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USE OF TRIPLOID ATLANTIC SALMON *(SALMO SALAR)* FOR AQUACULTURE

By

Tillmann J. Benfey
Department of Biology
University of New Brunswick
Fredericton, New Brunswick
E3B 6E1

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ABSTRACT

Induced triploidy is the only effective method presently available in Canada for the mass production of reproductively sterile salmonids for aquaculture. Pilot-scale culture of triploid Atlantic salmon in New Brunswick has revealed that these fish survive and grow well during freshwater smolt production, but less well during marine sea-cage grow-out to market size. Repeated studies at the Atlantic Salmon Federation's hatchery showed only minor differences between triploids and diploids in survival to S1 smolt age (15 mo), percentage of the population which became S1 smolts, and mean S1 smolt size. However, a similar study at a commercial hatchery was terminated due to exeptionally high mortality of triploids prior to the start of feeding. Marine grow-out trials in sea-cages showed that triploids grew well in seawater, but had reduced survival rates (leading to a 5 to 15% reduction in yield at harvest) and high rates of jaw abnormalities compared to diploids. Similar results have been reported with triploid Atlantic salmon in Newfoundland, British Columbia, Washington State, Scotland and Tasmania. Although induced triploidy can be used effectively as a management tool to ensure lack of reproduction in Atlantic salmon, it would at present be difficult to obtain the aquaculture industry's support to switch to their large-scale use. In light of fundamental biological differences between triploids and diploids, it is perhaps somewhat naive to expect triploids to perform as well as diploids using standard salmon culture methods. Triploids should be treated as a new species for aquaculture development, beginning with research to determine their optimum rearing requirements.

RÉSUMÉ

La triploïdie induite constitue actuellement la seule méthode efficace au Canada pour la production en masse de salmonidés stériles destinés à l'aquaculture. Des élevages à échelle pilote de saumons de l'Atlantique triploïdes réalisés au Nouveau-Brunswick ont montré que ces poissons présentaient une bonne survie et une bonne croissance pendant l'étape de production de saumoneaux en eau douce, mais que les résultats n'étaient pas aussi bons pendant l'étape de croissance à la taille commerciale en cages marines. Des études analogues effectuées à la pisciculture de la Fédération du saumon Atlantique n'ont montré l'existence que de différences mineures entre les triploïdes et les diploïdes en ce qui a trait à la survie jusqu'à l'âge de saumoneaux S1 (15 mois), au pourcentage de la population se transformant en saumoneaux S1 et à la taille moyenne des S1. Par ailleurs, une étude semblable réalisée à une pisciculture commerciale a dû être interrompue à cause de la mortalité exceptionnellement élevée des triploïdes avant le début de l'alimentation. Des essais de croissance au stade commercial effectués en cages marines ont montré que les triploïdes avaient une bonne croissance en eau de mer, mais des taux de survie réduits (donnant lieu à une réduction de rendement de 5 à 15 % à la récolte) et des taux élevés d'anomalies affectant les mâchoires. Des résultats semblables ont été signalés pour des saumons de l'Atlantique triploïdes à Terre-Neuve, en Colombie-Britannique, au Washington, en Écosse et en Tasmanie. La triploïdie induite est un moyen de gestion efficace pour garantir l'absence de reproduction chez le saumon Atlantique, mais il serait actuellement difficile d'obtenir l'appui de l'industrie aquacole pour l'utilisation à grande échelle de poissons triploïdes. Étant donné les différences biologiques fondamentales entre les triploïdes et les diploïdes, il serait plutôt naïf de s'attendre à ce que les triploïdes aient un rendement aussi bon que les diploïdes dans les conditions d'élevage standard du saumon. Les triploïdes devraient être traités comme une nouvelle espèce devant faire l'objet de travaux de développement débutant par des recherches visant à en déterminer les conditions d'élevage optimales.

Introduction

The aim of this paper is to summarize information available on triploid Atlantic salmon as it pertains to their use for aquaculture in New Brunswick. No original data are presented, but appropriate reference is made to published literature containing supporting data. In addition, the reader is referred to the more comprehensive proceedings of two workshops on this topic (Pepper 1991, Benfey 1996a).

The interest in triploids arises from the fact that they are sterile. Induced triploidy is by no means the only way to effectively sterilize salmon (or other fishes), but it is presently the only method available by which to sterilize large (commercial-scale) numbers of salmon without the use of chemicals that would otherwise affect consumer acceptance of the fish. Some of the alternate methods for the production of sterile salmon, such as surgical castration, hormonal sterilization, and induced gonadal autoimmunity, have been described elsewhere (Donaldson et al. 1993, Donaldson and Devlin 1996).

The use of triploids for aquaculture originated with the industry's need to prevent sexual maturation of production fish prior to their reaching market size, because maturing salmon, being chronically stressed, have reduced flesh quality and are more susceptible to disease (Mazeaud et al. 1977). Early maturation of Atlantic salmon is not, however, a concern for New Brunswick's aquaculture industry because precociously-mature males are culled prior to seawater transfer of smolts, and because rates of maturation as grilse are exceptionally low. The current interest in triploid Atlantic salmon is based on the perceived need for "genetic containment" of those fish which inevitably escape from aquaculture facilities, and is therefore driven by forces outside the industry.

Biological Effects of Induced Triploidy

As the name implies, triploids have three sets of chromosomes in their somatic cells rather than the normal (diploid) two sets. Although there are a few naturally-occurring triploid species of fishes that exist as all-female populations with unique reproductive strategies (Purdom 1984), it should be realized that for most fish species triploidy is not a natural condition. Tetraploidy has played a role in the evolution of many widespread and economically-important groups of fishes, including the salmonids (Allendorf and Thorgaard 1984). Triploidy, on the other hand, generally leads to such severe gametogenic impairment that triploid individuals are sterile (Benfey 1999). Among the salmonids, triploid males develop much larger gonads than triploid females and often produce functional spermatozoa, but these spermatozoa are aneuploid (Benfey et al. 1986) and therefore unable to yield viable offspring upon fertilization of eggs from diploid females (Ueda et al. 1987).

Impaired gametogenesis and its effects on gonadal development represents one of two fundamental effects of triploidy on basic fish biology; the second relates to changes in cell size and number. The volume of cell nuclei is increased in triploids to accommodate their extra genetic material, and a

corresponding increase in cellular volume typically results. In spite of this, triploid individuals are no larger than diploids, due to a corresponding reduction in cell numbers.

An important consequence of increased nuclear and cellular volume in triploids is the resulting decrease in nuclear and cellular ratios of surface area to volume. This could theoretically affect processes limited by surface area, such as nutrient and metabolite exchange, passive and active ion exchange, and membrane binding of hormones and other messengers. Due to decreased cell numbers, this decrease in ratio of surface area to volume applies to entire tissues and organs as well. A second important consequence of increased nuclear and cellular volume is that, depending on the shape of the cell and its nucleus, internal transport and diffusion distances may be increased. This could affect processes such as signal transduction from the cell surface to the nucleus, and resultant production and movement of RNA and proteins within and out of the nucleus and cell. Some of these potential disadvantages may be offset by the energetic advantages arising from reduced production and maintenance of cellular membranes and from the smaller relative surface area across which ionic and osmotic gradients must be maintained.

Aside from obvious effects of sterility, a comprehensive review of the literature on the physiology and behaviour of triploids (Benfey 1999) reveals remarkably little difference from diploids at the whole-animal level. None-the-less, it should not be assumed that triploids are identical to diploids in their culture requirements, and it has been argued (Benfey 1996b) that triploids should be treated as "new species" for aquaculture development. This is supported by the observation that triploid salmonids perform poorly under conditions of high oxygen demand and/or low oxygen availability (Quillet and Gagnon 1990, Johnstone et al. 1991, Blanc et al. 1992, Simon et al. 1993, Ojolick et al. 1995, Johnstone 1996).

Production and Identification of Triploids

Triploids are produced by retention of the second polar body, a package of maternal chromosomes which normally leaves the egg with the completion of meiosis shortly after fertilization. Triploidy is generally induced through either thermal or hydrostatic pressure treatment of eggs within the first hour of fertilization; these treatments disrupt spindle fibres and thereby interfere with the normal movement of chromosomes during meiosis. The ease with which triploid fish can be produced is evidenced by the extensive number of species in which this simple genetic manipulation has been performed successfully (Benfey 1989). Although thermal treatments are easier to apply to eggs and require less costly equipment, hydrostatic pressure treatments are more easily controlled and therefore preferred. The design of such systems is relatively simple (e.g., Benfey et al. 1988), and a local company (TRC Hydraulics Inc., Dieppe, NB) has manufactured several commercial-scale units for sale in Canada, USA and Chile.

The variables which must be controlled for the successful induction of triploidy are the time after fertilization at which to begin the treatment (which is itself temperature dependent and therefore

measured in °C-min) and the duration and magnitude of the treatment itself. The first successful production of triploid Atlantic salmon was achieved locally (Benfey and Sutterlin 1984), but the pressures and temperatures described in this early study are now considered to have been excessively high. Good results can be obtained using treatments of 5 min at 9500 psi, beginning 300°C-min after fertilization. This treatment was used successfully to produce all-triploid populations of 5 year classes of Atlantic salmon at the Atlantic Salmon Federation's hatchery in St. Andrews, New Brunswick (O'Flynn et al. 1997).

With the exception of characteristic jaw abnormalities (described later in this paper), triploid salmon are morphologically identical to diploids. Verification of triploidy-induction success is therefore generally done by measuring red blood cell dimensions, either microscopically or with the use of automated particle-sizing instruments (e.g., Benfey et al. 1984), or by measuring red blood cell DNA content by flow cytometry (e.g., Thorgaard et al. 1982, Allen 1983). Flow cytometry is the preferred method because it is rapid and yields unambiguous results, but the equipment required is expensive and generally only available through hospital facilities.

Single-sex (all-female) populations of triploids are generally used in salmonid aquaculture, since they remain sexually immature. (Triploid males, although sterile in the sense that they are unable to produce viable offspring, do go through the physiological processes associated with sexual maturation, exhibit normal spawning behaviour, and will mate with diploid females when placed in an appropriate spawning environment.) For commercial applications, all-female populations are generally produced by first treating a small population of potential broodstock with androgen (e.g., 3 ppm dietary 17α-methyltestosterone for the first 600°C-days after start of feeding), and then crossing the resulting masculinized females (i.e., functional males with the XX-genotype) with normal females. Such a protocol is easily incorporated into triploid production schemes. The only difficulty arises from problems in distinguishing masculinized diploid females from normal diploid males. This process has been greatly facilitated in some species by the development of Y-chromosome-specific genetic markers (e.g., Devlin et al. 1991), but such markers have yet to be developed for Atlantic salmon.

Pilot-Scale Aquaculture Evaluation of Triploid Atlantic Salmon in New Brunswick

As part of a collaborative study between the University of New Brunswick (UNB), the Atlantic Salmon Federation (ASF) and the New Brunswick Salmon Growers' Association (NBSGA), triploid Atlantic salmon were produced every year from 1990 to 1994 at the ASF's hatchery in St. Andrews, as described above. A variety of domesticated strains was used, with full-sib diploids as controls. Fish were reared to the smolt stage at the ASF hatchery (McGeachy et al. 1994, 1995, O'Flynn et al. 1997), and then transferred to sea cages at the NBSGA's demonstration farm in Lime Kiln Bay (McGeachy et al. 1996, O'Flynn et al. 1997). This was followed by the production of triploids in 1994 and 1995 at a commercial hatchery, but these fish were not carried past first-feeding due to unacceptable (and unexplained) high mortality of the triploids (O'Flynn et al. 1997).

Survival from fertilization to first-feeding was generally lower for triploids than for diploids at the ASF hatchery, although statistically significant differences were only observed for the 1991 year-class (Table 1). There was no consistent (or statistically significant) effect of ploidy on survival for the remainder of the freshwater production cycle in any year class. There was a general reduction in proportion of the population which became S1 smolts in triploids relative to diploids, but again a statistically significant difference was only observed for the 1991 year-class (Table 1). Triploid and diploid S1 smolts did not differ in size, but triploids had consistently lower condition factors (Table 1), giving them more the appearance of wild smolts.

Due to a lack of replicate cages, statistical analysis of survival rates after smolt transfer was not possible. However, survival rates in sea water were consistently lower for triploids than for diploids (Table 2). Surviving triploids were as large as, or larger than, diploids at harvest (Table 2), but considering their higher mortality rates, this should not be interpreted as better growth rates by the triploids. It may be that the smaller triploids were the ones to die prior to harvest, thereby skewing size estimates in favour of larger fish. As a result of their higher mortality rates, the actual yields (as kg at harvest per smolt stocked) were 5-15% lower for triploids relative to diploids (Table 2). Triploids showed a strikingly high incidence of deformities (Table 2), mainly of the lower jaw. Such lower jaw deformities have been previously described in triploid Atlantic salmon (Sutterlin et al. 1987, Jungalwalla 1991, Sutterlin and Collier 1991), but there has as yet been no definitive explanation of their cause. Fish with lower jaw deformities cannot be sold whole (gutted, head on), but are still suitable for value-added processing (steaks, fillets, etc.).

Other Pilot-Scale Aquaculture Evaluations of Triploid Atlantic Salmon

Research on a scale comparable to that described above has been conducted in both Newfoundland (Bay D'Espoir) and British Columbia. In both cases, triploids were on average smaller than diploids at harvest, and showed high rates of jaw deformities (V.A. Pepper and E.M. Donaldson, pers. comm., 1998). Research from Washington State reported similar freshwater growth but poorer growth and survival in sea water for triploid Atlantic salmon compared to diploids; no mention is made of lower jaw deformities (Galbreath et al. 1994, Galbreath and Thorgaard 1995). More long-term and larger-scale evaluations have been conducted in Scotland (Johnstone et al. 1991, Johnstone 1996) and Tasmania (Jungalwalla 1991). Again, the general impression has been one of poorer performance of triploids relative to diploids, especially during seawater growth. Interestingly, a high incidence of lower jaw deformities was also reported for triploids in Tasmania (using fish derived from Canadian stocks), but such deformities are quite rare in Scotland. Scottish triploids, on the other hand, show a higher incidence of cataracts (Wall and Richards 1992).

Management Considerations

Induced triploidy is presently the only practical method by which to ensure sterility of Atlantic salmon produced for aquaculture on a commercial scale. From a strictly management perspective, if sterility needs to be ensured then the present state-of-the-art dictates that triploids should be used. However, until it can be demonstrated that the performance of triploids is identical to (or, ideally, better than) that of diploids, the aquaculture industry will likely be opposed to their use. Although a large industry, salmon farming in New Brunswick is presently operating on an exceedingly small (if not negative) profit margin. Imposing the use of triploids at present, based on the data available (e.g., 5-15% lower yield and high incidence of jaw deformities), could well spell the end of this industry, and any management decisions involving the use of triploids should therefore not be taken lightly.

Research Recommendations

Although pilot-scale aquaculture results with triploids to date have not been good, they certainly have not been disastrous. In fact, if one accepts the suggestion (Benfey 1996b) that triploids should be treated as a "new species" for aquaculture development, then initial results with triploids are rather encouraging. Once optimum rearing conditions are determined for triploid Atlantic salmon, these fish may prove to be just as good as, if not better than, diploids as production fish for aquaculture. A general recommendation, therefore, is that research be conducted on determining the optimum culture requirements for triploid Atlantic salmon. More specifically, research is needed on determining environmental tolerances and optima (temperature, oxygen, salinity, etc.), nutritional requirements (energy, micronutrients, etc.), disease resistance, and behaviour (aggression, competition with diploids, etc.). The specific problem of lower jaw deformities must be addressed.

Although triploids are sterile, this does not preclude the fact that they may have unexpected ecological effects should they escape or be intentionally released into the environment. A second general recommendation is therefore that research be conducted on the ecological impacts of triploids in natural environments. More specifically, research is needed on migratory behaviour (especially in relation to freshwater homing), interaction with conspecific diploids and other species, and life history characteristics (e.g., lifespan). Although such research could perhaps be addressed through laboratory experiments, I would advocate some controlled releases of all-female triploids for a more comprehensive evaluation of ecological impacts. In light of regular escapes of diploid salmon from aquaculture facilities, I do not see any added risk from such an experiment.

It should be remembered that techniques other than induced triploidy can theoretically be used to sterilize fish, and that perhaps better methods can be developed to do this on a commercial scale with salmon. A final recommendation is, therefore, to support research directed towards the development of alternate methods for producing sterile salmon (and other species) for aquaculture.

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Table 1. Early freshwater survival (fertilization to first-feeding) and S1 smolt rate, size and condition factor (CF; calculated as [(weight/length^3) X 100]) for diploid (2n) and triploid (3n) Atlantic salmon reared at the ASF hatchery in New Brunswick (after O'Flynn et al. 1997).

Year Class	survival rate (%)		S1 smolt rate (%)		S1 smolt length (cm)		S1 smolt weight (gm)		S1 smolt CF	
	2n	3n	2n	3n	2n	3n	2n	3n	2n	3n
1990	56.2	42.9	80.8	76.5	18.9	18.8	73.3	72.0	1.06	1.02*
1991	63.4	41.0**	76.2	67.0*	17.0	17.1	52.3	52.9	1.05	1.02**
1992	66.9	67.8	87.6	86.0	18.0	17.9	64.1	62.8	1.08	1.06*
1993	51.7	41.9	94.6	95.5	16.7	17.0	51.5	55.3	1.08	1.11
1994	24.2	22.0	92.3	87.7	18.8	18.7	70.3	68.6	1.05	1.02**

(* significant at $p<0.05$, ** significant at $p<0.01$)

Table 2. Seawater survival (smolt transfer to harvest), size, yield (product of survival rate and harvest weight) and incidence of deformities at harvest for diploid (2n) and triploid (3n) Atlantic salmon reared at the NBSGA cage site in New Brunswick (after O'Flynn et al. 1997).

Year Class	survival rate (%)		harvest weight (kg)		yield (kg/smolt)		incidence of deformity (%)	
	2n	3n	2n	3n	2n	3n	2n	3n
1990	81.5	64.8	2.99	3.20	2.44	2.07	13.6	28.0
1991	65.2	60.4	3.72	3.79	2.43	2.29	1.5	23.2
1992	76.5	66.7	4.13	4.51**	3.16	3.01	4.1	11.8

(** significant at $p<0.01$)