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**Hybrids between chum *Oncorhynchus keta* and pink *O. gorbuscha* salmon:  
age, growth and morphology and effects on salmon production**

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Running head: INTERSPECIFIC HYBRIDIZATION AND ITS EFFECTS

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Mature hybrids between chum salmon *Oncorhynchus keta* and pink salmon *O. gorbuscha*, which were identified by an intermediate colour pattern, were caught at the Kurilskiy Hatchery, Iturup Island, Russia. Most of them were female and 3 years old (a partial freshwater year and two marine years), which is intermediate between the ages of maturity of the parental species. The hybrids exceed both parental species in the rate of growth, are large in size and robust and might successfully compete for mating in the wild or be chosen for artificial reproduction. The ratio of the scale length over width,  $R$ , is oblate ( $R < 1$ ), whereas scales of the parental species are prolate ( $R > 1$ ). From scale analyses, the C.V. in body size of hybrid females at the second marine year is twice that of *O. keta*, which suggests developmental instability in the hybrid. A dynamic model predicted that continuing hybridization at a low rate does not produce a substantial hybrid load due to selection against advanced-generation hybrids and backcrosses. A high hybridization rate, however, may be an additional risk for genetic management and should be taken into account in programmes of artificial reproduction of Pacific salmon *Oncorhynchus* spp., although such hybrids might have commercial use in confined production systems.

Key words: hatchery; interspecific characters; management production model; scale length; scale width.

## INTRODUCTION

Natural hybridization occurs in salmonids, particularly between Pacific salmon species *Oncorhynchus* spp. Suckley 1861. Hybrids between chum salmon *Oncorhynchus keta* (Walbaum 1792) and pink salmon *Oncorhynchus gorbuscha* (Walbaum 1792) have been caught in the open sea (Numachi *et al.*, 1979; Abe *et al.*, 2001). Fertile inter-specific hybrids have been obtained in experiments (Foerster, 1935; Smirnov, 1969; Chevassus, 1979; Joyce *et al.*, 1994). Some  $F_1$  hybrids survive and return to spawn (Chevassus, 1979), but the  $F_2$  generation and the progeny of backcrosses display low viability (Foerster, 1935; Simon & Noble, 1968; Smirnov, 1969). The frequency of interspecific hybridization may be increased by a breakdown in reproductive isolation following the introduction of a species into a catchment in which it is not native, after disturbance of the environment (Garcia & Veerspoor, 1989), or after escape from aquaculture (Pavlov, 1959; Kamyshnaya, 1961; Matthews *et al.*, 2000).

The ability of inter-specific hybrids to fertilize ova successfully depends upon a number of factors. For example, hybrids between *O. keta* and *O. gorbuscha* can attain the size of the larger parent (*O. keta*) and spawn at an earlier age (Smirnov, 1953; Kamyshnaya, 1961). These and other features that distinguish the hybrids from their parents may provide them success in spawning, especially if frequency-dependent selection occurs, although distinct mating rituals may reduce interspecific pairing. Even if natural hybridization is rare, but acts repeatedly over generations, it may allow foreign genes to introgress into a species, despite negative natural

selection and carry linked selectively neutral genes. Artificial reproduction might increase the frequency of hybrids released or escaping into nature. If the spawning time of two species overlap and little care is taken to separate species the increase in flow of the foreign genes may decrease the survival of the recipient population. Also, cultured fish might hybridize with and severely affect nearby small populations of this recipient species.

Although there is a long history of studying hybrids in *Oncorhynchus* spp., some questions remain open. Among those are: (1) to what degree do hybrids differ from their parental species phenotypically, (2) how fast do they grow in the ocean and (3) what demographic and genetic consequences might be expected from recurrent hybridization in a stream? These questions were addressed by using a case study of hybrids between *O. keta* and *O. gorbuscha* and developing a general model of genetic introgression to make quantitative estimates of the consequences of introgression at different survival rates for advanced-generation hybrids.

## MATERIAL AND METHODS

Eight mature putative hybrids between *O. keta* and *O. gorbuscha* were identified in October 2011 at the Kurilskiy Hatchery (Iturup Island, Russia; 45° N; 148° E) at the time of artificial reproduction of *O. keta*. The fish had small scales and dark spots on the caudal fin, which are typical of *O. gorbuscha*, but vertical lilac stripes across the body and large body size, both of which are typical of mature *O. keta*. The first two fish, 2 and 3 (see Table 1), were found in a sample of *O. keta* taken for a routine biological analysis at the hatchery. The

other six hybrids, 1 to 6 (Table I), were subsequently found among the hatchery fish used for artificial reproduction. The eight hybrids appeared and were identified between 15 and 17 October, 2011 following the return of *O. gorbuscha*. They were identified among *c.* 3000 mature *O. keta*.

Fin clips from the hybrids and parental species were fixed in 96% ethanol. In order to confirm the putative hybrids, PCR primers were used to amplify microsatellite markers OMM-1050, which is diagnostic for the respective species (Zhivotovsky *et al.*, 2013) and OMM-1015, which has different allele size ranges for *O. keta* and *O. gorbuscha*. DNA isolation, PCR amplification and genotyping procedures are described in Zhivotovsky *et al.* (2013). Identification of the sex of the parents of the hybrids was accomplished with diagnostic length polymorphisms in two regions of the mitochondrial DNA, *ND3–ND4* and *COI–COII/A8*, which were amplified with specific primers (Gharrett *et al.*, 2001) and cut with restriction enzymes Dde I, Msp I and Rsa I. The lengths of the restriction fragments were compared with those obtained for *O. gorbuscha* and *O. keta* (Churikov *et al.*, 2001).

Because the rate of scale deposition is often related to growth, the numbers and spacing of circuli on scales are commonly used to estimate the age and growth history of fishes (Hile, 1970). Scales were taken from rows two to four in the preferred area above the lateral line (MacLellan, 1987). Suitable scales were measured along their radii. Fork length ( $L_F$ ) at age  $t$  was backcalculated based on the Fraser-Lee model and the North Pacific Fisheries Commission (INPFC, now the North Pacific Anadromous Fish Commission, NPAFC) method (Martinson *et al.*, 2000). The total scale size and the scale shape were characterized by length

and the ratio of its length to width ( $R$ ). The scale analysis also was applied to the parental species. The *O. keta* analysed were from the same sample (15 October 2011) in which the first two hybrids were discovered. A sample of *O. gorbuscha*, taken at the same location, Kurilskiy Hatchery, on 14 August 2014, represented the even-year broodline to which the *O. gorbuscha* parents of the hybrids belonged.

To understand the consequences of recurrent interspecific crosses, a dynamic model (Supporting Information) of *O. keta*  $\times$  *O. gorbuscha* hybridization was developed. Survival of the *O. keta*  $\times$  *O. gorbuscha*  $F_1$  hybrid is similar to those in parental species, whereas second and advanced-generation hybrids and backcrosses have low survival (Simon & Noble, 1968; Smirnov, 1969). The reduced viability is probably a consequence of aneuploidy, as reflected by the unstable chromosome number observed in the surviving  $F_2$  hybrids (Simon & Noble, 1968). With the model, analyses were conducted that used low survivals of second-generation and other progeny of  $F_1$ -hybrids to evaluate the influence of hybrids on overall survival rate in the recipient population. Hybrid load, which is defined as the decrease in an average survival in the population due to a relatively high mortality of advanced-generation hybrids and backcrosses (Christiansen *et al.*, 2005), was estimated for introgression into the population of *O. gorbuscha*.

## RESULTS

The eight putative *O. keta* × *O. gorbuscha* hybrids each possessed the diagnostic marker alleles at loci *Omm-1050* and *Omm-1015* that were expected in  $F_1$ . At most, only 25% of advanced-generation hybrids would be expected to have this combination of markers.

## PHENOTYPIC FEATURES

All hybrids were mature and ready to spawn. All were age 2+ years, or 0.2 in another notation (+ and 0 mean a partial year in fresh water followed by 2 years at sea), that is, 3 years old. Therefore, the age of maturity of the hybrids was intermediate to those of the parental species: *O. gorbuscha* return after 2 years (age 0.1 years) and most *O. keta* in the Kuril Islands return at 4 or 5 years (ages 0.3 or 0.4 years). Seven of the eight fish were females. The adipose fin of the hybrid male was larger than those of the hybrid females. Five of the seven fish for which mitochondrial data were obtained had *O. keta* mothers; the mothers of the other two fish were *O. gorbuscha* (Table I). All hybrids had dark spots on the caudal fin, which is a characteristic of *O. gorbuscha* and lilac strips across the body as in mature *O. keta*. The hybrids were larger in body size than *O. gorbuscha* and nearly the same size as *O. keta*, although the *O. keta* in the same spawning run were older by 1 or 2 years (Table II).

## GROWTH RATE

Backcalculation of size at age from scales suggests that the hybrids grew faster than the parental species: the  $L_F$  of hybrid females at both one and two marine years,  $L_1$  and  $L_2$ ,

significantly exceeded the sizes of the parental species at those ages (Table II). Moreover, the difference in body size accelerated during the second marine year:  $L_2 - L_1$  was larger in hybrids. In addition, the C.V. in body size of hybrid females exceeded those in the parental species, especially for growth rate in the second marine year,  $L_2 - L_1$  (Table II). The single hybrid male could not be compared statistically with other male cohorts.

## SCALE SHAPE

Another distinguishing feature of the hybrids was the size and shape of the scales as compared with those of *O. keta* and *O. gorbuscha*. The scale length in female hybrids was similar to that in *O. gorbuscha*, (mean  $\pm$  S.D.)  $3.3 \pm 0.2$  and  $3.4 \pm 0.2$  mm, respectively, whereas their scales were smaller than in *O. keta*,  $5.2 \pm 0.1$  mm for age 0.3 years and  $5.6 \pm 0.2$  mm for age 0.4 years (as in Simon & Noble 1968). The scale shape, computed as the ratio  $R$ , was oblate in the *O. keta*  $\times$  *O. gorbuscha* hybrids (mean  $\pm$  S.D.;  $R = 0.82 \pm 0.05$ ), but prolate in the parental species ( $R = 1.38 \pm 0.08$  in *O. gorbuscha*; and  $1.16 \pm 0.04$  and  $1.11 \pm 0.05$  in *O. keta* at ages 0.3 and 0.4 years, respectively).

## HYBRID LOAD

If the rate of hybridization is low, results of the model suggest that the hybrid load will not be high and will depend weakly on the mortality of advanced-generation hybrids and



backcrosses (Fig. 1). At higher levels of introgression (in excess of 5%), however, the hybrid load can be substantial (20% or more).

## DISCUSSION

One of the research objectives of this study was to quantify the extent to which the  $F_1$  hybrids between *O. keta* and *O. gorbuscha* differ from their parental species. The hybrids (seven females and one male) differed from both parental species and were intermediate in colour pattern and scale shape. The hybrid male had a larger adipose fin than the hybrid females, as in all pure species of *Oncorhynchus* spp. (Beacham & Murray, 1983). The hybrids were robust, like *O. keta* and could be confused with true *O. keta* if attention was not paid to identifying hybrids. Such hybrids might successfully compete at natural spawning sites as well, since they are large, active and have developed eggs and sperm. Their distinctive morphological features might increase their reproductive fitness component *via* frequency-dependent assortative mating. The hybrids between *O. keta* and *O. gorbuscha* that were analysed had higher rates of growth as compared with both parental species, matured at the third year (0.2) [an observation that corresponds to that of Simon & Noble (1968) that most hybrid females return in the third year], exceeded the size of individuals of *O. gorbuscha* (age 0.1) and nearly attained the size of *O. keta*, although the majority of *O. keta* were of ages 0.3 or 0.4.

A second objective was to estimate the relative oceanic growth rate of hybrids. From scale analysis it was projected that hybrids have faster growth and earlier age at maturation than *O. keta* (Foerster, 1935; Smirnov, 1969; this study) but a lower survival component of fitness. This raises questions about the evolutionary fate of mixed genomes and about potential risks for salmonid management, as well as about their potential commercial utility.

The final question of this study considered the effect of recurrent hybridization on a recipient stock. Hybrids between the even and odd-year brood lines of *O. gorbuscha* demonstrated lower second-generation returns than the control (outbreeding depression; Gharrett *et al.*, 1999). Even stronger outbreeding depression in the progeny of inter-specific hybrids should be expected. Nevertheless, mixed *O. keta* × *O. gorbuscha* genomes may pass through multiple generations because the hybrids are partially fertile and produce backcross progeny, albeit with lower survival than  $F_1$  hybrids (Foerster, 1935; Smirnov, 1953, 1969; Pavlov, 1959; Kamyshnaya, 1961; Simon & Noble 1968; Bakkala, 1970; Chevassus, 1979). The model was developed for specific life spans (2 years for *O. gorbuscha* and mixed 4 and 5 years for *O. keta*) but could be formulated for other combinations.

It is possible to release artificially produced hybrids into the wild. For Kamyshnaya (1963) reported the discovery, in 1961, of mature *O. keta* × *O. gorbuscha* hybrids at the Taibolskiy Hatchery on the Kola River (which drains into the Barents Sea, Arctic Ocean). Kamyshnaya (1963) suggested that the hybrids had occurred among fertilized eggs of *O. gorbuscha* and *O. keta* transplanted to the rivers of the Kola Peninsula from Sakhalin Island hatcheries at the end of the 1950s. Many *O. gorbuscha* × *O. keta* hybrids were released to

rivers in the 1950s from Sakhalin Island hatcheries (Smirnov, 1953, 1969; Pavlov, 1959; Kamyshnaya, 1961). The hybrids in the present study might have been natural or mistakenly produced at the Kurilskiy Hatchery, which cultures both *O. gorbuscha* and *O. keta*, whose spawning runs overlap.

Release of artificially produced hybrids into the wild may bring potential long-term negative effects if the rate of hybridization is high. Under a naturally low hybridization rate (*c.* 1% or lower), the accumulated hybrid load does not exceed a few per cent. If artificial reproduction maintains higher rates of hybridization (*c.* 10%), however, then survival of the recipient population may decrease substantially and would require some form of mitigation (McClelland *et al.*, 2005). It is conceivable that cultured, for example, *O. keta* could severely affect nearby small native populations of, for example, *O. gorbuscha*. This issue raises concerns about the prospect of the by-product hybrid *Oncorhynchus* spp. for ocean ranching.

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## Supporting Information

A dynamic model of interspecific hybridization.

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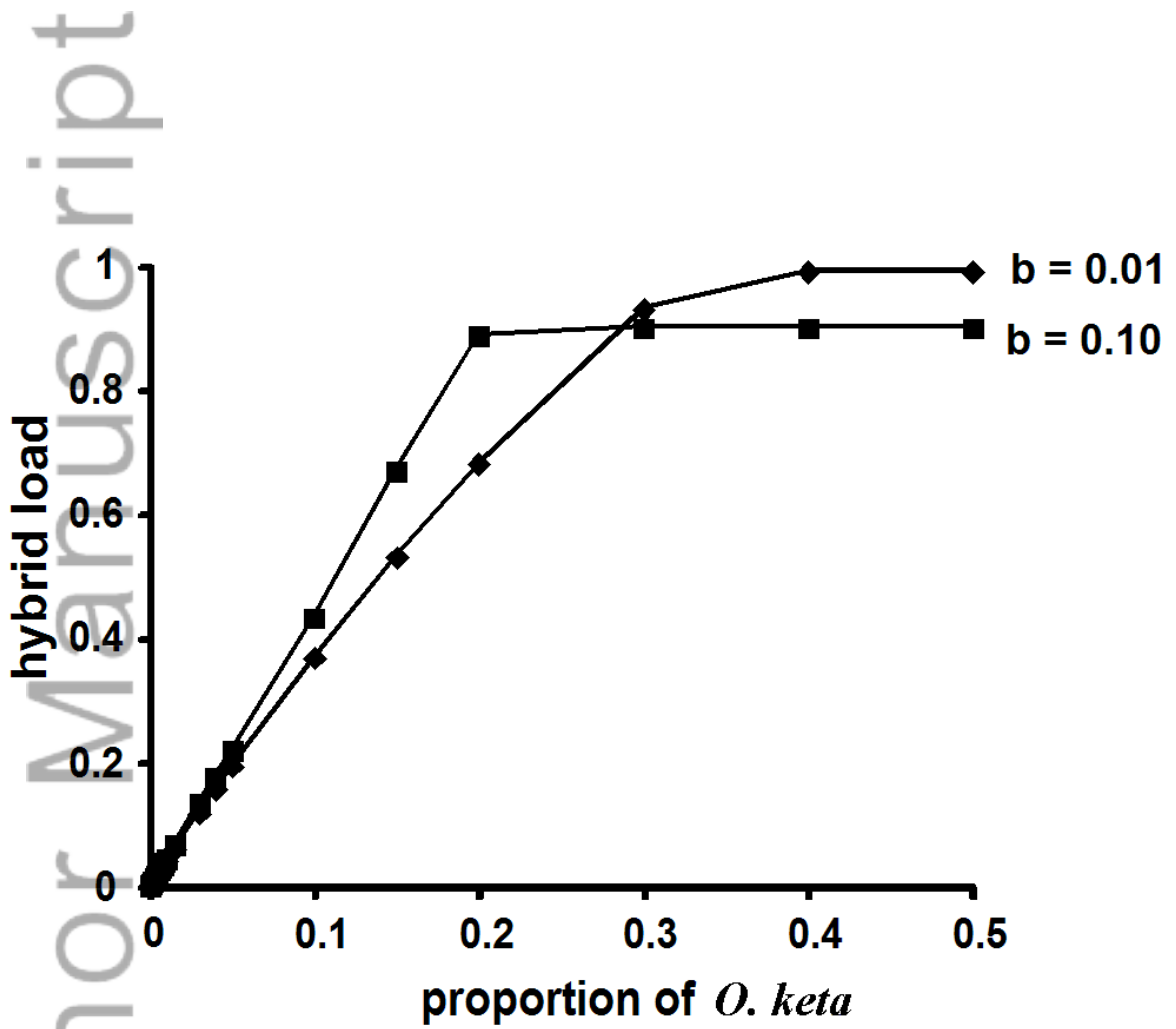


Figure 1.tif



## FIGURE CAPTION

FIG. 1. Model: hybrid load in a population of *Oncorhynchus gorbuscha* after 20 years of recurrent hybridization with *Oncorhynchus keta* at a proportion and for which survival of second and advanced-generation hybrids and backcrosses is (◆)  $b = 0.01$  and (■)  $b = 0.1$ .

Typesetter:

- 1 Delete  $b = 0.01$  and  $b = 0.10$ .
- 2 Change hybrid to Hybrid and proportion to Proportion.

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TABLE I. Description of the hybrids between *Oncorhynchus keta* and *O. gorbuscha* caught at the Kurilskiy Hatchery, Iturup Island, Russia between 15 and 17 October 2011

Hybrids	Sex	Age at capture <sup>1</sup> (years)	$L_F$ at capture (cm)	Size of the adipose fin	Dam	Sire
2	Female	0.2	66	Small	<i>O. keta</i>	<i>O. gorbuscha</i>
3	Female	0.2	72	Small	No PCR product <sup>2</sup>	
1	Female	0.2	64	Small	<i>O. keta</i>	<i>O. gorbuscha</i>
2	Female	0.2	66	Small	<i>O. keta</i>	<i>O. gorbuscha</i>
3	Female	0.2	68	Small	<i>O. keta</i>	<i>O. gorbuscha</i>
4	male	0.2	77	Large	<i>O. gorbuscha</i>	<i>O. keta</i>
5	Female	0.2	65	Small	<i>O. gorbuscha</i>	<i>O. keta</i>
6	Female	0.2	64	Small	<i>O. keta</i>	<i>O. gorbuscha</i>

<sup>1</sup>0.2 indicates one freshwater year and two marine years for a total of three.

<sup>2</sup>PCR products from the mitochondrial DNA were not produced, but microsatellite locus Omm-1050 was amplified to identify 3.

$L_F$ , fork length.

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TABLE II. Mean ( $\bar{x}$ )  $\pm$  S.D. and C.V.  $\pm$  S.E. of the estimated fork length ( $L_F$ ) at the first ( $L_1$ ) and second ( $L_2$ ) marine years of life and their difference ( $L_2 - L_1$ ) in hybrid and parental *Oncorhynchus keta* and *O. gorbuscha*

Category	Sex	Sample size (n)	Age at capture (years)	$L_F$ (cm) at capture	Estimated $L_F$ at the marine stage of life <sup>1,2</sup>					
					$L_1$ , 1st year in sea		$L_2$ , 2nd year in sea		$L_2 - L_1$	
					{ (S.D.)	C.V. $\pm$ S.E.	{ (S.D.)	C.V. $\pm$ S.E.	{ (S.D.)	C.V. $\pm$ S.E.
<i>O. keta</i>	Female	10	0.3	64.9 $\pm$ 2.6	31.1 $\pm$ 1.6	5.3 $\pm$ 1.2	46.2 (2.4)	5.2 $\pm$ 1.2	15.1 $\pm$ 2.0	13.5 $\pm$ 3.0
		11	0.4	68.3 (2.1)	30.1 (2.8)	9.4 $\pm$ 2.0	46.1 (2.1)	4.6 $\pm$ 1.0	16.0 (1.7)	11.1 $\pm$ 2.4
	Male	11	0.3	68.0 (2.9)	30.1 (2.3)	7.7 $\pm$ 1.6	46.6 (4.4)	9.7 $\pm$ 2.0	16.5 (3.1)	19.2 $\pm$ 4.1
		10	0.4	73.4 (5.4)	30.0 (1.6)	5.3 $\pm$ 1.2	48.2 (4.3)	9.1 $\pm$ 2.0	18.2 (3.5)	19.6 $\pm$ 4.4
<i>O. gorbuscha</i>	Female	5	0.1	49.2 (3.1)	33.5 (1.3)	4.0 $\pm$ 1.3	–	–	–	–
	Male	10	0.1	50.5 (4.0)	34.5 (1.9)	5.7 $\pm$ 1.3	–	–	–	–
Hybrids	Female	7	0.2	66.4 (2.8)	37.7 (3.3)	9.1 $\pm$ 2.4	59.5 (4.9)	8.5 $\pm$ 2.3	21.8 (5.3)	25.4 $\pm$ 6.8
	Male	1	0.2	77.0	34.6	–	59.6	–	25.0	–

Comment [J1]: Change all

<sup>1</sup>Estimated lengths of hybrid females exceeded those of the parental species with one-tailed significance levels ( $P < 0.05$ ) according to Wilcoxon-Mann-Whitney  $U$ -tests.

<sup>2</sup>C.V. in hybrid Females were significantly Larger ( $P<0.05$ ) than those in the parental species according to a Fisher combined test performed on significance values obtained with  $t$ -tests.