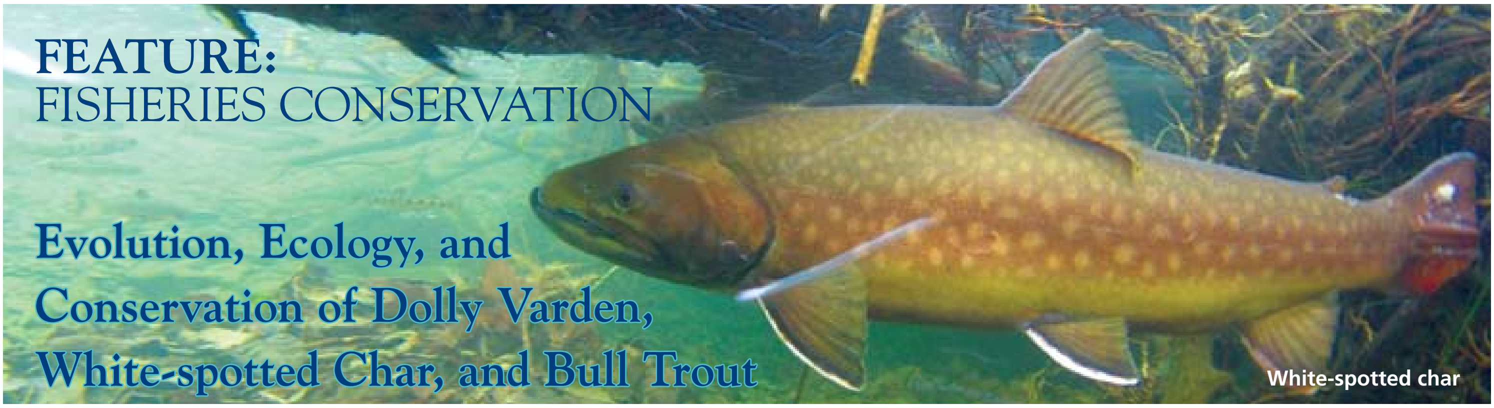

FEATURE:
FISHERIES CONSERVATION

Evolution, Ecology, and Conservation of Dolly Varden, White-spotted Char, and Bull Trout

White-spotted char

KENTARO MORITA

ABSTRACT: We review the ecology and conservation of three lesser-known chars (genus *Salvelinus*): Dolly Varden (*S. malma*), white-spotted char (*S. leucomaenis*), and bull trout (*S. confluentus*). Dolly Varden is distributed across the northern Pacific Rim and co-occurs with bull trout and white-spotted char at the southern extremes of its range. In contrast, bull trout and white-spotted char are naturally isolated, with the former restricted to North America and the latter distributed in northeastern Asia. Though the range of Dolly Varden overlaps with the two other chars, it is most closely related to Arctic char (*S. alpinus*), whereas bull trout and white-spotted char are sister taxa. Each species exhibits diverse life histories with respect to demographic characteristics, trophic ecology, and movement. This diversity appears to be tied to environmental variability (e.g., temperature, habitat connectivity), resource availability (e.g., food), and species interactions. Increasingly, these interactions involve nonnative species including nonnative salmonines and changes in food webs related to establishment of species such as *Mysis* shrimp in large lakes. As humans expand into the remote and pristine habitats that support these three chars, we encourage proactive consideration of the lessons learned where chars have already declined and internationally-based research and conservation.

Evolución, ecología y conservación de las truchas "Dolly Varden," "white-spotted" y toro

RESUMEN: Se revisa la ecología y conservación de tres truchas poco conocidas del género *Salvelinus*: Dolly Varden (*S. malma*), "white-spotted" (*S. leucomaenis*) y la trucha toro (*S. confluentus*). La primera se distribuye en el borde del Pacífico norte y co-ocurre con la trucha toro y la "white-spotted" en el extremo sur de su ámbito geográfico. En contraste, la trucha toro y la trucha "white-spotted" se encuentran naturalmente aisladas; la primera se restringe a Norte América y la segunda al noreste de Asia. A pesar de que el rango de Dolly Varden se sobrepone con el de las otras especies, está más relacionada con la trucha del Artico (*S. alpinus*) mientras que "white-spotted" y la trucha toro se consideran clados hermanos. Cada especie presenta diferente historia de vida con respecto a sus características demográficas, ecología trófica y movimiento. Esta diversidad parece estar determinada por la variación del ambiente (p. ej. temperatura y conectividad de hábitat) disponibilidad de recursos (i.e. alimento) e interacción con otras especies. Estas interacciones involucran cada vez más a especies no-nativas como algunos salmoninos y cambios en redes tróficas asociadas al establecimiento de ciertas especies como *Mysis* en los grandes lagos. En virtud de la expansión humana hacia hábitat más remotos y prístinos donde se distribuyen estas truchas, sugerimos que se tomen en cuenta de forma proactiva las lecciones tanto de aquellos casos en los que las poblaciones de truchas han declinado como del resultado de las investigaciones y esfuerzos de conservación a nivel internacional.

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Figure 1. Approximate known distributions of Dolly Varden, white-spotted char, and bull trout around the North Pacific rim. Given the remoteness of many areas where these species may occur, distributions are not fully described (e.g., Reist et al. 2002).

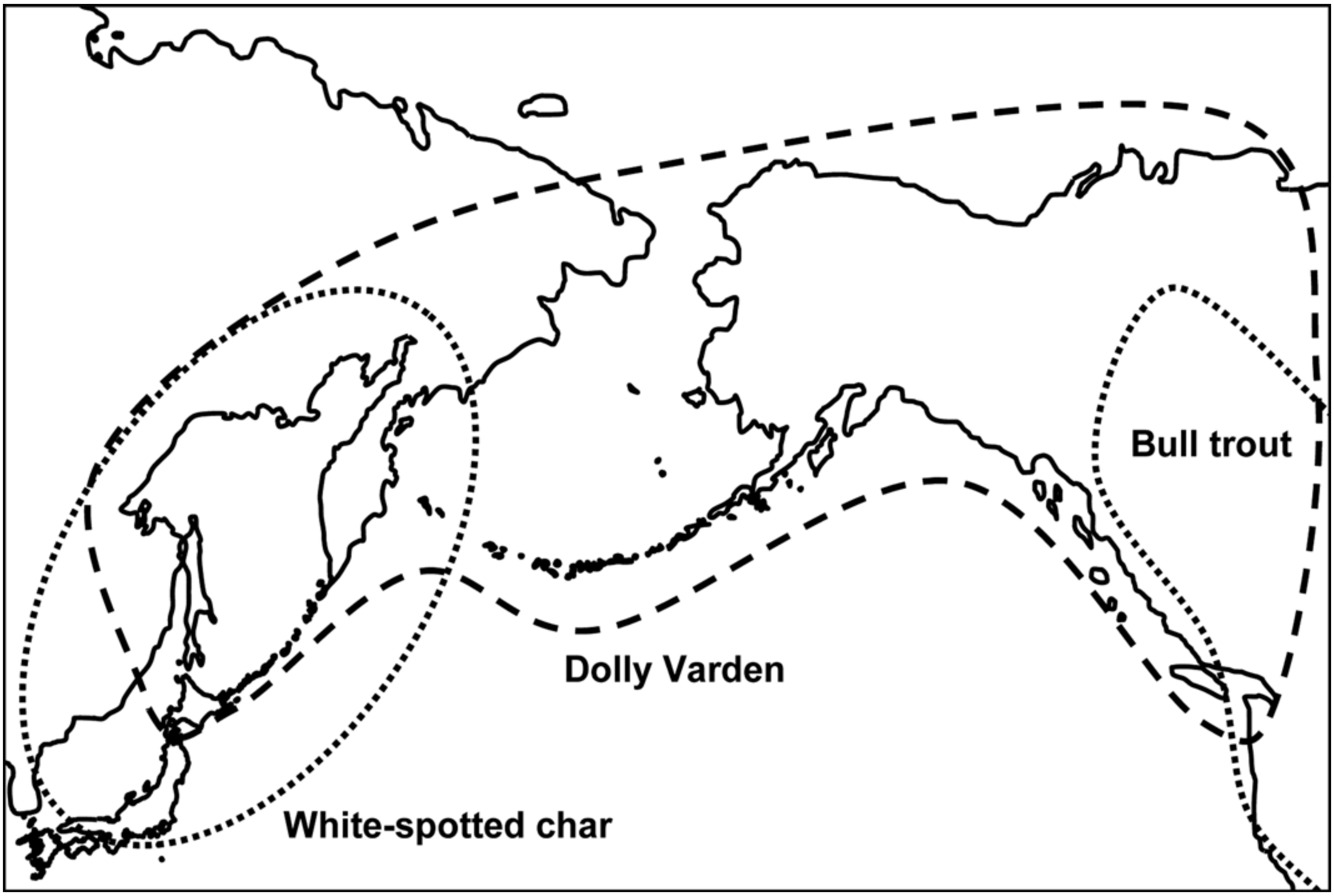

Figure 2. Photographs showing representatives of bull trout, Dolly Varden, and white-spotted char: upper left, the Miyabe char *S. m. miyabei* (Oshima), a subspecies of Dolly Varden from Hokkaido; upper right, white-spotted char from Russia; lower left, bull trout from Montana; lower right, white-spotted charr from Hokkaido.

INTRODUCTION

Most research on salmonine fishes has focused on the genera *Oncorhynchus* (e.g., Pacific salmon, cutthroat and rainbow trout) and *Salmo* (e.g., Atlantic salmon and brown trout). Within chars, genus *Salvelinus*, work has focused mostly on Arctic char (*S. alpinus*), lake trout (*S. namaycush*), and brook trout (*S. fontinalis*). Though research on these species has provided a broad foundation for understanding the biology, ecology, and conservation biology of salmonines, even within this well-studied group gaps in understanding and uncertainties pose significant management and conservation problems.

Here we focus on the biology and conservation of three lesser-known chars: Dolly Varden (*S. malma*), white-spotted char (*S. leucomaenis*), and bull trout (*S. confluentus*). We consider these species together because they share a similar Pacific Rim geography and evolutionary history, and provide an instructive comparison of the conservation problems and uncertainties associated with management of native chars in North America and Asia. Our specific objectives are to: (1) provide a brief and selective overview of major aspects of the evolution and ecology of these three species, (2) compare and contrast conservation issues within and among the species, and (3) suggest priorities for future research and conservation efforts.

BIOGEOGRAPHY AND EVOLUTIONARY HISTORY

Dolly Varden, white-spotted char, and bull trout are distributed across the North Pacific rim (Figure 1). Dolly Varden is the most widespread of these species, occurring from Puget Sound in Washington state, U.S.A., north to the Alaska Peninsula, Yukon, and Northwest Territories to far eastern Asia, including northern Siberia and neighboring islands, south to Hokkaido, the northernmost island of the Japanese archipelago (Armstrong and Morrow 1980; Reist et al. 1997; 2002). White-spotted char is distributed from Honshu (the main island of Japan) north to the Navarin Cape, Russia (Savvaitova 1980; Kawanabe 1989), on the Asian side of the North Pacific coast. Bull trout occupy coastal and inland drainages of western North America on both sides of the continental divide from Alaska and northern Canada to southern Oregon, but has been extirpated from the southernmost extent of its historical range in northern California, U.S.A. (Cavender 1978; Haas and McPhail 1991; Reist et al. 2002). Both white-spotted char and bull trout overlap with Dolly Varden in portions of their respective ranges.

Recent evidence indicates that these three chars share a complicated evolutionary history. Allozyme, nuclear DNA, and mitochondrial DNA (mtDNA) analyses all revealed sister groupings within *Salvelinus* that usually included one sister group comprising white-spotted char and bull trout, and one comprising Dolly Varden and Arctic char (Crane et al. 1994; Phillips et al. 1999; Crespi and Fulton 2003). A recent study based on mtDNA demonstrated, however, suggested that Dolly Varden and Arctic char do not constitute reciprocally monophyletic clades, which casts some uncertainty as to the distinct taxonomic status of these two species (Brunner et al. 2001). By contrast, a multilocus microsatellite (nuclear) DNA examination of sympatric populations of Dolly Varden and Arctic char in western Alaskan lake systems showed that sympatric forms were reproductively isolated from one another and acted as valid species (Taylor et al. 2008). Consequently, historical introgression may be responsible for the relationship between Dolly Varden and Arctic char mtDNA observed by Taylor et al. (2008). Historical and contemporary introgression has been reported between bull trout and Dolly Varden in populations that have a natural zone of overlap in North America (Taylor 2004), and between white-spotted char and Dolly Varden in Asia (Radchenko 2004; Yamamoto et al. 2006a). Evolutionary patterns within Dolly Varden, white-spotted char, and bull trout are unique for each species, both in terms of described subspecies and morphological variability.

Across the North Pacific rim, four subspecies of Dolly Varden are recognized: the northern Dolly Varden (*S. malma malma* Walbaum), the southern Asian Dolly Varden (*S. m. krascheninnikovi* Taranetz), the southern American Dolly Varden (*S. m. lordi* Günther), and the Miyabe char (*S. m. miyabei* Oshima; Figure 2). Chromosome and mtDNA data identified three phylogenetic groups, whose geographic distributions correspond to three Dolly Varden subspecies: *S. m. malma, S. m. krascheninnikovi,* and *S. m. lordi* (Phillips et al. 1999; Oleinik et al. 2005). Miyabe char inhabits only Lake Shikaribetsu, Hokkaido, Japan, which has been isolated historically due to volcanic activity. Miyabe char also has unique morphological characteristics in gill raker counts, pectoral fin length, the number of scales along the lateral line, and the muscle color compared to other conspecific populations (Maekawa 1984).

White-spotted char is presently separated into four subspecies based on zoogeographic patterns and morphological characteristics: *S. leucomaenis leucomaenis* (Pallas), *S. l. japonicus* (Oshima), *S. l. pluvius* (Hilgendorf), and *S. l. imbrius* (Jordan & McGregor). Populations north of Honshu Island, including Hokkaido Island, Japan, and Sakhalin Island and Kamchatka Peninsula, Russia, are classified as *S. l. leucomaenis*. They are characterized by large white spots (Figure 2; Savvaitova et al. 2007). The other three subspecies are endemic to Honshu Island, Japan, each with distinctive coloration. A recent phylogeographic study, however, has shown that the current subspecies designations of white-spotted char are not compatible with lineages identified with mtDNA markers (Yamamoto et al. 2004). Consequently, the taxonomy within *S. leucomaenis* remains in question.

At present, no subspecies of bull trout has been proposed, but the species was not formally described until relatively recently (Cavender 1978; Haas and McPhail 1991). Within bull trout, multiple lines of evidence suggest at least two major evolutionary lineages in western North America: coastal and interior bull trout (e.g., Taylor et al. 1999; Taylor and Costello 2006), with further subdivision of these lineages proposed by other authors (Leary et al. 1993; Spruell et al. 2003; Costello et al. 2003). As with Dolly Varden, these evolutionary groups within bull trout are associated with patterns of historical hydrographic connectivity (i.e., by the Coastal-Cascade Mountain Crest) across the geographic range of *S. confluentus* (Haas and McPhail 1991). Patterns of phenotypic variability among populations have not been rigorously analyzed, as with other salmonines within the range of bull trout (e.g., *O. mykiss*; Keeley et al. 2005).

DIVERSITY OF LIFE HISTORIES

Around the Pacific Rim, Dolly Varden, white-spotted char, and bull trout each inhabit a broad geography of habitats that present a range of physiological conditions and patterns of resource availability, as well as species interactions within distinct communities. This heterogeneity likely influenced resource polymorphisms and life history variation at a variety of scales, as has been observed in other species (e.g., Smith and Skúlason 1996). Here we use the term "life history" in a broad sense to represent a broad range of phenotypic characters, including body morphology, age and growth, and feeding and movement behaviors. Within individual river systems, key factors influencing life histories include: local variability in temperature and flow patterns; the presence of lakes, reservoirs, and marine habitats in addition to widely varying riverine habitats encompassed by small channels in headwaters to expansive flood plains further downstream; and the strength of ecological connectivity among these different habitats (Ward and Stanford 1995).

Age, growth, and reproduction

Dolly Varden and white-spotted char reportedly first mature between 1 and 7 years of age whereas bull trout are believed to mature later, generally between 5 and 7 years of age. Maximum life spans of these species may exceed 10–15 years (Rieman and McIntyre 1993; Savvaitova 1980; Yamamoto et al. 1999; Savvaitova et al. 2007). Rapid growth is often associated with movement into more productive environments, including the opportunity for piscivory. Dolly Varden, white-spotted char, and bull trout may reach maturity at sizes ranging from < 8 to > 80 cm (TL) depending on growth environments and differential selective pressure on reproduction by males and females (e.g., Jonsson and Jonsson 1993; Hendry et al. 2003). Migratory individuals that move from natal tributary streams into rivers, lakes, and the ocean occur in all three species; migratory individuals tend to mature at larger sizes (> 30 cm TL) compared to non-migratory or resident indivduals, which can mature at sizes down to 10 cm or less in small headwater streams (Koizumi et al. 2006a).

The timing and frequency of spawning can be highly variable. For example, in bull trout, spawning in inland habitats with colder winters and warmer summers may be initiated by late August, whereas in systems with lower seasonal variability (e.g., coastal environments; Brenkman et al. 2001) spawning may occur several weeks later. Spawning in white-spotted char and bull trout is believed to be restricted entirely to stream environments, but wholly lake resident Dolly Varden have been reported from Alaska (Armstrong and Morrow 1980), Kamchatka peninsula (Savvaitova 1973), and Kuril Onekotan (northern Kuril Islands; Savvaitova et al. 2000). All species are iteroparous, but patterns of mortality during spawning have not been well quantified.

Trophic ecology

The striking trophic polymorphisms observed in Arctic char (e.g., Jonsson et al. 1988; Johnston 2002) have not been reported in white-spotted char or bull trout, but Savvaitova and Kokhemenko (1971) reported discrete piscivorous and benthivorous morphs for Dolly Varden from large lakes in Kamchatka and the Kuril Islands (Savvaitova et al. 2000). It is not clear whether these species have less capacity for the trophic specialization observed in Arctic char or whether there has simply been too little work completed to recognize the full variability that may exist. At least one study suggested that some white-spotted char may develop dense gill rakers suited to foraging on plankton (Takami and Kinoshita 1990). Evidence of trophic polymorphisms for bull trout is lacking. Though trophic polymorphisms are not well documented for these species, considerable spatial and temporal variation in diet and plasticity in foraging behavior has been observed. Each species has achieved some notoriety for their opportunistic and often piscivorous habits (Behnke 1980; Takami and Aoyama 1997; Takami and Nagasawa 1996). Because of their proclivity to prey on salmon (*Oncorhynchus* spp.), all three chars were actively targeted for eradication in some early fishery management campaigns. For example, Colpitts (1997), elaborating on trout conservation in southern Alberta between 1900 and 1930, described an attitude he termed the "hierarchy of species" where "handsomeness, gaminess, and edibility" ranked high, and fish imported from the East were generally considered superior to native predators such as the bull trout. The "better classes of fish" such as brook trout, cutthroat trout, and grayling (*Thymallus arcticus*) were coveted and reared in hatcheries to fill the void created by eradicating undesirable species. As Colpitts (1997) opined:

> *The bull trout's failings—its image as a cowardly and lethargic sport fish, its flesh termed 'insipid,' and its character blighted by a reputation for cannibalism—targeted it among other species, for eradication by conservationists intent upon creating a perfect underwater world.*

In spite of these perceptions chars have diverse diets, varying from fish (including cannibalism) to invertebrates (e.g., Beauchamp and Van Tassell 2001). Moreover, these char display flexibility in their mode of foraging. For instance, Dolly Varden and bull trout have been observed to shift from drift-feeding on aquatic and terrestrially-derived invertebrates to picking benthic invertebrates from the benthos in response to diminished supply of drifting prey or competition with other salmonines for this resource (Nakano et al. 1992; Fausch et al. 1997; Nakano et al. 1999a). Likewise, all three species are known to opportunistically shift to scavenging of fish eggs, especially those of Pacific salmon, but also those of conspecifics (Maekawa and Hino 1987).

Movement

All three species commonly exhibit a great deal of variation in migratory behavior and related population characteristics. Migration typically is related to availability of food resources that are distant from natal habitat, and the relative benefits of migration may vary between the sexes (e.g., Jonsson and Jonsson 1993; Hendry et al. 2003; Koizumi et al. 2006a). Anadromy is common in white-spotted char and Dolly Varden but is more prevalent at higher latitudes (Yamamoto et al. 1999; Savvaitova et al. 2007) where freshwater food webs are less productive and marine waters provide alternative food resources (Maekawa and Nakano 2002). Anadromy is also known in bull trout (Brenkman et al. 2007), though apparently is less common, perhaps because the species' range is more inland in comparison to Dolly Varden and white-spotted char. Some variability in migratory behavior in chars may also relate to variability in thermal requirements of different life stages. Quinn (2005) suggested that juveniles may emigrate from cold natal areas to find relatively warmer habitats where they are able to grow faster. In accordance with this hypothesis, char require very cold water (< 10 °C) for successful egg incubation (e.g., McPhail and Murray 1979), yet these cold habitats are not ideal for juvenile growth (Selong et al. 2001). Likely, both food availability and temperature interact to influence movement and migratory behavior of these chars (e.g., Hughes and Grand 2000).

All three chars use a wide range of habitats, from small streams to large rivers, lakes, and marine habitats. However, few studies have been focused on their ecology during occupation of marine and large river habitats. Limited evidence suggests that within populations showing long-distance (> 20 km) migrations, larger (> 300 cm, TL) individuals tend to move quickly between natal habitats and migratory destinations, whereas behavior of smaller (< 30 cm) migratory individuals is more diverse and less predictable (Muhlfield and Marotz 2005; Monnot et al. 2008). Thus, there may be important age or life-stage dependent patterns of migration, with variability in migratory behavior more complex than classic definitions based only on origins or destinations. In many cases, the actual "destination" of migration is not clear, as fish may use multiple habitats during migration (e.g., Brenkman and Corbett 2005), or change destinations among years (O'Brien 2001).

Another less-studied factor influencing migratory behavior is sex. Small resident or so-called "precocious" males have been noted in Dolly Varden (Koizumi et al. 2006a; Savvaitova 1960), white-spotted char (Morita and Morita 2002; Savvaitova et al. 2007), and bull trout (Kitano et al. 1994; Baxter 2000). Even in populations considered to be largely migratory, mature, non-migratory males that adopt "sneaking" mating tactics probably occur, as this strategy is commonly observed in many other closely related salmonines (e.g., Esteve 2005). The occurrence of such individuals could be important, since they are unlikely to be considered in typical counts of adults or spawning surveys.

In summary, movement is a defining feature of these chars, but our understanding of their movements and migrations have been largely limited to descriptive studies and a focus on localized patterns. Only a few examples of process-based movement studies exist and clearly more work is needed to explicitly frame movement and migration in a broader ecological-evolutionary context (Jonsson and Jonsson 1993; Hendry et al. 2003).

SPECIES INTERACTIONS AND ECOSYSTEM ROLES

Biotic interactions can be critically important in shaping the local distribution and abundance of chars. Char distribution may be affected by the availability of prey species, competition for these or other resources, regulation by predation or parasitism, or additional indirect interactions within their ecosystems (Fausch et al. 1994). Research on biotic interactions involving these chars has largely focused on their potential competition with other native and nonnative salmonines, whereas relatively little is known about interactions involving these char as predators or prey of native biota, or other roles they may play in ecosystems.

Interspecific competition with native salmonines

Though the geographic ranges of white-spotted char and bull trout overlap with Dolly Varden, they usually do not co-occur in the same local habitats (e.g., within a stream network). In regions where the species overlap, Dolly Varden usually occurs in colder upstream segments whereas either of the other two species occurs downstream, and there is typically a narrow zone of sympatry, although there are exceptions. For example, in Hokkaido Island

this distribution pattern is observed for Dolly Varden and white-spotted char, and is correlated with changes in temperature across the region (e.g., climatic gradients) and within river networks (e.g., localized water temperatures; Fausch et al. 1994; Nakano et al. 1996). Presently, little is known about potential interactions that may occur between bull trout and Dolly Varden (but see Hagen and Taylor 2001).

Interspecific competition with other native salmonines is considered important in causing exclusion of these chars or regulating coexistence with the other salmonines. For example, in coastal British Columbia lakes native coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) exclude Dolly Varden from the productive near-shore littoral zone during summer where food resources are richest, causing them to shift to foraging in the open waters or deep benthic zone (Henderson and Northcote 1985; Hindar et al. 1988). In streams, salmonines compete for positions in mixed-species dominance hierarchies from which they can ambush drifting invertebrate prey (Nakano 1995). Stream-living Dolly Varden shift, however, between drift and benthic foraging as availability of invertebrates varies (Fausch et al. 1997; Nakano et al. 1999a). This may result in partitioning food resources between Dolly Varden and white-spotted char in zones where they overlap in Hokkaido mountain streams, and promote species coexistence. At a larger scale, coexistence of these chars is regulated by condition-specific interactions and physiological responses to water temperature (Taniguchi and Nakano 2000). White-spotted char appear to dominate Dolly Varden behaviorally and grow relatively faster at warmer temperatures in downstream reaches, but Dolly Varden can persist where they are better adapted than white-spotted char to colder temperatures in upstream reaches. Spatial patterns of segregation in other portions of the ranges of these two species may not parallel those observed in Hokkaido streams, however (e.g, Kamchatka; J. Stanford, personal observation). Other than in their common role as piscivores, interactions between bull trout and other native fishes have received less research attention than Dolly Varden and white-spotted char, despite the potential for strong interactions with bull trout and co-occurring native species such as cutthroat trout (e.g., Nakano et al. 1992; Jakober et al. 2004).

Interactions with nonnative salmonines

In contrast to interactions with native salmonines that shape char distribution, the introduction and invasion of nonnative salmonines has threatened to extirpate these three chars from many habitats throughout broad regions of their distribution via hybridization, competition, and disruption of spawning. Nonnative chars such as brook trout and lake trout have been most commonly implicated in the declines of native char, although other species can be important. Hybridization with nonnative brook trout has been reported for bull trout in northwestern North America (Leary et al. 1993; Kanda 1998; Kanda et al. 2002) and for white-spotted char in Honshu and Hokkaido Islands in Japan (Suzuki and Kato 1966; Kitano 2004; Kitano, unpublished data), and may result in displacement of the native char through gamete wastage (Leary et al. 1993). Although introgression has been observed in bull trout (Kanda et al. 2002), limited viability in post-F1 crosses may limit development of hybrid swarms (e.g., Allendorf et al. 2001). The reported ecological impacts of nonnative brook trout on bull trout are highly variable and likely dependent on habitat conditions and the spatial and temporal scales of observation (e.g., Nakano et al. 1998; Dunham and Rieman 1999; Rieman et al. 2006; McMahon et al. 2007). Impacts of nonnative lake trout on bull trout appear to be more consistently negative, but mechanisms of the interaction are similarly unclear (Donald and Alger 1993; Fredenberg 2002).

Rainbow trout (*O. mykiss*) and brown trout (*Salmo trutta*) are rapidly invading Hokkaido Island (Takami and Aoyama 1999; Takami et al. 2002), and have been reported to exclude Dolly Varden and white-spotted char from foraging positions or habitats in Hokkaido streams (Baxter et al. 2004; Morita et al. 2004; Hasegawa et al. 2004; Hasegawa and Maekawa 2006). In a field experiment, rainbow trout usurped terrestrial invertebrate prey on which Dolly Varden depend, and reduced their growth by 35% in 6 weeks compared to control reaches (Baxter et al. 2007). Rainbow trout introduced in North America could also compete with bull trout, but this has not been thoroughly investigated (Boag 1987). In addition, spring spawning rainbow trout can reduce reproductive success of native fall-spawning char by excavating their spawning redds before the fry emerge (termed superimposition; Taniguchi et al. 2000). Superimposition by fall-spawning kokanee salmon (*O. nerka*) on bull trout redds has also been documented, but at least in the latter case a study found that it was not harmful to bull trout due to the shallower depth at which the smaller nonnative kokanee (a form of landlocked sockeye salmon commonly introduced in lakes) excavated substrates for spawning relative to larger bull trout (Weeber 2007).

Despite evidence for apparent displacement, there are cases where several of these salmonines appear to coexist with chars where their native ranges overlap. For example, Dolly Varden coexist with rainbow trout or steelhead in Alaska and Kamchatka rivers, probably by partitioning food resources via the foraging mode shift described above (see Dolloff and Reeves 1990; Fausch et al. 1997). Since bull trout are naturally sympatric with either rainbow trout or cutthroat trout across most of their range, interactions with these species or with kokanee seem less likely to be negative and may even be beneficial in providing high quality food resources for bull trout. Indeed, many of the largest specimens of bull trout come from lakes with populations of introduced kokanee (Vidergar 2000; Beauchamp and Van Tassell 2001). Native lake trout and bull trout naturally coexist in certain drainages east of the continental divide in western North America, but when nonnative lake trout are established in lacustrine systems with native bull trout the latter are typically severely reduced or extirpated (Donald and Alger 1993). Examples of natural coexistence of lake trout with other chars are rare in other studied locations, and coexistence may be facilitated by natural geomorphic barriers (Hershey et al. 1999).

An important hypothesis is that the native char can resist invasion and persist in watersheds where intact habitat allows expression of the full range of life histories, including large, highly fecund, migratory individuals. When these migratory individuals are lost (e.g., through habitat loss or fragmentation, or overfishing), nonnative fishes may be better able to displace or replace the native char (Nelson et al. 2002). We view understanding the mechanisms that allow native chars to resist invasions by nonnative species, and the interactions of these mechanisms with habitat disruption, to be an important topic for future research.

Ecosystem roles

Relatively little is known about interactions involving these three char species as predators or prey in broader ecological communities, or other roles they may play in ecosystems. Bull trout are predators on other salmonines, especially *Oncorhynchus* spp. (*O. nerka, O. clarkii,* and *O. mykiss*) in lakes in the inland western United States, where they become more piscivorous with increasing size (Ricker 1941; Beauchamp and Van Tassell 2001). During periods when Pacific salmon are concentrated, such as spawning or the out-migration of smolts, salmon eggs or juveniles may become a temporarily important food for anadromous populations of Dolly Varden and white-spotted char (Armstrong and Morrow 1980; Kawanabe and Mizuno 1989). In turn, these chars may become prey for conspecifics and other piscivorous fishes and a host of semi-aquatic and terrestrial predators such as otters, bears, birds, or snakes.

Dolly Varden, white-spotted char, and bull trout likely have important effects on the structure of communities and the flow of energy and nutrients in the ecosystems they inhabit, though there have been few apparent investigations of these topics. Through their roles as predators on invertebrates and other fishes, these chars have the capacity to indirectly regulate organisms at lower trophic levels. For instance, two studies conducted in northern Japan (Nakano et al. 1999b; Baxter et al. 2004) showed that when terrestrial invertebrate prey were not available, Dolly Varden intensified their foraging on benthic invertebrates, which triggered an increase in the growth of algae but also reduced the emergence of adult aquatic insects and the abundance of spiders in the riparian forest. Studies like these have not been conducted for bull trout or white-spotted char, but similar indirect effects on algae have been described for brook trout in a Canadian stream (Bechara et al. 1992). If predation by these chars can regulate prey fish populations in lakes, they could indirectly control phytoplankton dynamics, as has been described for many other piscivorous fishes, including lake trout and Arctic char (Carpenter and Kitchell 1993). Moreover, these chars, through their migratory life histories, can play roles yet to be described to link the food webs of multiple habitats, and they may also transport energy and nutrients as has been found for other migratory fishes (e.g., Gende et al. 2002). In sum, there is good evidence that chars play important ecosystem roles, and local extirpations or declines in these species may have much wider impacts than is commonly recognized.

CHALLENGES FOR CONSERVATION

Many of the conservation problems for Dolly Varden, white-spotted char, and bull trout have been elaborated using the tools of contemporary conservation biology. Population viability analysis has been applied to assess long-term persistence of bull trout and white-spotted char (Rieman and McIntyre 1993; Morita and Yokota 2002; Post et al. 2003; Staples et al. 2005). In both species, sensitivity analyses have pointed to the importance of survival of older age classes to population persistence. Post et al. (2003) found that populations of migratory bull trout may be highly susceptible to declines from increased mortality of larger, older fish due to angling. Bull trout (especially females) in such systems do not attain first maturity until at least 5 years of age. Morita and Yokota (2002) similarly found that survival of adults was important for population persistence of white-spotted char in highly fragmented river systems. In their study system, however, white-spotted char matured at much smaller sizes and ages (e.g., most females were mature by age 2). Thus in both migratory bull trout and non-migratory white-spotted char, survival of older juveniles and adults appears to be a critical factor influencing population persistence.

Population viability analysis has provided important perspectives on the dynamics of individual populations of native char, but in most cases these local populations are embedded within a network of habitats and other populations. Within the context of a stream network, connectivity among populations (dispersal) and migrations among complementary habitats used for feeding, breeding, or refuge (Schlosser 1991) are relevant. Aggregations of local salmonine populations likely exhibit complex dynamics and structuring that represent a composite of different metapopulation, landscape, and historical processes (Costello et al. 2003; Koizumi et al. 2006b; Whiteley et al. 2006). Because many of these processes can operate on large (> 10 km) spatial and long (> 10 year) temporal scales, they are very difficult to study with conventional ecological methods. Single "snapshot" studies of large scale patterns of habitat or "patch" occupancy by bull trout (Dunham and Rieman 1999), white-spotted char (Morita and Yamamoto 2002), and Dolly Varden (Koizumi and Maekawa 2004) show that local population persistence in stream networks is strongly tied to patch size (stream or watershed size), connectivity, and quality (e.g., human influences, flow regime). The importance of habitat size and connectivity to persistence of chars documented by these studies is supported by several lines of evidence that examine temporal processes (e.g., dispersal, demographic variation, and environmental variability) driving these patterns. This includes evidence from models of population dynamics (e.g., Rieman and Allendorf 2001; Morita and Yokota 2002) and empirical applications of molecular genetic markers. Results from the latter show that disruption of connectivity can lead to lower effective size of local populations by simultaneously reducing dispersal and local adult population sizes of native chars (Griswold 2002; Costello et al. 2003; Yamamoto et al. 2004; Whiteley et al. 2006; Koizumi et al. 2006b; Taylor and Costello 2006; Yamamoto et al. 2006b).

Although many ideas from contemporary conservation biology have played an important role in our understanding of native chars, several fundamental challenges remain to be addressed for the conservation of these species. As with most fishes, threats to Dolly Varden, white-spotted char, and bull trout are associated with past and present human influences on water resources that lead to habitat loss and degradation, loss of connectivity, invasion of nonnative species, and excessive harvest (legal, poaching, and incidental mortality; Post et al. 2003). As described above, many of these influences have driven populations to extinction in just a few decades (see *Interactions with nonnative salmonines*, above). Our experience parallels that of many biologists working with chars (e.g., Al-Chokhachy et al. 2008) in that it can be extremely difficult to quantify the influences of specific threats and interactions among them, for example, evaluating the tradeoff between isolating char populations with barriers to prevent invasions by nonnative salmonines versus restoring connectivity to allow native chars the ability to move throughout networks (Fausch et al. 2006).

Overall, the status of Dolly Varden, white-spotted char, and bull trout appears to show a general north to south trend in the status of populations, with increasing imperilment near the southern margins of their ranges. For example, in the United States and Japan in particular, protected areas that support current strongholds of native chars are only small relicts of the range of habitats that were occupied in recent history. In the United States, many strongholds for bull trout are now located in higher elevation wilderness areas, whereas historically occupied areas were likely more expansive (Rieman et al. 1997). Distribution of bull trout has been consistently associated with unmanaged landscapes with low human population influence as exemplified by the density of roads (e.g., Rieman et al. 1997; Baxter et al. 1999; Dunham and Rieman 1999; Ripley et al. 2005). Lower elevation habitats such as floodplains and riparian corridors of large rivers are critical to many salmonines, but they are also most likely to be highly altered by humans (Ward and Stanford 1995; Beechie et al. 2003). In Japan, a large number of hatchery-reared white-spotted char have been stocked into lower elevation rivers and lakes. Consequently, populations of wild chars are often restricted to the upper reaches of rivers above natural waterfalls and human-constructed barriers that prevent the stocked fish from migrating upstream (Nakamura 2001). A focus on protecting only existing populations of native chars may therefore risk ignoring locations and/or habitats that are important for long-term viability.

Even though past changes are often clearly evident and important to Dolly Varden, white-spotted charr, and bull trout, possible future changes in populations and habitat are likely to pose even greater challenges. It appears likely that conditions will change substantially across landscapes in response to cycles of natural disturbance and succession processes (Reeves et al. 1995; Dunham et al. 2003). These natural processes will interact with human influences, such as climate change (Nakano et al. 1996; Rieman et al. 2007; Rahel and Olden 2008), human land and water use (e.g., habitat conditions), fishing (harvest and indirect impacts), and impacts of nonnative species. Many case studies suggest that even large populations can become highly vulnerable if present conditions change. For example, bull trout were once very abundant and thought to be secure in Flathead Lake and the Flathead River system in northwest Montana, but populations quickly crashed in the early 1990s, due to major ecosystem changes and cascading food web interactions as a result of the introduction of a single nonnative invertebrate species, the opossum shrimp (*Mysis relicta*). This introduction disrupted trophic relationships between native (bull trout and westslope cutthroat trout) and nonnative fishes (lake trout, kokanee, and lake whitefish [*Coregonus clupeaformis*]) that had been relatively stable for nearly half a century prior to the *Mysis* introduction (Spencer et al. 1991). We view analysis of these threats and planning for long-term persistence of chars (e.g., reserve design; Groves 2003) to be among the highest priority information needs for understanding long-term conservation of the native chars considered here. On a more positive note, there are some examples of native char expanding rapidly once threats are mitigated, such as the rapid increase in populations of bull trout in the Metolius River basin of Oregon (Ratliff 1992) and in Lake Kananskis in Alberta, Canada (Johnston et al. 2007) following decreased harvest mortality.

CONCLUSIONS

Our review suggests a number of fruitful areas of future investigation for learning more about the basic evolutionary biology and ecology of Dolly Varden, white-spotted char, and bull trout. Given the uncertain future for these species, we argue that these basic questions are directly relevant to applied conservation. For example, if we do not fully understand processes that contribute to the development of evolutionary and ecological diversity within and among chars, how can we develop long-term plans to conserve this diversity? How can these chars coexist with other fishes in some locations, yet apparently not in other locations? This question has direct relevance for managing invasive salmonines that may threaten native chars. What is the role of chars in aquatic ecosystems and how do food web interactions influence chars and ecosystems? In effect, the broad distribution of these species across both ecological and human geographies creates major challenges to addressing these critical questions about chars. More often our knowledge is based on a fragmented collection of isolated studies focused on narrowly framed issues of local interest. With this ad-hoc approach it can be very difficult to understand a species, and many of the questions we pose here are simply too broad to be adequately addressed in any particular locality. Accordingly, we encourage a stronger dialogue among biologists working across the ranges of these species and hope this synthesis represents an initial step in that direction.

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