Interspecific hybridization of salmonid fish. I. Hatching and survival up to the 15th day after hatching in F1 generation of hybrids

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INTERSPECIFIC HYBRIDIZATION OF SALMONID FISH

I. HATCHING AND SURVIVAL UP TO THE 15TH DAY AFTER HATCHING IN F 1 GENERATION HYBRIDS

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ABSTRACT

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Artificial hybridizations were carried out with 17 combinations using six species of Salmonidae, namely chinook and coho salmon, rainbow and brown trout, Atlantic salmon and brook trout. Success at the eyed stage, survival rates up to the 15th day after hatching, length of the incubation period and dispersion of hatching times were examined with reference to monospecific control lots.

Success and survival rates of hybrids were found to be inferior or at the best similar to those of parental species. Significant maternal effects were observed within most types of crosses.

Highly variable interaction factors were found to influence the length of incubation of hybrids, which could exceed that of either parental species. The dispersion of hatching times was greater in hybrids than in pure species and tended to be negatively correlated to survival.

A few types of hybrids showed promising results at the end of the experiment and their potential interest for aquaculture is discussed.

INTRODUCTION

In natural environment, interspecific hybridization among salmonids may be considered as a process leading to the elimination of some species through introgression (Behnke, 1968, 1970; Nyman, 1972). It also appears to be a way of obtaining new genotypes with features of interest both for fisheries management (Smith, 1972) and for aquaculture. Exact information on these hybrid potentialities is therefore of interest to fish farmers using traditional or more modern aquaculture techniques.

A large amount of research work has been carried out on this subject since the beginning of the century. However, the bibliographical reviews of Dangel et al. (1973) and Chevassus (1979) point out that a number of hybridizations, especially intergeneric ones, have never been attempted. They also show that experimental results are sometimes difficult to interpret due to lack of control crosses from the same parents under the same environmental conditions.

This report studies some characteristics of a number of salmonid hybrids to determine which might be used in aquaculture or in wild stocking and to appreciate the risks of introgression following the introduction of foreign species in waters already inhabited by salmonids, should interbreeding occur.

MATERIAL AND METHODS

Two species of the genus *Oncorhynchus* (*O. tsawytscha*, the chinook salmon and *O. kisutch*, the coho salmon), three of *Salmo* (*S. gairdneri*, the rainbow trout, *S. trutta fario*, the brown trout, and *S. salar*, the Atlantic salmon) and one of *Salvelinus* (*S. fontinalis*, the brook trout) were used in this study.

Brood stocks were obtained from the following hatcheries: yearling chinook males and 2-year old coho males and females from the Moulin-du-Roy hatchery at Touvre (Charentes); three-year old landlocked Atlantic salmon from the state hatchery at Augerolles (Puy-de-Dôme); yearling and 2-year old brook trout, 3-year old rainbow trout and brown trout from the I.N.R.A. hatcheries at Jouy-en-Josas (Yvelines) and Saint-Pée-sur-Nivelle (Pyrénées-Atlantiques).

Several experimental sets were initiated at the I.N.R.A. hatcheries between the end of November 1976 and the beginning of January 1977. Ova were stripped from individual females and the spawn was divided into subsamples; one was fertilized with sperm from the same species and the others were used for hybridization. Sperm from 3 to 5 males was mixed and subsampled for the corresponding types of crosses. We could thus estimate the individual maternal effect as well as determine any sign of poor sperm or ova quality from the control. However, due to mortalities and differences between spawning periods, several crosses could not be carried out or failed to give adequate data.

Fertilization and incubation were carried out using standard hatchery procedures. Recirculated water at a constant temperature of 8°C was used at Jouy-en-Josas, while incubators at Saint-Pée-sur-Nivelle were provided with filtrated pond water at a temperature varying between 5 and 13°C and averaging 9°C during the incubation period.

Numbers of dead and live eggs in each lot were estimated at the eyed stage from the volumes of water displaced by total samples and subsamples of 100 eggs. Eggs were considered as live when they showed embryonic eyes and blood vessels. Subsequent mortality was determined by actual count. Hatching was considered to be successful if the yolk sac emerged from the egg envelope.

The last count of survivors was 15 days after the mid-hatching date. Three variables were computed:
(1) success at the eyed stage,
(2) survival rate from the eyed stage to hatching, and
(3) survival rate from hatching to the 15th day after hatching.

At Saint-Pée-sur-Nivelle, the numbers of hatched alevins were recorded once or twice daily. Water temperature was recorded by a thermograph during incubation, which permitted rough standardization of the hatching curves of the various groups, using a common day-degree unit. This day-degree correction does not have an exact value (Blaxter, 1969), but was mainly used to compare types of crosses initiated simultaneously. Two variables were obtained from these data:
(1) length of the incubation period (LIP), measured in day-degrees from fertilization to mid-hatching time,
(2) dispersion of hatching times (DHT), measured in day-degrees between the 5% and 95% hatching points.

Data were processed with standard statistical methods (Snedecor and Cochran, 1967), but prior to any study, all data from abnormally bad spawns (less than 40% success at the eyed stage in the control lot) were discarded. The G-test (Sokal and Rohlf, 1969) was used to compare raw numbers of eyed eggs and alevins. Percentages were analyzed after the angular transformation to stabilize the variances of binomial origin. Student's t-test, linear regression and correlation analyses were used for paired hybrid-control comparisons. Since the number of individuals sampled could vary from one lot to the other, average sample size was calculated for any given type of cross as the harmonic mean (reciprocal of the arithmetic mean of reciprocals) of the sizes of the corresponding lots (Snedecor and Cochran, 1967).

RESULTS

Success and survival rates

Results obtained for the various types of crosses are presented in Tables I, II and III. Table IV summarizes the relative rates of hybrid success as compared to control lots over the whole experiment.

Crosses with Oncorhynchus kisutch

Coho females gave successful hybrid progeny only with the chinook salmon. Slightly lower survival rates for these hybrids were not significantly different from the controls.

Crosses using coho males and rainbow females gave good results, although survival rates were lower than those of pure rainbow trout control groups (averages up to the 15th day after hatching: 54% among hybrids vs 90% in corresponding controls; significant difference: $p = 0.01$).

TABLE I

Rate of success at the eyed stage

♀	♂	*Oncorhynchus*		*Salmo*			*Salvelinus*
		tsawytscha (chinook s.)	*kisutch* (coho s.)	*gairdneri* (rainbow t.)	*trutta* (brown t.)	*salar* (A. salmon)	*fontinalis* (brook t.)
Oncorhynchus kisutch (coho s.)	n_f	2	7	6	6	6	3
	n_o	78	65	87	103	110	166
	p	57.3	74.9	0.1	0	(0)	20.1
	r	(31.5—83.2)	(43.9—98.1)	(0— 0.5)	(0)	0	(1.1—32.3)
	S	86.3	—	0.1	0	0	20.7
Salmo gairdneri (rainbow t.)	n_f		12	12	12	5	8
	n_o		408	324	328	419	526
	p		68.6	86.2	54.6	21.6	57.1
	r		(23.2—92.8)	(40.0—96.8)	(1.4—88.8)	(3.2—49.9)	(19.8—80.3)
	S		77.8	—	61.4	23.0	68.3
Salmo trutta (brown t.)	n_f		10	10	10	7	4
	n_o		402	300	278	261	355
	p		20.6	3.9	85.0	76.3	46.9
	r		(0—96.2)	(0—17.5)	(72.9—96.0)	(7.6—92.2)	(41.5—52.8)
	S		21.9	4.7	—	88.8	52.9
Salmo salar (A. salmon)	n_f		3	3	3	3	3
	n_o		179	133	150	197	139
	p		1.5	0	86.4	94.7	39.3
	r		(0—4.0)	(0)	(80.2—90.4)	(86.2—99.5)	(9.2—80.8)
	S		1.6	0	91.3	—	41.2

n_f : number of females tested
n_o : harmonic mean number of ova sampled per female
p : mean percentage of eyed eggs
r : percentage range of eyed eggs
S : mean relative rate of hybrid success (as percentage of control samples from the same females)

TABLE II

Survival rate from the eyed stage to hatching

♀	♂	*Oncorhynchus* *tsawytscha* (chinook s.)	*Oncorhynchus* *kisutch* (coho s.)	*Salmo* *gairdneri* (rainbow t.)	*Salmo* *trutta* (brown t.)	*Salmo* *salar* (A. salmon)	*Salvelinus* *fontinalis* (brook t.)
Oncorhynchus	n_f	2	7	1			3
kisutch	p	91.6	99.6	0			0
(coho s.)	r	(83.2–100)	(97.3–100)	(0)	*	*	(0)
	S	92.8	—	0			0
Salmo	n_f		8	8	8	5	6
gairdneri	p		71.2	96.1	63.5	31.5	92.4
(rainbow t.)	r		(34.6–93.1)	(90.0–99.7)	(10.6–99.6)	(0–75.9)	(80.0–98.1)
	S		73.5	—	66.2	32.0	96.0
Salmo	n_f		7	5	10	7	4
trutta	p		8.5	0	97.7	33.2	88.3
(brown t.)	r		(0–37.1)	(0)	(92.6–99.5)	(0–78.9)	(75.9–95.0)
	S		9.0	0	—	33.4	91.2
Salmo	n_f		2				
salar	p		0				
(A. salmon)	r		(0)	*			
	S		0				

n_f : number of females with sampled progeny
p : mean percentage survival
r : percentage range of survival
S : mean relative rate of hybrid survival (as percentage of control samples from the same females)
* : all fish dead before eyed stage

TABLE III

Survival rate from hatching to the 15th day after hatching

♀	♂	*Oncorhynchus*		*Salmo*			*Salvelinus*
		tsawytscha (chinook s.)	*kisutch* (coho s.)	*gairdneri* (rainbow t.)	*trutta* (brown t.)	*salar* (A. salmon)	*fontinalis* (brook t.)
Oncorhynchus	n_f	2	7				
kisutch	p	99.6	99.8				
(coho s.)	r	(99.1—100)	(98.5—100)	*	*	*	*
	S	99.6	—				
Salmo	n_f		5	5	5	4	4
gairdneri	p		83.4	97.7	84.2	38.2	93.0
(rainbow t.)	r		(51.9—96.2)	(90.4—100)	(61.8—97.8)	(0—58.8)	(82.4—98.7)
	S		84.9		85.9	38.3	93.5
Salmo	n_f		2		7	5	3
trutta	p		56.1		97.2	19.1	83.6
(brown t.)	r		(38.5—73.7)	*	(89.6—99.4)	(6.5—47.1)	(65.9—95.0)
	S		58.9		—	19.3	86.9

n_f : number of females with sampled progeny
p : mean percentage survival
r : percentage range of survival
S : mean relative rate of hybrid survival (as percentage of control samples from the same females)
* : all fish dead before hatching

TABLE IV

Relative rate of hybrid success up to the 15th day after hatching

♀	♂	*Oncorhynchus*		*Salmo*			*Salvelinus*
		tsawytscha (chinook s.)	*kisutch* (coho s.)	*gairdneri* (rainbow t.)	*trutta* (brown t.)	*salar* (A. salmon)	*fontinalis* (brook t.)
Oncorhynchus kisutch (coho s.)	n_f	2	control	6	6	6	3
	S	85.8		0	0	0	0
Salmo gairdneri (rainbow t.)	n_f		5	control	5	5	4
	S		59.2		50.4	3.2	66.3
Salmo trutta (brown t.)	n_f		7	7	control	7	3
	S		0.8	0		5.2	37.5

n_f : number of females with sampled progeny
S : mean relative rate of hybrid success (as percentage of control samples from the same females)

Crosses between Salvelinus fontinalis *males and* Salmo *sp. females*

Rainbow trout ♀ × brook trout ♂ hybridizations were fairly successful, although rating lower than the control groups at eyed stage (57% vs 82%; significant difference: $p = 0.001$; mean relative rate: 68% of control). Little subsequent mortality was recorded.

Crosses with brown trout ♀ and Atlantic salmon ♀ resulted in somewhat lower survival (53% and 41% of control, not significantly different), especially in the first period of development.

Crosses within the genus Salmo

Hybrid alevins were obtained from the rainbow trout ♀ × brown trout ♂ cross, despite uneven losses before hatching (50% average relative success at the end of the experiment). The reciprocal cross produced only a few embryos which never hatched. Hybridizations between rainbow trout and Atlantic salmon followed a similar pattern, although with much lower success rates.

Lastly, brown trout ♀ × Atlantic salmon ♂ gave very good results to the eyed stage (76% vs 83% in corresponding controls; no significant difference), but poor subsequent survival resulted in small overall rates (5% of control). The reciprocal cross was about as successful to the eyed stage before being accidentally damaged.

Maternal source of variation

Significant differences between rates obtained from different females were found in all developmental periods, and within almost every type of cross, except those which totally failed. These differences existed even in the control series, although poor lots were discarded, with the sole exception of coho salmon controls exhibiting uniformly good survival subsequent to eyed stage.

The maternal effects in the three periods of development were not independent since positive correlations were generally found between rates obtained in two consecutive periods. The corresponding coefficients averaged 0.7 and were statistically significant in about one-half of the various types of crosses.

Comparisons between success rates in hybrid and control crosses showed significant positive correlations in several instances where enough pair data were available:

— rainbow trout ♀ × coho salmon ♂ lots and corresponding rainbow trout controls in any period studied (1: $r = 0.8$; 2: $r = 0.9$; 3: $r = 0.9$)

— rainbow trout ♀ × brook trout ♂ lots and corresponding rainbow trout controls in periods 1 and 2 (1: $r = 0.9$; 2: $r = 0.9$)

— brown trout ♀ × Atlantic salmon ♂ lots and corresponding brown trout controls in periods 1 and 2 (1: $r = 0.7$; 2: $r = 0.8$).

Regression analyses of hybrid rates on control rates never indicated sig-

TABLE V

Length of the incubation period and dispersion of hatching times

♀	♂	*Oncorhynchus*		*Salmo*			*Salvelinus*
		tsawytscha (chinook s.)	*kisutch* (coho s.)	*gairdneri* (rainbow t.)	*trutta* (brown t.)	*salar* (A. salmon)	*fontinalis* (brook t.)
Oncorhynchus kisutch (coho s.)	LIP	444	437	*	*	*	*
	DHT	23	32				
Salmo gairdneri (rainbow t.)	LIP		441	326	328	326	337
	DHT		54	31	46	50	67
Salmo trutta (brown t.)	LIP		501	*	399	429	429
	DHT		88		37	82	50

LIP: mean length of the incubation period (day - degrees)
DHT: average dispersion of hatching times (day - degrees between the 5% and 95% hatching points)
*: all fish dead before hatching

nificant y intercept values. This result shows porportionality between these rates. In all cases, however, the residual variances largely exceeded the error variance of binomial origin. Other sources of variation therefore occurred.

Incubation and hatching times

Fig. 1 shows the mean hatching curves of the hybrids and controls which were obtained in the second set of crosses at Saint-Pée-sur-Nivelle hatchery, plus the coho salmon ♀ × chinook salmon ♂ hybrid obtained in the first set. Other curves obtained throughout the experiment presented similar features. The numerical results presented in Table V were therefore compiled from the whole of the available data from hatchings at the Saint-Pée-sur-Nivelle hatchery.

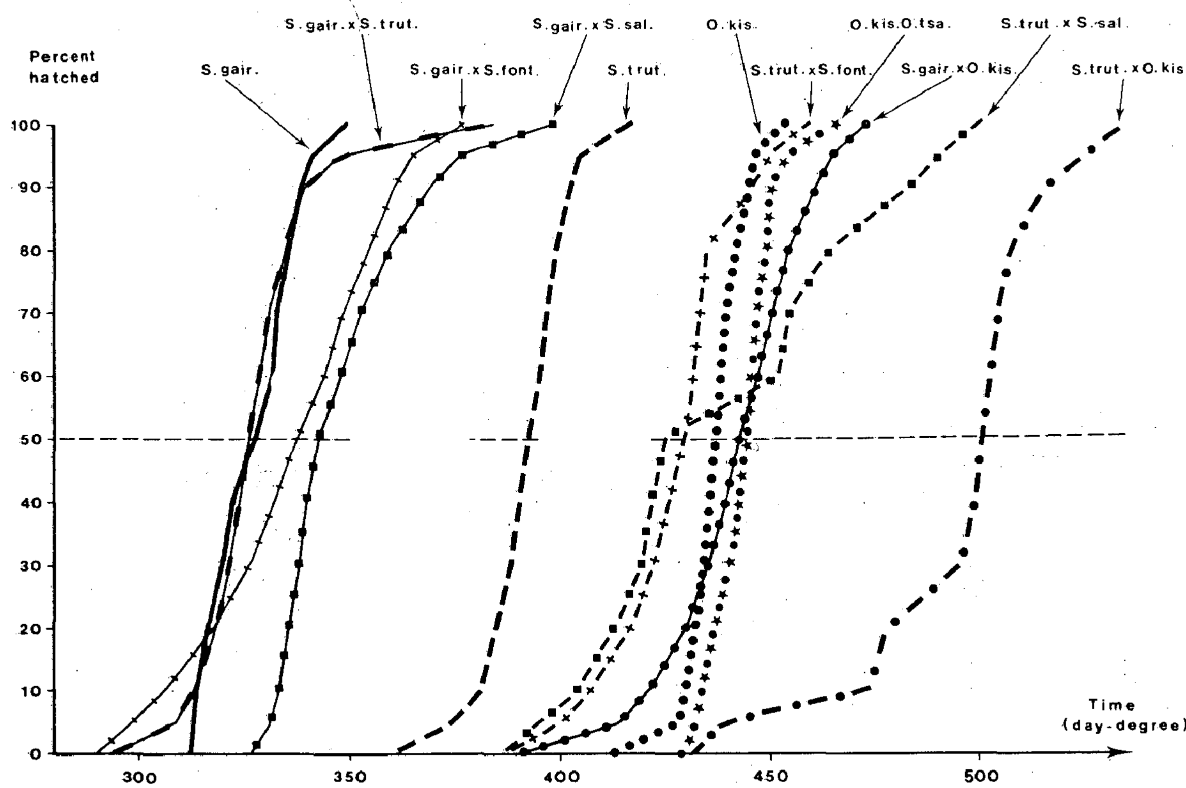

Fig. 1. Mean hatching curves of parental and hybrid genotypes.

———	*Salmo gairdneri* × *Salmo gairdneri*
– – – –	*Salmo trutta* × *Salmo trutta*
••••••	*Oncorhynchus kisutch* × *Oncorhynchus kisutch*
—■—■—	*Salmo gairdneri* ♀ × *Salmo trutta* ♂
—+—+—	*Salmo gairdneri* ♀ × *Salvelinus fontinalis* ♂
—•—•—	*Salmo gairdneri* ♀ × *Salmo salar* ♂
•••••	*Salmo gairdneri* ♀ × *Oncorhynchus kisutch* ♂
– + – + –	*Salmo trutta* ♀ × *Salvelinus fontinalis* ♂
– ■ – ■ –	*Salmo trutta* ♀ × *Salmo salar* ♂
– • – • –	*Salmo trutta* ♀ × *Oncorhynchus kisutch* ♂
•*•*•*	*Oncorhynchus kisutch* ♀ × *Oncorhynchus tsawytscha* ♂

Length of the incubation period (LIP). The LIPs which were found for the control groups do not differ greatly from those usually reported in the literature (Davis, 1970; Chevassus and Petit, 1975), although the brown trout and coho salmon times may have been somewhat underestimated. Unfortunately, monospecific samples of chinook salmon, Atlantic salmon and brook trout were not available.

Statistical comparisons of hybrid and control incubation periods corroborated the grouping which can be observed in the hatching curves (Fig. 1):

— LIPs of coho ♀ × chinook ♂ lots did not differ from those of corresponding coho salmon controls
— several hybrids obtained from rainbow trout females (rainbow ♀ × brown trout ♂, rainbow ♀ × Atlantic salmon ♂, and rainbow ♀ × brook trout ♂) had LIPs which did not differ significantly from those of corresponding rainbow trout controls, although they were much less than those of brown trout groups
— on the contrary, LIPs of rainbow trout ♀ × coho salmon ♂ lots did not differ from those of cohos, but were significantly greater than those of rainbow trout controls (influence of the male parental species)
— all types of hybrids obtained from brown trout females had LIPs significantly larger than those of corresponding brown trout controls; furthermore, LIPs of brown trout ♀ × coho salmon ♂ lots were significantly larger than any other LIP recorded in this experiment, including those of both parental species.

Highly significant differences were found among the mean LIPs from different females within almost all types of hybrids and controls, with the sole exception of two surviving lots of brown trout ♀ × coho salmon ♂. However, no significant correlation could be found between LIPs of hybrid lots and LIPs of corresponding controls, except in the case of brown trout ♀ × brook trout ♂ ($r = 0.98$ with corresponding brown trout controls).

Dispersion of hatching times (DHT). Low DHT values, which did not differ significantly from each other, were found for control groups, and for the coho ♀ × chinook ♂ hybrid. Other types of hybrids, whose survival rates were lower, had much larger DHTs (Table V). No statistical relationship could be found between the DHTs and the corresponding LIPs.

DISCUSSION AND CONCLUSION

Some of the results obtained in this study corroborate average findings from other authors. This is the case of the following crosses: rainbow trout × brook trout (Susuki and Fukuda, 1971 a), rainbow trout × Atlantic salmon (Refstie and Gjedrem, 1975; Sutterlin et al., 1977), rainbow trout × brook trout (Susuki and Fukuda, 1971 a), brown trout × Atlantic salmon (Piggins, 1970; Refstie and Gjedrem, 1975), brown trout × brook trout (Susuki and Fukuda, 1971 a), Atlantic salmon × brook trout (Sutterlin et al., 1977), and rainbow trout × coho salmon (Chevassus and Petit, 1975). Evidence of maternal variation within cross may explain small discrepancies between some results obtained for the same hybrid by different authors.

To our knowledge, failure of brown trout × coho salmon and Atlantic salmon × coho salmon hybridization, whatever species was used as male or female parent in these crosses, has not been previously reported. There is therefore little chance of introgression into native species of the genus *Salmo*, would coho salmon be introduced into European rivers.

Our results disagree with previous data on two points. Firstly, Foerster (1935) reported that coho salmon ♀ × chinook salmon ♂ hybridization aborted at the eyed stage, while we observed very good survival. This contradiction however may be explained by the fact that Foerster's study lacked a control cross, thus making it impossible to check the quality of coho female eggs. This was suggested by the author himself. Secondly, Uyeno (1972) reported good survival of 4-month old hybrids from coho salmon ♀ × brook trout ♂, while we never observed any hatch from that cross, although the coho ova showed good quality when used in control crosses and brook trout milt produced fairly successful progeny with brown trout. However, since Uyeno reported a karyotype in his hybrids identical to that of coho salmon ($2n = 60$), the true hybrid nature of these animals may be questioned. The problem of hybrid identification is important in salmonids since phenotypic variability in parental species renders morphological or anatomical criteria difficult to apply (Susuki and Fukuda, 1973a). Safer techniques based on karyological (Lieder, 1956; Sasaki et al., 1968; Nygren et al., 1972) or biochemical (Nyman, 1970) studies therefore are necessary for hybrid identification. Biochemical work done on the various progenies which we could raise to the feeding stage confirmed the hybrid nature of those fishes (Guyomard, 1978).

Data obtained on the length of the incubation period do not permit us to draw overall conclusions. Hybrid values may be paternal-like, maternal-like, or even higher than in either parental species. On the other hand, within a case where the mean value of the LIP seems to be due to the paternal species influence (rainbow trout ♀ × coho salmon ♂), Chevassus and Petit (1975) analyzed the variability of the results and showed a preponderance of individual maternal effects. These data therefore corroborate those of Withler and Morley (1970) studying three species of the genus *Oncorhynchus*, which showed highly variable interaction effects in the determinism of hybrid LIP.

The dispersion of hatching times does not seem to be a valuable specific character. Instead, it might simply be a consequence of the average physiological condition of the hatching embryos.

Among the various types of hybrids showing good survival to the 15th day after hatching, a number were reported to have poor survival subsequent to that stage. This is particularly true of the rainbow trout ♀ × brown trout ♂ and rainbow trout ♀ × brook trout ♂ crosses (Susuki and Fukuda, 1971 b). Contrastingly, other hybrids seem to show promise, such as the Atlantic salmon ♀ × brown trout ♂ (Piggins, 1970) and brown trout ♀ × brook trout ♂ crosses (Susuki and Fukuda, 1971 b). The latter provides a sterile hybrid (Susuki and Fukuda, 1973 b) which could be used in marine aquaculture to prevent unfavorable consequences of sexual maturation. Another interesting hybrid is the rainbow trout ♀ × coho salmon ♂ which has proven to be partly resistant to a rainbow trout viral disease (Ord et al., 1976). The coho salmon ♀ × chinook salmon ♂ hybrid, although it has not been studied much, should also be of interest. Further investigations will deal with the survival and growth of such hybrids and with the appreciation of their practical value.

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RESUME

Blanc, J.M. et Chevassus, B., 1979. Hybridation interspécifique chez les salmonidés. I Eclosion et survie jusqu'au 15ème jour après l'éclosion chez les hybrides de première génération. *Aquaculture*, 18: 21–34 (en anglais).

Des hybridations artificielles représentant 17 combinaisons ont été réalisées à partir de 6 espèces de Salmonidés, à savoir les saumons chinook et coho, la truite arc-en-ciel, la truite brune, le saumon Atlantique et l'omble de fontaine. La réussite au stade oeillé, les taux de survie jusqu'au 15e jour après l'éclosion, la durée d'incubation et la dispersion des éclosions ont été examinés par référence aux lots témoins monospécifiques.

Les taux de réussite et de survie des hybrides se sont révélés inférieurs ou au mieux semblables à ceux des espèces parentales. Des effets maternels significatifs ont été observés dans la plupart des types de croisements.

Des facteurs d'interaction très variables se sont avérés agir sur la durée d'incubation des hybrides, qui pouvait dépasser celles des espèces parentales. La dispersion des éclosions était plus importante chez les hybrides que dans les espèces pures et tendait à être négativement corrélée à la survie.

Quelques types d'hybrides ont donné des résultats prometteurs au terme de cette expérience. Leur intérêt potentiel pour l'aquaculture est considéré dans la discussion.