

Population structure and partial anadromy in *Oncorhynchus mykiss* from Kamchatka: relevance for conservation strategies around the Pacific Rim

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Abstract – Conservation of life-history diversity found in *Oncorhynchus mykiss* requires knowledge of the underlying population structure and genetic basis of this variability. We analysed variation at 10 microsatellite loci from seven rivers across Kamchatka to identify population structure and to test for divergence between life-history forms. We found lower heterozygosity in Kamchatkan populations compared with North American populations, but population structure was substantial (region-wide $F_{ST} = 0.11$) and followed an isolation-by-distance pattern similar to that reported for older North American populations. We found no evidence for genetic divergence between resident and anadromous individuals in the Sopochnaya River or between typically anadromous individuals and ‘half-pounders’ in the Utkholok River. A review of other studies of reproductive isolation, in combination with our results, suggests: (1) that pristine populations of steelhead should be expected to exhibit partial anadromy; and (2) that managing anadromous and resident individuals separately without demonstrating reproductive isolation is biologically unsound.

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Introduction

The extensive biological diversity that occurs within the genus *Oncorhynchus* reflects the successful evolutionary journey of this group throughout its divergence from other salmonids over the past 10 million years (Behnke 1992). Such diversity, including physiological, morphological and life-history variation, reflects broad adaptive potential where anadromy (migration to the sea) is the major life-history variant within most species (reviewed in Reisenbichler et al. 2003).

The extent of reproductive isolation between co-occurring resident and anadromous individuals varies across species and populations, although the two forms typically share most recent common ancestors (Quinn 2005). Ranging from anadromous and resident siblings determined purely by physiological processes (e.g., Savvaitova et al. 1997) to the

accumulation of sufficient isolating mechanisms to prevent gene flow, a full spectrum of possibilities has been recently explored by Hendry et al. (2004). Both of these extremes have been observed in sockeye salmon (*Oncorhynchus nerka*) within the Snake River basin (Winans et al. 1996; Waples et al. 1997). Similarly, previous studies of sympatric resident and anadromous (steelhead) rainbow trout (*Oncorhynchus mykiss*) have detected both extensive gene flow (Seamons et al. 2004; Olsen et al. 2006; Pearsons et al. 2007) and apparent genetic isolation (Narum et al. 2004) between forms (although cross-basin transfers might have affected findings of genetic isolation; Narum et al. 2004).

The rainbow trout is an excellent candidate for applying insights from pristine salmonid populations towards managing and protecting disturbed ones. Highly regarded as sport fish, rainbow trout have been widely harvested, cultured and introduced throughout

temperate waters of the world (MacCrimmon 1971). Along with habitat loss and migratory issues, these activities have contributed to conservation problems for indigenous populations (Busby et al. 1996). Introduced rainbow trout have adversely affected other fish species in temperate waters around the world (Crowl et al. 1992; Leary et al. 1995). Remedial actions, such as through the U.S. Endangered Species Act (ESA) of 1978, have been instigated in response to these overall concerns (McElhany et al. 2000).

Rainbow trout populations of the Kamchatka Peninsula (Russian Federation) at the north-western edge of the species' range provide contrast to those at the south-eastern limit. Despite a growing interest in many resources of this region (Savvaitova et al. 2003), Kamchatka resident and steelhead populations persist in an essentially undisturbed condition. Their close kinship to degraded coastal populations of south-eastern Pacific drainages (Okazaki 1984; Pavlov & Kuzishchin 1999; McCusker et al. 2000) suggests that they would make appropriate comparative models for understanding patterns of gene flow among populations and life

histories prior to habitat degradation and barriers to migration. This knowledge is important in Russia as well because *O. mykiss* is listed in the Russian Red Data Book of endangered species (Savvaitova et al. 2003).

The objectives of this paper were twofold. First, we used patterns of genotypic (microsatellite) variability of *O. mykiss* sampled from rivers of the Kamchatka Peninsula to estimate gene flow within and among sampled populations and rivers and between life-history types within a river. Second, we reviewed existing studies about genetic differentiation between sympatric resident and anadromous *O. mykiss*. In combination with our Kamchatka data, we then used this information as a basis for evaluating current and alternate management strategies of populations around the Pacific Rim.

Methods

Adult *O. mykiss* were sampled using hook and line or in rare cases with gill nets (80 mm × 80 mm mesh) from seven rivers across the Kamchatkan Peninsula in 2002–2004 (Fig. 1, Table 1). Fin clips were taken

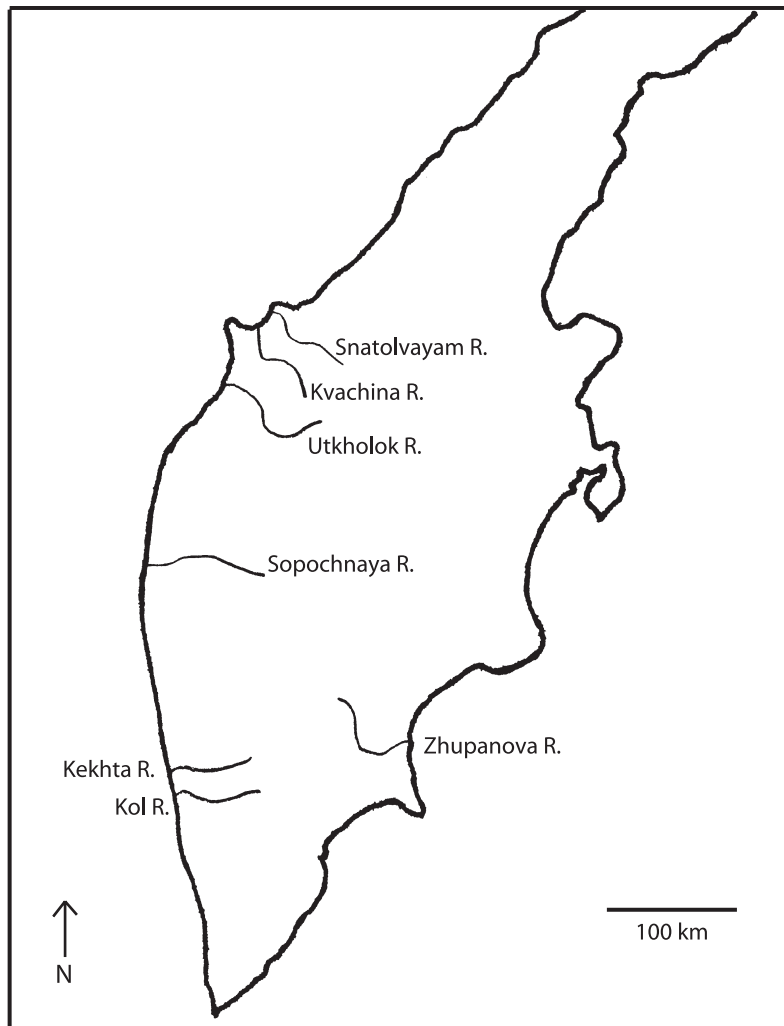


Fig. 1. Rivers of the Kamchatka Peninsula from which genetic samples were collected.

Table 1. Sample size by river and life history.

River	Year	Sample code	Sample size	Resident	Anadromous	Half-pounder
Snatolvayam	2002	SNA	39	0	39	0
Kvachina	2002	KVA	94	0	94	0
Utkholok	2003	UTK	81	0	45	36
Sopochnaya	2002	SOP	81	35	46	0
Kekhta	2004	KEK	12	0	12	0
Kol	2003	KOL	46	46	0	0
Zhupanova	2002	ZHU	29	29	0	0

Sample code refers to Table 3 and Fig. 3.

from the anal or pectoral fins and preserved in 95% ethanol. Scales were collected from the fourth row above the lateral line between the dorsal and adipose fins and used to assign individuals as resident or anadromous following Kuzishchin et al. (1999). ‘Half-pounders’ (Snyder 1925) were defined as individuals who smolted, went to sea, and then were collected in the river as over-wintering immature individuals (Savvaitova et al. 2005). ‘Typically anadromous’ fishes were mature anadromous individuals whose life history did not include the half-pounder stage, as determined by the scale analysis.

DNA was isolated from ethanol-preserved fin clips using proteinase K digestion followed by salting out of proteins and two ethanol washes. We amplified 10 microsatellite loci using nine microsatellite primer pairs (one locus, *Str60INRA*, is duplicated in *O. mykiss*; K. Knudsen, personal communication). Amplification was conducted using fluorescently labelled forward primers, following the PCR conditions described in the original primer reference (Table 2). PCR products were separated by electrophoresis and visualised by either a Hitachi FMBIO II fluorescent imager or an Applied Biosystems 3130 Genetic Analyzer. Approximately 5% of the individuals were scored using both visualisation techniques to standardise allele sizes between methods.

Table 2. Microsatellite loci, PCR conditions and number of alleles.

Locus	T_A (°C)	Allelic size range (bp)	Total no. alleles	Mean no. alleles per population	Reference
<i>Ogo4UW</i>	58	115–133	5	4.0	Olsen et al. (1998)
<i>OMM1050</i>	58	234–342	19	9.8	Rexroad et al. (2002)
<i>OMM1060</i>	58	95–104	3	3.0	Rexroad et al. (2002)
<i>Omy0004DIAS</i>	62	134–142	7	3.8	Holm & Brusgaard (1999)
<i>Oneμ11ASC</i>	56	143–145	3	2.2	Scribner et al. (1996)
<i>Oneμ14ASC</i>	54	147–159	6	4.6	Scribner et al. (1996)
<i>Ots100SSBI</i>	50	168–186	7	4.9	Nelson & Beacham (1999)
<i>Ssa20.19NUIG</i>	58	75–83	3	3.0	Sánchez et al. (1996)
<i>Str60INRA*⁻¹</i>	58	106–132	2	1.9	Estoup et al. (1993)
<i>Str60INRA*⁻²</i>		124–130	3	2.2	

Asterisk (*) indicates a duplicated locus.

Samples from each river were tested for deviation from Hardy–Weinberg proportions (HWP) at each locus using Guo & Thompson’s (1992) exact test, implemented in ARLEQUIN v. 2.000 (Schneider et al. 2000). We corrected significance levels for multiple tests within each population using the false discovery rate (FDR) method, which is less stringent than the sequential Bonferonni correction (Benjamini & Hochberg 1995). Expected heterozygosity was calculated over all loci in ARLEQUIN.

Pairwise genetic divergence between samples was calculated as F_{ST} and R_{ST} (based on the square of the size difference between alleles in repeat number; Slatkin 1995) and permutation of genotypes between populations was used to test the null hypothesis of no divergence between sample pairs. Isolation by distance (Slatkin 1993) was examined by regressing pairwise geographic distance (distance between river mouths, km) against pairwise genetic divergence, expressed as $F_{ST}/(1-F_{ST})$ after Rousset (1997). The correlation between genetic and geographic distances was evaluated using the Mantel test (Mantel 1967), implemented in F-STAT (Goudet 2001). Clustering of samples based on variance in allele frequencies was determined using a principal component analysis (PCA) implemented in PCAGEN 1.2 (Goudet 1999).

We tested for genic and genotypic differentiation between life-history types within the Sopochnaya and Utkholok rivers using Fisher’s exact test for homogeneity of allelic and genotypic distributions, respectively (Raymond & Rousset 1995). These tests were performed in GENEPOP, using 100 batches, at 1000 iterations per batch, following a burn-in period of 1000 iterations.

Results and discussion

Genotypic data and analyses

All 10 microsatellite loci were polymorphic across the region, with the total number of alleles per locus ranging from two to 19, and the mean number of alleles per locus per sample ranging from 1.9 to 9.8 (Table 2). Most samples exhibited Hardy–Weinberg proportions at all loci. However, conformation to HWP was rejected after controlling for multiple tests in Sopochnaya residents at *OMM1050* and in Utkholok half-pounders at *Ssa20.19* and *Str60–2* (Appendix I). In these three cases, an excess of homozygotes was observed, but we did not remove these loci from the analysis because overall there was no reason to suspect the presence of null alleles. Expected heterozygosity over all loci ranged from 0.24 in Utkholok River half-pounders to 0.54 in anadromous individuals from the Sopochnaya River (Table 3).

Table 3. Pairwise F_{ST} (below diagonal), R_{ST} (above diagonal) and overall expected heterozygosity along diagonal in italics.

	SNA	KVA	UTK-A	UTK-HP	SOP-A	SOP-R	KEK	KOL	ZHU
SNA	<i>0.44</i>	0.005	0.010	0.004	0.072	0.047	0.117	0.199	0.390
KVA	0.003	<i>0.45</i>	-0.003	-0.012	0.105	0.063	0.132	0.203	0.352
UTK-A	-0.001	0.002	<i>0.42</i>	-0.026	0.085	0.048	0.109	0.179	0.360
UTK-HP	-0.009	-0.010	-0.016	<i>0.24</i>	0.073	0.051	0.137	0.172	0.451
SOP-A	0.049	0.047	0.053	0.037	<i>0.54</i>	-0.007	-0.005	0.045	0.189
SOP-R	0.052	0.044	0.060	0.045	-0.003	<i>0.51</i>	0.006	0.059	0.237
KEK	0.103	0.084	0.107	0.123	0.012	0.015	<i>0.51</i>	-0.020	0.202
KOL	0.103	0.095	0.106	0.091	0.019	0.024	-0.005	<i>0.51</i>	0.088
ZHU	0.191	0.180	0.187	0.199	0.074	0.090	0.045	0.065	<i>0.45</i>

A = anadromous, HP = half-pounder, R = resident. F -statistics in bold are significantly greater than zero.

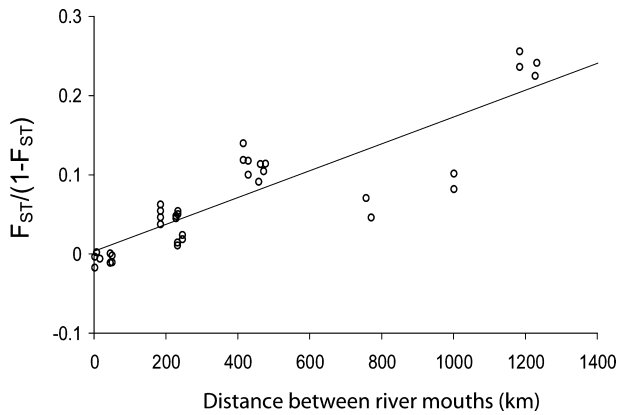


Fig. 2. Pairwise genetic differentiation as a function of pairwise geographic distance (between river mouths).

Genetic divergence, reflected in pairwise F_{ST} and R_{ST} (Table 3), was consistent with geographic separation. Divergence followed an isolation-by-distance pattern (Fig. 2), ranging from negligible values between neighbouring rivers to $F_{ST} = 0.19$ between the Snatolvayam and Zhupanova rivers. Pairwise genetic (F_{ST}) and geographic distances were significantly and strongly correlated (Mantel test, $r = 0.87$, $P < 0.0005$).

A principal component analysis (Fig. 3) suggested three genetically distinct groups: (1) Snatolvayam, Kvachina and Utkholok; (2) Sopochnaya, Kekhta and Kol and (3) Zhupanova. This grouping was based predominantly on the first principal component (PC1), which explained 72.8 % of the variance in allele frequencies among samples, and was augmented by PC2 (11.6 %). Overall F_{ST} was 0.11 and significantly greater than zero ($P < 0.0001$).

In the Sopochnaya River, anadromous and resident individuals did not differ significantly according to allele frequencies (d.f. = 20, $P = 0.35$) or multi-locus genotypes (d.f. = 20, $P = 0.35$). Similarly, no significant differentiation in allele frequencies (d.f. = 20, $P = 0.68$) or multi-locus genotypes (d.f. = 20, $P = 0.73$) was detected between half-pounders and mature anadromous individuals from the Utkholok River. These results are supported by an otolith

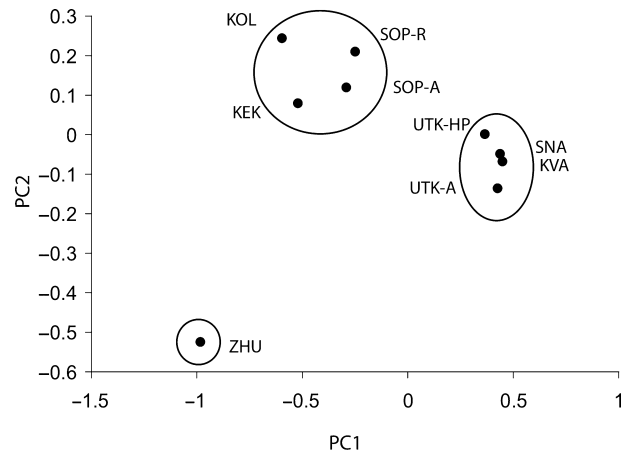


Fig. 3. Results of principal components analysis of genetic variation among samples. PC1 explained 73.0% of the variation and PC2 explained 11.6%. Sample codes are described in Table 1.

microchemistry study of *O. mykiss* from the Saichek River of western Kamchatka (Zimmerman et al. 2003). Anadromous females gave rise to both anadromous and resident offspring, in accordance with our finding of gene flow between both forms in Kamchatka.

Comparability of Kamchatka and eastern Pacific *O. mykiss* populations

Although once considered a separate species (Behnke 1966), conspecificity of Kamchatka populations with *O. mykiss* in North America is now well established (Behnke 1992). Molecular data from nuclear (Okazaki 1984; Pavlov & Kuzishchin 1999) and mitochondrial (McCusker et al. 2000) loci suggest a closer relationship of Kamchatka populations to coastal groups extending through Oregon and California, and separate from sublineages putatively descended from Queen Charlotte (mtDNA) and North American interior (nuclear loci) refuges. A phylogeographic analysis (McCusker et al. 2000) suggests that Kamchatka was the last region of the Pacific Rim to be colonised by *O. mykiss*, via the Bering Strait.

Previous studies have reported reduced allozyme and mitochondrial DNA variability in Kamchatkan populations (the north-western edge of the species' range) compared with North America (Osinov & Pavlov 1994; Pavlov 2000; Pavlov et al. 2004). We also found evidence for reduced microsatellite diversity in populations from Kamchatka. Expected heterozygosity in our study populations (0.24–0.54) was low compared with microsatellite studies of *O. mykiss* from other regions. For example, expected heterozygosity based on previous microsatellite studies ranged from 0.55–0.59 in Alaska (Olsen et al. 2006), 0.51–0.87 in British Columbia (Heath et al. 2001; Hendry et al. 2002; Heggenes et al. 2006), 0.68–0.86 in Washington (Ardren & Kapuscinski 2003; Narum et al. 2006) and 0.62–0.79 in California (Aguilar & Garza 2006). We were able to compare single-locus measures of observed heterozygosity from these studies for five of our 10 loci. Three of the five loci showed reduced heterozygosity in Kamchatka compared with North American populations, while one (*Ogo4*) showed greater heterozygosity and the other was within the range found in North America (data not shown). Thus, although reduced overall heterozygosity could be due simply to differences between loci across studies, lower genetic diversity might also reflect the later colonisation and isolation of Kamchatkan populations compared with those in North America. However, we found considerable divergence across the peninsula and isolation by distance was on a scale similar to that reported by Aguilar & Garza (2006) for steelhead populations from California (the oldest *O. mykiss* lineages, McCusker et al. 2000), suggesting that the genetic structure of these populations has approached equilibrium.

Despite apparently reduced genetic diversity, Kamchatka *O. mykiss* populations express the full spectrum of life-history variability found throughout the species' range (Pavlov et al. 1999; Savvaitova et al. 2003). The presence of all-anadromous, all-resident or mixed life histories in Kamchatka rivers is similar to western Alaska streams that support *O. mykiss* populations at similar latitudes. For instance, only all-resident populations occur on the Alaska mainland north of the Alaska Peninsula, while steelhead predominate on much of the Alaska Peninsula and both forms coexist to the southeast in the Copper River (Olsen et al. 2006). Such a geographical pattern is expected if the difference between freshwater and marine productivity, thought ultimately to drive the evolution of diadromy, varies broadly with latitude (Gross et al. 1988). While latitude is apparently a major factor in the level of anadromy versus residency in *O. mykiss* populations at the range-wide scale, at the regional scale life history diversity is likely also a function of the biophysical complexity of rivers (Stanford et al. 2002).

Gene flow in sympatry

Our results, indicating a lack of reproductive isolation between sympatric life-history forms in Kamchatka, generally support those of other studies seeking evidence for gene flow between sympatric resident and anadromous *O. mykiss* over a broad geographic range in North America (Table 4). No genetic divergence between forms was found in 11 of 12 streams where nuclear data were collected, and divergence in the aberrant stream (Walla Walla River) may reflect out-of-basin stocking of steelhead (Narum et al. 2004). The other two instances indicating nonrandom mating were based on female-restricted data where breeding with male parents could not be excluded (Zimmerman & Reeves 2002; Docker & Heath 2003). Such one-way gene flow from small 'satellite' males is common in salmonids (e.g., Quinn 2005) and may explain these results. Thus, from this review we conclude that gene flow commonly, perhaps predominantly, occurs in *O. mykiss* when resident and steelhead populations spawn in sympatry.

Relevance of present observations and current management directives

Based on the results presented and reviewed in this paper, we suggest that in many (if not most) rivers, sympatric rainbow trout and steelhead should be considered members of a common population. Furthermore, expression of such life-history diversity in a single population probably has adaptive significance. Atlantic salmon (*Salmo salar*) populations, evolving in parallel North Atlantic ecological settings to *O. mykiss*, have complex and dynamic age and maturity structures, and this retention of divergent life histories within common taxonomic units is interpreted as an evolutionary strategy that promotes adaptive flexibility in streams that are subject to unstable temperatures and stream flows and reduces inbreeding through matings of predominantly younger males with predominantly older females (Valiente et al. 2005; Juanes et al., in press). However, it is worth pointing out that the presence of younger males in the breeding population would also increase the rate of loss of heterozygosity due to finite population size by decreasing generation time (R. Waples, personal communication).

The capability to balance life-history options fits understandings of anadromy as '...a suite of life history traits...expressed as points along continua for each species and population.' (Quinn & Myers 2005) as '...a function of variation in costs and benefits...' (Hendry et al. 2004) in specific situations. An alternate response in more stable lake environments is exemplified in the sympatric divergence of resident sockeye

Table 4. Summary of studies comparing reproductive isolation between sympatric anadromous and resident *O. mykiss*.

Location	Description	Data type	Reproductive isolation	Reference
Kamchatka Peninsula Russia	No within-drainage divergence detected between resident and anadromous fish. Isolation by distance evident among populations sampled over a 1200 km range.	Microsatellite (10 loci)	No	This study
Copper River Alaska	Spawning resident and anadromous fish sampled at two adjacent upstream tributaries were indistinguishable within locations ($F_{ST} = 0.000-0.003$) but differed significantly between locations ($F_{ST} = 0.019-0.028$). Comparison with downstream steelhead populations highly significant ($F_{ST} = 0.170-0.202$)	Microsatellite (13 loci)	No	Olsen et al. (2006)
British Columbia Canada	Sympatric steelhead and resident fish from five rivers diverged significantly for mtDNA in one river (Meziadin). Remaining mtDNA and all nuclear comparisons were nonsignificant.	mtDNA (ND3, D-loop) Nuclear GH2D (3,4GATT)	Yes? (mtDNA) No (nuclear)	Docker & Heath (2003)
Yakima River Washington	Visual evidence of anadromous and resident interbreeding consistent with allele frequencies of progeny subsequently collected in the same reaches.	Allozyme (22 loci)	No	Pearsons et al. (in press).
Deschutes River Oregon	Resident female parentage (low ratios) dominated in mainstem progeny while steelhead (high ratios) dominated below falls and in tributaries.	otolith Sr:Ca ratios	Yes? (female parent)	Zimmerman & Reeves (2002)
Quileute River Washington	Mating behaviour observed during late spawning season between wild resident males and steelhead females in all reaches studied.	observation	No	McMillan et al. (in press)
Walla Walla River Washington	Genetic divergence of resident and anadromous populations in mainstem, but not in Touchet R. tributary. Mainstem differences may reflect out-of-basin stocking.	microsatellite	Yes & No	Narum et al. (2004)

In cases marked 'Yes?' the potential for male-mediated gene flow could not be eliminated.

salmon (kokanee) from anadromous lake-type sockeye where kokanee have evolved through positive assortative mating and distinct spawning locations (Wood & Foote 1996). We find no evidence to suggest that such a fixed and genotypically determined life history is common in *O. mykiss*.

The biological significance of gene flow among life-history variants has important conservation and management implications. Given their reproductive independence, regulations promoting separate protection, restoration and harvest of coexisting kokanee and sockeye populations are biologically appropriate. Despite their overlapping distributions, each entity is affected independently by hydrological, habitat and harvest issues. Conversely, in species like steelhead and Atlantic salmon where interbreeding among life-history classes prevails in sympatry, these issues become interdependent. In the interest of sound management and conservation, the expression of multiple life histories within a common gene pool mandates parallel protection of each component and their interaction.

The lack of simple genetic determination of life history in *O. mykiss* has implications for restoration, as well. On the one hand, it suggests that genetic variation for life history will not be lost rapidly from a population even under strong selection against a particular form (e.g., Thrower et al. 2004). Such retention provides hope that, for example, populations

that have lost the anadromous form due to artificial barriers to migration might be restored from local resident individuals on time scales relevant to most management schemes. However, given how poorly we understand the interaction between environment and genome in the determination of salmonid life history, this idea remains a hypothesis and should not be a basis for management actions. Yet more challenging is the implication that proper restoration must focus on identifying and restoring habitat features that promote expression of life-history diversity as opposed to managing numbers of adults through artificial propagation.

Recently, the National Marine Fisheries Service ruled that distinct population segments (DPSs) of steelhead subject to protection under the U.S. ESA would be considered separately from resident *O. mykiss* (National Marine Fisheries Service, NMFS 2005). This ruling noted '...Despite the apparent reproductive exchange between resident and anadromous *O. mykiss*, the two life forms remain markedly separated physically, physiologically, ecologically, and behaviorally. Given the marked separation between the anadromous and resident life history forms in physical, physiological, ecological, and behavioural factors, we may conclude that the anadromous steelhead populations are discrete from the resident rainbow trout populations within the DPSs under consideration...'

While this ruling is in keeping with the history of separate management by NMFS and USFWS of the DPSs in question, it is biologically unsound for reasons discussed above. For instance, the biological reality is that resident and anadromous populations interbreed in the Yakima River, a tributary to the Middle Columbia River (Pearsons et al. 2007) where steelhead are presently listed as threatened under the ESA (McClure et al. 2003). Exclusion of the resident life history in the protection and recovery of Middle Columbia River steelhead prevents adequate assessments of current and future population dynamics, and precludes full awareness of the status of *O. mykiss* in this large area.

Management recommendations

The lack of reproductive isolation between anadromous and resident forms suggests a strong role for environment in determining the expression of life history in *O. mykiss*. Thus, conservation of *O. mykiss* requires knowledge of how the many components of habitat (freshwater spawning and rearing habitat, marine feeding conditions and migration pathways) interact to influence life history and population size. Furthermore, demographic and evolutionary independence of spawning populations, in addition to underlying geomorphologic differences between neighbouring streams, indicates that the exact nature of genotypic and environmental effects is likely to vary at a fine spatial scale. Currently, we lack an understanding of the mechanistic determination of life history in *O. mykiss*, and detailed information on both forms from a single river is scarce. We suggest that a first step in understanding and conserving the true complexity of *O. mykiss* life history would be to abandon the typological thinking ('steelhead' and 'rainbow trout' as biologically independent units) that has pervaded the biology and management of this species in North America and around the Pacific Rim.

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Supplementary Material

The following supplementary material is available for this article:

Appendix S1: Allele frequencies, observed and expected heterozygosity, and P-value of exact test for Hardy-Weinberg proportions by locus and sample.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1600-0633.2007.00248.x> (This link will take you to the article abstract).

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