

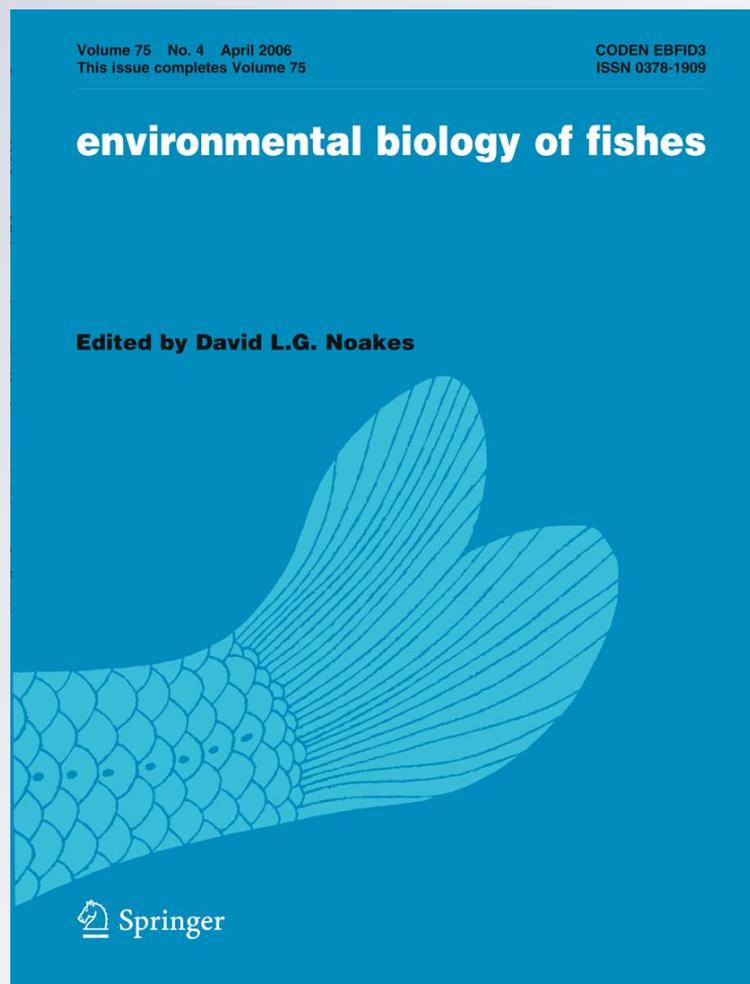
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Rapid expansion of an enhanced stock of chum salmon and its impacts on wild population components

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Abstract A harvested stock of chum salmon homing to Kurilskiy Bay, Iturup Island, consists of two genetically distinct river populations that reproduce in two rivers that drain into the bay and are characterized by limited gene flow. One of these is small and can be regarded as wild, whereas the other is much larger and, until recently, was composed of naturally reproducing components spawning in the river's mainstem and tributaries, with almost no hatchery reproduction during the past two decades. The only human impact on reproduction of the chum salmon stock was regulation of the escapement, with

officially accepted limits to avoid 'over-escapement'. Recently the hatchery began to release a large amount of chum salmon juveniles. As confirmed by data on variation in both age composition and microsatellite DNA, first-generation hatchery-origin fish that returned from the first large releases occupied spawning grounds and presumably competed directly with, and potentially displaced wild fish. The most dramatic example is a genetically distinct beach-spawning form of chum salmon that was swamped by much more numerous hatchery-origin fish of the river-spawning form. In order to restore and support naturally

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reproduced population components, careful estimation of the carrying capacity of natural spawning grounds is necessary with efforts to increase escape-ment to these habitats. We also recommend concerted efforts to restore and conserve a unique beach-spawning population of chum salmon. We further recommend development of a marking program for direct estimation of straying and evaluation of ecological and genetic impacts of hatchery fish on neighboring wild and natural populations.

Keywords Chum salmon · Hatchery population expansion · Microsatellite DNA marker · Age composition · Release-return dynamics · Wild-hatchery fish

Introduction

Enhanced reproduction of salmon populations through hatchery programs has been developed to maintain depleted salmon stocks or increase their abundance and fishery yields (Lichatowich 1999; Naish et al. 2007). Hatchery population may negatively influence neighboring wild populations through both genetic and ecological risks. Genetic risks occur through straying and introgression of hatchery-selected genes that may result in lower fitness in the wild environment (Ford 2002; Araki et al. 2007). Gene flow from hatcheries into wild salmon populations may be strong (Palm et al. 2003), but even if the risk from captive breeding occurring over a single generation is low (Schroder et al. 2008), effects can accumulate and become significant over multiple generations, particularly if the hatchery population is managed independently of wild populations. Ecological risks may act faster because they are introduced by hatchery environments that modify phenotypes and behavior of fish and influence wild populations even after only one generation in the hatchery (Pearsons et al. 2007).

Hatchery releases may represent a trade-off with productivity of wild fish (Hilborn and Eggers 2000; Nickelson 2003; Oosterhout et al. 2005). To minimize negative genetic effects from hatchery operation, it is important to conserve natural reproductive components (Dannewitz et al. 2004). It has been shown that the overall production of a wild salmon population is indirectly related to the contribution of hatchery returns (Chilcote 2003) and wild salmon productivity

in at least one case has been shown to increase following a reduction in hatchery releases (Buhle et al 2009). These are examples of species with prolonged freshwater periods prior to smoltification; the effect stemming from artificial selection is presumed to be less pronounced for species with only brief juvenile freshwater phases (e.g. pink salmon and chum salmon). However, even for those species with limited periods of captivity and for hatchery strains that are derived directly from the local wild population, increase in hatchery-origin returns can disrupt natural reproduction as a result of phenotypic changes that are not necessarily heritable (Kostow 2009). This disruption could lead to displacement of wild salmon populations, as has been described by some authors (e.g. Hilborn and Eggers 2000). However, building a strong case for competitive displacement based on empirical observations is difficult and fraught with uncertainty (Wertheimer et al. 2001; Brannon et al. 2004).

In this paper, we provide a summary of historical and more recent data to describe the temporal dynamics and population structure for a chum salmon stock homing to Kurilsky Bay, Iturup Island. Based on examination of abundance, and demographic and genetic data, we tested the hypothesis that recently developed chum salmon hatchery programs have greatly increased abundance of chum salmon recruits in this region, including hatchery fish that stray to natural spawning grounds and potentially disrupt and replace locally adapted, wild chum salmon populations. We conclude by suggesting measures to support naturally reproduced components of the stock in the future.

Material and methods

Definitions of wild, hatchery and natural chum salmon

We consider salmon wild if they originate (i.e. hatch) from natural stream gravel and have a largely wild pedigree. Hatchery salmon are defined as those that result from artificial means of reproduction performed in hatcheries. We call salmon natural if they hatch from natural stream gravel (with fertilized eggs produced from natural spawning parents) but have a mixed parentage consisting of some combination of

wild and hatchery pedigree. We do not consider the degree in which these populations have been influenced by fisheries exploitation and escapement regulation in these definitions, but we do note the possible impact these practices may have on their overall biological characteristics and fitness.

Background on study area

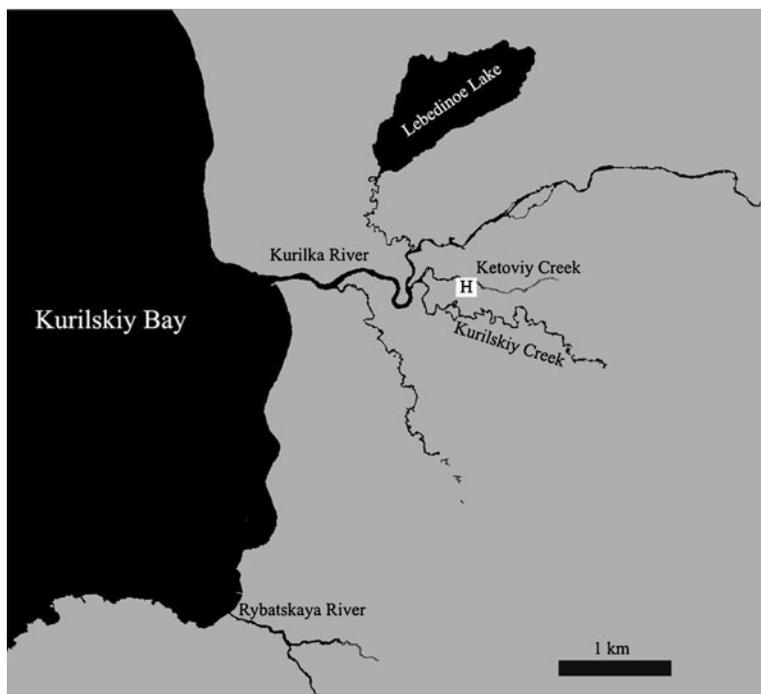
Chum salmon homing to Kurilskiy Bay are composed of two separate populations originating in Kurilka River and Rybatskaya River that both drain into the bay (Fig. 1). The Kurilka River contains spawning habitat in the upper mainstem and in its tributaries, Kurilskiy Creek and Lebedinoe Lake. Lebedinoe Lake in the past has supported a rare beach-spawning population of chum salmon (Ivankov 1985). The area of chum salmon spawning grounds of the Kurilka River's mainstem, Lebedinoe Lake, and Kurilskiy Creek have been estimated to be 11500, 6750, and 2000 m², respectively. Artificial reproduction is maintained by the Kurilskiy hatchery located on Ketoviy Creek, close to Kurilskiy Creek (Fig. 1). Neighboring Rybatskaya River contains 3600 m² of chum salmon spawning grounds and its population was never enhanced artificially. There is an additional, small river (Kitovaya River) that drains into

the bay. In the past, the river supported a very limited amount of natural reproduction of chum salmon, but the river has never been surveyed.

Escapement is regulated for both rivers to prevent 'over-escapement'. The current regulation rule in Sakhalin Oblast, which includes Iturup Island, is based on achieving a goal of 'optimal density' of spawners (160 fish per 100 m² of spawning grounds). This escapement goal has been established as a means to maximize the natural production of chum salmon juveniles (Program of Field Observation 2003).

Historically, the management plan of Kurilskiy hatchery focused mainly on reproduction of pink salmon (around 100 million juveniles produced per year in the 1970–80s, and 50 to 70 million juveniles produced per year in the last decade). Unlike pink salmon, chum salmon were reproduced in the hatchery intermittently. During the middle of the 1980s, overharvest decreased the chum salmon population size dramatically, and Kurilskiy hatchery stopped reproduction of this species (Fig. 2). The Kurilka River chum salmon population was maintained by natural reproduction until 2003, with the exception of a few small releases from the hatchery (Fig. 2). Up until the year 2003, we consider the Kurilka River chum salmon wild. While the Rybatskaya River population has a history of

Fig. 1 Map of Kurilka River and Rybatskaya River at Kurilskiy Bay, Iturup island, Russian Federation. Note. "H" stands for the Kurilskiy hatchery



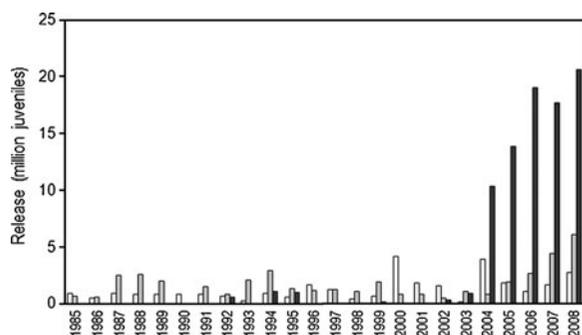


Fig. 2 Production (# of juveniles emigrating per year) of wild, natural and hatchery chum salmon juveniles in the Kurilskiy Bay system, Iturup island. *Note.* Prior to 2004, this was largely wild production, after 2007 they are juveniles produced by a mixture of wild and hatchery straying parents. *Notation:* black bars—releases from the Kurilskiy hatchery, grey bars—juveniles emigrating from spawning grounds of the Kurilka River system, white bars—wild juveniles emigrating from spawning grounds of Rybatskaya River

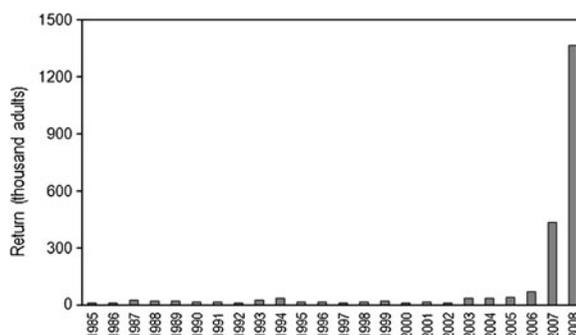


Fig. 3 Abundance of adult chum salmon returning to Kurilskiy Bay

fishery exploitation, it has never received hatchery releases and therefore we consider it entirely wild.

Recently hatchery biotechnologies have improved, and the managers of the Kurilskiy hatchery decided to apply these new technologies to augment the chum salmon stock for the benefit of the commercial fishing industry. Initially, the hatchery releases increased to 10.4 and 13.8 million chum salmon juveniles in 2004 and 2005, respectively. Production has now reached a level of ~20 million juveniles annually (Fig. 2). Efforts at limiting unlawful catch (poaching) were strengthened. It is thought that these anti-poaching efforts have contributed to an overall increase in natural production in these river systems, although this natural contribution was still small in 2004 and 2005 when the hatchery released the first large amounts of chum salmon juveniles (Figs. 2 and 3).

Samples and microsatellite markers

For DNA analysis, 33 separate sample collections (Table 1) were drawn from chum salmon populations of Kurilka and Rybatskaya rivers from 2004 to 2008 (1589 fish total). Tissues (mainly a clip of the pectoral fin) were fixed in 96% ethanol. Our sampling efforts were designed to characterize the spatial (across tributaries) and temporal (within spawning runs and across years) genetic variation (Fig. 4).

Additionally, we collected scales from returning chum salmon to determine ages by counting scale

circuli (Pravdin 1966, pp. 168–179). Ages reported here (2+, 3+ and 4+) represent years since hatching. We estimated age composition of the reproductive population by river and year for our collections (Table 1). Data on hatchery releases, catch, and escapement counts were taken from annual reports of SakhalinRybvod and SakhNIRO (institutions of the Fishery Agency of Russia), and ZAO Gidrostroy (private fishing company operating on Iturup).

All chum salmon individuals were typed using the following microsatellite loci: *Ssa197* (O'Reilly et al. 1996), *Ssa20.19* (Sanchez et al. 1996), *Ogo2* (Olsen et al. 1998), *Oke3* (Bucholz et al. 2001), *Okell* (Bucholz et al. 2001), *One101* (Olsen et al. 2000), *One103* (Olsen et al. 2000), *One109* (Olsen et al. 2000), *Ots3* (Small et al. 1998), and *Okil* (Smith et al. 1998). The fragment profiles at *One101* appeared to be identical to those at *One103*, with a constant difference of 18 bp, and thus we used a shorter variant, *One103*. Using the primers for *Okil*, we obtained two distinct zones on a gel that can be interpreted as a result of duplication followed by evolutionary molecular divergence into two microsatellite loci with identical flanking regions; both loci were used in this study with notation *Okil-1* (180–270 b.p.) and *Okil-2* (90–110 bp). The procedures for DNA extraction, amplification, fragment analysis, and standard statistics of microsatellite variation at the loci used have been described elsewhere (Afanasiev et al. 2008).

Data analyses

We used the GDA software (Lewis and Zaykin 2001) for estimating F_{ST} values and performing multi-way

Table 1 Samples for genetic analysis from populations of Kurilka River (Kurilskiy hatchery, Lebedinoe Lake, Kurilskiy Creek) and Rybatskaya River

Year	Locale	Date	Sample size	
2004	Hatchery	October 12	51	
	Rybatskaya River	October 8	50	
2005	Hatchery	October 6	50	
		October 17	51	
	Rybatskaya River	October 26	50	
		October 23	50	
2006	Hatchery	October 18	50	
		October 30	50	
		November 7	50	
	Kurilka River mouth	October 4	50	
		October 31	50	
	Rybatskaya River	October 19	50	
	2007	Hatchery	October 11	48
			October 20	50
			November 1	48
		Kurilka River mouth	October 8	48
October 17			48	
October 29			48	
November 9			48	
Lebedinoe Lake		November 8	42	
Kurilskiy Creek		October 12	48	
Rybatskaya River		October 10	48	
2008	Hatchery	October 4	48	
		October 20	48	
		October 31	48	
	Kurilka River mouth	September 29	48	
		October 9	48	
		October 14	48	
		October 21	48	
	Lebedinoe Lake	October 17	31	
	Kurilskiy Creek	October 10 and 13	48	
	Rybatskaya River	October 9	48	
October 19		48		

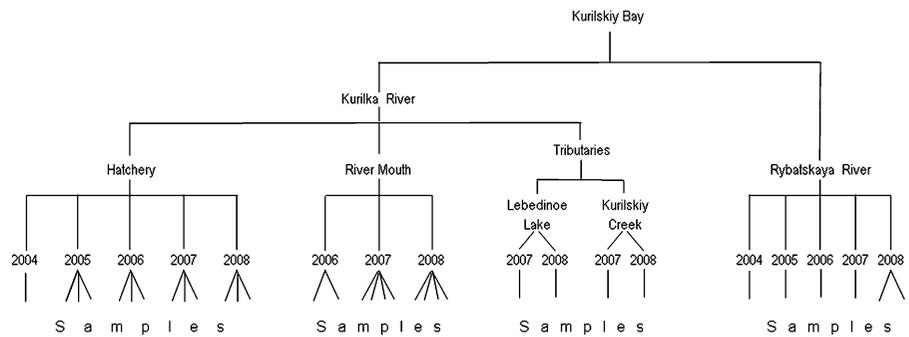
analyses on allele frequencies. The 95%-confidence intervals were obtained by bootstrapping across loci (Weir 1996). A matrix of F_{ST} -values between all pairs of samples was obtained for constructing principal component plots using SPSS software (Darren and Mallery 2005). Differences in age compositions are reported based on one-tail significance tests; the significance value is denoted by p .

Assuming the escapement to the hatchery consists of exclusively hatchery-origin fish and that the natural spawning population consists of a mixture of hatchery-origin and wild fish, the fraction f_{WA} of wild fish of age class A (A is 2+, 3+, or 4+) in the same age class of the mixture of wild and hatchery fish that are naturally spawning in the river was estimated by the formula $f_{WA} = \frac{P_{HA} - P_{RA}}{P_{HA} - P_{WA}}$, where P_{HA} and P_{RA} are the frequencies of the age class A counted among fish sampled at the hatchery that are considered as hatchery-origin and among fish that are naturally spawning in the river, respectively. The P_{WA} is a frequency of the same age class A among wild-origin fish, but its value cannot be counted directly. We estimated P_{WA} for each of the age classes 2+, 3+, and 4+ as the average age composition in the Kurilskiy Bay returning stock measured during years prior to the period of significant hatchery release of chum using available data on the years 1974–1995 (Report of SakhNIRO 2010). The average P_{WA} s during this pre-hatchery release period appeared to be 4.4%, 62.4%, and 32.6% for age classes 2+, 3+, and 4+, respectively. Here we assume the deviation from this long-term mean age composition of the run observed following large releases in years 2004–2005 was a result of returning hatchery chum salmon. Based on this, we calculated f_{WA} for age 3+ in 2007, and for both 3+ and 4+ age classes in 2008. Standard error of f_{WA} was computed by using the delta method (Cramér 1946).

Results

In the year 2004, after many years of low abundance, the release of chum salmon juveniles from Kurilskiy hatchery increased exponentially (Fig. 2). The very first indication of chum salmon expansion in population size occurred in 2006 when the frequency of fish of age 2+ that escaped to the hatchery ($24.6 \pm 2.5\%$) exceeded greatly its typical, low level of around 3 to 5%. We did not obtain samples from spawning grounds of Kurilka River that year, but instead, analyzed samples obtained from the mouth of the river. The estimated frequency of age 2+ was observed to be lower ($15.5 \pm 2.1\%$) than that observed at the hatchery ($p=0.0027$). It is highly unlikely that the lower frequency of age 2+ in the Kurilka River's mouth was due to immigration from rivers other than

Fig. 4 The structure of chum salmon samples that have been collected for genetic analysis from Kurilka and Rybatskaya rivers during 2004–2008



the Kurilskiy Bay river system because this would require an unusually high rate of between-stock straying. Therefore, the smaller contribution of age 2+ in the run observed at the Kurilka River's mouth might be explained by the presence of both hatchery and wild fish that returned back into the river that year.

The first large return of chum salmon to Kurilskiy Bay was observed in 2007 (Fig. 3), with an unusually large frequency of age 3+ represented in the run. This age was the dominant age class observed at the hatchery ($92.7 \pm 1.50\%$). Age 3+ composition in the run during this year was much greater ($p < 0.01$) than the year prior ($42.9 \pm 2.9\%$ in 2006) and the year after ($53.8 \pm 2.9\%$ in 2008). We found the frequency of age 3+ in the run in the Kurilka River's tributaries to be intermediate ($86.0 \pm 3.6\%$), but still significantly less than that observed at the hatchery ($p = 0.030$). Based on these percentages, we estimated wild chum salmon to account for $22.0 \pm 7.0\%$ of the natural spawning population in the tributaries within age class 3+ in the year 2007. This estimate, although approximate and potentially biased, suggests that the year 2007 represented a marked shift from a wild population to a hatchery-supported population in the Kurilka River.

In 2008, the return of chum salmon to the Kurilskiy Bay doubled in abundance relative to the previous year (Fig. 3) as a result of large releases from the hatchery in 2004 and 2005 (Fig. 2). Average fractions of ages 3+ and 4+ in the hatchery and in the tributaries were $53.8 \pm 2.9\%$ and $43.3 \pm 2.9\%$, and 53.3 ± 6.4 and 45.0 ± 6.4 , respectively. This age composition represents a significant shift away from the age composition of returns observed in the pre-hatchery period suggesting hatchery fish swamped the wild population. Therefore, in 2008, hatchery-origin fish of both ages represented a substantial portion of the natural spawning population in the Kurilka River.

Although noting shifts in age composition of returning salmon is an indirect method to estimate the composition of wild and hatchery-origin salmon in the population, it does provide some compelling evidence of a marked increase in abundance of hatchery-origin chum salmon in the Kurilka River in 2007 and 2008. Our data suggest these returning fish strayed from the hatchery and entered natural spawning grounds in the mainstem and tributaries of the Kurilka River, potentially competing and displacing wild salmon in these systems.

In order to genetically compare wild and hatchery-origin fish in the tributaries, we subdivided each of the samples that were drawn from Lebedinoe Lake and Kurilskiy Creek in 2007 into two subsamples based on age at return ($\geq 4+$ and $\leq 3+$). The older age class subsample represented the fish that had emigrated from the system as juveniles prior to 2004 predating the dramatic increase in hatchery releases. We assume this subsample was entirely wild. The younger age class subsample represented returns from broods dating from 2004 and thus are presumed to be mainly hatchery-origin. The two subsamples from Lebedinoe Lake differed from each other at DNA markers ($p = 0.05$). This difference is evident in the principal component plot (Fig. 5), in which the older age class subsample diverges away from the younger age class subsample. These wild Lebedinoe Lake chum salmon also appear to be diverged from the rest of the Kurilka River samples suggesting this lake population was reproductively isolated prior to hatchery expansion. Additional analysis showed the genetic profile of this age class subsample ($\geq 4+$), which is considered as wild, is close to that of the beach-spawning form of chum salmon (data not shown). This result is consistent with our previous study that described genetic divergence between river- and beach-spawning forms of chum salmon using the

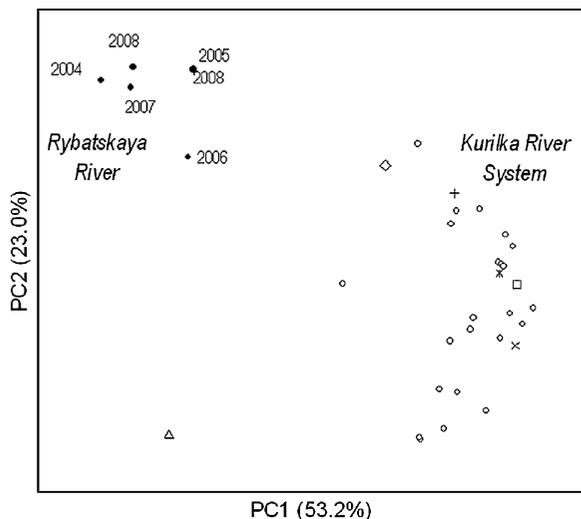


Fig. 5 PC-plot of chum salmon samples based on microsatellite data. Genetic divergence is evident between the Kurilka River (hatchery-influenced population) and the neighboring wild population in Rybatskaya River. Genetic swamping from the expanding hatchery population is evident in the beach spawning population found in Lebedinoe Lake in the Kurilka River drainage (see text for additional description). *Notation:* Rybatskaya River (filled circles); Kurilka River, the hatchery and the mouth (open circles); Lebedinoe Lake: subsample of age class $\leq 3+$ in 2007 (diamond), that of age class $\geq 4+$ in 2007 (triangle), 2008 (open square); Kurilskiy Creek: subsample of age class $\leq 3+$ in 2007 (cross), that of age class $\geq 4+$ in 2007 (plus), 2008 (asterisk). PC1 and PC2 are principal components (loadings are in the brackets)

same set of microsatellite markers (Report of Zhivotovsky 2006; Kaev et al. 2008). The 2008 sample from Lebedinoe Lake was within the cluster containing the rest of the samples (Fig. 5). These results suggest that Lebedinoe Lake chum salmon was swamped by a rapidly expanding hatchery population in this river system, representing a potential loss of biological diversity in the Kurilka River. Unlike subsamples from Lebedinoe Lake, the analogous subsamples from Kurilskiy Creek did not differ genetically from each other and from the hatchery fish (see also Fig. 5). We suspect this is a result of the fact that genetic variation among river-spawning populations of chum salmon in this river system is very small, and that Kurilskiy Creek is located close to the hatchery and is very likely to receive fish straying from the hatchery.

It is impossible to estimate how much the Kurilka River chum salmon population was genetically subdivided prior to the large returns of hatchery fish. Nevertheless, it is still structured genetically, with

statistically significant within-run temporal differentiation. A two-way hierarchical variance analysis revealed no significant between-year differences, but did discriminate significant within-run variation. We determined that both the hatchery population and the mixed hatchery-wild population sampled at the Kurilka River mouth were both structured genetically. The F_{ST} for both collections had a value of 0.43%, with wider confidence interval for the mixed run at the river mouth, [0.07, 0.97], compared to the hatchery returns, [0.17, 0.78]. This genetic heterogeneity within spawning runs probably reflects the existence of discrete subpopulations with different run-timing that might have existed in the Kurilka River population prior to the current expansion of the hatchery program. The F_{ST} -value across annual runs was positive, but not statistically significant ($F_{ST}=0.14\%$, confidence interval [-0.02, 0.31]), suggesting little or no interannual genetic variation.

The Rybatskaya River population, sampled during 2004–2008, was greatly diverged genetically from the Kurilka River population (Fig. 5), with $F_{ST}=0.90\%$ (confidence interval [0.57, 1.27]). As reported above for the Kurilka River, we did not find significant between-year genetic differentiation in the Rybatskaya River population. We might expect a shift in allele frequencies in the latter part of this time series if there was increased gene flow from an expanded hatchery population in a neighboring river system. These results suggest the Rybatskaya River population is independent of the Kurilka River population. We found significant differences in age composition ($p<0.01$) between the Rybatskaya and Kurilka River runs in 2007 and 2008, providing additional support that these two populations are independent.

Discussion

The management unit of chum salmon homing to Kurilskiy Bay consists of two ecologically and genetically distinct populations reproducing in Kurilka and Rybatskaya rivers that drain into the bay. Before the first large returns in 2007 and 2008, the Kurilka River population was nearly wild and composed of several spawning components in the river's mainstem and tributaries, including the genetically distinct beach-spawning life history form of chum salmon in Lebedinoe Lake. Our demographic and genetic

results suggest that the current Kurilka River population of chum salmon consists of two genetically similar components, namely the fish that migrate to the hatchery and hatchery-origin fish that spawn naturally in the system. Although it is difficult to demonstrate unequivocally without a marking program and supporting field studies, we suggest these hatchery-origin chum salmon that are straying to natural spawning grounds have replaced the wild population that once existed in this river. The most dramatic case is the genetic swamping of a unique and rare beach-spawning population in Lebedinoe Lake. Based on our results, we infer that this swamping will have deleterious impacts on this locally-adapted, unique population of wild chum salmon. Indeed, it is still an open question as to whether natural reproduction occurring in this river-lake system since the hatchery expansion is successful. Ivankov (1985) and Kaev and Romasenko (2003) describe important phenotypic difference between the river- and beach-spawning chum salmon in Iturup and Kunashir Islands, with the beach-spawning population exhibiting larger and deeper bodied forms, with females carrying smaller eggs. Phenotypic adaptations to beach spawning have also been observed in beach-spawning populations of sockeye salmon (*O. nerka*) in Bristol Bay, Alaska (Blair et al. 1993). It is highly likely that reproductive success of hatchery strays in this system is poor, underscoring the importance of developing and implementing a recovery plan for the Lebedinoe Lake chum population. It is worth mentioning that the beach-spawning form of chum salmon is unusual and very rare; it has been described in Asia on Iturup and Kunashir islands only (Ivankov 1985; Kaev and Romasenko 2003), and in North America in the Yukon territory (Wilson 2006).

The Rybatskaya River population is relatively small and can be considered as wild except for direct fisheries exploitation and fishing regulation to avoid over-escapement. It greatly differs genetically from the Kurilka River population, and thus they are likely to be reproductively isolated from each other, although a small gene flow is still possible given the large amount of hatchery fish returned to the bay. In other words, the chum salmon of Kurilskiy Bay can be regarded as an ecologically and genetically structured metapopulation.

This study shows that the effect of an artificially enhanced population on neighboring wild populations

within a watershed can be very rapid following only a couple of years of large returns of hatchery fish. We suggest here that this level of straying may be sufficient to completely replace wild populations of chum salmon. Short-term effects are generally limited to neighboring populations, but longer-term effects are possible on more distant wild populations. Therefore, ecological and genetic monitoring of hatchery and neighboring naturally produced populations are important for management of enhanced salmon stocks and we encourage the development of precautionary measures to conserve wild populations and to support natural reproduction.

Since the expansion in size of the hatchery population, the overall return of chum salmon to Kurilskiy Bay has increased exponentially. Therefore, one of the measures that might support natural reproduction of chum salmon would be an increase in production of natural juveniles from spawning grounds through larger escapements. Indeed, the target ('optimal') level of escapement enforced through the current regulation rule in Sakhalin Oblast (which includes Iturup Island) is set at 160 fish per 100 m² of spawning grounds (Program of Field Observation 2003). The spawning grounds in Kurilka and Rybatskaya rivers amount to 20000 and 3600 m², respectively, and we observed in 2007–2008 around 150 spawning fish per 100 m², which is very close to the official 'optimal value'. Assuming a sex ratio of 1:1, fecundity of 2000 fertilized eggs per female, and survival rate (from egg to emigrating juveniles) of 20%, the current potential of naturally produced juveniles from Kurilka and Rybatskaya rivers is around six and one million emigrating juveniles, respectively, which is roughly a third of the current annual release of chum salmon juveniles from the hatchery.

The regulation rule assumes the 'optimal' escapement for naturally reproduced chum salmon to be constant regardless of the nature of the population. We question whether this value is appropriate and whether it applies to the river systems in our study area. Indeed, the carrying capacity of spawning grounds may vary markedly across rivers, and may be above the currently suggested 'optimal' value for a particular river's environment. Thus, there could potentially be untapped natural production from these systems and current exploitation rates and regulation rules could be contributing to under-escapement in

some cases. One of the authors of this paper (LZh) has conducted a multi-year analysis of chum salmon escapement and juvenile production in the Rybatskaya River, and preliminary results suggest that the system is currently 'under-escaped', and overall natural production could be increased through increase escapement into this river system. Therefore, more research is needed to estimate more meaningful targets of escapement for natural and wild populations of the Kurilskiy Bay stock of chum salmon.

One can argue, based on genetic heterogeneity of the Kurilka River population, that natural populations of chum salmon of Kurilka River have the ability for local adaptation and development of a genetic structure characteristic of a wild population. In particular, the beach environments of Lebedinoe Lake are unusual for chum salmon, except for the beach-spawning form, and populations using these habitats are subjected to unique forms of selection that may differ markedly from the river-form and from the hatchery population. Therefore, a more productive use of the Lebedinoe Lake resources can be achieved by restoration of the beach-spawning form of chum salmon. The beach-spawning populations of Iturup Island are closer genetically to each other than to the river-spawning populations (unpublished), suggesting that these fish represent a unique evolutionary lineage. Since the lake-spawning form of Lebedinoe Lake has been genetically swamped by the hatchery population, the only way to restore it would be using the sources of neighboring populations. It is unlikely that this form can be restored naturally by immigrants from other beach-spawning populations of chum salmon in Iturup Island that are known to exist (our observations) because natural between-stock straying is weak. Another possibility might be transfer to Lebedinoe Lake adult fish or/and artificially reproduced fry from a genetically and ecologically similar neighboring beach-spawning population of chum salmon in the island.

The wild status of Rybatskaya River chum salmon is more secure given they appear to be reproductively isolated from the Kurilka River system, suggesting these fish represent an independent population unit. However, we acknowledge the limitation of the current study in detecting hatchery straying and gene flow. The mouth of this river is less than 4 km distant from the mouth of the Kurilka River, suggesting that straying may be occurring (Fig. 1). In order to

estimate the magnitude of straying of hatchery fish, it is important to develop a marking program on the Kurilskiy Bay stock and neighboring stocks of chum salmon that includes monitoring of both enhanced and naturally reproduced populations.

The challenge for the future in this system is to strike a balance between natural and artificial reproductive components of this exploited stock and explicitly understand how they interact, which was a major theme of the State of the Salmon conference. Although our study has its limitations, it does provide new insight into the ecological and genetic effects of a rapidly increasing hatchery population. These challenges are shared among many hatchery-supported salmon fisheries in the North Pacific region. We hope this study will encourage more focused attention and debate on the sustainability of salmon fisheries that exploit a combination of wild and hatchery salmon.

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