* in Alaska and the Canadian Arctic. The distribution of *S. malma* includes riverine and anadromous char west of the Mackenzie River to and including the Gulf of Alaska, southeast Alaska, British Columbia and northwest Washington. The distribution of *S. alpinus* includes lacustrine char from the Gulf of Alaska north to and east of the Mackenzie River and anadromous and lacustrine char from east of the Mackenzie River (Reist et al., 1997). These data refuted the idea that there was a Bering Sea-western Arctic form of *S. alpinus* (McPhail, 1961; McCart, 1980) and these fish were demonstrated to be Dolly Varden (Reist et al., 1997).

Finally, several morphological, ecological, and genetic studies of interior forms of "Dolly Varden" sensu McPhail (1961) have illustrated that most populations found in inland areas of western and some eastern tributaries of the Mackenzie River, east of the Coastal-Cascade mountain crests, and east to the headwaters of the Saskatchewan and Missouri rivers in western North America are bull trout (*S. confluentus*) and not Dolly Varden (Cavender, 1978; Haas & McPhail, 1991; Baxter et al., 1997; Redenbach & Taylor, 2003; Mochnacz et al., 2013). A few Dolly Varden populations, however, are found east of the continental divide in the interior of Yukon (e.g. Peel River basin) and Northwest Territories (Reist et al., 2002) as well as in the Peace River basin in British Columbia as a result of historical watershed exchanges (Baxter et al., 1997).

In summary, the study of char over the last 54 years has peeled away skins of the onion-like *S. alpinus* "complex". There are, at least, three species in western North America (Fig. 1): Arctic char, Dolly Varden, and bull trout (in addition to the native populations of lake trout, *S. namaycush*, which have never been considered part of the *S. alpinus* complex). The taxonomic situation in western North America contrasts markedly with myriad forms, many of uncertain taxonomic status, that occur in many tributaries of the western Pacific basin (e.g. Oleinik et al., 2007; Osinov et al., 2015; Senchukova et al., 2015). For instance, consider the three enigmatic char of Lake El'gygytgyn in eastern Siberia. Here, the long-finned char (*Salvethymus svetovidovi*), the small-mouth char (*Salvelinus elgyticus*), and Boganida char (*S. boganidae*) are all strikingly morphologically and genetically distinct from one another in sympatry. Despite their distinct taxonomic designations, including one form constituting a monotypic genus, some genetic data suggest that they cluster tightly with members of *S. malma*/*S. alpinus* from other regions of the North Pacific basin (Osinov et al., 2015). A geographically and genetically comprehensive Pan-Pacific analysis of the phylogenetic affinities of all *Salvelinus* and closely related forms (e.g. *Salvethymus*) is required to better understand the level of diversity in these chars, i.e. if some taxa should be synonymized and perhaps new forms recognized.

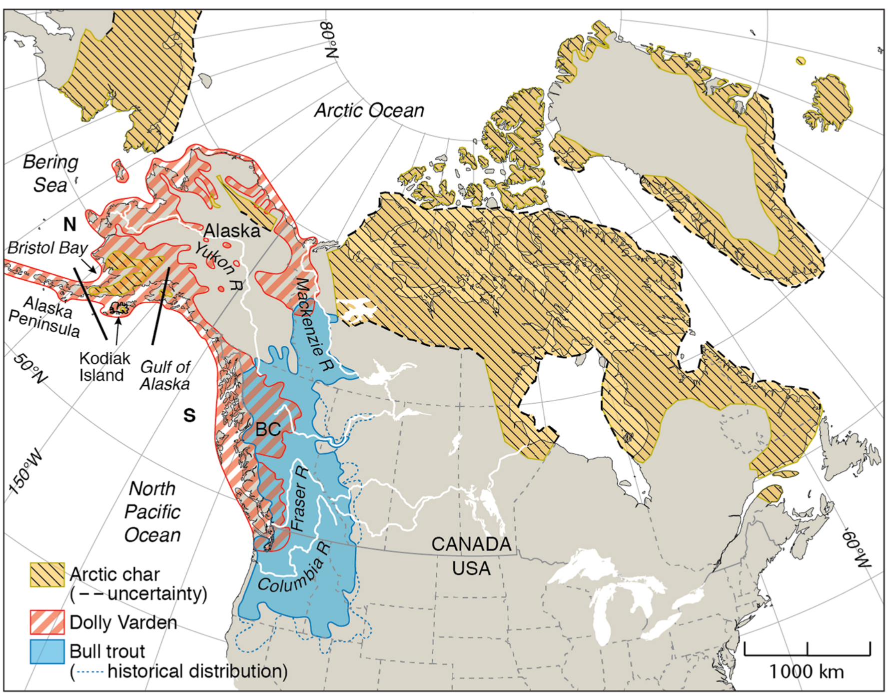

Fig. 1 Current approximate distributions of Arctic char (*Salvelinus alpinus*: brown shading), Dolly Varden (*S. malma*: red hatched shading), and bull trout (*S. confluentus*: light blue shading) in western North America and adjacent areas. The area between the two *thick solid angled lines* in western Alaska denotes a genetic admixture zone between the two subspecies of eastern North Pacific Dolly Varden: northern Dolly Varden (*S. m. malma*, N) and southern Dolly Varden (*S. m. lordi*, S; see Taylor & May-McNally, 2015 and Fig. 4). *Black dashes* associated with Arctic char distribution indicate uncertain geographical limits. The maximum extent of all distributions constituted the distribution of the *S. alpinus* species "complex" in North America (sensu McPhail, 1961). The distributions were based on information provided at http://www.arcticbiodiversity.is and in Kowalchuk et al. (2010) and COSEWIC (2012)

Hybridization and gene flow

The life history and morphological studies of DeLacy & Morton (1943) and McPhail (1961) were fundamental to suggesting that there were at least two biological species within the northwestern North American component of the Arctic char complex. These studies clearly demonstrated the temporally stable co-existence of two phenotypes in several lake systems. Arguably, the most compelling evidence of the existence of two distinct biological species, an "acid test" in the phraseology of Avise (1994), is the maintenance of genetic distinction in the face of potential or actual gene flow in sympatry. Gharrett et al. (1991)'s allozyme study (see above) substantiated the distinct biological species status of sympatric Arctic char and Dolly Varden in Alaska despite evidence of some gene flow between them. Notwithstanding these complementary studies, suggestions that Dolly Varden and Arctic char were not distinct species occasionally resurfaced (e.g. see Savvaitova, 1976; Brunner et al., 2001). Taylor et al. (2008) and May-McNally et al. (2015a) have, however, extended the approaches used in earlier studies and provided compelling evidence of genetic distinction of the two char in sympatry with almost a complete lack of hybridization between them. Sympatric populations in three western Alaskan lake systems (Iliamna Lake, Lake Aleknagik, and Lake Nerka) were examined using morphological and microsatellite DNA. Over a variety of habitat types (lakes, rivers, smaller streams, ponds), hybridization levels (i.e. the percentage of samples deemed to be of mixed ancestry) ranged between 0.52% (or lower) and 7% (Taylor et al., 2008; May-McNally et al., 2015a). Despite some evidence of a low level of gene flow between species (no unequivocal first-generation hybrids have been encountered), sympatric Dolly Varden and Arctic char maintain themselves as two distinct gene pools (e.g. Fig. 2; cf. Gharrett et al., 1991).

May-McNally et al. (2015a) also presented evidence of a greater reliance on stream residence by juvenile Dolly Varden relative to Arctic char which tend to be found only in the lakes after about age 3+ which is consistent with the greater use of lakes by Arctic char reported by DeLacy & Morton (1943). Further, the two species appear to have distinct diet and migratory habits as inferred from stomach contents and otolith microchemistry analyses (Dennert et al., unpublished data).

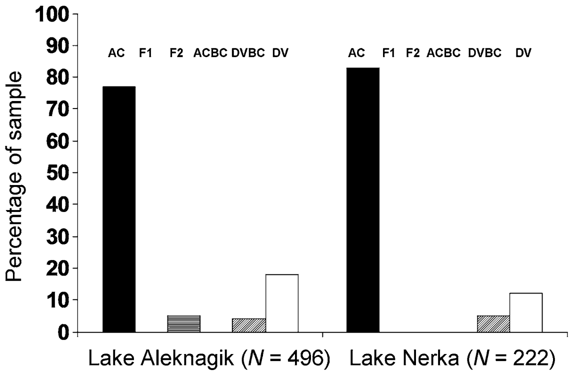

Fig. 2 Genetic classification of 718 sympatric Alaskan Arctic char (*S. alpinus*) and Dolly Varden (*S. malma*) across two years (2012, 2013) from Lakes Aleknagik and Nerka, southwestern Alaska. Classifications were based on assays across 12 microsatellite loci and model-based Bayesian assignments generated using the Newhybrids algorithm (see Anderson & Thompson, 2002) are shown. *AC* Arctic char, F_1 first-generation hybrid, F_2 second-generation hybrid, *ACBC* backcross to Arctic char, *DVBC* backcross to Dolly Varden, *DV* Dolly Varden

In summary, the distinct species status of Dolly Varden and Arctic char is supported by strong evidence from natural populations and maintenance of discrete gene pools in sympatry despite some gene flow between them. This distinction is consistent with fixed differences at allozyme loci between *S. malma* and *S. taranetzi* (a taxon of uncertain validity that is very closely related to *S. alpinus*) in Russia (Salmenkova et al., 2000). Analyses using nuclear DNA in sympatric populations stands in contrast to some mtDNA studies that indicate Arctic char and Dolly Varden mtDNA are not reciprocally monophyletic lineages (Brunner et al., 2001; Taylor et al., 2008; Yamamoto et al., 2014). The mtDNA results, however, are likely the result of historical hybridization and introgression between the species, a not uncommon phenomenon (see Toews & Brelsford, 2012) especially in *Salvelinus* (Hammar et al., 1989; Bernatchez et al., 1995; Redenbach & Taylor, 2002).

Interestingly, the level of hybridization between sympatric Dolly Varden and bull trout from several areas in British Columbia appears to be generally higher (up to 25% of some samples; Redenbach & Taylor, 2002, 2003) than between Dolly Varden and

Arctic char (May-McNally et al., 2015a). Further, although post-F_1 hybrids predominate in Dolly Varden–bull trout systems, F_1 hybrids are regularly observed, whereas none have yet been recorded between Dolly Varden and Arctic char (Redenbach & Taylor, 2003; Taylor et al. 2008; May-McNally et al., 2015a). Here, life history differences between species may be critical to explaining these different patterns of hybridization and introgression. Arctic char and Dolly Varden are well segregated during mating with the former spawning on submerged lake beaches and the latter spawning in streams (DeLacy & Morton, 1943; Gharrett et al., 1991; Schwanke, Alaska Department of Fish and Game, Dillingham, personal communication). When they are sympatric with Dolly Varden, however, bull trout migrate to adjoining lakes or larger rivers after several years of residence in streams, where they achieve body sizes of 1 m or more in total length, before returning to streams for spawning. By contrast, Dolly Varden are typically permanent residents of streams and mature at 20–30 cm or less when they are sympatric with bull trout (see Hagen & Taylor, 2001; Mochnacz et al., 2013). Consequently, the use of the same stream habitats with some temporal overlap for spawning may promote hybridization between Dolly Varden and bull trout, especially if the smaller Dolly Varden act as "sneak-spawners" on larger bull trout male–female pairs (see Hagen & Taylor, 2001; Taylor, 2004). In either case of hybridization between sympatric species of char, the exact processes that constrain hybridization or limit gene flow (e.g. ecological, genetic factors) are only beginning to be understood through studies of comparative ecology and genomic analysis of loci under selection in sympatry and allopatry (e.g. Hagen & Taylor, 2001; Mochnacz et al., 2013; Dennert et al., unpublished data).

Observations from the study of sympatric populations of Arctic char and Dolly Varden and of Dolly Varden and bull trout also suggest that character displacement of life histories may be common. All species tend to show the same range of life history patterns (anadromous, stream resident, lake resident) when allopatric, but appear to adopt different life histories when sympatric. Dolly Varden, when allopatric from bull trout, may be anadromous or lacustrine (e.g. Cowichan Lake and Buttle Lake on Vancouver Island, Duncan Lake in the upper Peace River watershed, both in British Columbia), yet in sympatry they are permanent residents of streams (e.g. Baxter et al., 1997; Hagen & Taylor, 2001; McPhail, 2007; Mochnacz et al., 2013). Bull trout may be lacustrine, anadromous, or permanent residents of streams, the expression of which is often associated with the presence or absence of Dolly Varden (Hagen & Taylor, 2001; McPhail, 2007). Similarly, Arctic char may be anadromous (and grow to a very large size), lacustrine, or stream resident east of the Mackenzie River where there are no known Dolly Varden (e.g. Reist et al., 1997). Conversely, in the presence of Dolly Varden (which are typically anadromous or stream resident) west of the Mackenzie River, Arctic char appear to be exclusively lacustrine, except for brief periods of foraging in streams as juveniles (DeLacy & Morton, 1943; Morrow, 1980; Reist et al., 1997; May-McNally et al., 2015a). The replicated nature of sympatric and allopatric species of char would make an excellent model system to test the hypothesis that life history diversity has facilitated not only the broad use of habitats by allopatric species, but probably also promotes their persistence in sympatry via character displacement.

Phylogeography and subspecies

McPhail (1961) discussed the "validity of subspecies" within both *S. alpinus* and *S. malma*. With respect to Dolly Varden, McPhail (1961) described the rationale for three subspecies: *S. malma malma*, found north of the Gulf of Amur in the northwestern Pacific, the Bering Sea, east to the Mackenzie River and south to the Alaska Peninsula; *S. m. krasheninnikovi*, found south of the Gulf of Amur in the western North Pacific; and *S. m. lordi*, found south of the Alaska Peninsula in the eastern North Pacific. He discussed myriad proposed subspecies of *S. alpinus*, and there are four taxa that have most commonly been referred to or proposed: *S. alpinus alpinus* found throughout most of the Holarctic in Europe, *S. a. erythrinus* in Arctic Canada and the central Asian Arctic, *S. a. oquassa*, a lake-dwelling form in Québec and New England, and *S. a. taranetzi*, a lake-dwelling form in eastern Siberia.

The three subspecies of Dolly Varden (commonly known as the northern Dolly Varden [Asia and North America], southern Dolly Varden [North America]), and Asian Dolly Varden [Asia]) are not contentious (see Oleinik et al., 2007; Kowalchuk et al., 2010). The two North American subspecies are also considered distinct from a conservation viewpoint in Canada (see COSEWIC, 2011). What is interesting about the subspecies of Dolly Varden is their phylogeography relative to *S. alpinus* and, in particular, the position of the western North Pacific Asian Dolly Varden. Studies have demonstrated a distinction between *S. m. krasheninnikovi* and *S. m. malma* in the western North Pacific (e.g. Oleinik et al., 2007). The most geographically comprehensive mitochondrial DNA-based phylogeographic analyses involving Dolly Varden and Arctic char (e.g. Taylor et al., 2008; Yamamoto et al., 2014; Osinov et al., 2015) suggest that a "western" Pacific lineage of Asian Dolly Varden, centred around the Sea of Japan/Sea of Okhotsk (representing *S. m. krasheninnikovi*), is ancestral and that some lineages of *S. alpinus* are the most derived ones. There are also at least two instances of lineages composed of mixtures of Dolly Varden and Arctic char mtDNA, both involving fish collected largely from areas of sympatry in the eastern North Pacific (Yamamoto et al., 2014). These data suggest three things: (i) Dolly Varden is, at least for mtDNA, paraphyletic with respect to Arctic char, (ii) some ancestral lineages of *S. alpinus* are more closely related to some lineages of *S. malma*, and (iii) the origin of the group lies in the western Pacific in and around the Sea of Japan/Sea of Okhotsk area (cf. Cavender, 1984; Osinov, 2001; Frolov, 2000 cited in Oleinik et al., 2007; Osinov et al., 2015; but see Phillips et al., 1999). This part of the western Pacific and adjacent freshwater habitats were also suggested by Oleinik et al. (2007) to be the centre of speciation for *Salvelinus* and have been linked to speciation in *Oncorhynchus* (Neave, 1958), *Thymallus* (Stamford & Taylor, 2004), and *Gasterosteus* (Higuchi & Goto, 1996), and several taxa of marine fishes (see discussion in Yamamoto et al., 2014). Indeed, given the growing evidence of the basal status of *S. malma* lineages and the geographic importance of the western Pacific as a well-spring of divergence, perhaps the evolution of the group of North Pacific and adjacent Arctic *S. malma*/*S. alpinus* is better thought of as the Dolly Varden complex.

Sympatric populations

There is a long history of studying the ecology and genetics of co-existing populations within *S. alpinus*. These populations are typically morphologically distinct, exploit different food resources, exhibit differences in growth and life history patterns, and in many cases are genetically distinct from one another. Perhaps, the best known case involves the four morphs of char in Lake Thingvallavatn, Iceland (e.g. Sandlund et al., 1992; Skúlason et al., 1996), and cases, typically involving a pair of morphs, have been documented in many areas of Eurasia and eastern North America (Alexander & Adams, 2000; Alekseyev et al., 2002; Power et al., 2005, 2009). It is, however, not always the case that sympatric morphs are genetically distinct from one another (Adams, 1999); they may also result from phenotypic plasticity driven by environmental differences (Nordeng, 1983; Arbour et al., 2011; Moore et al., 2014). Recently, Woods et al. (2013) and May-McNally et al. (2015b) presented the first evidence of sympatric morphs of *S. alpinus* in Alaskan lakes and that they were distinguishable ecologically and genetically (Fig. 3). The finding of genetically distinct morphs of *S. alpinus* is not surprising given earlier work and the diversity of environments in Alaska, and it adds to the generality of the phenomenon in *S. alpinus*.

Given the co-occurrence of *S. malma* as well as the taxonomic and numerical abundance of *Oncorhynchus* spp. in many Alaskan watersheds, the geographic extent and distribution of morphs in *S. alpinus* may be very different in Alaska compared to other areas of the Holarctic. Increased survey effort and integration of information on Alaskan populations of *S. alpinus* would allow for a pan-distributional comparative analysis that may identify factors critical to the evolution of sympatric morphs in Arctic char (cf. Kristjánsson et al., 2011; Woods et al., 2012).

Curiously, the investigation of sympatric morphs of *S. malma* is not as common as in *S. alpinus.* This may be because much of the range of *S. malma* includes sympatric populations of *S. alpinus* and *S. confluentus* in North America. In such cases, Dolly Varden tend to be stream specialists either as a prelude to seaward migration or as permanent residents (see discussion above). Whether or not stream residency and/or anadromy place greater constraints on the development of sympatric morphs is an interesting question. Lakes and streams differ in various physical and chemical attributes, and their variability, as well as in productivity (Wetzel, 2001), that may influence ecological opportunity and the evolution of different

Fig. 3 Images of three body-size morphs of Arctic char from Lower Tazimina Lake, southwestern Alaska, discovered by Woods et al. (2013). The *values* to the *left* represent mean total gill raker counts and those joined by a *vertical line* are not significantly different from one another. The *values* on the *right* and joined by *square brackets* indicate F_{ST} comparisons between morphs based on variation at 11 microsatellite DNA loci (May-McNally et al., 2015b). The values accompanied by * are not significantly greater than 0 after correction for multiple comparisons. Images are from Woods et al. (2013). *Scale bar* represents 10 cm

morphs. Also, the behavioural and physiological demands of anadromy may constrain the evolution of sympatric morphs in *Salvelinus*.

Nevertheless, lake-dwelling populations of *S. malma* do occur (there are at least three occurrences in British Columbia) and these may contain divergent, sympatric populations. Ostberg et al. (2009) documented just such a case in Kronotsky Lake, Kamchatka, where a "limnetic piscivorous" morph and a "benthic morph" were identified. Each was genetically distinct from the other as well as from anadromous *S. malma* in the lower Kronotsky River (cf. Salmenkova et al., 2005). The emerging results from studies of lacustrine populations of Dolly Varden in Asia suggest that closer scrutiny of lacustrine populations of Dolly Varden in western North American lakes may reveal greater diversity than is currently appreciated.

Contact zones

Applying the idea of contact zones, where genetically divergent populations come into parapatry or sympatry and where they may hybridize across a landscape, is challenging for many aquatic systems. These challenges arise because of the small spatial context in many lake and stream environments, the dendritic structure of streams, and because freshwater habitats are often physically isolated from one another. Aquatic contact zones, therefore, often exist as a "patchy" collection of independent habitats with sympatric and interacting populations within them, rather than as a broad interconnected contact zone that characterizes many terrestrial systems (e.g. Remington, 1968). Still, in large river, lake, or coastal systems, broad contact zones have been observed (e.g. Planes & Doherty, 1997; April & Turgeon, 2006). In *Salvelinus*, areas of contact between *S. malma* and *S. alpinus* are perhaps better understood in western North America (e.g. Oleinik et al., 2007; May-McNally et al., 2015a; Senchukova et al., 2015). Taylor & May-McNally (2015), however, assayed *S. malma* samples with microsatellites collected from across the entire North American range and presented evidence of a contact zone between northern and southern Dolly Varden—from Cook Inlet, Alaska, to the southern margin of the Alaska Peninsula. The distance between samples that were highly (i.e. >20%) admixed between the two subspecies and localities that were northern Dolly Varden (i.e. <1% admixture) was less than 300 km, but could be much smaller once more intervening localities are examined (Fig. 4). Further, the two subspecies appear to have different propensities for

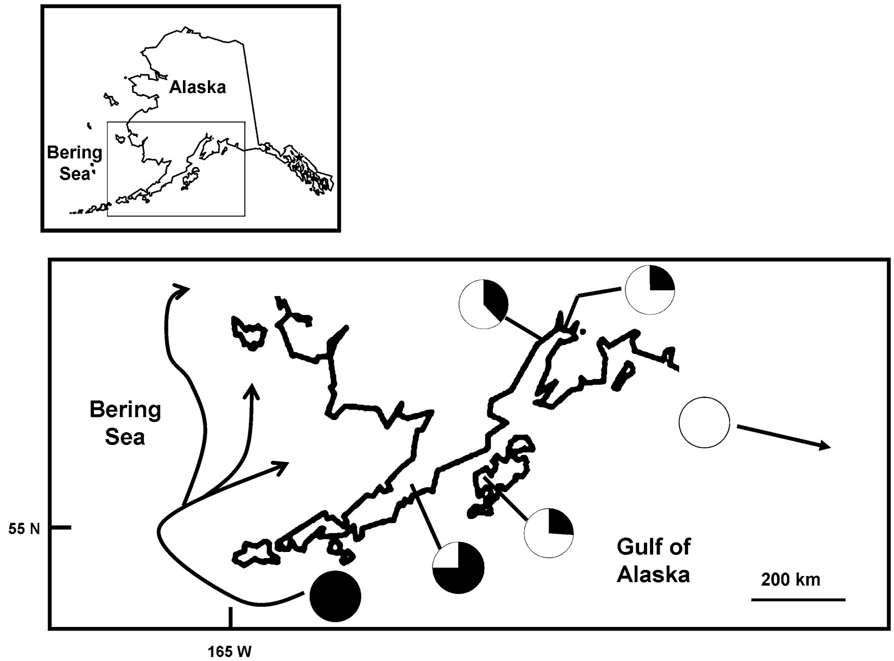

Fig. 4 Proportional composition of two genetic groups of Dolly Varden as determined by assays at 13 microsatellite DNA loci in samples from the Alaska Peninsula area of southwestern Alaska and adjacent areas (*bottom map*). The *white region* of each circular symbol represents the proportion of the genome consisting of southern Dolly Varden (*S. m. lordi*), and the *black region* represents the proportion of the genome consisting of northern Dolly Varden (*S. m. malma*). The *single symbol* that is all *black* represents the average proportion (0.99 ± 0.009) consisting of northern Dolly Varden for samples across 20 sites west, north, and east of that *point*, and the *single symbol* that is all *white* represents the average proportion (>0.99 ± 0.016) consisting of southern Dolly Varden for samples across 35 sites south and east of that *point* (see Taylor & May-McNally, 2015). The *map* at *top left* indicates lower map in the context of Alaska

long-distance migration (see Crane et al., 2004), so it remains to be determined if the contact zone is a vestige of historical isolation and re-contact or involves contemporary interactions between the subspecies. If the latter, such contact zones could provide the basis for testing whether or not the two subspecies should, in fact, be elevated to species status.

Concluding remarks

The various works that have been summarized above provided considerable clarification of the nature and origin of biodiversity of the *S. alpinus* "complex" in northwestern North America. These efforts, over the last 50 years, have contributed to a better understanding of char diversity and helped integrate this understanding over a broader geographic context. In addition, work on the *S. alpinus* complex has contributed substantially to conservation initiatives for the various taxa in western North America. First, and most fundamentally, there is now broad recognition of the existence of three distinct biological species within the original complex: Arctic char, Dolly Varden, and bull trout. Each of the species is now considered a distinct entity for conservation purposes both under the US *Endangered Species Act* (e.g. United States Fish and Wildlife Service, 1999) and Canada's *Species-at-Risk Act* (SARA, e.g. COSEWIC, 2011, 2012). This has led to fundamental changes in environmental impact assessments (e.g. separate monitoring and mitigation strategies for sympatric populations, e.g. Bustard, 2014) and stimulated much work to better understand the distribution of each taxon (e.g. Reist et al., 2002; Mochnacz et al., 2013, Fig. 1). Further, the subspecies of Dolly Varden are assessed separately under SARA, and the distributional information of the subspecies collected since McPhail (1961) has been critical to these assessments (e.g. see review in Kowalchuk et al., 2010; COSEWIC, 2011). Finally, phylogeographic and population genetic data collected for bull trout have been used to recognize five distinct "designatable units" for separate conservation assessment and listing under SARA (see review in COSEWIC, 2012). By any measure of effort, however, studies of the distribution and status of southern Dolly Varden, at least in Canada, are far behind those of Arctic char, northern Dolly Varden, or bull trout. A greater effort toward the study of southern Dolly Varden in Canada would be prudent given the seemingly ever-increasing developmental pressures it faces, particularly in the southern portions of its range. The focussed study of sympatric populations in northwestern North America using new genomic tools and analyses provides an exciting opportunity to better understand the ecological and genetic phenomena that promote co-existence between Dolly Varden and Arctic char, as well as the loci associated with variable life histories. Despite the potential for such fine-scale analyses of interacting populations, we still lack a firm understanding of the level of taxonomic diversity in Pan-Pacific *Salvelinus*, a limitation that can only be addressed with comprehensive geographic sampling and international co-operation.

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