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GROWTH, PHYSIOLOGY AND BEHAVIOUR OF SALMONID HYBRIDS

by

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ABSTRACT

Attempts were made to complete all possible interspecific hybrid crosses between Atlantic salmon *(Salmo salar)*, rainbow trout *(Salmo gairdneri)*, brook trout *(Salvelinus fontinalis)*, lake trout *(Salvelinus namaycush)*, and Arctic char *(Salvelinus alpinus)*. Survival was appreciable only in lake ♀ x brook ♂, salmon ♀ x char ♂, brook ♀ x char ♂ and char ♀ x brook ♂. Growth rates over a weight increment of 3-30 grams averaged 2.14% wet weight per day for all species and hybrids (14.5-17.0°C - excess rations). The highest growth rate, 2.74%, was obtained with the brook ♀ x char ♂ hybrid and the lowest, 1.63%, in lake trout. Salmon ♀ x char ♂ hybrids grew faster than salmon; brook trout ♀ x char ♂ hybrids grew faster than brook trout. *Salmo* species grew no faster than *Salvelinus* species but became silvery and had greater salinity tolerance at a smaller size and earlier age. Intergeneric hybrids between *Salmo* spp. ♀ and *Salvelinus* spp. ♂ more closely resembled the female parent in processes related to smoltification (silvering and salinity tolerance).

Salvelinus spp. and their intrageneric hybrids prefer temperatures 3-4°C cooler than those of the *Salmo* genus. Progeny resulting from a female salmon crossed with either male brook trout or char resembled the salmon in temperature preference.

Interspecific differences in breathing frequency and in the breaths:gulp ratio were observed - *Salmo* spp. having higher breathing rates than *Salvelinus* spp. *Salmo* spp. also appeared more susceptible to hypoxia than *Salvelinus* spp. as indicated by the dissolved oxygen level following asphyxiation.

INTRODUCTION

Survival and growth rates of different salmonid species and hybrids have seldom been compared under accelerated rearing conditions. In some studies only the final weight or length of the fish obtained at completion of experiments has been used as a growth index, and variations in hatching time, and egg and embryo size have not been taken into account in the assessment of growth. Attempts are made here to examine growth in several salmonid species common to eastern Canada, along with their possible hybrids, under conditions that are considered optimum for many salmonids. Physiological aspects of smoltification, salinity tolerance and susceptibility to hypoxia are also considered in an attempt to assess the hybrids' suitability for culture in fresh and salt water and their tolerance to stress. The basis for inheritance of some behavioural traits such as temperature selection and breathing patterns is also examined.

METHODS, RESULTS AND DISCUSSION

I. Hatchability, Growth and Survival in Fresh Water

Brood stock (Table 1A) to be used in the hybridization experiments were held in either of two tanks maintained at different temperatures (4 and 12°C). To accelerate ripening, certain species were transferred to the tank containing colder water. Eggs from three to five females of the same stock were pooled and thoroughly mixed; milt from three to five males was similarly pooled. The eggs and milt were divided into batches and used to complete the straight and hybrid crosses (Table 1). With some char crosses it was impossible, due to incompatability in ripening time, to use the same eggs in the self and hybrid crosses. In such instances, however, eggs and milt from at least three of parental species were pooled prior to fertilization; thus, the self cross is not a strict control for variations in egg and milt viability.

Between 2000 and 3000 eggs from each of the crosses were incubated at temperatures between 7 and 8°C (Fig. 1). Twice a week eggs were treated with malachite green and dead eggs removed. The surviving fry were transferred to 1-m^2 tanks shortly after they started feeding and were reared for an additional 3-4 months on excess rations until they had reached a weight of 1-5 g. The increase in temperature and photoperiod (fluorescent lights) during this early rearing and the subsequent growth experiment is shown in Fig. 1.

In most instances 100 fish from each group were selected randomly for the growth experiment and retained in the 1-m^2 tanks. Deformed individuals were excluded from the sample. During the next 4 months the fish were reared under a gradually increasing temperature, 14.5-17.0°C, and a rapidly increasing photoperiod, from 14.5 to 20.0 h of daylight (Fig. 1). Excess food was delivered to each tank by automatic feeders operating on a 50-min cycle for the entire daylight period. Canadian-produced Ewos salmon grower of the following composition was used as food: moisture, 10%; crude protein, 52%; fat, 10%; calories per gram, 5.0. Water flow and water current in the tank were standardized by a water jet delivery system, and dissolved oxygen remained above 95% of air saturation.

Fish were anaesthetized with 3% amyl alcohol and fork length and weight of all fish in each tank were determined approximately every 25 days during the 4-month growth period. Replicates of the different crosses were not included because of limitations in tank space; however, past studies using such tanks under identical conditions indicate differences in tank and position account for less than 7% variability in growth rates of Atlantic salmon.

Hybrid survival

The majority of hybrids had poor survival past the eyed stage (Table 1C). Within this group, crosses involving female salmon x male brook and lake trout hatched normally but died within 1 or 2 weeks. Survival comparable to their parental crosses was only obtained in four instances (Table 1B). Similar survival has been reported by other workers (Stenton 1952; Alm 1954; Buss and Wright 1956; Suzuki and Fukuda 1971; Refstie and Gjedrem 1975; also see bibliography by Dangel et al. 1973). To the contrary, however, we obtained poor survival with brook x lake (splake) and char x salmon, both of which are reported to be viable hybrids (Buss and Wright 1956; Refstie and Gjedrem 1975). Crosses attempted here, which to our knowledge have not been reported elsewhere, are lake x char, char x lake, salmon x lake and lake x salmon. No survival to feeding was obtained with any of these.

The reason why the intergeneric hybrid salmon x char has good survival, while salmon x lake and salmon x brook hybrids die shortly after hatching, cannot be explained by simple incompatibility in egg size or chromosome number (Table 1A). Hybridization between brook trout and lake trout and between brook trout and char is possible, while lake trout and char appear incompatible. Hybrids between brook trout and Arctic char are reported to be reproducing naturally in lakes in eastern U.S.A. and Canada (Wooding 1959; Maine Department of Fish and Game, personal communication, 1977. Whether or not these hybrids were created naturally or have been introduced cannot be accurately established.

Growth rates

A logarithmic increase in weight with time at a constant growth rate appears to provide a reasonable fit for most of the 11 species and hybrids (Fig. 2). The specific growth rate (percent increase in wet weight (W) per day) has been determined for the slope of these lines. The fork length (L) cubed is also plotted

(Fig. 2). All species and hybrids except lake trout had condition factors (W x 100 x L^{-3}) greater than unity throughout the experiment (Fig. 2). There was also a tendency among several groups for the condition factor to increase during growth (Fig. 2 and last two columns of Table 2).

A reduction in growth rate with size does not appear to occur with most of the species and hybrids examined. The combination of a relatively short growth period, a 2.5°C increase in temperature and increasing photoperiod during the growth period might account for this.

For aquaculture, change in weight is probably more important than change in length although in some instances it might be advantageous to look at both. The rate of change in length is plotted against the rate of change in weight for the 11 species and hybrids (Fig. 3). A correlation coefficient of 0.955 indicates that either method of comparing growth is probably satisfactory but a vectorial distance between species in Fig. 3 might be used as well. Specific growth rates for weight varied from a low of 1.63% in lake trout to a high of 2.74% in brook trout-char hybrids. The low growth rate of lake trout, however, may be questioned because of their consistently low condition factor during the experiment and high mortalities from an outbreak of septicemia near the end of the experiment. The difference in growth rate between the sea-run wild and hatchery brook trout is probably not significant, and differences between landlocked and sea-run salmon may be different if length changes are considered (Fig. 3). The salmon-char hybrids grew faster than their salmon parental cross, an observation similar to that of Refstie and Gjedrem (1975). The splake hybrid (lake x brook trout) grew faster than the parental cross involving lake trout and about as fast as the parental brook trout cross. The char x brook hybrids grew as fast as their brook trout parental cross, while the brook-char hybrids grew considerably faster than their parental brook trout cross. The rainbow trout grew no faster than the straight salmon or brook trout crosses.

An unexpected result of this experiment was the relatively high growth rate observed in the two Atlantic salmon stocks, which was comparable to that of brook trout and rainbow trout. Most hatchery managers rearing the three species together will consistently say that Atlantic salmon are slower growing, as indicated by the apparent fact that the same year-class of salmon parr in a hatchery is always smaller than the trout. Possibly some combination of larger egg size, longer hatching time and initial slower growth rates during yolk sac absorption and early feeding of Atlantic salmon results in an initial disparity in size that is always apparent during the remainder of the freshwater rearing stage. Unfortunately, comparative hatching time and growth rates of fish smaller than 1-2 g were not carefully examined during this experiment. A second possible explanation is that the usually colder water and/or higher stocking densities in hatcheries favor trout growth over salmon. The temperatures used in our growth studies (14.5-17.0°C) were felt to encompass a range shown to be optimum for a number of salmonids although specific requirements for all species are lacking (Brett et al. 1969; Brett 1974). Rearing density of Atlantic salmon, however, could be especially critical, in that Refstie and Kittelsen (1976) have shown nearly a 40% reduction in growth rate as a result of increased rearing density of salmon parr. At the exceptionally low rearing densities used in our experiments perhaps the growth potential of salmon could be more fully expressed than in most hatchery situations.

Char x brook trout and the reciprocal cross have been described by Day (1882), Soguri (1936), and Suzuki and Fukuda (1973). Alm (1954) reported that the char x brook hybrid grew faster than either parent species, was "easier to rear" than char and "lived longer" than brook trout. The hybrid resulting from brook x char and not the reciprocal grew faster than its parent brook trout progeny during our study. Similarly, this hybrid is also said to grow faster than its parental char cross (Suzuki and Fukuda 1972). The brook x char hybrid and its reciprocal are reported to be indistinguishable in external appearance from each other (Suzuki and Fukuda 1973), an observation we can also confirm. These workers observed a high proportion of maturing male and female brook x char and their reciprocal hybrids at the end of the second summer, although the gonads of maturing males were small. Thus it is apparent that hybridization, while perhaps improving growth rates, will not overcome the problems of early sexual maturity that is a hindrance to brook trout culture in both fresh and salt water (Sutterlin et al. 1976).

II. Smoltification and Salinity Tolerance

Throughout the spring and summer, the salmon x char hybrids resembled char more than salmon. Lateral parr marks numbered between 10 and 12 but were often not discrete bars. The dorsal surface was mottled with an irregular array of wedges and spots. During the first half of September this pattern was occluded by a guanine deposition in what resembled a natural smoltification process. This same transition occurred simultaneously both in their parental salmon cross and in the landlocked salmon. By October the salmon-char hybrids were hardly distinguishable from the salmon except for a reddish-yellow coloration of the fins and slightly more pointed caudal fin lobes. The rainbow trout and the salmon-brook trout hybrids also underwent a process resembling smoltification at approximately this same time. The rapid growth, perhaps induced by a continuing increase in temperature and photoperiod, resulted in 85% of both salmon groups "smoltifying" by September 15 at a body weight of 15-20 g and with a length of 10-12 cm.

The salinity tolerance of various species and hybrids was examined in a recirculation system of 200-ℓ volume, consisting of a holding and an aeration tank, pump, heater, and thermostat. Ocean salt was added to raise the salinity to 40‰ so that mortalities would occur in all groups. Seven fish of each of the different species or hybrids were placed together in the tank and the time to cessation of breathing was determined. Salinity tolerance tests were performed in November after the growth experiments had been completed.

Despite a considerable variation in weight among the eight groups tested, there are significant differences in the mortality rate and time necessary for all fish to die when stressed by high salinity (Fig. 4). The different species and hybrids may be divided into four groups exhibiting increasing tolerance to salinity as follows: CxC = LxL = BxB = BxC < SxB = SxS < RxR < SxC. It is apparent that *Salvelinus* spp. and their intrageneric hybrids have less tolerance to salinity than the *Salmo* spp. Although these salmon were of smolt size and appearance, their tolerance to salinity does not compare with that of "natural" smolts tested during the spring. True smolts (1+ or 2+ years and 40+ g) will tolerate 40‰ for up to 100 h with less than 10% mortality (R.L. Saunders, unpublished data). Inheritance of salinity tolerance in the two hybrids SxC and SxB appears to be predominantly contributed by the female salmon. Tolerance tests conducted the following spring (June 6-10), prior to placing the fish in the ocean, revealed a similar rank (12°C, 40‰): BxB (152) = BxC (132) < CxB (146) = RxR (133) < SxS (125) = SxC (137). The mean weights of the lots tested are indicated as grams in brackets. Although the previous observations related to silvering seem to be correlated with salinity tolerance, further long-term studies on growth and survival in sea water are required to assess the suitability of these groups for culture.

Comparison of growth rates among different species as well as comparisons of hybrids with their parental crosses should be interpreted with caution. Quite apart from intraspecific genetic variability in different stocks, environmental influences further complicate comparisons. With the great number of variables such as temperature, photoperiod, diet quality, water velocity, shading, and rearing density, all of which have different degrees of influence on species-specific growth, it might be said that the relative growth of different species depends on how these variables interact to produce ultimate conditions that depart from or approach the optimum. We have attempted to stimulate the rearing conditions that seem to provide optimum growth for a number of salmonids, with no pretense at satisfying all specific requirements.

Presently these hybrids are being reared together in a large saltwater tidal impoundment and preliminary observations suggest that growth rates and survival in salt water can be vastly different than in the fresh water studies reported here. The SxC hybrids have developed a very slinky appearance and the CxB hybrids appear to be surpassing the BxB and BxC in growth.

III. Temperature Selection

Five fish from a selected cross were placed in each channel of an 8-channel, horizontal temperature gradient

(Peterson 1976). Observations on eight different groups were conducted simultaneously one hour after they were introduced to the channel. The position of each fish in the gradient was noted every 2 minutes for a period of 64 minutes, giving a total of 160 observations on each group. The arithmetic mean of the frequency distribution with respect to temperature was used as a measure of preferred temperature. Skewness in the distribution did not appear to introduce significant errors in any of the experiments. At the time of the experiments the fish were being reared at a hatchery temperature of 12.7°C; for complete thermal history, see Fig. 1.

Two series of experiments were performed (Table 3). In series 1 the various groups of fish had feeding about two weeks prior to testing; series 2 followed series 1 and the fish were approximately 2 weeks older. The mean lengths of the various groups (Table 3) varied depending on egg size, hatching time and time of feeding. Because the preferred temperature of the different groups did not change significantly from series 1 to series 2 (Table 4), fish size will not account for the difference in preferred temperature among the different groups.

Progeny from all pure crosses of the genus *Salmo* and from all crosses involving a female parent of the genus *Salmo* selected 13-14°C (Table 4). All intrageneric crosses with *Salvelinus* selected a somewhat lower temperature (9-10°C). The only intergeneric hybrid involving a female *Salvelinus* spp. (BxS) appeared intermediate in preferred temperature (11.9°C). Significant differences between groups are summarized in Figure 5.

A difference in preferred temperature of 3-4°C between fry of *Salmo* spp. and *Salvelinus* spp. seems to correlate well with the general observation that Atlantic salmon, brown and rainbow trout naturally inhabit and probably tolerate warmer water. It is possible that intrageneric differences in thermal preference develop at a later period than the fry stage which would account for the differences observed by Goddard and Tait (1976) in lake and brook trout and their hybrids.

IV. Breathing Patterns

Because of the intrinsic variability in behaviour traits, it is often difficult to find behavioural parameters that are easily quantified in genetic studies, especially with salmonids. Breathing or gill ventilation and its periodic interruption by "gulps" associated with gill cleaning was chosen as a behaviour index to which a numerical value could be easily assigned and which was hoped to be species specific.

A 12-compartment chamber for measuring this activity was constructed, permitting the breathing and gulping frequency to be recorded electrically on a polygraph. Electrodes mounted on the end of each chamber were connected by a rotary switch which allowed activity from any one of the 12 fish to be recorded. Combinations of straight crosses and hybrids (8-10 cm length) were placed in each compartment and tested at least twice (AM and PM) the following day; each recording period lasted approximately 10 minutes. Acclimation and testing temperatures were held at 15°C during the experiments and at least 6 individuals from each cross were tested. Interspecific differences are greater for breathing frequency than for breaths/gulp ratio (Fig. 6). *Salmo* spp. have higher breathing rates than *Salvelinus* spp. or their intrageneric hybrids at the designated test and acclimation temperature. The ventilation frequency of the SxB hybrid was significantly lower than in the SxS cross but no different than in the BxB offspring. Hybrids, BxC, CxB, LxB, did not differ from their BxB parental cross. Unfortunately the straight lake trout and char crosses are not available for comparison with the above hybrids.

V. Tolerance to Hypoxia

A stress factor often associated with fish mortalities is low dissolved oxygen levels that periodically occur due to malfunction in the rearing plant. Preliminary observations during anaesthetizing and measuring fish indicated that differences between the species and hybrids in susceptibility to hypoxia could quite easily be demonstrated. A bank of 3-ℓ Erlenmeyer flasks, painted black, was arranged in a cooling bath and a single fish was placed in the flask which was continually flushed with water overnight. The next morning the water samples were removed and the flask sealed. The time to loss of equilibrium of the fish, the time to cessation of breathing, and the final oxygen content of the flask were determined.

Ten fish from each cross were tested and most species required about 3 hours to die under these conditions. The final DO levels of four species and one hybrid are shown in Table 5. *Salmo* spp. died at higher DO levels than *Salvelinus* spp. and the hybrid. With the exception of the spring spawning rainbow group, Table 5 might indicate that larger fish died at lower DO levels. This is probably not the case in that very poor correlations were obtained within each group between body weight and final DO. Similarly the time to death and final DO levels were also poorly correlated, possibly indicating that differences in activity levels may not be the only deciding factors. It is probably incorrect to relate such tolerance studies to DO as being the only limiting factor. Build-up of CO_2, NH_3, and other metabolites could partially contribute to death.

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Table 1. Crosses performed and resulting hybrid survival.

A. Straight crosses

No.		Origin	Egg volume (cm^3)	Chromosome no.	Survival to feeding (%)
1	Atlantic salmon (sea-run)	Middle Brook, Nfld.	0.142	58	73
2	Atlantic salmon (landlocked)	Chamcook Lake, N.B.	0.178	58	25
3	Rainbow trout (hatchery domestic)	Cobequid Fish Cult. Sta., N.S.	0.061	60	96
4	Brook trout (hatchery domestic)	" " " " "	0.058	84	85
5	Brook trout (sea-run)	Sheet Harbour, N.S.	0.056	84	93
6	Arctic char (landlocked)	Walton Pond, N.B.	0.049	80	5[a]
7	Lake Trout (landlocked)	Chamcook Lake, N.B.	0.110	84	69

B. Interspecific hybrids with survival to feeding comparable to parental cross

Parents	Female		Male	Survival from fertilization to:	Eyeing (%)	Hatching (%)	Feeding (%)
1 x 6	salmon	x	char		97	97	91
4 x 6	brook	x	char		93	91	89
6 x 4	char	x	brook		79	76	68
7 x 4	lake	x	brook		87	87	82

C. Interspecific hybrids with poor survival to feeding

4 x 7	brook	x	lake		75	63	8
1 x 4	salmon	x	brook		89	83	5
4 x 1	brook	x	salmon		73	3	0
6 x 1	char	x	salmon		35	3	0
1 x 7	salmon	x	lake		95	93	0
7 x 1	lake	x	salmon		5	0	0
7 x 6	lake	x	char		30	25	0
3 x 1	rainbow	x	salmon		51	23	0
3 x 4	rainbow	x	brook		73	52	0
3 x 7	rainbow	x	lake		35	0	0
1 x 3	salmon	x	rainbow		20	0	0
6 x 3	char	x	rainbow		13	0	0
4 x 3	brook	x	rainbow		43	21	0
7 x 3	lake	x	rainbow		12	0	0

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[a] An exception - hybrids survived better than straight cross.

Table 2. Comparative growth rates

Ref. no.	Cross	Female	Male	Initial - final numbers of fish	Initial - final weights (g)	Increase[a] wet weight per day (%)	Increase[a] L^3 per day (%)
1	S x S	salmon	x salmon (SR)	100-100	1.5-13.0	2.07	1.99
2	S x S	salmon	x salmon (LL)	148-146	1.7-21.0	2.22	2.24
3	R x R	rainbow	x rainbow	100-99	3.0-31.5	2.17	2.02
4	B x B (SR)	brook	x brook (SR)	100-97	4.5-39.0	1.95	1.84
5	B x B	brook	x brook (H)	15-13	4.8-54.0	2.12	1.97
7	L x L	lake	x lake	100-87	1.4-5.5	1.63	1.48
1 x 6	S x C	salmon	x char	100-99	1.8-28.0	2.52	2.23
4 x 6	B x C	brook	x char	100-98	2.0-51.0	2.74	2.56
6 x 4	C x B	char	x brook	64-56	4.0-23.0	2.08	2.04
7 x 4	L x B	lake	x brook	14-14	6.3-60.0	1.93	1.93
1 x 4	S x B	salmon	x brook	28-27	3.0-15.5	1.92	1.89
Average						2.12	2.02

[a] Based on regression in Fig. 2
SR, sea-run; LL, landlocked; H, hatchery domestic.

Table 3. Size (range) and thermal history of fish used in temperature selection studies. Series 1 was performed from March 5-17; series 2 from March 18-April 30. Mean rearing temperature for each experiment is also given.

	Fish Lengths (mm)	
	Series 1	Series 2
S x S (SR)	29.7(27-32)	35.5(30-38)
S x B	30.7(27-36)	35.1(30-42)
S x C	30.0(29-31)	31.5(27-36)
S x S (LL)	36.8(32-45)	35.6(31-44)
R x R	28.4(26-32)	44.8(41-47)
B x B	25.4(25-26)	29.2(24-33)
B x L	26.2(23-28)	25.7(24-27)
L x B	37.0(33-42)	36.9(32-43)
L x L	31.8(30-34)	36.6(34-48)
C x C	-	23.5(20-27)
C x B	29.0(26-30)	30.1(24-40)
B x S	-	29.5(26-33)
B x C	-	29.2(24-33)

Mean rearing temperature:	March 5-17	12.7(12.1-12.8)
	March 18-April 13	12.7(12.3-12.9)

Table 4. Mean (range) in selected temperatures in progeny from the different crosses. M - mean for the two series.

	Mean Selected Temperature		
	Series 1	Series 2	M
S x S (SR)	13.4(10.6-15.1)	14.0(11.8-15.2)	13.7
S x S (LL)	13.2(11.4-15.0)	13.6(12.2-16.2)	13.4
S x B	14.6(13.1-15.9)	13.4(11.5-16.5)	14.0
S x C	13.0(11.7-14.2)	13.0(12.5-13.6)	13.0
R x R	14.8(13.2-17.8)	13.8(11.5-16.2)	14.3
B x S	-	11.9(10.9-12.6)	11.9
B x B	8.0(6.5-9.4)	9.4(8.5-10.9)	8.7
B x L	9.0(8.2-9.7)	9.4(7.8-12.4)	9.2
B x C	10.0(8.4-11.4)	10.5(9.1-12.5)	10.2
L x B	10.1(8.4-12.2)	9.5(7.4-10.4)	9.8
C x B	10.3(7.6-12.4)	9.2(8.6-9.5)	9.8
L x L	10.0(8.4-10.9)	9.9(9.3-10.6)	10.0
C x C	-	9.2(7.7-10.1)	9.2

Table 5. Dissolved oxygen remaining at the time of death. Brackets include species showing non-significant differences (0.05 level, Duncan's Multiple Range Test).

Cross	n	Wt ± 2SE	DO ± 2SE
		g	mg/ℓ
S x S	10	84.4 ± 29.4	1.91 ± 0.56
R x R (FS)	9	99.2 ± 32.92	1.30 ± 0.21
R x R (SP)	10	41.4 ± 8.33	1.18 ± 0.25
B x B (SR)	10	103.8 ± 14.2	0.88 ± 0.19
B x C	9	139 ± 40.1	0.63 ± 1.12

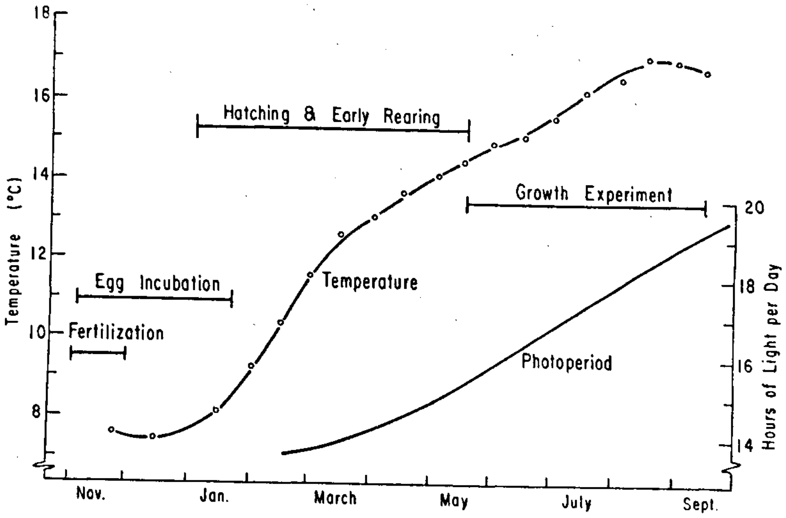

Fig. 1. Temperature and photoperiod conditions during egg incubation and rearing.

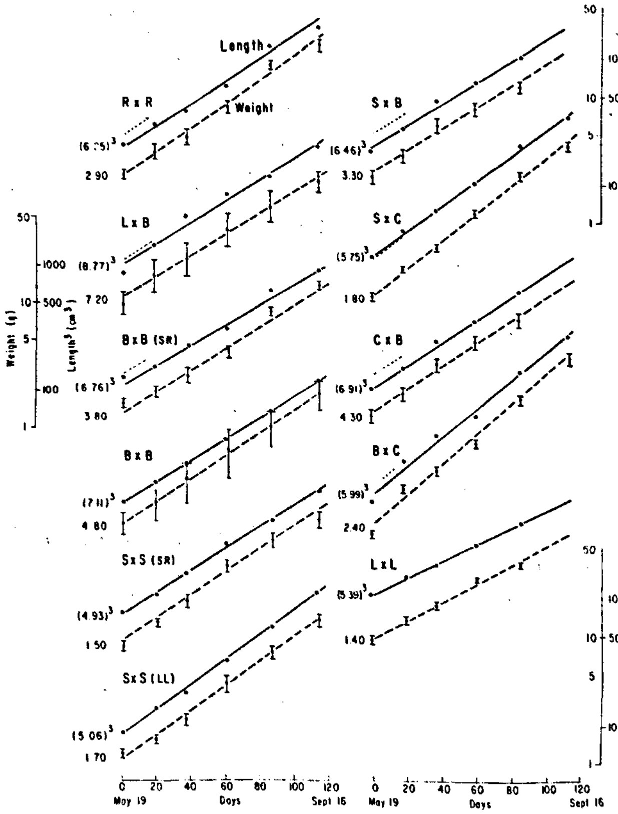

Fig. 2. Growth of different species and hybrids. Weight ± 2SE (---) and length^3 (——) are plotted against time using the logarithmic scale indicated. The length^3 plots have been arranged relative to the weight intercept at time zero so that any change in condition factor (wt x 100 x L^{-3}) is apparent. If the condition factor is unity and remains so during growth, then the L^{-3} line would fall on the hatched line and remain parallel to the weight line. If the L^3 line approaches the weight line, the condition factor approaches 2. Regression lines have been determined by least squares method. Initial weight and length intercepts are indicated to the left of each set of lines.

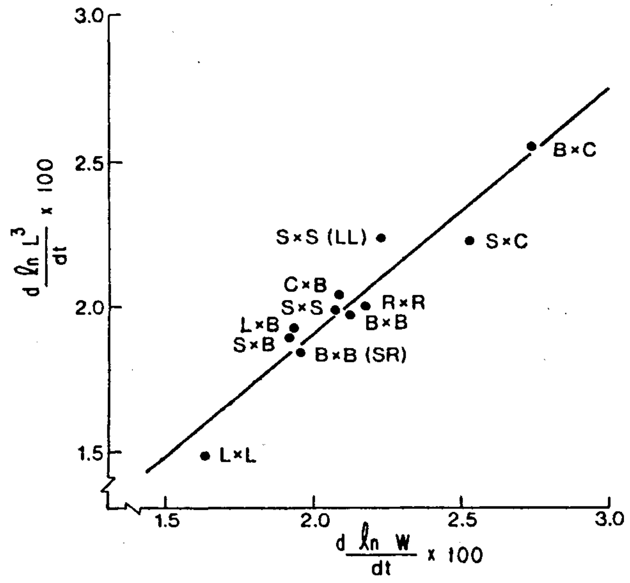

Fig. 3. Relationship between the rate of change in weight and that in length cubed (Table 2) as an index of growth.

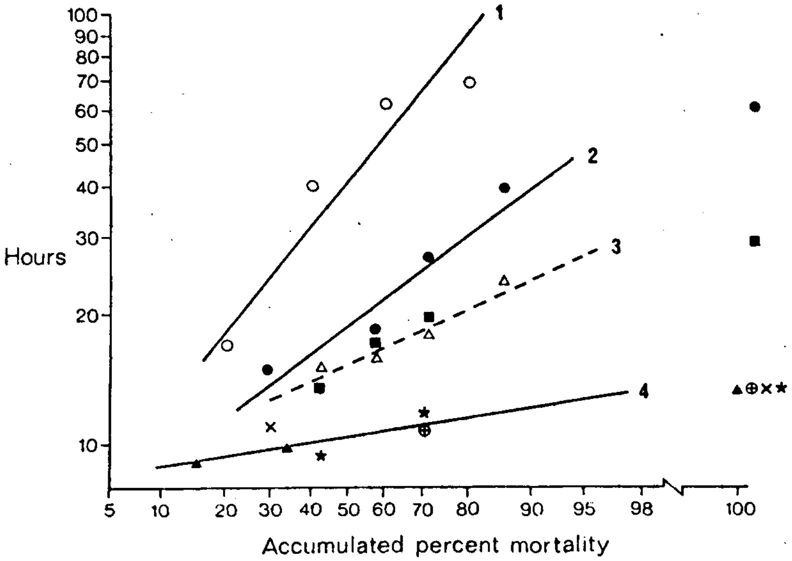

Fig. 4. Log-probit plot describing survival time (salinity: 39.4‰, temperature: 12°C). ○, S x C, 52 g; ●, R x R, 42 g; ■, S x S, 40 g; △, S x B, 39 g; ▲, B x B, 69 g; ×, B x C, 63 g; ⊕, LxL, 30 g; ★, C x C, 60 g. Seven fish from each group were used. The C x C group is not the same char stock as that used in the hybrid crosses, B x C and S x C, although they are approximately the same age.

	RxR	SxB	SxS (SR)	SxS (LL)	SxC	BxS	BxC	LxL	LxB	CxB	BxL	CxC	BxB
R x R						*	*	*	*	*	*	*	*
S x B						*	*	*	*	*	*	*	*
S x S (SR)						*	*	*	*	*	*	*	*
S x S (LL)							*	*	*	*	*	*	*
S x C							*	*	*	*	*	*	*
B x S								*	*	*	*	*	*
B x C													
L x L													
L x B													
C x B													
B x L													
C x C													
B x B													
	———	———	———	———	———								
					———	———							
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							———	———	———	———	———	———	———

Fig. 5. Differences in temperature selection between groups. Significant differences are indicated by an asterisk (Duncan's Multiple Range Test - 0.05 level). Groups that are not different are underscored by a common line.

Cross	S x S (LL)	S x S (SR)	S x C	R x R	B x C	B x B (SR)	B x B (D)	S x B	L x B	C x B
Number breaths/min	110.4	106.5	105.4	99.8	89.5	86.7	82.4	78.5	77.7	77.5
S x S (LL)			x	x	x	x	x	x	x	x
S x S (SR)					x	x	x	x	x	x
S x C					x	x	x	x	x	x
R x R						xo	xo	x	xo	x
B x C										
B x B (SR)										
B x B (D)										
S x B									o	
L x B										
C x B										

Fig. 6. Differences in breathing frequency and in the breaths:gulp ratio. x and o indicate significant differences (0.05 level, Duncan's Multiple Range Test) between groups in breathing frequency and breaths:gulp ratio.