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Performances of auto and allotriploids in salmonids I. Survival and growth in fresh water farming

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Abstract

Survival and growth performances of autotriploids in rainbow trout (*Salmo gairdneri*) and three types of triploid hybrids between female rainbow trout and brown trout males (*Salmo trutta*), coho salmon males (*Oncorhynchus kisutch*) and brook trout males (*Salvelinus fontinalis*) were analysed relatively to the parental species in freshwater farming conditions. At the end of the immature period, autotriploids exhibit moderate but significant depression relative to the control for both survival (about 25% depression) and growth (10 to 15% depression). Most of this depression is established during the first three months of life, triploids appearing very similar to the control later on. At the onset of sexual maturation at 2 years old, relative value of triploids becomes higher than that of the control, for both survival and growth. Long term evaluation (2⁺ or 3⁺) balances in favor of triploids with particular advantage for triploid females. Triploid hybrids exhibit much more important depression in early survival (up to 60%). Later on, their survival remains always lower than those of parental controls. Their growth performances are intermediate between their two parental species. Despite a relative advantage for these groups during the onset of sexual maturation in control groups, especially for growth, long term evaluation is in favor of diploid rainbow trout, but in some specific cases.

Keywords : Salmonids, triploidy, hybridization, survival, growth.

Performances chez des salmonidés auto et allotriploïdes. I. Survie et croissance en élevage intensif en eau douce.

Résumé

Nous avons comparé les performances de survie et de croissance de truite arc-en-ciel triploïdes (*Salmo gairdneri*) et de trois hybrides triploïdes entre des femelles de cette espèce et des mâles de truite commune (*Salmo trutta*), de saumon coho (*Oncorhynchus kisutch*) et d'omble de fontaine (*Salvelinus fontinalis*) à celles des différents témoins parentaux dans le cadre d'un élevage intensif en eau douce. Les truites arc-en-ciel triploïdes présentent à la fin de la période immature (1⁺) une dépression modérée, mais significative de leurs performances de survie (environ 25%) et de croissance (-10 à -15%). L'essentiel de cette dépression s'établit au cours des 3 premiers mois, l'écart entre diploïdes et triploïdes étant plus réduit par la suite. Lors de la maturation sexuelle, les triploïdes deviennent supérieurs au témoin, en survie comme en croissance. Le bilan à long terme (2⁺ ou 3⁺) s'établit en faveur des triploïdes, un avantage particulièrement net apparaissant dans le cas des femelles triploïdes. Les hybrides triploïdes présentent une dépression de survie précoce beaucoup plus marquée. Ultérieurement, leur survie reste toujours inférieure à celle des témoins parentaux. Leurs performances de croissance sont comprises entre celles des espèces parentales. Malgré un avantage relatif de ces groupes lors de la maturation sexuelle (en croissance notamment), le bilan à long terme reste en faveur de la truite arc-en-ciel diploïde, sauf dans certains cas particuliers.

Mots-clés : salmonidés, triploïdie, hybridation, survie, croissance.

INTRODUCTION

The chromosome set manipulation techniques have been extensively investigated in fish in recent years. Theoretic and practical interest of resulting individuals (gynogenetics, androgenetics, induced polyploids) was extensively discussed (see reviews of Purdom, 1983; Thorgaard, 1983, 1986; Chevassus, 1987; Chourrout, 1987). Triploidy is valuable for production of sterile individuals. It also proved to be an efficient way of increasing survival of interspecific hybrids, (Chevassus *et al.*, 1983; Scheerer and Thorgaard, 1983; Arai, 1984) which may be helpful to produce hybrids with desirable qualities of both parental species. Particular interest lies in hybrids with specific resistance to disease (Dorson and Chevassus, 1985 *a, b*; Parsons *et al.*, 1986). Up to now, much of the work has been done on optimization of induction techniques (see review of Chourrout, 1987). In salmonids, heat shocks proved to be a very efficient technique in inducing high frequency of triploids, and a much more appropriate technique than others (i. e., pressure shocks, that are also efficient; see review of Chourrout, 1987) to be used for large scale production. As a matter of fact, this technique is already diffused in private farms. Nevertheless, there is still few information on performances of these animals.

If much has been done on surveying sexual maturation of triploids (Benfey and Sutterlin, 1984; Benfey, 1985 in Atlantic salmon; Johnson *et al.*, 1986, in coho salmon; Lincoln, 1981 *a, b*; Lincoln and Scott, 1983, 1984; Solar *et al.*, 1984; Jalabert, pers. comm. 1985, in rainbow trout), data on survival and growth are less accurate, as they have sometimes been established with very few animals (Utter *et al.*, 1983; Benfey and Sutterlin, 1984; Johnson *et al.*, 1986; Thorgaard, 1986). Purpose of the present study was to provide extensive information on survival and growth performances of triploid rainbow trout and its triploid hybrids with other salmonids over a complete breeding cycle in freshwater farming.

MATERIAL AND METHODS

Brood stock

Four salmonid species were collected. In all cases, but for experiment 82C (table 2), rainbow trout (*Salmo gairdneri* R.) and brown trout (*Salmo trutta* L.) breeders were kept in INRA experimental fish farm at Gournay-sur-Aronde (Oise) (INRA strains in both cases). In experiment 82C, rainbow trout and brown trout breeders were obtained from the stocks of INRA experimental fish farm at Lees-Athas (Pyrénées Atlantiques). Coho salmon (*Oncorhynchus kisutch*) were introduced from private

freshwater (80A, 82A) and seawater (81A) French farms. Only brook trout males (*Salvelinus fontinalis*) were available and came from domestic population in north of France (Etrun; Pas-de-Calais).

Fertilization procedure

Nine successive experiments were performed, from November 1980 to January 1983 (tables 1, 2). In each

Table 1. — Crossing design and nomenclature of the different groups.

	Male	Rainbow trout (R)	Brown trout (B)	Coho salmon (C)	Brook trout (O)
Rainbow trout (R)	NF HS	R2 R3	RB ⁺ R2B	RC ⁺ R2C	RO ⁺ R2O
Brown trout (B)	NF	/	B2	/	/
Coho salmon (C)	NF	/	/	C2	/

NF : normal fertilization.

HS : heat shock (26°C, 20 min).

* : diploid hybrids, with poor or no survival at early stages.

case, eggs of several females per species were stripped by abdominal pressure, and artificial fertilization performed using saline buffered diluent (Billard, 1977). Eggs from rainbow trout females were fertilized by a sperm mixture from 3 to 10 males of all the available species, while brown trout and coho salmon eggs were fertilized only by homologous semen, as presented in table 1.

Eggs from the different females were usually pooled, except in experiment 80B, in which eggs of the individual females were fertilized and kept separately until the end of hatching. Triploidization treatment was the one described by Chourrout (1980) and Chourrout and Quillet (1982) (heat shock at 26°C lasting 20 min), which proved to be highly efficient on rainbow trout eggs; the same treatment also proved to induce very high rates of triploid hybrids involving that species as maternal species (Chevassus *et al.*, 1983).

Control of the nature of individuals

Early karyological and biochemical controls were performed in exp. 80A and 80B. Results are presented in the paper by Chevassus *et al.* (1983). Later on, we have admitted that the nature of the individuals resulting from the treatments was the expected one. Now, Chourrout (1986) has recently demonstrated across karyological examinations that when heat shocks are applied, diploids are directly replaced by triploids, with very limited occurrence of aneuploidy, conversely to what is observed with suboptimal pressure shocks. Therefore, in the case of homospecific

crosses, heat shocks would result in only diploids (fertile) and triploids (supposed to be sterile). Following maturation up and examination of gonads after maturation provided a control *a posteriori* of the frequency of triploids in experimental populations. This was done in autotriploids in several experiments: whatever experiment, we usually found very few fertile animals (usually 3 to 5%, up to 13% in exp. 82A), thus indicating high efficiency of the triploidization treatments.

Rearing facilities

Rearing facilities were the following, depending on the experiments (see table 2):

— a recirculated system (Jo) stabilized at $10 \pm 0,5^\circ\text{C}$ used for incubation and early fry development, and located at INRA station of Jouy-en-Josas (Yvelines). When long term rearing was planned, eggs were transported into experimental farms at eyed stage.

— the INRA experimental fish farm of Gournay-sur-Aronde (Gr) supplied with spring water (temperature ranging from 6 to 16°C).

— the INRA hatchery of Saint-Péc-sur-Nivelle (Sp), supplied with filtered water from river Nivelle (temperature ranging from 8°C to 13°C).

In all cases, eggs of the different groups were hatched in separated trays until the end of start-feeding, and then reared separately up to 7 to 12 months (20 to 50 g) in fiber tanks and kept under standardized conditions.

Later on, the different groups were tagged by fin-clipping (at least 100 individuals per group) and mixed in large concrete ponds for long term growth study. During the first year, all fish were fed *ad libitum* twice a day on commercially produced dry pelleted food. Later on, standard rationing tables were applied.

Study of performances

Three main periods were defined during the life of the fish to study performances: (1) hatchery period P_1 , from fertilization to about 50 days after start of

feeding; (2) immature period P_2 , which extends until the fish are about 20 months (1^+); (3) maturation period P_3 , which includes both the first maturation cycle at 2 years and the following maturation cycle when it is analysed. Exact durations of P_1 , P_2 , P_3 for the different experiments are reported in table 2.

Survival

Survival was recorded at the end of each period. Daily mortality rate (m) for the different periods was defined as:

$$N_f = N_i(1 - m)^d$$

where N_i and N_f are the initial and final numbers of fish (or ova in the case of P_1), and d the duration in days of the period; m is given in per thousands per day.

Growth rate

Early growth rate was evaluated by mass weighing of 50 to 100 fish per group.

Later on, weight was individually recorded on 50 fish per group. Daily specific growth rate α (in percent of body weight) is calculated from:

$$Wf = Wi(1 + \alpha)^d$$

with Wi = mean weight at the beginning of the period, Wf = mean weight at the end of the period and d = duration in days of the period.

At two years old, maturing fish were recorded on a phenotypic basis, and tagged with Aleyan blue spots on fins, hence their further growth could be analysed separately.

Consequences of triploidy on sexual maturation of both auto and allotriploids will be dealt with specific analysis in another paper (Chevassus *et al.*, unpublished data), but some informations about occurrence of maturation in the populations analysed here are necessary with regards to growth analysis: in the rainbow trout strains analysed and in our rearing conditions, 97% of males and about 75% of females first mature at 2 years, whereas in brown trout populations, more than 80% of males but only few females

Table 2. — Experimental groups and characteristics of the different experiments.

Experiment	Number of Rainbow trout females	Experimental groups	Place of incubation (*)	Hatching and raising (*)	Age at the different period (°)		
					P1	P2	P3
80A	12	R2, R3, R2B, R2C, R2O	Jo	Gr	0-105	105-656	656-1412
80B	5	R2, R3, R2C	Jo	Jo	0-110	/	/
81A	6	R2, R3, R2B, R2C, B2, C2	Jo	Gr	0-90	90-593	593-1194
82A	28	R2, R3, R2B, R2C, B2	Jo	Gr	0-110	110-593	593-1043
82B	41	R2, R3	Gr	Gr	0-90	90-575	575-1024
82C	4	R2, R2B	Sp	Sp	0-93	/	/
82D	4	R2, R3	Jo	Gr	0-83	/	/
83B	2	R2, R3	Jo	Go	0-81	/	/
83C	34	R2, R3	Jo	Sp	0-96	/	/

(*) see in text for description of experimental structures. (°) age in days post fertilization.

mature at that age. All fish are mature at 3 years old. In autotriploids, only males are affected by sexual maturation (gonadal growth is observed, but they keep lower gonado-somatic index than diploids), and females remain fully sterile as this was described in several studies previously cited. The same phenomenon is encountered in the case of allotriploids (Chevassus *et al.*, 1985; Quillet, 1986).

Within group variability

At each date of measurement, individual data allowed for each group calculation of the coefficient of variation CV, as standard deviation expressed as a percentage of the mean.

In the particular case of experiment 82A, when fish were about 9 months old, number of data was extensively increased (250 fish per group) in order to get more precise estimation of within group variability and to describe the distributions of the different populations.

Statistical methods

Normality of weights was tested by computation of Spearman's coefficients for skewness (g_1) and kurtosis (g_2) (as defined in Sokal and Rohlf, 1981). Asymetry to the right was usually detected in young fish, but this asymetry tended to decrease as time goes, and was not important enough for a log-transformation (Chevassus, 1976) to be required. So, normality was

Table 3. — Early survival rate (in percents of inseminated ova) in the different experiments.

Control Experiment (*)	R2	B2	C2
80A	54.6	nr ^(b)	/
80B	58.3	/	/
81A	77.1	83.5	14.6
82A	89.7	67.7	26.3
82B	79.6	/	/
82C	71.3	/	/
82D	70.9	/	/
83D	88.2	/	/
83C	48.4	/	/
Mean	70.9	75.6	20.5

(*) Age at measurement for the different experiments is given in table 2.

(b) Not recorded.

accepted, and analysis performed on non transformed data.

Analysis of variance was performed with classical models (one or two way ANOVA, with or without replicates. Sokal and Rohlf, 1981).

Some multiple comparisons were also performed with test of Student-Newman-Keuls (Scherrer, 1984).

Analysis of percentages p (i. e. survival rates) were performed on transformed data $p' = \arcsin \sqrt{p}$.

Finally, assuming that coefficient of variation remains constant over short range of growth within

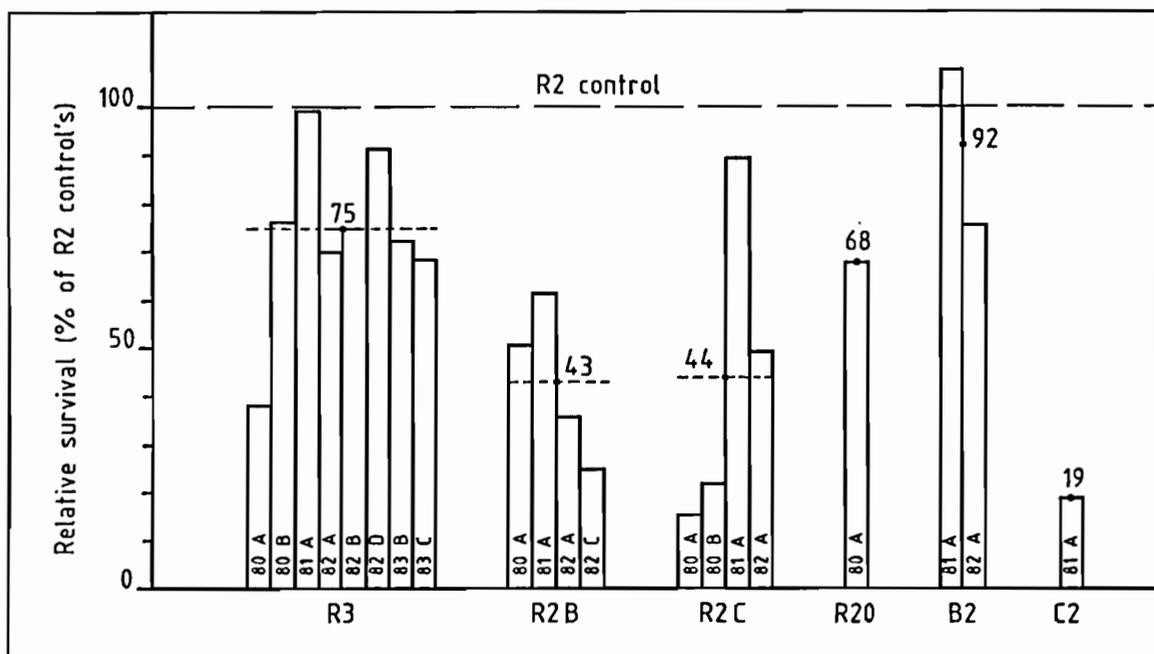


Figure 1. — Early survival (end of P₁) of auto and allotriploids.

a given population, we could test equality of coefficients of variation as equality of variances, as indicated by Sokal and Rohlf (1981).

RESULTS

Survival

Early survival (P_1)

— *Mean performances:* At the end of P_1 , early survival in pure species controls was usually high (more than 70% of ova in both R2 and B2 groups), except for coho salmon C2, for which low survival was supposed to result from poor egg quality (table 3). Relative survival rate of the other groups are presented in figure 1. At that time, all diploid hybrids had died, while relatively high survivals were observed in all triploid groups; autotriploids R3 and rainbow trout \times brook trout hybrids exhibited the best survivals, but all groups were significantly weaker than the diploid rainbow trout control (from 43 to 75% relative to the control). Mortality occurred regularly from fertilization to the end of P_1 and was not typically connected with any particular phase of early development.

— *Variability:* Wide variation of mean relative success was detected among the different experiments, especially in R2C groups (see fig. 1—the lowest data observed in R3 groups was related with miss—handling of eggs after heat shock, and may not be considered as representative of actual variability). Between-female variability was analysed as possible origin of the observed variation from data of experiment 80B, in which progenies of 4 females were kept separately. Test of homogeneity of survivals in the different genotypes actually revealed important female effect on early survival in all hybrid and triploid groups (R3, RC and R2C), though such an effect could not be detected among the diploid R2 batches (table 4).

Immature period (P_2)

Daily mortality rates of the different groups are reported in figure 2. Detailed analysis of data (general

test of Newman and Keuls, and restricted paired comparison between R2C and C2) showed that mortality rate in autotriploids R3 did not differ from R2 control one, but that all triploid hybrids exhibited higher mortality rates than their two parental controls when available.

First maturation cycle and later on (P_3)

Absolute daily mortality rate in R2 and B2 control at that time was about twice as high as it was during the immature period (fig. 2). Conversely, mortality rate in both autotriploids R3 and triploid hybrids was reduced, when compared to the previous P_2 period. Result of these two concurrent evolutions was that R3 groups exhibited at that time better survival than their R2 control (Student's *t*-test significant for $P < 0.05$) and that triploid hybrids did not differ any more from their parental control.

Evolution over the three periods

Long term evolution of the different groups (summarized in fig. 3) leads to the following conclusions: better survival of autotriploids during the maturation period and later on is enough to balance initial depression relative to the diploid, so that cumulated survivals at 3 years are similar in both groups. On the other hand balancing is not observed in allotriploids, important initial depression, increasing all along the immature period associated with relative survival rate at best equal to the control one contributes to lower final survival in these groups (about half to one third of the parental controls).

Growth performances

Early growth (fig. 4)

Differences in growth performances of the different groups were detected as soon as the end of P_1 : autotriploids R3 exhibited slight but significant depression (about 6%) when compared with their diploid control. Triploid hybrids, as well as the two paternal species B2 and C2 presented a much more accurate inferiority in weight relative to diploid rainbow trout.

Immature period

— *Mean performances:* Initial depression tended to increase all along the following immature period. Anyhow, deviation was kept restricted in autotriploids R3 as their final weight by the end of P_2 reached 87% of that of their diploid control (fig. 5). Conversely, discrepancy was highly emphasized in triploid hybrid groups, that exhibited relative growth performances similar to their paternal control; yet the only available paired comparison (between R2B and B2) indicated that hybrids have had better growth rate than pure paternal brown trout control (table 5).

— *Within-group variation:* Analysis of coefficients of variation CV of the different groups when growth goes on revealed no difference of within-group

Table 4. — Analysis of female effect on survival of the different groups (data of experiment 80B).

Group Stage	R2	R3	RC	R2C
Eyed stage	S 89.3	92.0	84.0	89.4
	K 7.3 NS	23.5**	88.3**	31.7**
Hatching	S 97.0	95.0	62.0	93.0
	K 3.9 NS	15.6**	43.4**	21.2**

S = survival (in percents).

K = χ^2 test (3 df) for homogeneity between the different females.

* : significant for $P < 0.05$.

** : significant for $P < 0.01$; NS : non significant).

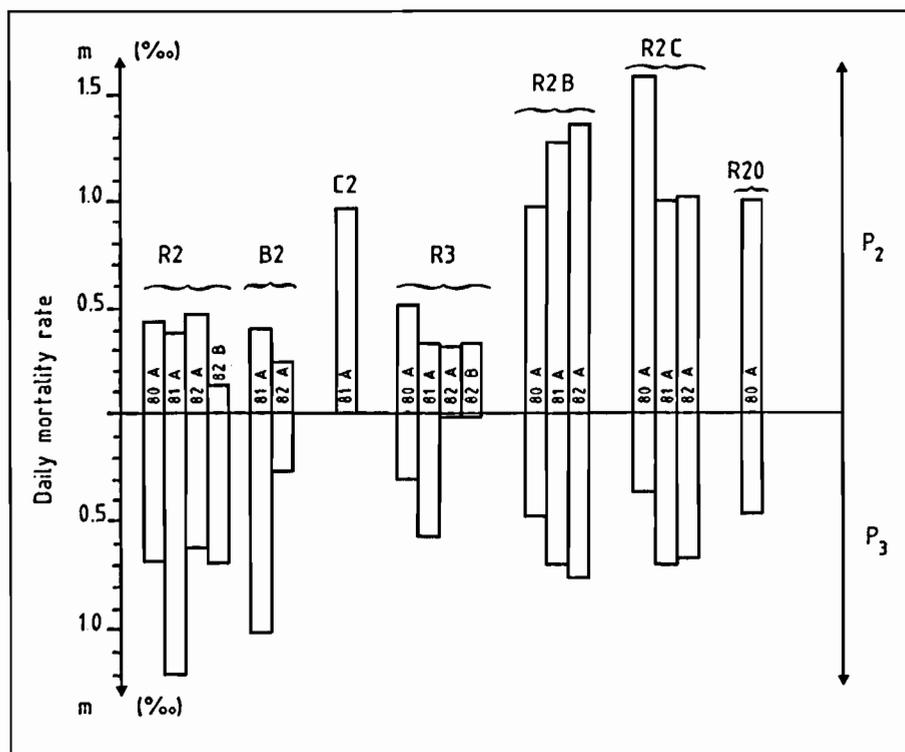


Figure 2. — Daily mortality rate during the immature (P_2) and the maturation (P_3) periods.

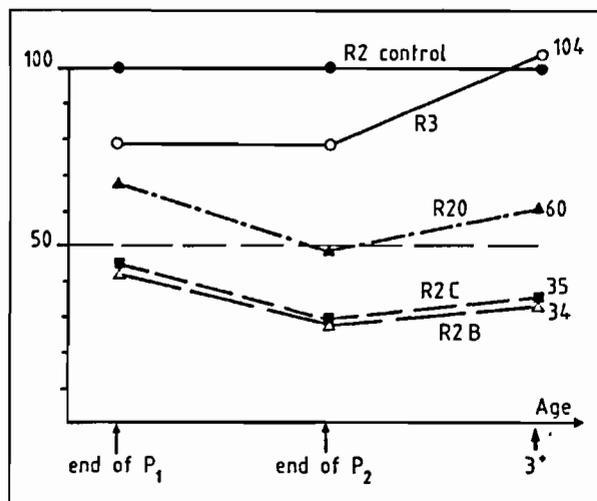


Figure 3. — Evolution of the relative survivals of the different groups over the whole breeding cycle.

variation between parental diploid controls, autotriploids R3 and R2B triploid hybrids. Though tests were not very powerful, due to low sample sizes (50 data), and therefore usually not significant, R2C triploid hybrids exhibited systematically higher variability than controls.

Extensive measurements in experiment 82A confirmed that observation, the only group with

higher variability than controls being R2C (table 6). Simultaneously, coefficient of kurtosis was also particularly high in R2C groups, indicating a tendency towards bimodal distribution in that particular group (about 9% of total population heavier than antimode), while others were much more similar to the controls.

Maturation period

On and after first sexual maturation cycle, diploid rainbow trout females were considered as common reference for comparison of the different groups. Relative weights of the different groups after the two first maturation cycles at 2^+ and 3^+ are presented in figure 6.

After the first sexual maturation at two years, an important dimorphism was observed between still immature fish and maturing males, weight of which represented 82.0 and 79.5% of that of immatures in R2 and B2 controls respectively. The same dimorphism was observed in autotriploids R3: weight of maturing males after the first maturation was only 80.4% of immature triploid population (table 7). However, it was clear that during maturation, R3 triploid males kept higher growth rate than their R2 maturing control. Similarly, triploid sterile females grew faster than maturing diploid females, but did not have significant difference in growth rate with the small proportion of residual immatures of the control population (table 8).

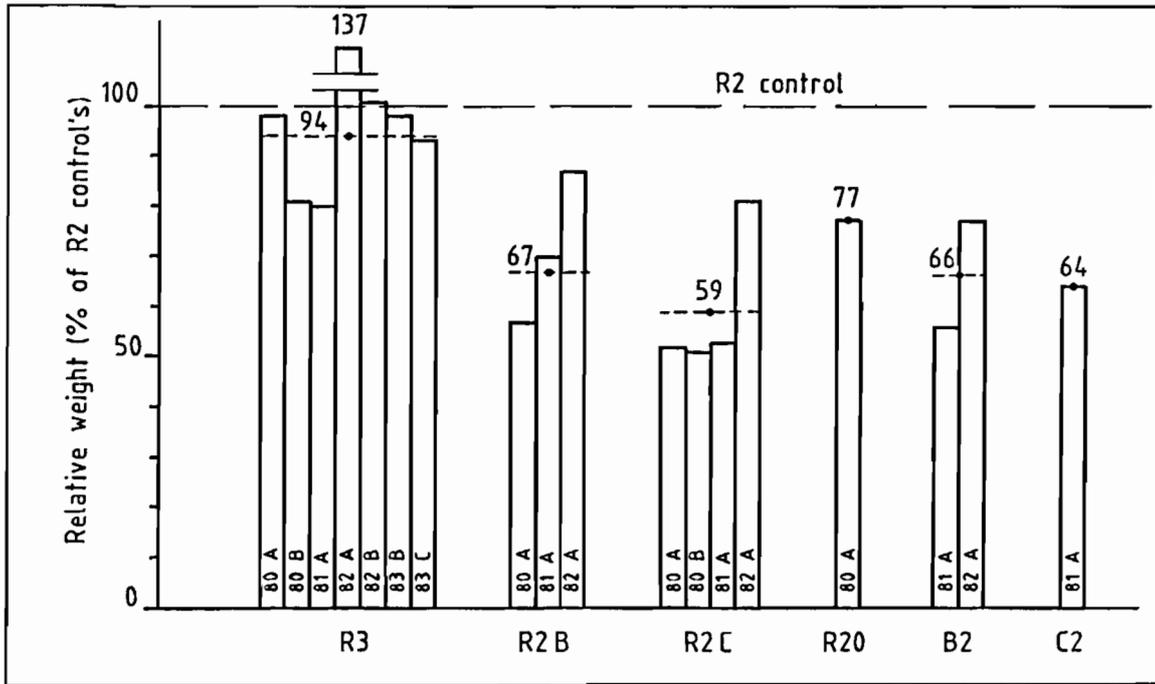


Figure 4. — Early growth (end of P₁) of auto and allotriploids (in R3 groups, weighted mean according to the number of batches in each experiment).

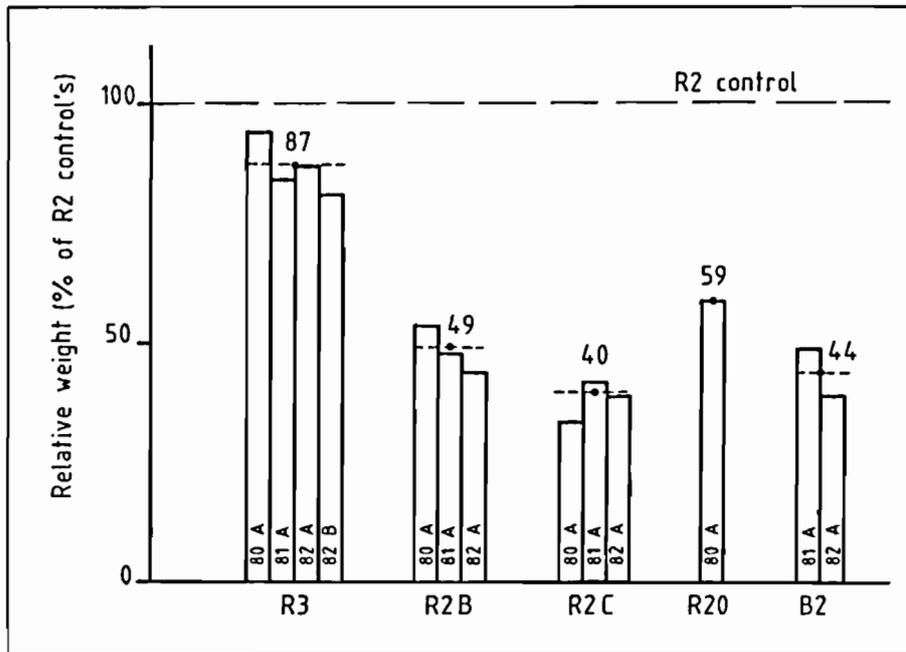


Figure 5. — Weights of the different groups at the end of the immature period P₂.

As a result, triploids gradually took advantage from every successive maturation cycles. Their relative weight which was 87% of the diploid one by the end of the immature growth became 104 and 107% of diploid males and females respectively after the first maturation cycle, and reached 116 and 119% at 3⁺

after the 2nd maturation cycle. Same general trends were observed in triploid hybrids (fig. 6), despite some specific aspects. Thus, level of dimorphism between mature and immature fish widely depended on hybrids: therefore mature males weighed only 64 and 46,5% relative to their immature sibs in F₂C

Table 5. — Analysis of variance for weights at the end of P2.

	Source of variation	SS	d. f.	MS	F
R2/R3	Group	430992	1	430992	33.83 **
	Experiment	1.03×10^6	3	341 752	26.83 **
	Interaction	109 888	3	36 629	2.87 *
	Residual	4.99×10^6	392	12 739	
R2/R2B	Group	4.13×10^6	1	4.13×10^6	312.36 **
	Experiment	381 192	2	190 596	14.43 **
	Interaction	151 696	2	75 848	5.74 **
	Residual	3.88×10^6	294	13 207	
R2/R2C	Group	5.57×10^6	1	5.57×10^6	440.51 **
	Experiment	216 848	2	108 424	8.57 **
	Interaction	243 676	2	121 838	9.64 **
	Residual	3.72×10^6	294	12 643	
R2/R2O	Comparison of 2 means Student _(98 df) = 8.57 **				
R2/B2	Group	7.00×10^6	1	7.00×10^6	1045.91 **
	Experiment	203 000	2	101 500	15.16 **
	Interaction	337 280	2	168 640	25.18 **
	Residual	1.97×10^6	294	6 697	
B2/R2B	Group	554 274	1	554 274	96.48 **
	Experiment	205 896	2	102 948	17.92 **
	Interaction	94 056	2	47 028	8.18 **
	Residual	1.69×10^6	294	5 745	

** : Fisher's (or Student's) test significant for $P < 0.01$. * : Fisher's test significant for $P < 0.05$.

Table 6. — Within-group variability and distribution of population in experiment 82A.

Group	n	W	SD	CV	g_1	g_2
R2	249	17.28	7.53	43.6	0.577 **	+0.342
R3	248	22.34	9.82	43.9 ^a	0.818 *** ^c	+0.719 ** ^c
R2B	232	12.93	6.69	51.7 ^{ab}	0.513 *** ^{cd}	-0.600 ** ^{cd}
R2C	237	13.06	7.72	59.1 ^c	1.608 *** ^c	+3.421 *** ^c
B2	235	6.98	3.25	46.6 ^a	0.814 *** ^c	+0.491 ^c

n : number of data.

W : weight (grams).

SD : standard deviation.

CV, g_1 , g_2 : see definition in text.

a, b : non significant difference with R2 and B2 controls respectively ($P < 0.01$).

c, d : significant difference with R2 and B2 respectively ($P < 0.01$).

* : coefficient (g_1 or g_2) significant for $P < 0.05$.

** : coefficient (g_1 or g_2) significant for $P < 0.01$.

and R2O groups respectively, whereas no significant differences could be detected between males and immatures in R2B groups (Student (48d f) = 1.09; NS) (table 7).

Maturing hybrid males also kept better growth rate than the parental diploid males, so that their relative weight increased with every sexual maturation cycle: R2C males were 49% of diploid rainbow trout at 2⁺ and 78% at 3⁺. Similarly, R2B hybrids were 71% at 2⁺ and 82% at 3⁺ of rainbow trout control; corresponding figures were 65.5 and 96% respectively for the comparison with brown trout males.

Concurrently, relative value of hybrid females also increased relatively to their diploid controls, in even greater proportions as they were completely sterile.

Nevertheless, females hybrids between brook trout and rainbow trout were the only ones to become heavier than the R2 female control at 2⁺.

Evolution over the three periods

Relative growth of the different groups over a three year long breeding period is summarized in figure 7. In our experimental conditions, rainbow trout was the best growing group all over the immature period. When occurring, maturation involved in most groups clear discrepancies between males and females, the males exhibiting lower growth at that time than their sisters. Anyhow, despite their initial depression, two groups recovered their inferiority relative to the rainbow trout reference: these are pure rainbow trout triploids and rainbow trout × brook trout hybrids, in which females passed beyond the rainbow trout as soon as the first sexual cycle. Next maturation periods went with increase of this relative advantage. All the other groups also show relative improvement after the rainbow control has matured, but they remain lighter within the experimental 3 year long period.

DISCUSSION - CONCLUSION

Autotriploids

Survival

Reduced survivals in early stages have often been recorded in triploids resulting from application of heat shocks (Chourrou and Quillet, 1982, Lincoln and Hardiman, 1982, Solar *et al.*, 1984, Happe *et al.*,

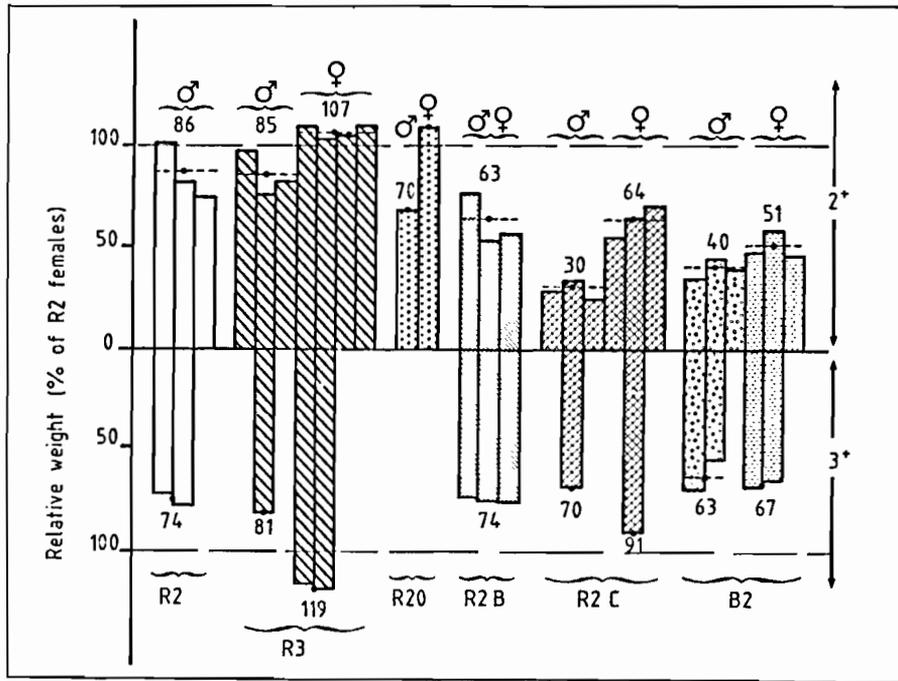


Figure 6. — Weights of the different groups after the first (2⁺) and the second (3⁺) sexual maturation cycles.

Table 7. — Sexual dimorphism in the different groups.

		a R2 b	R3 a	R2B a	R2C a	R2O a	a B2 b
2 ⁺	80A	97.9 (102.2)	90.4	92.4	51.9	64.3	73.1
	81A	74.6 (81.4)	73.1	—	51.9	—	79.4
	82A	73.5 (74.4)	78.7	143.1 ^c	35.6	—	85.9
	Mean	82.0** (86.0)	80.4**	92.4 NS	46.5**	64.3**	79.5**
3 ⁺	80A	(71.2)	—	—	—	—	(101.0)
	81A	(77.7)	67.4	99.1	76.5	—	(88.1)
	Mean	(74.4)	67.4	99.1	76.5	—	(94.6)

a : relative value of males over immatures. b : relative value of males over mature females. c : only 2 males are recorded.

Table 8. — Comparison of growth rates during sexual maturation in diploid and triploid rainbow trout.

	Source of variation	SS	d. f.	MS	F
♂ R2/♂ R3	Group	1.13×10^{-2}	1	1.13×10^{-2}	7.10*
	Experiment	3.43×10^{-2}	5	6.86×10^{-3}	4.31 NS
	Residual	7.95×10^{-3}	5	1.59×10^{-3}	
♀ R2/♀ R3	Group	4.91×10^{-2}	1	4.91×10^{-2}	10.43*
	Experiment	1.16×10^{-1}	6	1.93×10^{-2}	4.09 NS
	Residual	2.82×10^{-2}	6	4.71×10^{-3}	
Im. R2/Im. R3(*)	Group	1.55×10^{-2}	1	1.55×10^{-2}	3.36 NS
	Experiment	1.81×10^{-1}	8	2.26×10^{-2}	4.91*
	Residual	3.69×10^{-2}	8	4.61×10^{-3}	

(*) Immature fish at 2 years. * : Fisher significant for $P < 0.05$.

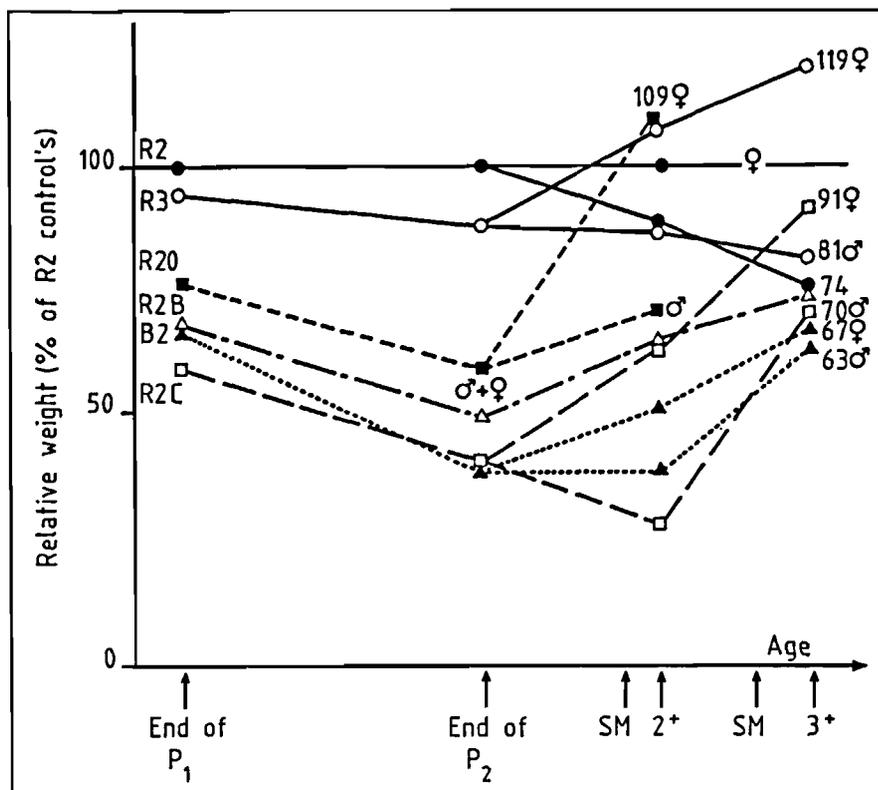


Figure 7. — Evolution of the relative weights of the different groups over the whole breeding cycle.

in press, in rainbow trout; Scheerer and Thorgaard, 1983, in brown trout; Benfey and Sutterlin, 1984, Johnstone, 1985 in Atlantic salmon). Lower survivals may result from persistent deleterious effect of thermal shock on egg quality (i. e. integrity of yolk component). One indication is that eggs appear particularly susceptible to handling at the end of the thermal treatment. Nevertheless, it does not seem that use of other treatments (i. e. pressure shocks) improves survival.

One possible approach of treatment effect is comparison of such triploids with second generation triploids, obtained by mating diploid females and tetraploid males (Chourrout *et al.*, 1986), as production of the latter does not involve any treatment of the ova. There are several results indicating that second generation triploids may have better survival than heat-shock ones (Chourrout *et al.*, 1986), at least in very early stages (yolk resorption, Blanc *et al.*, 1987).

Later on, however, no difference was detected between triploids and their control all over the immature period. These results are similar with several data available in the literature (Gervai *et al.*, 1980 in carp; Lincoln and Hardiman, 1982, in rainbow trout; Suzuki *et al.*, 1985, in the cyprinid loach) but are not totally consistent with other observations that point out decreases in the frequency of triploids as fish grow old in populations initially containing diploids and triploids (Thorgaard *et al.*, 1982, in rainbow trout; Utter *et al.*, 1983, in coho salmon).

Yet, previous results were generally recorded under so called "optimal" rearing conditions, but it must also be underlined that, when kept under more restrictive conditions, triploids may eventually exhibit greater weakness than diploids: Johnson *et al.* (1986) once reported special susceptibility of triploid coho salmon to the stress of seawater challenge, Quillet *et al.* (1987) also recorded higher mortality in triploid rainbow trout than in diploids during summer time in seawater farming on French coast. On another hand, Dorson and Chevassus (1985 *a*, 1985 *b*) did not detect differential mortalities in diploid and triploid rainbow trout after challenge with IPN and VSH virus. Despite disputable results, one can not exclude the possibility that triploids may be weaker than diploids in some conditions, though that should not be a nuisance in most cases.

Growth

Growth of triploids follows the same general trend than survival, triploids being smaller than diploids up to the onset of sexual maturation, and getting heavier later on. If our results are somewhat variable from an experiment to another concerning early stages (relative value of triploids ranging from 80 to 137% at the end of P₁), depression by the end of P₂ is well established from our data. Such an observation is in agreement with many results available in literature: most of the authors find that triploids grow less than

diploids, or at best, as much as them (see table 9), though, in most cases, few information is available concerning emergence of the discrepancy if any. Nevertheless, several arguments indicate that origin of the depression should not lie in early embryonic and larval development; indeed, measurements by

Happe *et al.* (in press) and Quillet *et al.* (in press) establish that triploids hatch slightly before diploids: triploids are therefore most likely to take relative developmental advance at that time rather than delay.

Similarly, observations of Oliva-Teles and Kaushik (1987) on embryonic metabolism and of Happe *et al.*

Table 9. — Comparison of growth of diploids and triploids in different experiments.

Species	References	Rearing conditions	Immature phase		After maturation of control	
			Period	Ratio T/D(°)	Age	Ratio T/D(°)
SALMONIDS						
<i>Salmo gairdneri</i>	1. Lincoln and Hardiman, 1982	Mixed with control, fed to satiation	22 to 50 weeks	0.79		—
	2. Lincoln and Scott, 1984	Mixed with control, fed to satiation			23 months	NS
	3. Solar <i>et al.</i> , 1984	Separated tanks (up to 5-6 feedings per day)	24 to 48 weeks	0.38		—
	4. Chourrout <i>et al.</i> , 1986	Separated tanks fed to satiation	83 to 360 days	0.90	890 days	1.10
	5. Thorgaard, 1986	Mixed with control n.p.	2 years	NS	3.5 years	1.35
	6. Happe <i>et al.</i> , in press	Replicated separated tanks, fed to satiation	0 to 106 days	0.91		—
	7. Blanc <i>et al.</i> , 1987	Separated tanks n.p.	0 to 175 days	0.89		—
<i>Salmo salar</i>	8. Benfey and Sutterlin, 1984	Separated tanks excess food	9 to 18 months	NS		—
<i>Oncorhynchus kisutch</i>	9. Utter <i>et al.</i> , 1983	Mixed with control n.p.	0 to 17 months	0.87		—
	10. Johnson <i>et al.</i> , 1986	Mixed or separated n.p.	0 to 20 months	NS		—
OTIHER SPECIES						
<i>Cyprinus carpio</i>	11. Gervai <i>et al.</i> , 1980	Mixed, same initial weight, fed to satiation	Juvenile (3 weeks period)	NS		—
<i>Misgurnus anguillicaudatus</i>	12. Suzuki <i>et al.</i> , 1985	Mixed with control	0-year old	♀ 0.63 ♂ 0.92	1-year old	♀ 1.31 ♂ 1.03 NS
<i>Ctenopharyngodon idella</i>	13. Cassani and Caton, 1986	Mixed with control	fry fingerling	0.46		
		Separated tanks, fed to satiation	fingerlings	0.96 NS		
<i>Ictalurus punctatus</i>	14. Wolters <i>et al.</i> , 1982	Separated tanks, fed to satiation	0 to 4 months	1.00 NS	8 months 16 months	1.06 1.16
<i>Silurus glanis</i>	15. Kraznai and Marian, 1986	Replicated separated tanks, fed to satiation	7 to 14 weeks	1.43		
<i>Clarias gariepinus</i>	16. Richter <i>et al.</i> , 1987	Mixed with control, varying feeding levels			163 to 219 days	NS
<i>Tilapia aurea</i>	17. Valenti, 1975	Separated tanks	0 to 6 weeks	0.97 NS		
<i>Oreochromis aureus</i>	18. Penman <i>et al.</i> , 1987	Mixed or separated	Measured at 20 to 32 weeks (depending on experiment)			≤ 1 (one exception)
<i>O. mossambicus</i>						
<i>(P. platessa × P. flesus)</i>	19. Lincoln, 1981 c	Separated tanks, fed to satiation	5 months before spawning of diploids at 3 years	0.91	2 months after spawning	1.15
					4 months after spawning	1.03 NS

a : T/D = Weight of triploids/Weight of diploid control. n.p. : no precision.

(in press) on larval growth during yolk resorption are consistent one with the other, and indicate no difference in utilization of endogenous reserves between diploid and triploid larvae.

It seems from experiment by Happe *et al.* (in press) that emergence of the discrepancy goes with introduction of exogenous feed at swim up; this suggests that differences either in feeding behavior or (and) in long term metabolism are involved.

Results of Cassini and Caton (1986) on triploid grass carps reared in various conditions (density, feeding level, competition with diploids or no) comfort such hypotheses. Similarly, Bricout *et al.* (unpublished data) showed that keeping triploids rainbow trout fingerlings in separated tanks instead of mixing them with diploids, as well as changing rate of feeding could modify the relative ranking of the two groups for both growth rate and food conversion efficiency.

So, differences in rearing conditions may contribute to the inconsistency of the above cited results on relative growth of triploids. More over, it seems that restrictive conditions for survival previously discussed may also emphasize the tendency of triploids to grow slower than diploids (Cassini and Caton, 1986; Johnson *et al.*, 1986; Quillet *et al.*, 1987).

On the other hand, relative superiority of triploids during the onset of sexual maturation is also generally recorded, though absolute gain is variable (table 9), and can be interpreted as a direct consequence of sterility of triploids, which invest few or no for gonadal growth and keep good somatic growth rate during this period. As a matter of fact, triploid females, that were completely sterile, displayed the greatest advantage during this period in our experiment. Nevertheless, gonadal development is sometimes observed in triploid females (Penman *et al.*, 1987 in tilapia *O. aureus*).

Comparing diploid and triploid plaice × flounder female hybrids, Lincoln (1981) described rapid growth in diploids following spawning, so that they compensated their loss in weight. We have no data to confirm such an evolution, but even if similar phenomenon occurred in our case, it was not enough to overcome the relative loss of diploids, as we observed an increase of relative advantage of triploids after several maturation cycles.

Allotriploids

Survival

All three hybrids we have studied in the present paper are highly inviable when diploid (Chevassus, 1979). Despite noticeable increase of viability by triploidization treatment (Chevassus *et al.*, 1983; Scheerer and Thorgaard, 1983), these animals remain weaker than the parental controls all over the immature period. No specific disease was identified as causal agent of the death of fish, and mortality was regularly distributed in time. At the onset of sexual

maturation, triploid hybrids display same evolution of gonads than pure species triploids and are not very affected by maturation. Nevertheless, this is not sufficient to overcome their general weakness, and they just equalize maturing controls at that time.

Another trait of triploid hybrids is the important variability of success of hybridization. Large variability of survival rates is a general feature in diploid interspecific crosses (Ayles, 1974; Chevassus and Petit, 1975; Blanc and Chevassus, 1979) and it seems that female effect could be a major cause of this variability (Blanc and Poisson, 1983). The same phenomenon is observed in triploid hybrids. In both cases however, survival of hybrids is not correlated with survival of monospecific crosses, and that will make selection for better survival (if desired) much more difficult to manage.

Growth

Two main factors are likely to influence growth rate of triploid hybrids that are (1): triploid state previously discussed in the case of triploid rainbow trout, and (2): hybrid state and potential effect of genic balance between the genomes of the different species. Additive inheritance in interspecific hybrids was demonstrated by Purdom (1972) in diploid hybrids, triploid hybrids and the back-cross between plaice and flounder for some characteristics as number of vertebrae or larval pigmentation.

Our data indicate that growth of triploid hybrids is influenced by both parental species. This can be stated in the case of rainbow trout × brown trout hybrid, for which both parental species are available. Similarly, though data on pure brook trout are not available in our experiments, hybrid involving that species exhibit good growth, which is consistent with previous works on this species and its hybrids (Refstie and Gjedrem, 1975; Sutterlin *et al.*, 1977).

Nevertheless, caution must be kept when considering values of R2C hybrids in our study, because both survival and growth of coho salmon are extremely poor in our experimental conditions, and certainly not representative of actual potential of this species.

No clear effect of triploidy on within-group variability during immature growth is detected from our data, but in rainbow trout × coho salmon hybrids. Whether this variability results from only paternal inheritance or is emphasized because of triploid status remains questionable, due to lack of reliable coho salmon control in our experimental conditions. Bimodal distribution, associated with this high variability, may also be related to partial smoltification of hybrids, but further observations will be necessary to conclude on the particular point.

At last, reduction of growth depression of hybrids relative to rainbow trout control during the onset of maturation can also be interpreted as the main consequence of sterility of those groups. Maintenance of good growth rate of triploid females before and

during spawning had already been observed by Lincoln (1981) in flatfish hybrids. Yet in our conditions, hybrid involving brook trout is the only one that passed beyond rainbow control at 2⁺.

Practical interest of triploids

Practical interest of triploids will depend on economical consequence of their characteristics relative to diploid populations in specific breeding schemes. Some authors have concluded from analysis of their data that triploidy would not confer any particular advantage for fish farming (Lincoln, 1981 *c* in flatfish; Penman *et al.*, 1986 in tilapia; Richter *et al.*, 1986) except for body composition (gutted weight, muscle composition). We provide here preliminary calculations from our data in order to compare the different groups in term of total production they allow, taking both survival and growth into account (*table 10*). This clearly indicates that triploidy confers a benefit as soon as production of large animals (implying rearing fish over at least one maturation cycle) is planned that should certainly be enhanced if economical costs of production were also taken into account: for instance, most of the mortality in triploids occurs at early stages, while late mortality in diploids affects animals with high individual value; similarly, Wolters *et al.* (1982) recorded better feed conversion in triploid tilapia than in maturing diploids. Time when triploids become superior to their control will depends on several factors as the age at sexual maturation in the local control, the extend to which growth and survival are reduced by maturation.

Yet, in some specific cases (disease attack for instance), relative superiority of triploid hybrids may also raise earlier in the breeding cycle. Anyhow, rearing all female triploid populations should be recommended as a complementary technique, to take full advantage of their complete sterility. Beside an absolute increase of biomass production, this could also allow a distribution of sales all over the year, both survival and growth into account (*table 10*). This clearly indicates that triploidy confers a benefit as soon as production of large animals (implying rearing fish over at least one maturation cycle) is planned that should certainly be enhanced if economical costs of production were also taken into account: for ins-

Table 10. — Productiveness of the different groups in terms of total biomass (same initial number of fry in every case).

		Total biomass (%)		
		1 ⁺	2 ⁺	3 ⁺
R2	♂	100	86	74
	♀		100	100
R3	♂	85	97	93
	♀		122	137
R2B	♂	33	40	65
	♀			
R2C	♂	28	22	66
	♀		48	77
R2O	♂	44	70	—
	♀		110	
B2	♂	42	48	69
	♀		61	73

(*) Relative production, taking both growth and survival into account.

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