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Studies in individual spawnings of *Salmo salar*: a model to explain chromosome polymorphism patterns

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Summary. Atlantic salmon fry from nine offspring belonging to individual spawnings were karyotyped. Different patterns of Robertsonian chromosome polymorphism were obtained. A theoretical model is developed to explain the different chromosome polymorphism patterns in *Salmo salar* offspring in terms of the chromosome numbers of the parents.

Key words: *Salmo salar* – Offspring – Robertsonian polymorphism – Genetic pattern – Chromosome number

Introduction

Atlantic salmon, *Salmo salar* L., is a species with inter- and even intra-individual polymorphism in the number of chromosomes, as are some other Salmonids (Hartley 1987). This polymorphism often follows a Robertsonian pattern, with a varying chromosome number (2n) but the same fundamental number of chromosome arms (NF). This can be explained by translocations in which two acrocentrics are fused into one metacentric, or vice-versa (Roberts 1968, 1970).

Wild and reared European populations of *Salmo salar* present very diverse patterns of Robertsonian polymorphism (Hartley 1988; García-Vázquez et al. 1988, 1991). The standard European *Salmo salar* karyotype is 2n=58 with NF=74 including 16 M (metacentrics), 24 LA (large acrocentrics) and 18 SA (small acrocentrics). The small acrocentric pairs are the ones involved in the Robertsonian translocation (Hartley and Horne 1984a). No successful chromosome banding (R or G) was obtained before the work of Gold et al. (1990), but C and Q chromosome banding (Phillips and Hartley 1988), and other facts such as the existence of multivalents in meiosis (Nygren et al. 1972; Wright et al. 1983), and linkage relationships (May et al. 1982), support the conclusion that the Robertsonian fusions involve non-homologous chromosomes (see Hartley 1987). Diter et al. (1988) showed the existence of preferential pairing of homologous (not homeologous) chromosomes at meiosis-I and the subsequent segregation of homologues to different gametes.

The inheritance of polymorphism patterns in *Oncorhynchus mykiss* (rainbow trout) has been described by Thorgaard (1976) and developed by Ueda and Oiima (1984). These authors provided a model to explain Robertsonian chromosome polymorphisms in strains of rainbow trout, involving fertilization between individuals with both different and the same chromosome numbers (an individual with Robertsonian translocations is able to produce gametes with different haploid numbers).

In this study we analyse chromosome distribution in offspring from different pair matings of the Atlantic salmon, in order to develop a model to explain inheritance of Robertsonian chromosome polymorphism in *Salmo salar* L., and so contribute to an understanding of the diverse patterns observed in European populations.

Materials and methods

We recorded chromosome numbers (2n) of fry from spawnings belonging to nine individual crosses of *Salmo salar*. In each individual cross, ova from one female were fertilised with milt of one male, both captured in the River Narcea (Asturias, northern Spain). Offspring were kept in similar environmental conditions in the same hatchery; they were maintained separately and a sample of fry was taken from each one to obtain metaphase chromosomes.

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Five crosses (Narcea-90) were made in January 1990; samples were taken after yolk sac reabsorption. An average of 21.2 fry per spawning were analysed.

Four crosses (Narcea-91) were made in January 1991; samples were taken before yolk sac reabsorption. An average of 33.5 fry per spawning were analysed.

The method used to obtain karyotypes from fry follows the protocol of Chourrout (1984) as modified by P. Morán. Fish were kept in 0.02% colchicine for 12 h, then gills were removed and homogenized in 0.075 M KCl. Hypotonic treatment was in 0.075 M KCl for 1 h 15 min. A cell suspension was centrifuged at 1,700 rpm for 10 min and the pellet rinsed three times in methanol/acetic 3/1. The suspension was then dropped onto slides, rinsed in 45% acetic acid and flamed. Staining was with 5% Giemsa in phosphate buffer at pH 6.8.

We also obtained the karyotypes of parents of one Narcea-90 cross (N-5) and two Narcea-91 crosses (N-13 and N-15) by leukocyte culture, following Hartley and Horne's (1983) method. Unfortunately, sampling of other parents was not possible.

Chromosome polymorphism is presented as the number (and percent) of individuals with chromosome numbers ranging from $2n=55$ to $2n=59$. We counted five metaphases per individual.

The statistical tests used were: contingency χ^2 to test differences between observed polymorphism patterns and χ^2 to fit observed and expected patterns.

Results

Except in a few cases where the very low NF indicates a loss of chromosomes (these cells were ignored) metaphases always had NF = 74. We found occasional intraindividual polymorphism that followed a Robertsonian pattern but this was not taken into account in data analysis.

Table 1 presents the number (and percent) of individuals of each chromosome number in the five spawnings analysed in 1990. The five distributions differed statistically ($\chi^2=15.22$, 8 *df*, $P<0.05$), the difference being due mainly to N-5. All the distributions had $2n=58$ as a modal chromosome number, but N-5 had a higher proportion of individuals with $2n=59$ but did not have any individuals with low chromosome numbers ($2n=56$ and $2n=57$).

Table 2 shows the number (and percent) of individuals of each chromosome number in the four spawnings analysed in 1991. In four offspring we obtained individuals of only four chromosome numbers per spawning. N-13 and N-14 had individuals from $2n=55$ to $2n=58$; N-15 and N-16 had individuals from $2n=56$ to $2n=59$. We did not find any individuals with a modal chromosome number of $2n=60$, but did observe two cells with this number in two individuals classified as $2n=59$, indicative of a Robertsonian fission in the parents. Cells with $2n=54$ or less were not found. The four offspring were significantly different as a whole, but N-13 and N-14 did not show a significant difference; neither did N-15 and N-16 (Table 2).

Table 1. Number (and percent) of individuals of each chromosome number, in each spawning from Narcea-90 stock. N = number of individuals

Spawning	N	Chromosome number			
		56	57	58	59
N-3	20	4 (20.0)	1 (5.0)	12 (60.0)	3 (15.0)
N-4	21	2 (9.5)	5 (23.8)	11 (52.4)	3 (14.3)
N-5	22	0	0	15 (68.2)	7 (31.8)
N-6	25	3 (12.0)	4 (16.0)	17 (68.0)	1 (4.0)
N-7	18	4 (22.2)	2 (11.1)	11 (61.1)	1 (5.6)

Table 2. Number (and percent) of individuals of each chromosome number, in the four individual spawnings from Narcea-91 contingency χ^2 to test the homogeneity between samples. N = number of individuals

Spawning	N	Chromosome number				
		55	56	57	58	59
N-13	34	5 (14.7)	17 (50.0)	7 (20.6)	5 (14.7)	0
N-14	31	3 (9.7)	12 (38.7)	9 (29.0)	7 (22.6)	0
N-15	35	0	2 (5.7)	6 (17.1)	20 (57.1)	7 (20.0)
N-16	34	0	5 (14.7)	7 (20.6)	16 (47.1)	6 (17.6)
Totals	134	8 (6.0)	36 (26.9)	29 (21.6)	48 (35.8)	13 (9.7)

Between all spawnings: $\chi^2=48.923$, 9 *df*, $P<0.001$
N-13/N-14: $\chi^2=1.811$, 3 *df*, N.S.
N-15/N-16: $\chi^2=1.870$, 3 *df*, N.S.
[N-13 + N-14]/[N-15 + N-16]: $\chi^2=46.677$, 4 *df*, $P<0.001$

Table 3. Chromosome number (2n) of parents of three analysed offspring: N-5, N-13 and N-15

Spawning	Chromosome number	
	Male	Female
N-5	58	59
N-13	57	56
N-15	58	58

From Tables 1 and 2 it is clear that: (1) All the offspring had a Robertsonian polymorphism (at least two different chromosome numbers per offspring with the same NF = 74). (2) No offspring had more than four different 2n numbers, though this does not exclude the possibility that, because of the limited number of individuals analyzed, offspring exist with other chromosome numbers in a lower proportion. (3) The distributions of the four chromosome numbers were statistically different (see Table 2): some offspring (N-13 and N-14) had individuals with a lower 2n (from 55 to 58), others (N-15 and N-16) with a higher 2n (from 56 to 59).

Table 3 presents the results obtained from the parents. The parents of all three spawnings analysed were

different. N-5 offspring came from a 58 × 59 cross, N-13 from a 56 × 57 cross and N-15 from a 58 × 58 cross. The patterns of these three offspring were statistically different ($\chi^2 = 55.214$, 6 *df*, $P < 0.001$): crosses between parents with different chromosome numbers thus produced different patterns in the offspring.

A model

Significant differences among offspring distributions can be explained in terms of the chromosome numbers of the parents by following the hypothesis proposed by Ueda and Ojima (1984) for *Oncorhynchus mykiss*. Any individual heterozygous for one Robertsonian translocation (RT) could produce gametes with a different n and a different NF depending on the segregation of chromosomes at Anaphase-I. Consider a heterozygous 2n = 57 individual with two acrocentric pairs involved in RT and with 17 M, 24 LA, 16 SA. If this heterozygote produces a trivalent of meiosis, then by the non-disjunctional segregation of this trivalent (Fig. 1a, WA) unbalanced gametes would be obtained, a half with a double dose of one acrocentric (n = 29, NF = 38) and a half without this acrocentric (n = 28, NF = 36). Disjunctional segregation (Fig. 1a, WB) would give rise to gametes with different chromosome numbers (28 and 29) but the same NF (37), both being balanced because they carry complete sets of chromosome arms. Other authors have cited different rates of Non-Robertsonian polymorphism in *Salmo salar* in which individuals have a different NF (Bolla 1987; Hartley 1988), but we have no evidence of this in our results. In our case all the fry analysed had NF = 74. Our results are interpretable in terms of three hypotheses:

(1) Only the WB pathway is followed at meiosis.
(2) The only viable balanced gametes are those with NF = 37, or else they are the only gametes able to fertilize (gametic selection), as found by Wright et al. (1983) in *Salvelinus fontinalis*.
(3) Unbalanced gametes (with a NF higher and lower than 37) may fuse to produce balanced zygotes with NF = 74 but the probability of this is very low. *Salmo salar* is the Salmonid species with the lowest NF (Hartley 1987), thus the loss or excess of one single acrocentric would represent more damage for the zygote or embryo than in species with a higher tetraploidy.

Whichever hypothesis is correct (1, 2 or 3) we are of the opinion that balanced gametes are the main contributors to the chromosome distributions observed in offspring.

There is another question to be resolved: what number of acrocentrics are involved in RT in any one population? If RT involving two acrocentric (AP) pairs of non-homologous chromosomes is present in a polymorphic population, then the minimum variation expect-

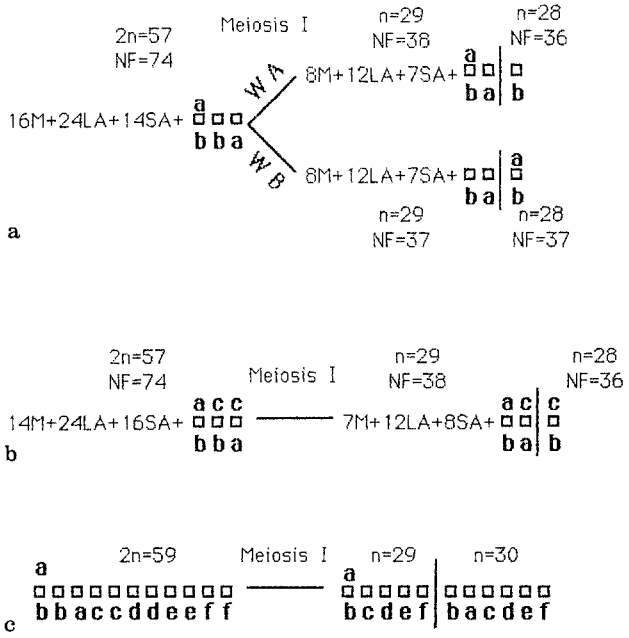

Fig. 1a–c. Meiotic segregations. **a** Two possible modes of segregation in a heterozygote for one Robertsonian translocation producing unbalanced (*WA*) and balanced (*WB*) gametes. **b** Unbalanced segregation in the meiosis of an individual with three acrocentric pairs involved in Robertsonian translocations. **c** Meiotic segregation of 2n = 59 individuals with six acrocentric pairs involved in Robertsonian translocations. *Little squares*, centromeres; *letters*, chromosome arms

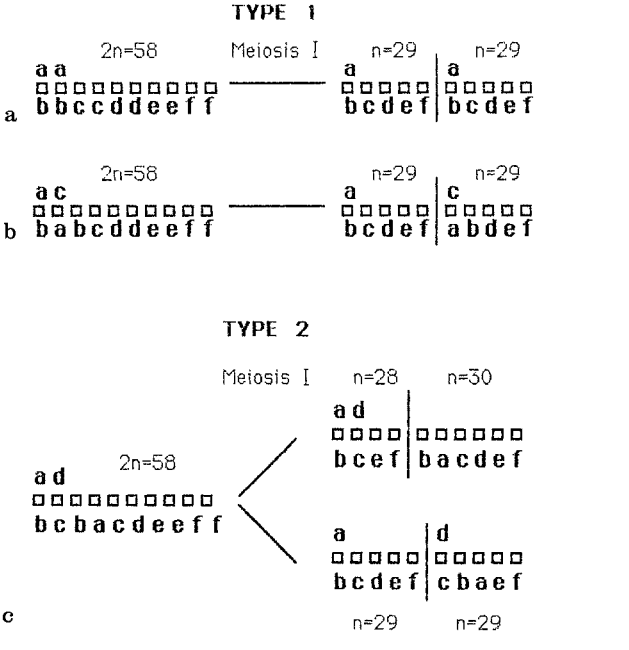

Fig. 2a–c. Meiotic segregations of individuals with 2n = 58. **a** and **b** Type 1 (with only one way of producing balanced gametes). **c** Type 2 (with two ways of producing balanced gametes)

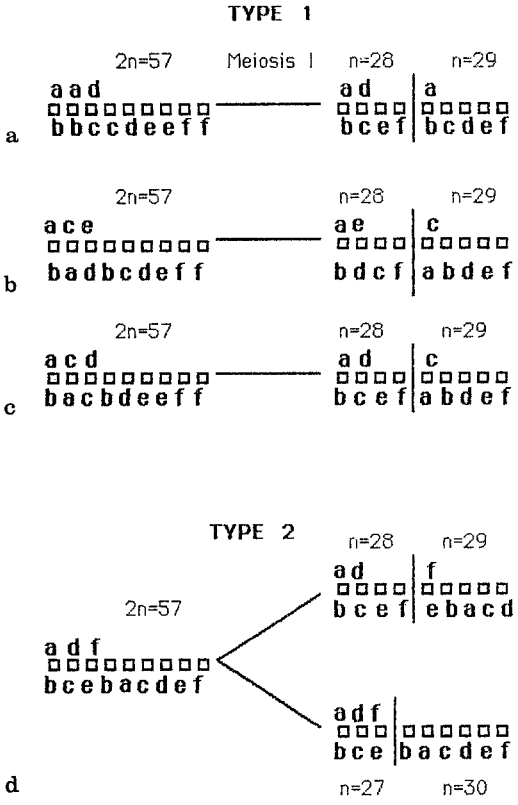

Fig. 3a–d. Meiotic segregations of individuals with 2n=57. **a**, **b** and **c** Type 1; **d** Type 2

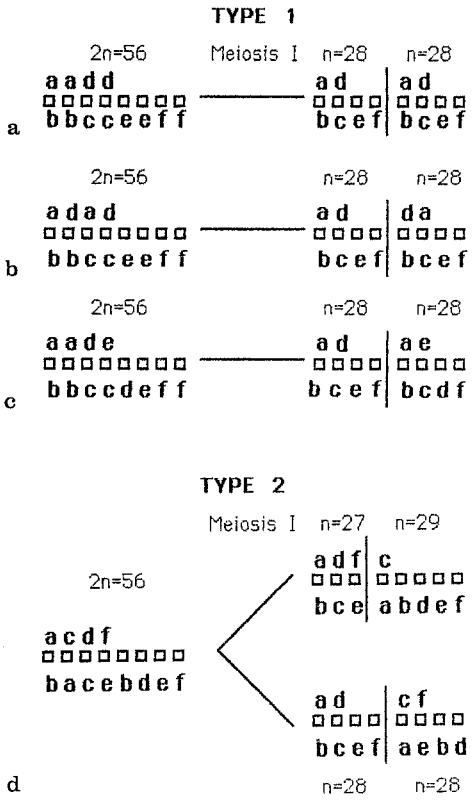

Fig. 4a–d. Meiotic segregation of individuals with 2n=56. **a**, **b** and **c**: Type 1; **d** Type 2

ed is three different chromosome numbers: the standard 2n=58 and polymorphisms with 2n=56 to 2n=58 for two fusions, 2n=58 to 2n=60 for two fissions, and from 2n=57 to 2n=59 with one fusion and one fission. Again assuming that RTs are between non-homologous chromosomes, then a RT involving three AP cannot lead to a stable Robertsonian system even when one acrocentric is involved in one fusion and its homologue is fused with another acrocentric (very low probability). In such a circumstance (Fig. 1b), individuals having the lowest 2n (57) are unable to produce balanced gametes. This allows us to discard the possibility that stable Robertsonian patterns can be produced by translocations involving an odd number of AP.

In the Narcea population, the variability in chromosome numbers ranges from 2n=55 to 2n=60, a pattern with six chromosome numbers. Here six AP must be involved in RT because we can again reasonably discard the proposition that five pairs would produce a balanced Robertsonian pattern. We might expect an extreme variation from 2n=54 to 2n=60, which was probably not detected because of the limited size of our sample (just 18 parents in nine spawnings). More than six translocated pairs would imply greater variability in chromosome numbers, which so-far have not been found in Asturian populations (García-Vázquez et al. 1992).

The next step is to calculate the type of gametes produced by each individual. We can expect that individuals (or cells) with 2n=60 are homozygous for three fissions and that individuals with 2n=59 are heterozygous for one fusion (Fig. 1c). Fusion events being at random between small acrocentrics, 2n=58 individuals could be of several types: homozygous for one fusion (Fig. 2a), heterozygous for two fusions with fusion events involving one acrocentric from a pair previously involved in RT (Fig. 2b) and individuals doubly heterozygous for two independent fusions (Fig. 2c). 2n=58 individuals from Fig. 2a, produce identical gametes with n=29 whereas 2n=58 individuals (Fig. 2c) can give rise to different gametes by following two possible modes of segregation at Anaphase-I. By virtue of their contribution to the next generation, we can distinguish two types of individuals: those producing gametes by Type 1 meiotic segregation and those able to follow two different modes of segregation at meiosis (Type 2). In Fig. 3a, b, c we can distinguish between different Type 1 individuals with 2n=57 whereas in Fig. 3d Type 2 segregation is again possible. Individuals with 2n=56 can also give a Type 1 (Fig. 4a, b, c) or a Type 2 segregation (Fig. 4d). Finally, 2n=55 individuals (homozygous for two fusions and heterozygous for another one) can produce gametes with n=27 and n=28. As we have no contrary evidence, we can

Table 4. Expected proportion of each chromosome number in offspring from crosses between individuals of the Atlantic salmon with different chromosome numbers. -1 and -2 indicate the type of chromosome constitution (depending on the mode of segregation at Meiosis-I, see text). Expected rates of each chromosome number are obtaind by crossing gametes from each mating in the absence of either gametic or zygotic selection

	56-1	56-2	57-1	57-2	58-1	58-2	59
56-1	56 1	55 56 57 1: 2: 1	56 57 1: 1	55 56 57 58 1: 3: 3: 1	57 1	56 57 58 1: 2: 1	57 58 1: 1
56-2		54 55 56 57 58 1: 4: 6: 4: 1	55 56 57 58 1: 3: 3: 1	54 55 56 57 58 59 1: 5:10:10: 5: 1	56 57 58 1: 2: 1	55 56 57 58 59 1: 4: 6: 4: 1	56 57 58 59 1: 3: 3: 1
57-1			56 57 58 1: 2: 1	55 56 57 58 59 1: 4: 6: 4: 1	57 58 1: 1	56 57 58 59 1: 3: 3: 1	57 58 59 1: 2: 1
57-2				54 55 56 57 58 59 60 1: 6:15:20:15: 6: 1	56 57 58 59 1: 3: 3: 1	55 56 57 58 59 60 1: 5:10:10: 5: 1	56 57 58 59 60 1: 4: 6: 4: 1
58-1					58 1	57 58 59 1: 2: 1	58 59 1: 1
58-2						56 57 58 59 60 1: 4: 6: 4: 1	57 58 59 60 1: 3: 3: 1
59							58 59 60 1: 2: 1

assume that there is no selection against any type of balanced gamete, and that their frequencies can be calculated from Type 1 and 2 meiotic segregation.

It is thus possible to calculate the theoretical chromosome polymorphism patterns expected in offspring from crosses involving parents with different 2n numbers (Table 4). In any given population, the most frequent crosses would obviously be those between individuals with the most frequent 2n numbers. In the Narcea population the mode is $2n=58$, followed by the classes $2n=57$, $2n=56$ and $2n=59$ (García-Vázquez et al. 1992); thus the most frequent crosses would be 58×58, 57×58, 56×58 and 59×58. Crosses involving individuals with $2n=55$, $2n=54$ or $2n=60$ have a very low probability of occurrence.

Discussion

Our hypothesis that six AP are involved in RT in the Narcea population, with no evidence of $2n=54$ cells, can be discussed in the following terms: a polymorphism with six different 2n numbers could be obtained by RT in five AP. But the inability of individuals with $2n=55$ to produce balanced gametes in this case (Fig. 1 b) would imply that they have poor fitness, being produced in each generation by the segregation of crosses between individuals with a higher 2n (for example 57×57). We are not able to reject this possibility without chromosomal markers allowing us to identify each acrocentric and hence to identify number of pairs involved in RT in each population. Nevertheless, the evolutionary trend (diploidization) to decrease the chromosome number in Salmonids (Ohno 1974) is not consistent with the existence of selection against a low 2n in wild populations; this is especially important in Spanish populations with high proportion of 2n lower than 58 (García-Vázquez et al. 1992).

Table 5 presents the results of a χ^2 to test the goodness of fit between observed and expected patterns. In the three spawnings where karyotypes of parents were recorded (N-5, N-13 and N-15; Table 3) the results obtained fit those expected, thus confirming our model. N-3, N-4, N-6, N-7 and N-16 have patterns from $2n=56$ to $2n=59$ with a mode at $2n=58$ and must be tested with the expected distributions from the crosses 57×58 or 58×58 (Table 4). N-14 has individuals from $2n=55$ to $2n=58$, with a mode of $2n=56$; it must be compared with patterns expected from 56×56 or 56×57. N-4 fits a 58×58 cross; N-14 a 57×57 cross and N-16 a 57×58 cross. It is thus possible to explain all the polymorphisms of N-4, N-14 and N-16 by simple segregation from the one cross given.

Nevertheless, N-3, N-6 and N-7 from Narcea-90 do not fit the distribution expected from their respective individual crosses because they have a strong mode at $2n=58$, higher than that expected from any cross. As there are no significant differences between them (the contingency χ^2 is 3.953 with 6 *df*, $P=0.683$), they probably belong to crosses between $2n=58$ adults, though we cannot be sure of this.

Table 5. χ^2 to test the goodness of fit of the polymorphism pattern observed and expected in each offspring

Offspring	Possible cross	χ^2	*df*	*P*<
N-3	58-2 × 58-2	14.000	3	0.01
N-4	58-2 × 58-2	3.894	3	N.S.
N-5	58-1 × 59	2.227	1	N.S.
	58-2 × 59	9.348	1	0.01
N-6	58-2 × 58-2	14.299	3	0.01
N-7	58-2 × 58-2	15.259	3	0.01
N-13	56-2 × 56-2	9.137	3	0.05
	56-1 × 57-2	4.275	2	N.S.
N-14	56-2 × 56-2	18.263	3	0.001
	56-2 × 57-2	4.203	3	N.S.
N-15	58-2 × 58-2	7.015	3	N.S.
N-16	57-1 × 58-2	4.275	2	N.S.
	57-2 × 58-2	6.189	3	N.S.
	58-2 × 58-2	7.849	3	0.05

N.S.; not significant

Two observations can be made from our results. First, the numbers of individuals with a higher 2n (59 or 60) were always less than expected, probably because the possibility of chromosome loss is higher in gametes with n = 30. Second, in all the offspring analysed we found the same trend (reaching statistical significance in N-3, N-6 and N-7): the frequency of 2n = 58 individuals observed is always higher than expected.

A possible explanation for these observations is that the expected frequency of gametes could be different. Diter et al. (1988) showed preferential pairing between homologous chromosomes, but this does not exclude some pairing between homeologues, though in at a low frequency. The possible presence of homeologues pairing and further segregation might disturb the expected proportions of gametes, though this remains highly speculative.

Another possible explanation could be the existence of selection increasing the modal 2n = 58. Roberts (1968, 1970) and Thorgaard (1976, 1983) suggest that the various karyotypes in the Robertsonian pattern of *Salmo salar* show different adaptative values. Hartley and Horne (1982) proposed that the chromosome polymorphisms reported in hatchery stocks may reflect different selection pressures to those operative in the wild; in fact, wild Scottish populations of *Salmo salar* are less polymorphic than the farmed ones (Hartley 1988). There is also variability of results between different life stages: in-vivo studies in eggs and early fry of Salmonids (Bolla 1987; García-Vázquez et al. 1988, 1991 and 1992; Morán et al. 1989) report greater variability in polymorphism patterns than those observed in adults (Hartley and Horne 1984a and b; Hartley 1988; García-Vázquez et al. 1992). In our results, offspring with the highest mode, 2n = 58, were those from Narcea-90, analysed after yolk sac reabsorption. The yolk sac reabsorption stage is very sensitive; populations at this stage show a high mortality. Thus, selection against non-modal individuals might act intensely at this time, producing a significant increase of 2n = 58 individuals in some offspring.

In conclusion, polymorphism patterns might be the result of a balance between:

(1) A smaller probability of chromosomes loss in low 2n individuals, thus favouring 2n = 56 and 57 types.
(2) The better adaptation of modal individuals, favouring 2n = 58.
(3) The continuous appearance of individuals with a higher 2n in each generation as result of gamete segregation, thus favouring a 2n = 59 type.

Our model could be tested by the identification of each acrocentric once adequate banding techniques become available.

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