A study of Atlantic salmon (*Salmo salar*) maturation using individually identified fish

by

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A Billy, sans qui rien n'aurait été possible.

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ABSTRACT

This thesis studies the variability of several Atlantic salmon (Salmo salar) reproductive traits, with a particular emphasis on the sea age at first maturity, a trait of foremost importance for both management of natural stocks and commercial salmon aquaculture.

Three groups of salmon, belonging to several families were followed from spawning to grilse maturation. A combination of cold-branding and jet-injection of Alcian Blue in several fin locations proved to be satisfactory to identify fish at the individual and family levels and has allowed the compilation of precise growth and maturation history for each fish.

A considerable diversity of maturation patterns was observed among individual fish, as well as important variation among families in maturation rates. A complex pattern of interactions between growth and maturation was evidenced. A model of maturation "triggering" is proposed to explain these observations: a fish appears to initiate maturation if its level of energy stores in spring is above a sex specific threshold level. For fish having the same previous maturation history, the level of energy store in spring appears mostly dependent on the fish growth over the winter, and to a lesser extent on the level of energy stores at the beginning of the winter. Differences among families for rate of maturation appear to be mostly due to differences among families for the relative allocation of surplus energy into somatic growth versus energy stores maintenance, and to a lesser extent to differences among families for winter growth capabilities.

Some practical considerations about genetic and environmental manipulation of maturation in the aquaculture context are discussed.

ABBREVIATIONS AND SYMBOLS

1Y81.	Cohort of 1-year-old smolt from the 1981 spawning year class.
2Y81.	Cohort of 2-year-old smolt from the 1981 spawning year class.
2Y80.	Cohort of 2-year-old smolt from the 1980 spawning year class.
(0+)	Refers to precocious maturation observed at age 0+ in the three cohorts.
(-6)	Refers to precocious maturation observed at age 1+, 6 months before smoltification in the 2Y80 and 2Y81 cohorts.
(+6)	Refers to post-smolt precocious maturation observed 6 months after smoltification in the three cohorts.
(+18)	Refers to grilse maturation observed 18 months after smoltification in the three cohorts.

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GENERAL INTRODUCTION

Atlantic salmon (Salmo salar) is a euryhaline anadromous fish, native to rivers in North America and Europe. Born in freshwater, it characteristically migrates to feeding grounds in the ocean and migrates back again to freshwater for the purpose of spawning. Some populations however, never migrate to sea and spend their complete life cycle in freshwater (Netboy, 1968).

On the western side of the Atlantic ocean, Atlantic salmon is now found in rivers extending from Ungava Bay (Northern Quebec) to Maine (U.S.A.). It disappeared from all rivers between Southern Maine and Long Island where it was found in early colonial times, but it was reintroduced in a few places (Netboy, 1968; Carter, 1975). On the eastern side of the Atlantic ocean, the Atlantic salmon range extends from Northern Norway and the Kola peninsula (U.S.S.R.) to southern France and northern Spain, but it disappeared from most rivers it originally inhabited in continental Europe (Netboy, 1968). It is also found in Icelandic rivers and in at least one river from Greenland (Netboy, 1968).

Atlantic salmon spawns in fall, from early October to early January, with the peak of spawning activity occuring generally in November. The female digs a nest (redd) in the gravel and deposits the eggs which are immediately fertilised by the male. The female then covers the fertilised eggs with a shallow cover of gravel (Jones, 1959). These eggs hatch in winter or early spring, the length of the incubating period depending mostly on the water temperature (Netboy, 1968; 1973).

Upon hatching, the young fish, called alevin, remain buried and rely on the attached yolk sac as the primary source of nutrition (Netboy, 1968; Allen and Ritter, 1977). Upon absorption of the yolk sac, the fry (as they are tnen called) emerge from the gravel and remain in the vicinity of tne redd for a few weeks (Allen and Ritter, 1977).

Upon dispersal from the redd, the young fish are called parr, up until tney become fully silvered and start their seaward migration as smolts (see below) (Allen and Ritter, 1977). The number of years that the parr remain in the river varies with latitude, from one year in southern France and Spain, up to 7 - 8 years in Ungava Bay (Netboy, 1968; Power, 1969). The parr stage is often sub-divided by age and the convention of Allen and Ritter (1977) has been used in the present study: a 0+ parr is a parr less than one year old; a 1+ parr is a parr aged one year or older but less than two year old, etc. Male parr commonly mature during their freshwater residency (Jones, 1959) and are generally designated as precocious parr (Allen and Ritter, 1977).

The seaward migration generally occurs in May/June and the young migrants are known as smolts. The parr-smolt transformation (smoltification) is accompanied by numerous pnysiological and behavioural changes which preadapt the young fish while still in the river to tneir future life in the sea (Saunders, 1969). The same age classification convention that is used for the parr stage is generally used for tne smolt stage as well (Allen and Ritter, 1977). For example, a 1+ smolt (or a 1-year-old smolt) is a young fish ready to migrate to sea in May/June, slightly over one year after hatching.

Most of tne growth or the salmon occurs during its extensive ocean

migrations of which little is known. A feeding ground common to multi-sea-winter salmon (see below) from North America and Europe has been identified off the southwest coast of Greenland, and more recently, another common feeding ground for grilse (see below) and multi-sea-winter fish from Europe has been discovered in the vicinity of the Faeroe Islands (Netboy, 1968; 1973).

One of the truly amazing characteristics of Atlantic samon is its homing instinct. The salmon is known to undertake very long journeys at sea, yet about 95% of the adults that survive to migrate back in freshwater return to their natal stream to reproduce, the remainder ones straying into other streams (Hasler and Scholz, 1983). Homing and straying are very important phenomena from a population dynamics point of view. Homing reduces reproductive wastage by ensuring that spawning is mostly confined to waters suitable for survival. Straying maintains gene flow between separate river populations and allows the colonisation of newly available habitats (Hasler and Scholz, 1983).

In contrast to Pacific salmon, the Atlantic salmon does not always die after reproduction. Some fish, known as kelt, survive the mating and stay in the rivers for a variable length of time before migrating back to sea again. Some of them will come back to spawn for a second time ("previous" or "repeat" spawners). A few will spawn three times, four times or even more, always returning to the ocean between each spawning (Netboy, 1973).

For the last twenty years, much of the research dealing with Atlantic salmon has concentrated on aspects of its reproductive life

cycle. Atlantic salmon shows a remarkable plasticity in that respect (Saunders and Schom, 1985).

- The duration of the sea absence (i.e. the sea age at first maturity) is quite variable. Some fish, known as grilse or as 1-sea-winter fish come back to the river about one year after smoltification, weighing on average 1.5 to 2 kg. Other fish come back after 2 or more years spent at sea and are designated as multi-sea-winter salmon (meaning that they spent at least 2 winters in the sea, as opposed to grilse that only spent one). They are considerably heavier than grilse and weigh between 4 and 14 kg on average (Netboy, 1968; 1973; Gardner, 1976; Allen and Ritter, 1977). Multi-sea-winter fish are most commonly 2-sea-winter or 3-sea-winter salmon (i.e. fish spending about 2 or about 3 years at sea, respectively), 4-sea-winter, 5-sea-winter, and older fish are considerably rarer (Netboy, 1973).

- In the case of salmon spawning more than once (repeat spawners), the interval between consecutive spawnings is as well quite variable (Saunders and Schom, 1985).

- There is also a considerable variability in the season of ascent of the river. Some fish may ascend the river in early spring (spring run), while others may wait until the fall (fall run), even though all fish will eventually spawn around the same time, in late fall (Netboy, 1968; 1973).

- As previously mentioned, male parr commonly mature in freshwater before smoltification and participate in the spawning of anadromous adults (Jones, 1959). Some will do so repeatedly, while others might mature precociously only once or not at all. (Leyzerovich, 1973;

Mittans, 1973; Saunders and Schom, 1985).

This variability in life history parameters has wide implications for the dynamics of Atlantic salmon populations (Saunders and Schom, 1985). Much of the management of the Atlantic salmon resource is now focussed on these aspects and particularly on the sea age at first maturity, i.e the grilse versus multi-sea-winter fish phenomenon. Grilse are smaller and less valuable to both sport and commercial fishermen (Saunders, 1896).

Age at first maturity also bears considerable economic importance in the context of the commercial salmon aquaculture. This activity has expanded remarkably for the last ten years and now represents a considerable source of earnings for some countries, Norway and Scotland among the first. Grilse maturation in cage reared salmon is detrimental. As maturity approaches, the growth rate decreases and the meat quality deteriorates (Tveranger, 1985; Aksnes et al., 1986). Fish farmers also claim that grilse maturation is associated with increased mortality (Naevdal et al., 1978 b). Late maturation (multi-sea-winter maturation) has the additional advantage that the slaughtering season may be lengthened (Naevdal, 1983).

Yet, our knowledge of this important life history parameter is still fragmentary. In an extensive review of the factors which may influence the Atlantic salmon sea age at maturity, Gardner (1976) concluded that "no single factor can be identified as regulating the time at which maturing salmonids return to freshwater. The evidence is confusing and no other conclusion can be justified." Ten years later, Saunders (1986), in the prologue of an international workshop on

"Salmonid age at maturity" stated that "effective management of the species demand a fuller understanding than we now have of the genetic and environmental influences..." on the sea age at maturity.

In the same workshop, Bielak and Power (1986) concluded that "integrated studies of genetic factors, effects of freshwater and marine environments on growth rates, and of the interactions between them, are more likely to contribute to our understanding of how age at first maturity is controlled." This approach was used in the present study of Atlantic salmon maturation. Three groups of salmon, belonging to several different families were followed from spawning to grilse maturation. Each salmon was individually identified before or shortly after smoltification, and growth and maturation data were individually collected approximately every 6 months, until some fish matured as grilse (18 months after smoltification). This compilation of precise individual life histories permitted an analysis of: the relationships between precocious maturation and grilse maturation, the relationships between growth patterns and maturation patterns, the influence of the fish sex and smolt ages, and the influence of the fish genetic background.

The present work is sub-divided into five separate chapters.

- Chapter I presents and discusses the individual and family marking techniques used in the present study. This Chapter I does not therefore directly deal with the primary goal of this study, the understanding of how age at maturity is controlled in Atlantic salmon, but it should rather be viewed as an important preliminary technical chapter.
- Chapter II presents an overview of the methods used for rearing the

salmon and of the data collection procedures. It presents and discusses results concerning survival, the various maturation patterns observed among individually identified salmon, the sex specific incidence of maturation in the different groups of salmon and the relationships between successive maturation episodes.

- Chapter III presents and discusses results concerning family variability for incidence or maturation.

- Chapter IV analyses the relationships between growth patterns and maturation patterns and proposes a model of maturation "triggering".

- Chapter V tries to reconcile the observations of Chapters III and IV, i.e. the genetic/environmental interactions in the control of age at maturity.

- The General Conclusion discusses briefly some practical considerations about genetic and environmental manipulation of the Atlantic salmon age at maturity in the aquaculture context.

CHAPTER I INDIVIDUAL MARKING OF ATLANTIC SALMON. EVALUATION OF COLD-BRANDING AND JET INOCULATION OF ALCIAN BLUE IN SEVERAL FIN LOCATIONS.

1. Introduction

In a variety of situations, from laboratory experiments to breeding programs in commercial aquaculture, there is a growing need for the identification of individual fish, or at least for a system with which to recognize a number of "codes" generally larger than those generated by batch marking techniques. In addition, most situations require (with various degrees of priority) that the information remain available for a minimum period of time, that the marking technique does not interfere with fish behaviour and physiology, that marks can be applied to small fish, and that it is not necessary to sacrifice the fish to retrieve the information. This ideal marking technique should also not be too expensive and should require little time and labour.

Many techniques have been described and a few are widely used. However, none can fulfill all requirements. External tags tend to impair growth and survival, and tag losses can be high (Refstie and Aulstad, 1975; Herbinger, unpublished). Fin clipping does not allow for many distinct classes to be identified and imposes a certain degree of mutilation upon the fish, with the exception of adipose clipping in salmonids (Piggins, 1972). Cold and hot brandings are widely used for batch marking and can generate a few combinations. However, a high variability in quality and subsequent recognition of the brand has been noted (Raleigh et al., 1973; Raymond, 1974). Jet inoculation of dyes in several locations on the fish fins and body could generate more

combinations, but there are conflicting reports on the known duration of such marks (Refstie and Aulstad, 1975; Pitcher and Kennedy, 1977; Cane, 1981). Nose tags require the sacrifice of the fish. Two recently developed techniques appear promising, the use of "X-ray microtags" in which the binary coded notches can be read with an X-ray apparatus (Higgins, 1985; Miles et al., 1985), and the use of internal magnetic tags that can be detected by passing the fish through an identification coil (Harache et al., 1978; Dumas and Prouzet, 1982). However, both methods are fairly expensive and only allow a maximum of 127 different individual tags to be recognized.

In the present study, an identification system was needed for Atlantic salmon (Salmo salar L.), that could provide family and individual identification (12 families and up to 60 individuals per family), from the earliest possible time to grilse maturation times. The marking system that was chosen consisted of a combination of adipose clipping (the least mutilating fin clipping), cold-branding (restricted to optimal conditions) and jet injection of Alcian Blue in several fin locations. The overall period of study was slightly more than 3 years from family marking to the last individual fish census, but data collection sessions were performed at intervals of approximately 6 months, allowing remarking to be performed if fading was detected. From the time when individual marking was first performed (parr/smolt stage) until the end of the experiment, a reading score was assigned to each cold brand and each jet injected dot, allowing an evaluation of each technique as well as an evaluation of the practicability of such a system for marking individual salmon.

2. Preliminary experiment

Hot-branding several signs or symbols to different body locations was tried in a preliminary work (unpublished). The fish used were from the 1980 spawning year class. The device used for hot-branding, an electrically heated nickel-chrome wire, was similar to the one described in Joyce and El-Ibiary (1977). The different symbols used were: a single horizontal bar, a single vertical bar, a left arrow, a down arrow, a right arrow, an up arrow (symbols # 0,1,2,5,7,8 in Joyce and El-Ibiary, 1977), as well as double parallel horizontal bars and double parallel vertical bars. The positions used were mostly the anterior dorsal area between the head and the dorsal fin, above the lateral line, and the posterior dorsal area between the dorsal fin and the adipose fin, above the lateral line. A few mid ventral positions, just above the pelvic fins below the lateral line were tried as well.

Overall results were not satisfactory. After 6 months, very few symbols could be easily recognized although the presence of a brand could be detected. Brand fading and complete disappearance occured over longer periods of time, but in a variable and unpredictable way. In a few cases, paradoxical phenomena were even observed: considerably faded but identifiable symbols seemed to reappear on some large fish (over 1 kg) whereas these same symbols were absolutely undetectable at earlier times. Furthermore, rebranding proved to be awkward because of the changing size and shape of the symbol. Topical locations, branding techniques and changes in hue of the fish affect cold brand recognition on salmonid fish (Raleigh et al., 1973), and several of these reasons are probably involved in this inconsistency of the brands. However, this preliminary work showed that, over a period of 6 months, the place

of branding could almost always be located, even when the specific symbol could not be recognized. The most easily identifiable symbol was a single horizontal bar (#0 in Joyce and El-Ibiary, 1977), and the best location was the anterior dorsal area between the head and the dorsal fin, just above the lateral line (Fig. 1.1). Raleigh et al. (1973) found as well that symbols with open design and with clean line produced the best quality cold brands, and that the anterior dorsal area was the best for branding brown trout and rainbow trout.

Jet injection of Alcian Blue in several fin locations was tried as well, and appeared satisfactory. The method is described below.

3. Material and methods

A new marking system was designed to mark fish of the 1981 year class. Based on the conclusion of the preliminary work, Alcian Blue jet injection was used, in combination with adipose clipping and branding restricted to the optimal condition previously mentioned. Only one symbol, a single horizontal bar, at one location, the anterior dorsal area, on the left or right side of the fish, was used.

Alcian Blue injections were performed using an unmodified Madajet dental inoculator (Mada Medical Products Inc. Carlstadt NJ 07072 U.S.A.), similar to the Panjet inoculator used by Hart and Pitcher (1969), filled with an aqueous suspension (65 mg/ml) of Alcian Blue, as first recommended by Kelly (1967) and used by Hart and Pitcher (1969). In October 1982, for family marking (Fig. 1.2) hot-branding was performed with the same device used in the preliminary experiment.

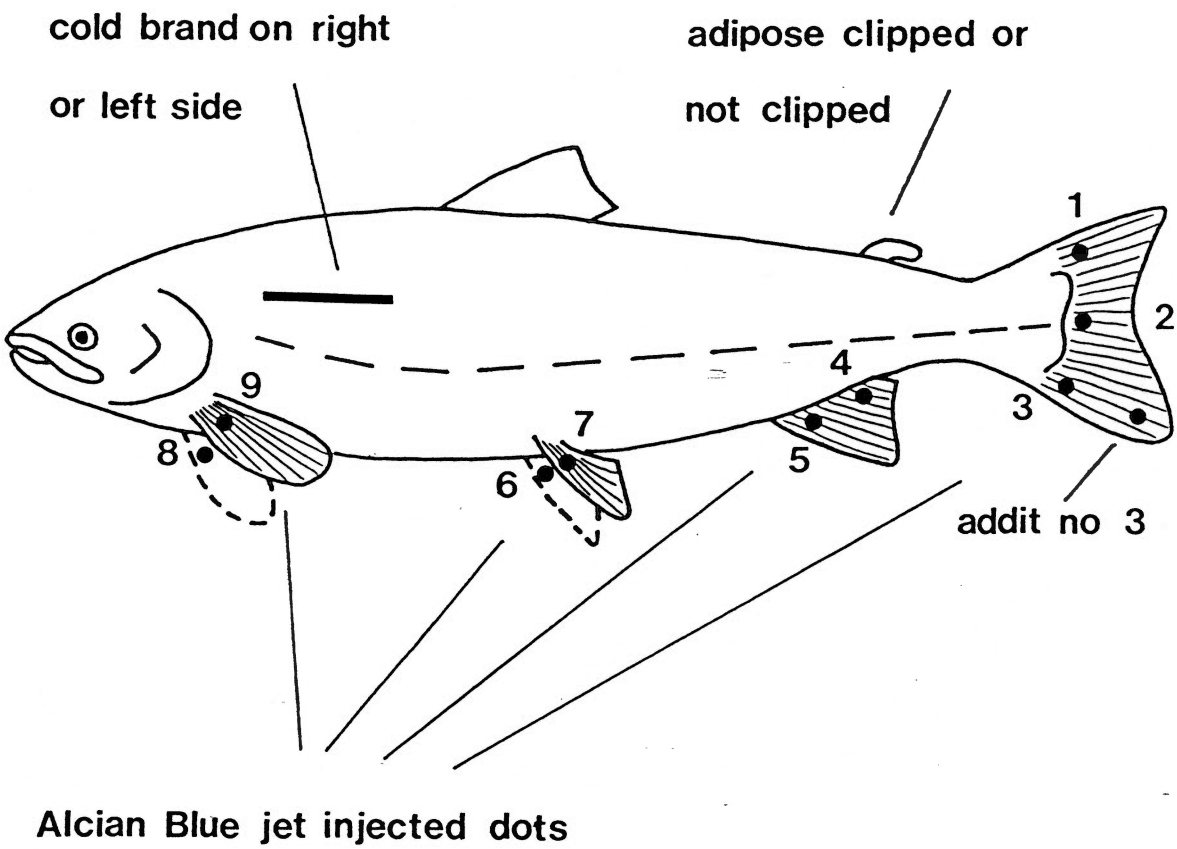

Fig. 1.1: Location of the different types of information used for family and individual identification.

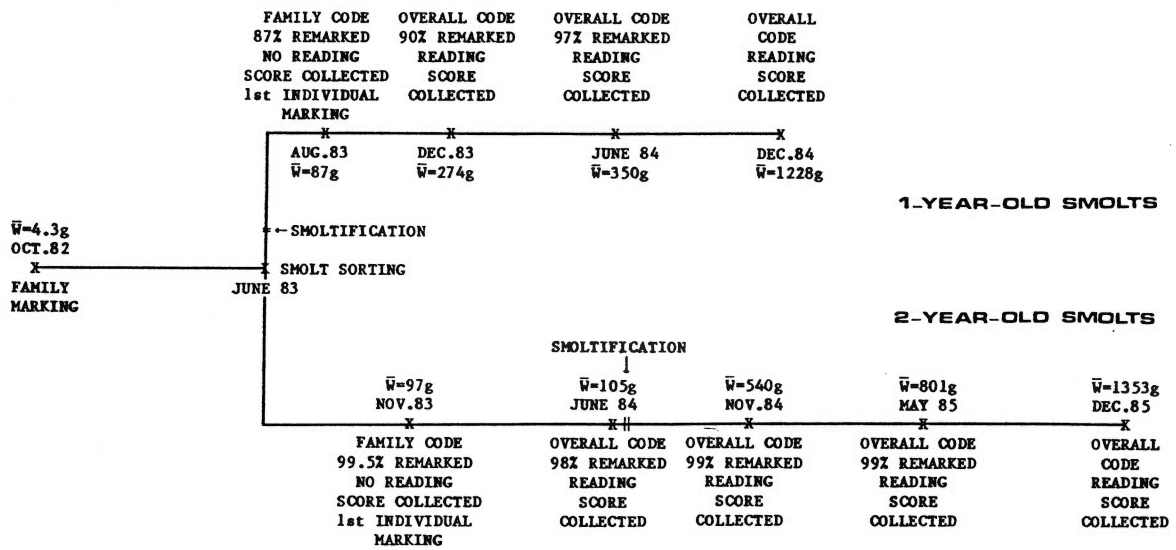

Fig. 1.2: Summary of the different marking/remarking and reading operations performed on family and individual codes.

W: Mean weight of the fish at the data collection session.

After this marking operation, hot-branding was abandoned in favour of cold-branding, because of the risk of injury to the fish. Cold-branding was performed by gently applying for 1.5 to 3 seconds, depending on fish size, a copper branding tool previously dipped in liquid nitrogen. The branding tools were similar in design to those described by Groves and Novotny (1965), but with simpler tips since only one sort of symbol, a single horizontal bar, was to be used. Two sizes of branding tips (length=20mm, width=1.5mm; and length=50mm, width=5mm) were used to allow for the change in fish size with time. Raleigh et al. (1973) and Refstie and Aulstad (1975) recommended that the width of the branding tips should be 1 mm or less to distinguish different symbols. Wider tips were used in this study since only one symbol was to be identified and because there were indications that using large branding tips might improve long term retention (Park and Ebel, 1974).

Figure 1.1 shows the position of the brand as well as the different fin locations used for jet injections. Family codes had to be marked in October 1982 (Fig. 1.2), when the fish were still very small (mean weight: 4.3 g; range: 2 to 40 g) and the jet innoculator could be safely used only on positions 1 and 3 (upper and lower caudal fin). With the additional information provided by the adipose "Clip"/"No Clip" and by the brand placed on the "Right" or "Left" side of the fish, 12 different families could be identified:

Clip Left 1	Clip Left 3	Clip Left 13
Clip Right 1	Clip Right 3	Clip Right 13
No Clip Left 1	No Clip Left 3	No Clip Left 13
No Clip Right 1	No Clip Right 3	No Clip Right 13

More than 12 combinations could be formed with this information, but this conservative combination code insured that each fish would bear

one and only one brand and at least one dot on the upper or lower caudal fin, insuring thus a safer and easier family recognition. In August 1983, for the 1-year-old smolts, and in November 1983, for the 2-year-old smolts (Fig. 1.2), with the fish weight ranging from 24 g to 270 g, individual identification was assigned to each fish within each family. The individual code consisted of a unique combination of the yet unused Alcian Blue dot positions 2, 4, 5, 6, 7, 8, 9. The position 4 (posterior part of anal fin, see Fig. 1.1) was found to be too fragile for satisfactory use and hence was used only when absolutely necessary. With bigger fish (over 150/200 g), however, the use of that position did not cause any more problems. Most cold brands and jet injected dots were systematically rebranded/remarked at each census session.

In August 1983 (1-year-old smolts) and November 1983 (2-year-old smolts), no reading scores of the family codes were collected (Fig. 1.2). Afterwards each jet injected dot was systematically scored, as set out in Table 1.1, on a scale ranging from 1 (Absent) to 6 (Very Clear).

It can be noted that the only difference between the scores 5 and 6 was the size of the dot, the color of the dot being the same. Hence, having to choose between 5 and 6 for a good dot was probably the most subjective of all score assignments and as well the most prone to variation between censuses.

A reading score was also systematically assigned to cold brands, ranging from 1 to 6. Each cold brand having the same shape and the same location (Left or Right side of the fish), scores were based on the easiness to detect the brand, ie. on the contrast between the branded area and the body background.

Table 1.1: Bases on which reading scores were assessed for jet injected dots.

Reading score	Color of the dot	Size and shape of the dot	Comments
Very clear (6)	Not faded. Dark turquoise blue	Very elongated along fin rays, over 5mm to 1cm in longer axis	Very conspicuous. Could easily be detected by untrained observers.
Clear (5)	Not faded. Dark turquoise blue	Oval, around 3 to 5mm in longer axis	Conspicuous. Could easily be detected by untrained observers.
Light (4)	Faded. Light turquoise blue	Oval, around 2 to 3mm in longer axis	Not too obvious. Could still be detected by untrained observers exercising care.
Very light (3)	Very faded. Light bluish	Roundish, around 1mm in diameter	Very inconspicuous. Would be overlooked by most untrained observers.
Quasi absent (2)	One or a few blue grains embedded in fin	Minute points.	Almost invisible. Could be detected only with prior knowledge.
Absent (1)	None detected	No dot detected	Absolutely undetectable

Except for family marking in October 1982, all marking and reading operations were performed by the same operator throughout the experiments.

In addition to the normal dots positions used for family and individual identification (Fig. 1.1), a number of atypical dots were created because of the fish movements during the marking/remarking operations. These dots, mostly located on the caudal fin, being dispensable for absolute identification, were not systematically remarked. Nevertheless, reading scores were still collected for most of them, thus allowing an evaluation of longer term stability.

In order to look at extension potentials of this marking system, an additional position No. 3, located along the same fin rays but further away from the caudal peduncle (Fig. 1.1) was tried on a few fish. Similarly, a few dozen jet injected dots were created, using a chromium oxide dispersion (75 mg/ml) (Kelly, 1967) instead of Alcian Blue. During the time the fish were kept in the Dalhousie University Aquatron facilities (Aug. 1983 - Dec. 1984 for the 1-year-old smolts and June 1984 - Dec. 1985 for the 2-year-old smolts), mortality and causes of mortality were checked every day.

Non parametric statistical tests (ranking test) were used; Kendall rank order correlation, Mann-Whitney U test (2 group comparison) and Kruskall-Wallis' one-way analysis of variance (multigroup comparison) (Nie et al., 1975; Nie and Hull, 1981).

4. Results and Discussion

With the exception of the mortality results which encompass the totality of the 1-year-old smolts and 2-year-old smolts cohorts, all

other reading/marking results were drawn from two subsamples of 100 fish, randomly taken among the 238 1-year-old-smolts and the 245 2-year-old-smolts used for this study.

4.1 Mortality

Overall mortality was low during the time the fish were kept in the Dalhousie University Aquatron facilities: 45 fish died (9.3%) out of the original 483 fish followed during this period. Mortality causes can be broken down as follow:

- non smoltification: 4 fish (0.8%)
- accidental oxygen level drop: 12 fish (2.5%)
- diseases, wounds, background mortality: 13 fish (2.7%)
- mechanical causes (net tangling, jumps out of tanks): 9 fish (1.9%)
- anaesthesia, handling, marking stress: 7 fish (1.4%)

Mortality attributable directly or indirectly to the marking was very low (1.4%), particularly when keeping in mind that 4 or 5 different marking/remarking and data collection sessions were performed on all fish, and that these data collection sessions were extensive, therefore increasing the handling and anaesthesia stresses. Unfortunately, no precise mortality data were collected earlier on smaller fish, particularly after the family marking. However, the hatchery operators did not detect, at the time, any apparent mortality due to marking.

Apart from the already noted problem with the posterior anal fin position 4, few fin damages (fin splitting etc.) from jet injection and skin damages from cold-branding were noted. Pitcher and Kennedy (1977) and Cane (1981) (using jet injections), Mighell (1969), Laird et al. (1975) (using cold-branding), recorded few, if any, mortalities or problems associated with both marking techniques, although Raleigh et al. (1973), Refstie and Aulstad (1975) and Nahhas and Jones (1980) noted

that mortality can occur if cold-branding is performed too long or with too high a pressure.

4.2 Evolution of jet injected dots and cold brands legibility when systematically remarked/rebranded every 6 months or so.

Both marking systems, jet injection and cold-branding, performed very satisfactorily when systematically remarked at each data collection session (Fig. 1.3 a,b,c,d). Jet injection was particularly good with mean scores ranging from 5.64 to 5.90 on the 1 to 6 scale (Fig. 1.3 a,b). The mean overall score (2303 jet injected dots) breaks down as follow:

- Very Clear: 84.0%
- Clear: 11.7%
- Light: 3.7%
- Very Light: 0.5%
- Quasi-Absent and Absent, lumped together: 0.1%

As noted by Hart and Pitcher (1969) and Pitcher and Kennedy (1977), best results were obtained when pigment was injected in the fin rays rather than in the dermal/connective tissues only. Mean scores did not vary notably with time, for both 1-year-old and 2-year-old smolts, although fish size and fish relative growth greatly varied with time (Fig. 1.3 a,b).

With the already noted exception of position 4 (rear anal fin) on small fish (mean score: 4.4 in Dec. 1983), all other positions proved to be equally satisfactory, no single position scoring less than 5.2 at any time in any groups. There is a significant but slight tendency for pectoral/pelvic fin positions to be better and caudal fin positions to be worse (Table 1.2).

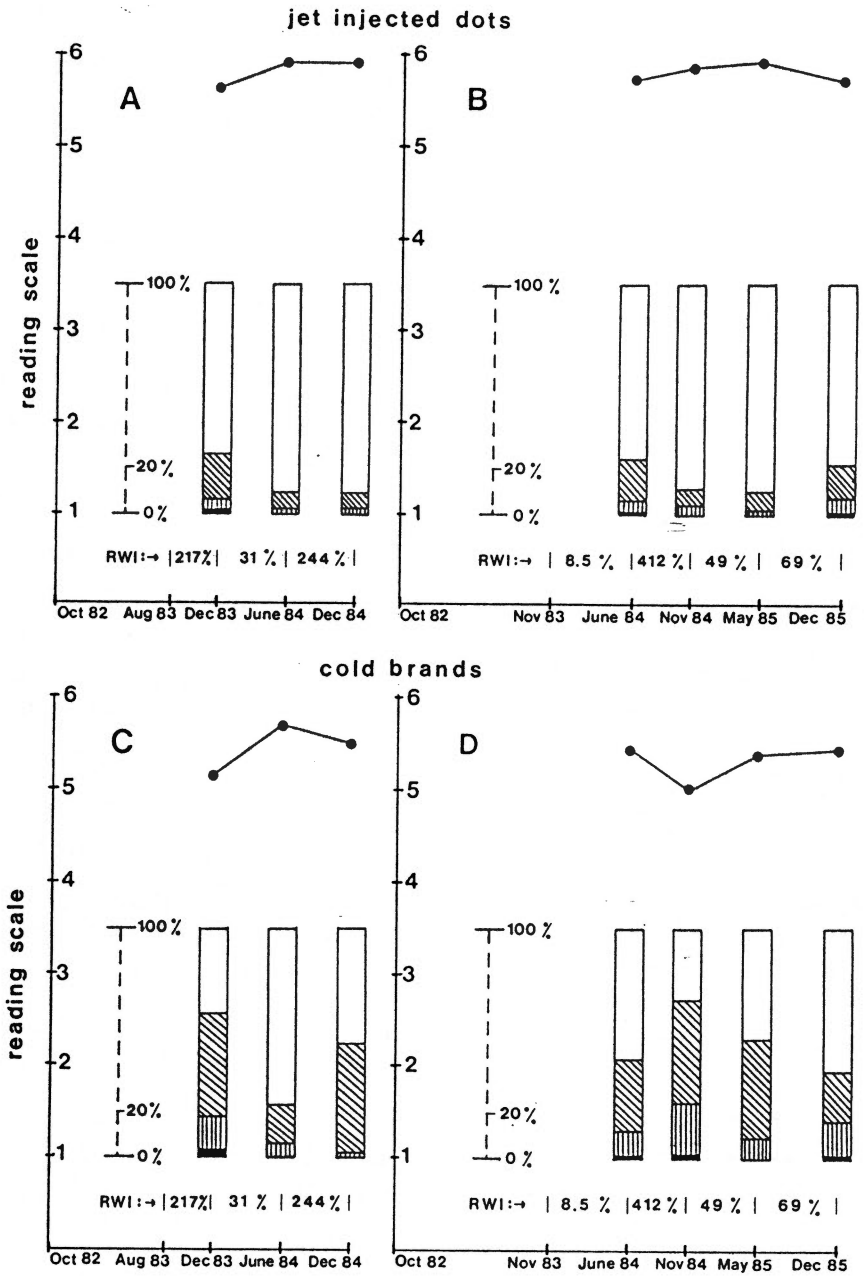

Fig. 1.3: Mean score of marks with systematic remarking at all data collection sessions.

A= 1+ smolts (281 cases), B= 2+ smolts (366 cases).

C= 1+ smolts (82 cases), D= 2+ smolts (93 cases).

RWI: Relative Weight Increase between two data collection sessions.

Solid lines and dots: mean scores.

Rectangular boxes: distribution of the mean score at eacn data collection sessions.

score 1/2/3 score 4 score 5 score 6

Table 1.2: Mean reading scores for the different jet injected dot positions and pooled for the different fins.

Dot position	1	2	3	4	5	6	7	8	9
Number of cases	361	62	388	15 10(1)	365	328	313	265	208
Mean reading score	5.69	5.73	5.72	5.27 5.90(1)	5.76	5.90	5.81	5.83	5.90

Between positions comparison: Kruskall-Wallis 1 way anova $X^2=43.8$ $p<0.1\%$

Fin	Caudal	Anal	Pelvic	Pectoral
Mean reading score for the fin	5.71	5.74 5.76(1)	5.86	5.86

1: Number of cases and mean score for position #4 and for anal fin when results of position #4 in Dec. 83 are excluded. See text.

However, differences are small and mostly due to a slightly different proportion of 5 (Clear) and 6 (Very Clear) scores, for which the distinction is small and relatively subjective. Hence, for practical marking purposes, all positions can be considered equally good. Pitcher and Kennedy (1977) found as well no significant difference in quality of the mark on the different fins of slow growing roach (Rutilus rutilus L), although they noted a tendency for pelvic fin marks to be worse than the others.

Cold brands were also found to be satisfactory, with mean scores ranging from 5.02 to 5.71 on the 1 to 6 scale (Fig. 1.3 c,d). Mean overall score (617 cold brands) breaks down as follow:

- Very Clear: 52.2%
- Clear: 35.2%
- Light: 11.5%
- Very Light: 0.8%
- Quasi Absent and Absent, lumped together: 0.3%

Cold brand mean scores were consistently inferior to those of jet injected dots at all data collection sessions for both 1-year-old and 2-year-old smolts. However, a strict statistical comparison was not done, because of the essentially subjective nature of such a comparison, cold brands not being evaluated exactly in the same way as jet injected dots. In addition, it can be noted that the relative proportion of problematic scores (Absent, Quasi Absent and Very Light) did not differ significantly between cold-branding and jet injection ($X^2=1.88$ 1df NS). Cold brand mean scores varied more widely with time (Fig. 1.3 c,d) than jet injected dots mean score (Fig. 1.3 a,b). The lowest mean scores were generally observed after periods of highest relative growth.

4.3 Stability of jet injected dots and cold brands over periods longer than 6 months.

Most jet injected dots and cold brands were systematically remarked (Fig. 1.2) to avoid losing vital information. The non-remarked dots and brands that will be discussed in this section do not constitute a random sample of the entire population of dots and brands. Indeed, a significant proportion of the non-remarked dots consisted of the non-vital atypical dots that were created accidentally during remarking sessions (see section 3. Materials and methods). Six months after first marking, these accidental dots were generally characterised by a mean score quite inferior to that of the dots created on purpose (4.11 versus 5.71 respectively). To circumvent this bias, stability for periods longer than 6 months was assessed by looking at the mean change in score (6 to 12 months; 12 to 18 months; 18 to 24 months) associated with non-remarking rather than by directly looking at mean scores.

- Evolution of reading scores from 6 to 12 months after marking. Mean score after 12 months was about 0.83 units lower than the mean score after 6 months for 59 non-remarked jet injected dots (Table 1.3), hence demonstrating significant fading. However, estimates of this mean change in score varied significantly between periods, higher losses being observed after periods of highest relative growth. In contrast, fading did not seem to be significantly dependent on the number of times a dot had been remarked (Table 1.4); mean changes in scores did not differ significantly whether the dots had been marked only once or had been already marked and remarked twice or thrice.

Table 1.3: Comparison of the different estimates of mean change in score from 6 to 12 months (jet injected dots).

Smolt cohort	1year old smolt		2 year old smolt			mean estimate
Last time marked	Aug. 83	Dec. 83	Nov. 83	Jun. 84	Nov. 84	/
Period of evaluation	Dec. 83 to Jun.84	Jun. 84 to Dec. 84	Jun. 84 to Nov. 84	Nov. 84 to May 85	May 85 to Dec. 85	/
Relative weight increase	31%	244%	412%	≃ 49%	69%	/
Number of cases	33	9	13	2	2	59
Mean change in score	-0.42	-0.89	-1.85	-1.00	-0.50	-0.83
Comparison of estimates	Kruskall-Wallis (1 way anova) $X^2=20.01$ $p<0.1\%$					

Table 1.4: Influence of the number of times a dot was marked on the mean change in score from 6 to 12 months (jet injected dots).

Smolt cohort	1 year old smolt	1 year old smolt
Last time marked	Aug. 83	Dec. 83
Period of evaluation	Dec. 83-Jun. 84	Jun. 84-Dec. 84
Relative weight increase	31%	244%
Mean change in score Last marking was first marking	-0.41 (17 cases)	-0.67 (3 cases)
Mean change in score Last marking was a remarking	-0.44 (16 cases)	-1.00 (6 cases)
Between last marking type statistical comparisons	Mann-Whitney U-test Z=0.19 (NS)	Mann-Whitney U-test Z=0.69 (NS)

No significant correlation was found between scores after 6 months and changes in scores from 6 to 12 months (Kendall correlation coefficient=.16, p=9% NS). Hence, good quality dots do not seem to fade less than poor quality dots. This seems to contradict the observation of Pitcher and Kennedy (1977) that "deterioration of quality did not proceed at the same rate in all marks and that there was a non random distribution of quality decay skewed heavily towards low loss rates in the marks scored as 'very clear' at 3 1/2 years."

In contrast to jet injected dots, cold brands did not show any significant fading from 6 to 12 months after marking, mean score after 12 months being only .05 units lower than mean score after 6 months. Figure 1.4, showing the distribution of change in score from 6 to 12 months, for both jet injected dots and cold brands, allows some insight into this contrasting fading behaviour. For both marking techniques, the most commonly observed change in score is 0 (no change). However, for cold brands, there are more cases where the change in score is positive (denoting an improvement of the brand legibility) than negative (denoting fading). With jet injected dots, on the other hand, except for one sole observation of a positive change, all other changes are either null or negative, and predictably distributed in a Poisson like fashion. For cold brands, positive changes in score were mostly observed on fairly low quality brands. Therefore, this phenomenon seems to be quite similar to the paradoxical "reappearance" of lost hot-branded symbols, observed in the preliminary experiment (see section 2. Preliminary experiment).

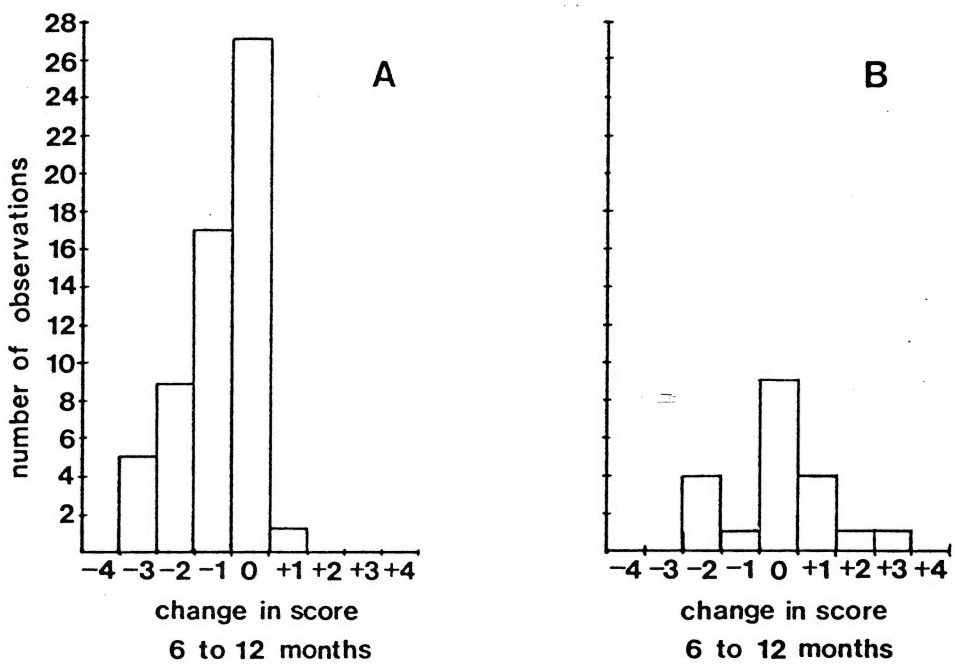

Fig. 1.4: Distribution of the change in score from 6 to 12 months after marking. A: jet injected dots (59 cases). B: cold brands (21 cases).

Laird et al. (1975) showed that, after 1 week and up to 16 weeks, cold brand legibility was mostly due to the invasion of the branded area stratum spongiosum and hypodermis by melanin containing cells, such as those that are found in healing teleost wounds. These cells are responsible for the darker coloration of the brand. However, in other forms of wounds, they appear to remain for up to 2 years only (Roberts et al., 1973). It is likely that after an initial period of proliferation (probably 6 months to 1 year at the most), the number of melanin containing cells begins to decrease, resulting in a decrease of the cold brand legibility. This brand degradation seems to be compensated by an increased detectability of the brand area iridescence when the scales get bigger. Regenerating scales of the brand area are generally smaller and deformed (Piggins, 1972). The brand can then still be recognised even though it is not darker than the surrounding area. Most authors did not specifically recognise these two aspects of cold brand legibility, but it is of significance that in long term studies (for over 1 year), it has been noted that brands were faint (Raleigh et al., 1973; Refstie and Aulstad, 1975) but could be recognised when held at the proper light angle. Most short term studies only mentioned the darker coloration of brands as the key factors with which to recognise brands. Cane (1981), in a four month study, noted that cold brands at later stages were less well defined in direct light as dark areas but still visible if the angle of incidence of light was varying. It seems that the paradoxical phenomenon of cold brands and hot brands disappearance/reappearance, reported in the present study, can be explained by the early disappearance of the brand legibility linked to melanin containing cells, before the fish could got big enough

to allow increased iridescence detectability to compensate for that loss. It also seems to explain two observations on cold brand behaviour that are apparently contradictory. After 6 months, lower mean scores were observed after periods of highest growth (Fig. 1.3 c,d), but, from 6 to 12 months, mean change in scores did not seem to be significantly affected by growth rate. High growth rate probably affects negatively cold brand legibility linked to darker coloration (melanin containing cell phenomenon.), but probably affects positively cold brand legibility linked to scale iridescence.

- Evolution of reading scores from 12 to 18 months and 18 to 24 months after marking.

From 12 to 18 months and 18 to 24 months, fading behaviours of both jet injected dots and cold brands appear quite similar to those observed from 6 to 12 months (Table 1.5). There does not seem to be any accelaration of fading with elapsed time in the case of jet injected dots; the estimates for the 3 different periods are quite similar and amount to a loss of 1 unit every 6 months. There were not enough cases to statistically test the influence of the relative growth rate on the amount of fading, but in the case of changes from 12 to 18 months, the same tendency for higher losses after periods of highest relative growth was observed. Jet injected dots were shown to be initially quite robust to varying growth rates (see section 4.2, Fig. 1.3 a,b) with mean scores after 6 months around 5.79. Under subsequent conditions of moderately high growth rate (30%-150% relative weight increase per 6 months), mean score after 1 year, 1.5 year and 2 years, can probably be estimated to be around 5, 4, and 3, hence satisfactory, mediocre and unsatisfactory respectively.

Table 1.5: Comparison of mean change in score, from 6 to 12 months, from 12 to 18 months and from 18 to 24 months for both marking techniques.

Marking system	Jet injection			Cold branding	
Period of evaluation after last marking	6 to 12 months	12 to 18 months	18 to 24 months	6 to 12 months	12 to 18 and 18 to 24 months
Number of cases	59	10	5	21	3
Mean change in score	-0.83	-0.90	-1.00	-0.05	0.00
Between period estimates comparison	Kruskall-Wallis 1 way anova X^2=0.59 (NS)			Mann-Whitney U-test Z=-0.09 (NS)	

Nevertheless, under conditions of sustained very high growth rate (over 200% relative weight increase per 6 months), decrease in mean score could be much faster and mean score could only be partly satisfactory, already 1 year after marking. In the only other long term study of jet injected dots, Pitcher and Kennedy (1977) reported almost no loss of marks for 3.5 years and no loss at all during the first 2 years. However, the fish they used, (Rutilus rutilus L.), had a growth rate considerably lower (length varying from 18.8 cm to 22.3 cm in 3.5 years) than that of the salmon used for this study (length changed from about 21 cm to about 49 cm in 1.5 year).

In this study, cold brands appear to be on average more resistant to fading than jet injected dots. Although the number of cases on which this evaluation is done is low, cold brand mean score after 1 year and 1.5 year would probably still be satisfactory. Piggins (1972) reported a 94% readability of cold brands from smolt stage to grilse stage (period slightly longer than 1 year) and Refstie and Aulstad (1975) reported similar results (86.5% to 99.4% for various salmonids, 9 to 13 months after marking). However, as already indicated, this better resistance to fading seems mostly due to the compensating phenomenon of increased iridescence detectability on bigger fish. Cold brand legibility based solely on the brand darker coloration appears shorter lived, probably in the range 6 months to 1 year at the most. Under several conditions, this compensation due to increased iridescence might not occur: for instance, salmon are known to loose a large number of scales when kept in indoor tanks; other finely scaled species might simply not show such an increased iridescence.

4.4 Problems encountered and possibilities of extension of the jet injection system.

In this study, because of the relatively low number of fish involved (483 fish), and because many data, other than marking data, were collected on each fish, a complete identification of the fish at all times proved to be possible. All problems that led, or could have led, to identification errors could be traced. The individual identification of 100 1-year-old smolts (for 4 consecutive times) and of 100 2-year-old smolts (for 5 consecutive times), necessitated 5083 marking/remarking/reading operations on the different items of information (adipose clip, cold-brand, jet injected dots) in the course of which 74 problems occured:

- 16 of these problems were purely due to operator error, mostly reading or marking/remarking inversion between symetrical pieces of information: Clip or No Clip adipose, Left or Right brand, Upper or Lower caudal fin, Left or Right pectoral fin, Left or Right pelvic fin.

- 30 of these problems were due to the marking system: 17 pieces of information disappeared and 13 pieces of information almost disappeared.

- Finally, on 28 occasions, additional unwanted pieces of information were created during marking/remarking operations. On 7 occasions (frequency of occurence=0.8%), the branding tool was applied next to the brand area instead of directly on it, resulting in the appearance of a new symbol, a double parallel horizontal bar, at subsequent data collection sessions. Only 2 of these 7 cases were immediately detected. In this study, this did not cause any real problem since only one sort of symbol was used. However, if several symbols are to be used, improper rebranding of this sort could create

some troubles. On 10 occasions (frequency of occurence=1%), a dot was created on the caudal fin in a place other than the one originally planned. However, 7 of these problems were immediately detected, and furthermore, only 4 of these resulting dots could be mistaken for a normal dot, the other ones occupying atypical positions, hence reducing considerably the impact of this problem. Finally, on 11 occasions (frequency of occurence=1.2%), a dot was mistakenly created on one pelvic fin when marking the other one. This last problem was more serious since only 2 of these problems were immediately detected, and furthermore, all resulting dots looked like regular ones, although generally lighter. It seems that upon marking one fin, part of the jet is sometimes diverted and hits the other pelvic fin located quite close. A careful and systematic washing and checking of the marking operations can help to reduce this problem.

- Extension of the jet injection system.

More positions and/or more sorts of dyes could increase the number of individual combinations. On 5 fish, one additional position No. 3 (Fig 2) was tried in addition to the normal one. On all 5 fish, 6 months later, both positions No. 3 could not be distinguished from one another. The Alcian Blue seemed to be able to migrate quite extensively along bony structures such as fin rays. On the other hand, Alcian Blue did not seem to migrate much across connective tissues: most atypical dots located on the caudal fin remained quite distinct, even though they were sometimes located just a few fin rays across a normal dot. Therefore, if more positions are to be used, they should be located on an axis perpendicular to the fin rays axis. For this reason, it appears impractical to have more than one position on the pelvic and pectoral

fins. More positions could possibly be used on caudal and anal fins, although this would be practical only on large fish and would probably greatly increase the number of problems associated with accidental additional dots. On the dorsal fin, 2 or 3 positions could probably be satisfactorily used, even on small fish. No dorsal fin positions were used in this study, since most fish lacked their dorsal fin, a common occurence with hatchery reared Atlantic salmon. Jet injection can as well be used to tattoo marks directly on the fish body (Kelly, 1967; Hart and Pitcher, 1969). However, this can be used safely only on large fish, and these body marks seem to be shorter lived than fin marks (Refstie and Aulstad, 1975; Pitcher and Kennedy, 1977).

Hydrated chromium oxide (75 mg/ml), a green pigment, had been recommended by Kelly (1967). None of the few dozens of jet injected marks tried in the present study were recovered after 6 months. In the course of this study, an extensive variation of the fin background colour was noted, from light yellowish green to dark blue-grey. Therefore, orange/red pigments would seem to be the most promising ones to ensure easy recognition of marks independently of the fin background colour and easy differentiation between the two dyes.

Mercuric sulphide (100 mg/ml), a red pigment, proved satisfactory with subcutaneous needle injection (Kelly, 1967; Schoonoord and Maitland, 1983), however, its poisonous nature is certainly a major drawback for its general use.

5. Conclusion

Jet injection of Alcian Blue in several Atlantic salmon fin locations proved to be a very satisfactory method by which to produce

good quality marks, enabling individual identification for at least 6 months. All positions used in this study were equally good, and the mark quality appeared initially quite robust to various growth conditions. Remarking was very easy and good marks could be maintained this way for a seemingly unlimited time. When dots were not remarked, fading occurred in a fairly regular and predictable way. The decrease in mark quality for periods longer than 6 months seemed to be mostly influenced by growth rate, higher decreases being observed after periods of highest growth, but independently of the initial mark quality or of the number of times it was remarked. No acceleration of fading with time was observed. Under most growth conditions, jet injection would probably be satisfactory after 1 year, only partly satisfactory after 1.5 year, and unsatisfactory after 2 years, for this sort of study where every piece of information must remain readable to secure individual identification. In studies with less stringent requirements, for example, if a 10% to 20% rate of mark loss is acceptable, then Alcian Blue jet injection would certainly remain satisfactory for longer periods. There were few mortalities and few problems associated with this technique, even when used on very small fish. Among significant improvements to this technique would be: the modification of the jet inoculator nozzle allowing a more precise positioning, the automation of the hand driven pressure system, and ways to control the pressure of the jet as well as the amount of liquid injected (if one does not want to be turned into a Smurf). If a red/orange pigment, behaving as well as Alcian Blue, could be found, the number of individual combinations would be greatly increased.

Cold-branding proved to be quite satisfactory to produce good

quality marks for 6 months. A lower brand quality was observed after initial periods of high growth. Rebranding was easy because of the simple design of the symbol used in this study. Cold-branding was used in optimal conditions as defined by a preliminary experiment. Only the best symbol, a single horizontal bar, and the best body location, the anterior dorsal area just above the lateral line, were used. Even under these fairly restrictive conditions, cold brand quality was found to be slightly inferior to that of jet injected dots, 6 months after marking. Cold brands appeared more resistant to fading than jet injected dots and would probably still be satisfactory after 1 year, 1.5 year, and possibly after 2 years. However, cold brand legibility appeared to be linked to 2 independent events: a darker coloration due to an increased number of melanin containing cells, and an increased iridescence of the brand area that can be detected by varying the light incidence when the regenerated scales are fairly large. The asynchrony between these 2 events led to an annoying variability and unpredictability of the cold brand fading behaviour that tended to offset the advantages associated with a better average resistance to fading.

This combined system using jet injections, adipose clipping and cold-branding proved to be successful for the recognition of individual salmon of various sizes for at least 6 months. Adipose clipping, cold-branding and jet injection on 2 caudal fin locations could be successfully used for family identification on very small fish (2 g-40 g). With bigger fish, (24 g-270 g), 6 other fin locations could be safely used for individual identification and a seventh one could be used with fish over 150-200 g. If the dorsal fin is present, 2 or 3 more locations can probably be used, even on small fish. The only major

drawback to the use of this system is that it is time-consuming. In some cases, reading and remarking the different pieces of information could take several minutes per fish.

CHAPTER II. SURVIVAL, SEX RATIO, AND MATURATION PATTERNS.

1. Introduction

As developed in the General Introduction, Atlantic salmon maturation patterns are variable and complex (Saunders and Schom, 1985), and important from an economic point of view. The sea age at first maturity is a characteristic of great economic importance for both the management of natural population (Saunders, 1986) and aquaculture production (Naevdal, 1983).

Part of the difficulty in dealing with this problem of sea age at first maturity among natural or sea-ranched populations is that little is known about the life-history of salmon at sea. Cage rearing operations offer an unusual opportunity to document survival, growth and sexual maturation (Saunders et al., 1983), and indeed, much of the present knowledge about salmon at sea came from such cage reared salmon studies, mostly in Norway.

Male and female salmon have different maturation histories (Gardner, 1976); however, sexes can be externally differentiated only around the time of sexual maturity. Furthermore, it is generally not possible to tell from an adult salmon what might have been its previous maturation history, particularly with regards to precocious maturation in freshwater. Hence, relationships between successive maturation episodes are still largely conjectural, or based on group means.

This chapter will present an overview of the experimental method through which 3 cohorts of salmon were documented from spawning to grilse maturation, the use of individual identification allowing the

compilation of maturation patterns and the analysis of relationships between different maturation episodes. Survival, particularly in relation to maturation, will be presented as well.

2. Material and methods

2.1 Overview of the experimental design

Three groups of Atlantic salmon were used in this study. Two main groups consisted of 1-year-old smolts and 2-year-old smolts of the 1981 spawning year class. They will be referred as 1Y81 and 2Y81 respectively. A third small group (2Y80) consisted of a few 2-year-old smolts from the 1980 spawning year class.

Most of the broodstock fish (parent-fish of the 1980 and 1981 year class fish) were held in two places, located along the Bay of Fundy shore, New Brunswick, and matings were performed there. The stock origin of the parent fish, as well as information on the family created, will be described in Chapter III section 2. Late in the fall of 1980 and 1981, shortly after fertilisation, the eggs were transferred to the IMA Aquatic Farming hatchery. IMA Aquatic Farming Ltd is a private enterprise located in Argyle Head, Nova Scotia, that started a salmonid commercial breeding program in 1980. The fish were held in the hatchery facilities until May 1983, when IMA Aquatic Farming decided to terminate the breeding program. The fish ready to smoltify (the 1Y81 and 2Y80 fish) were transferred at that time to the Dalhousie University Aquatron seawater facilities. The fish which were not yet smolt (the 2Y81 fish) were transferred to the Fraser's Mill hatchery (N.S. Department of Fisheries, St Andrews, N.S.) and reared in freshwater one more year, until June 1984, when they were transferred to the Dalhousie University

Aquatron seawater facilities. The experiments were terminated when the fish reached the grilse stage; in December 1984 for the 1Y81 and 2Y80 fish, and in December 1985 for the 2Y81 fish. Figure 2.1 provides a general synopsis of the experimental design. Figure 3.1 (Chapter III) shows the geographic locations of the different rearing places. From the hatching time to the termination of the experiments, all fish were fed ad libitum at all times.

All fish were family and individually identified. The family and individual marking techniques have been described in Chapter I. The 2Y80 fish were the ones on which the preliminary marking work (cf. Chapter I sect. 2) was performed. The 1Y81 and 2Y81 fish were the fish on which the final marking technique was used (cf. Chapter I sect. 3) and for which marking results were given (cf. Chapter I sect. 4)

The 1Y81 fish were followed individually during 16 months of growth in seawater (Aug. 83 to Dec. 84). The 2Y81 fish were followed individually during 25 months of growth, in freshwater (7 months) and in seawater (18 months) (Fig. 2.1).

The 2Y80 fish were family and individually marked before the 1981 year class fish (Fig. 2.1). As problems with the marking technique that had been originally used (cf. Chapter I sect. 2) resulted in considerable losses in both family and individual identifications, a second individual marking was performed in August 1983.

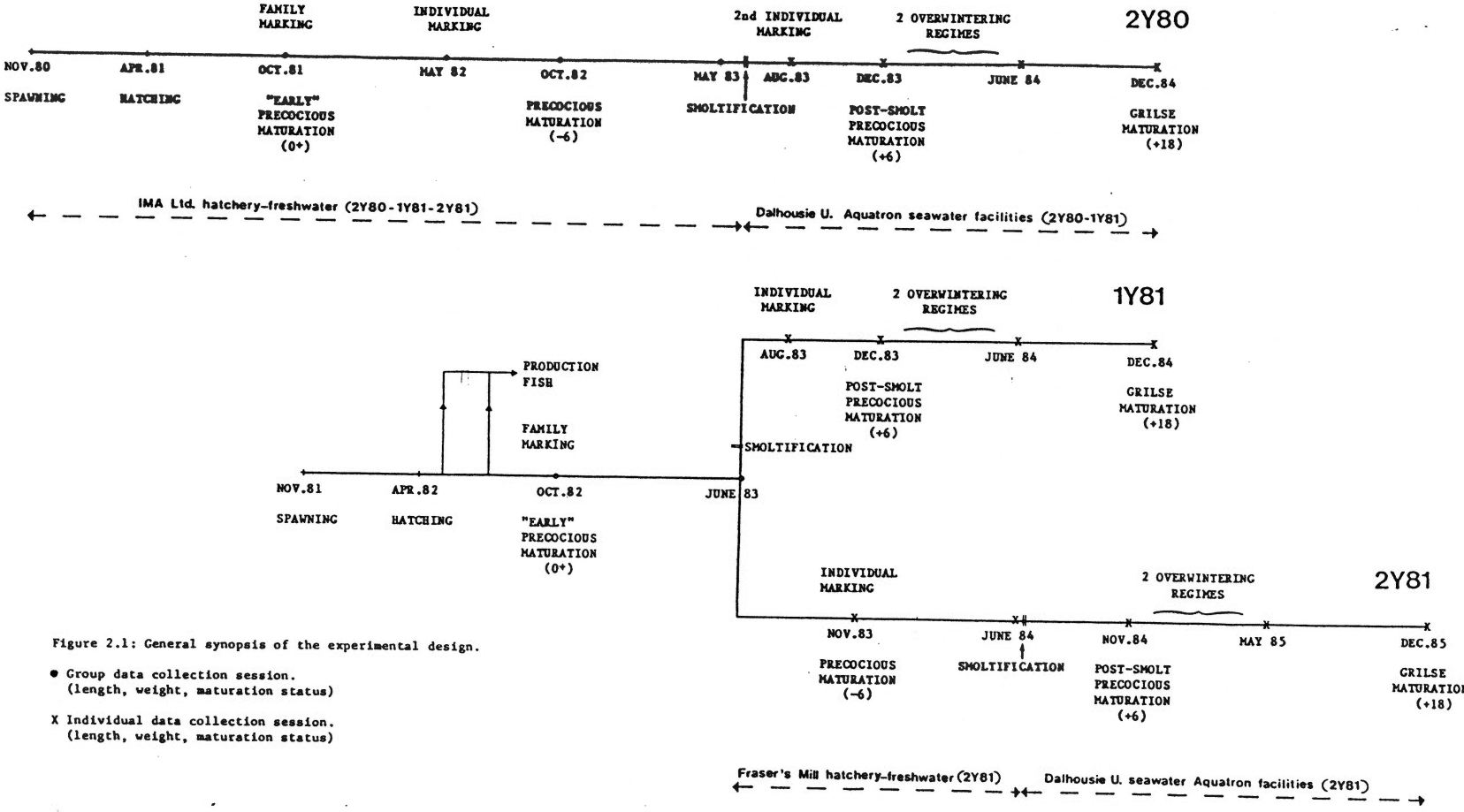

Figure 2.1: General synopsis of the experimental design.

- ● Group data collection session. (length, weight, maturation status)
- X Individual data collection session. (length, weight, maturation status)

The 2Y80 were then followed individually for 16 months of growth in seawater, along with the 1Y81 fish (Fig. 2.1). However, family identities were completely lost for the 2Y80 group.

In this study, the data collected before the second individual marking have been used as group data only. No attempt has been made to use them as individual data.

In each group, individual data concerning length, weight and maturation status were collected approximately every 6 months from individual marking time to the end of the experiment (Fig. 2.1).

Maturation status was determined externally by assessing characteristics such as the fish colouration, the skin thickness, the overall fish shape, the aspect of the genital area, the presence of kype or groove on large male fish. In addition, the emission of seminal fluid or eggs when exerting a gentle abdominal pressure was checked on all fish that were presumed mature. No attempt was made to verify if all males maturations were complete and fully functional in a physiological sense, but it should be noted that the great majority of presumed mature males did produce a significant amount of seminal fluid, even in the case of post-smolt precocious maturation. Sex was determined either externally for mature fish, or by gonad inspection after sacrifice, for fish still immature at the end of the experiment. Unfortunately, immature fish of the 1Y81 cohort could not be all sacrificed in December 1984 and a significant proportion of these fish are thus of unknown sex.

2.2 Terminology used

The terminology used to refer to the 3 cohorts has already been

defined (1Y81, 2Y81, 2Y80).

The periods of growth in seawater, 18 months from smoltification to grilse maturation time, comprised 3 subperiods, separated by individual data collection sessions (Fig. 2.1). For the sake of convenience, these 3 subperiods have been named first summer (in seawater), winter (in seawater), second summer (in seawater).

For the 1Y81 and 2Y80 cohorts, these were the same: first summer = Aug. 83 to Dec. 83; winter = Dec. 83 to June 84; second summer = June 84 to Dec. 84. (Fig. 2.1).

For the 2Y81, these subperiods were: first summer = June 84 to Nov. 84; winter = Nov. 84 to May 85; second summer = May 85 to Dec. 85. (Fig. 2.1).

Four different maturation episodes were covered in the present study:

(1) "Early" precocious maturation (0+), refers to the precocious maturation that was observed in the first fall after spawning, in freshwater, when the fish are 0+ parr. (Fig. 2.1).
To facilitate their recognition, the three other maturation episodes are referred to by the approximate number of months that have elapsed since or before smoltification.

(2) Precocious maturation (-6) refers to maturation observed 6 months before smoltification, ie. at the parr stage in freshwater, when the fish are 1+ parr. This maturation episode could be observed <u>only</u> on 2-year-old smolts (2Y80 and 2Y81), since the 1Y81 fish had been transferred to seawater by this time (Fig. 2.1).

(3) Post-smolt precocious maturation (+6) refers to maturation

observed 6 months after smoltification. As noted by Allen and Ritter (1976), the term "pre-grilse" would seem more appropriate to describe these fish, but the term post-smolt precocious mature fish has been used most often in the few references dealing with this phenomenon and was hence used here.
(4) Grilse maturation (+18) refers to maturation observed 18 months after smoltification. Hence, "grilse" in this study is equivalent to 1 sea-winter fish.

2.3 Freshwater husbandry

- November 1980-May 1983: IMA Aquatic Farming hatchery.

For both year classes 1980 and 1981, from spawning (in November) to family marking (the following October), all families were kept in separate small tanks. In October, fish bigger than 2g were selected for family marking, then pooled together in several large tanks after marking.

Family marked fish of the 1981 year class were graded by size, before pooling in October 1982, to minimize competitive interaction and, hopefully, to increase the proportion of future 1-year-old smolts. At this time, all family marked fish of this year class (1981) were checked for "early" precocious maturation (0+) (Fig. 2.1).

From hatching time (April 1982) to family marking time (October 1982), densities in the small family tanks were adjusted to avoid overcrowding and possible stunting of the future family marked fish. In May and again in July 1982, "surplus" fish were taken from the family tanks and pooled in two large tanks. These "production" fish beared no family mark, but were later adipose clipped according to the source of

parent-fish (see Chapter III sect. 2).

In April 1983, mean length and weight were estimated for each families. In May and in June 1983, all family marked fish of the 1981 year class were sorted out as 1-year-old smolts or future 2-year-old smolts. Smolt sorting was performed on the basis of size and external appearance.

The few survivors of the 1980 year class were, from May 1982 to June 1983, kept aside from the 1981 year class fish. In May 1983, they were all smolts. In June 1983, all smolts (1Y81 and 2Y80) were transferred to the Dalhousie University Aquatron facilities. The non smolts (2Y81) were transferred to the Fraser's Mill Hatchery (N.S. Dept. of Fisheries, St Andrews N.S.) to be reared one more year in freshwater before smoltification.

During this whole freshwater rearing period, November 1980-June 1983, all fish were submitted to a natural photoperiod regime. To promote growth, a well water supplement was added to the normal ambient water, and a heat pump was used, and this both to increase low temperature during winter and to decrease high temperature during summer.

- June 1983-June 1984: Fraser's Mill hatchery, N.S. Dept. of Fisheries.

The 2Y81 fish were reared in a large outside concrete pond from June 1983 to June 1984. They were mixed with a large number of "production fish" (fish of the same stocks that had not been family marked). In November 1983, the 2Y81 fish were sorted out from the production fish, individually marked, checked for precocious maturation (-6) and put back with the production fish. During the winter (December/January to March/April), the water temperature was very low

and feeding was much reduced because of the ice covering the outside pond. In June 1984, individually marked fish were again sorted out from the production fish by the Hatchery staff and they were transferred to the Dalhousie Aquatron facilities.

2.4 Saltwater husbandry

During the first summer and the following winter in seawater, all fish (2Y80, 1Y81 and 2Y81) were reared in several square tanks (Fig. 2.2 A,B). Each unit consisted of a tank of aproximately 1.8 m3 (1.5m x 1.5m x 0.8m) with a sheet of fiberglass inside defining a cylindric volume of seawater (1.4m3) available to the salmon (Fig. 2.2 B). The water input flow was directed to create a slow rotating movement of the water (Fig. 2.2 B). Water drainage was located on the bottom center of the tank, with an articulated outside pipe allowing the control of the water level as well as the rapid flushing of waste (Fig. 2.2 A). Due to the water rotating movement, waste tended to accumulate near the drain and, to a lesser extent, in the four corners outside the fiberglass sheet, thus allowing a convenient waste flushing and cleaning without much interaction with the salmon. During the second summer in seawater, the fish were transferred to a 40m3 square net pen (4m x 4m x 2.5m) floating in the large Dalhousie Aquatron pool tank (684 m3) (Fig. 2.3). Waste cleaning was performed every 10 days (minimum) by moving the cage and sucking the waste accumulated on the bottom with a water vacuum cleaner.

Upon their arrival at Dalhousie University in June 1983, the 1Y81 and 2Y80 fish were inadvertantly submitted to a 24 hour constant daylight photoperiod regime until mid-August when the situation was

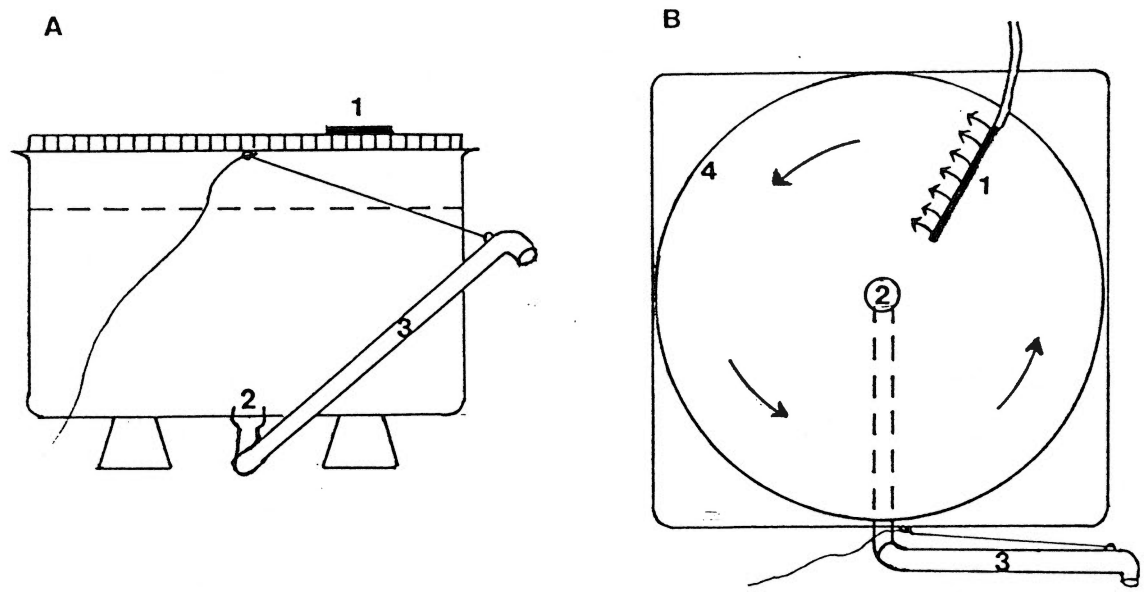

Fig. 2.2: Tank unit. A Side view B Top view.

1 - water input
2 - water drainage
3 - articulated outside pipe
4 - fiberglass sheet

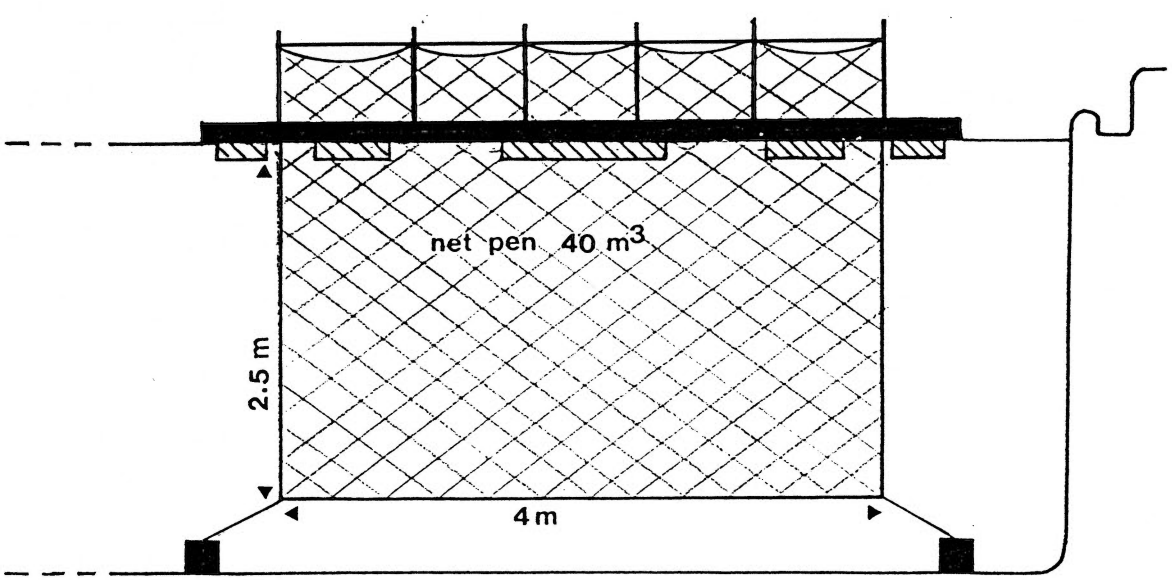

Fig. 2.3: Net pen ($40m^3$) floating in the Aquatron pool tank ($684m^3$)

corrected. From then on, the artificial photoperiod regime was adjusted every 10 to 15 days to match the natural photoperiod regime prevalent in Halifax, N.S., until the end of the seawater experiment in December 1985. The seawater used for both the tank units and the net pen was pumped from the North West Arm and filtered. Hence, the Dalhousie Aquatron seawater physico-chemical characteristics closely followed the natural variations of the seawater characteristics at the pumping location.

During the winter periods, the fish were divided between two overwintering temperature regimes. Ambient tanks were supplied with normal ambient seawater and heated tanks with seawater warmed through a heat exchanger. Heating was adjusted so that warmed seawater temperature varied between 5 °C and 6 °C during the winter periods. During the remaining rearing periods (first summer and second summer of growth in seawater) all fish were submitted to the same ambient temperature regime. Additional specific information about the temperature regimes, fish densities, and tank replication will be given in Chapter IV section 2., when the effects of these environmental parameters will be analysed.

2.5 Data treatment.

Group data were used for all results related to maturation episodes observed before individual marking (Fig. 2.1). For results related to episodes observed <u>after</u> individual marking, only the fish with complete data sets, i. e. the fish for which grilse maturation (+18) status could be assessed have been included. These fish consisted of the fish that were alive at the end of the experiments, and the fish that had died within 4 months of the end of the experiments, since their maturation

status could be assessed by gonads inspection. All earlier mortalities among individually marked fish have been excluded. As mortality among individually marked fish was fairly low (see sect. 3.1), the exclusion of these data is not likely to have affected the validity of the results.

The X^2 (chi-square) test was used to compare observed percentages either with other observed percentages or with theoretically expected percentages. When X^2 cells had expected frequencies lower than 5 but higher than 3, the Yates' corrected X^2 was used. If an expected cell frequency was lower than 3, the exact Fisher's probability was computed (Schwartz, 1969). One-way analysis of variance was used for comparisons of means between several groups (Nie et al., 1975)

3. Results.

3.1 Mortality.

During early rearing at the IMA Aquatic Farming hatchery, both the 1980 and 1981 year class fish experienced levels of mortality in the range usually seen in Atlantic salmon hatcheries. From spawning to 1-year-old smolts sorting time (Nov. 80 to May 82 for 1980 year class, Nov. 81 to May 83 for 1981 year class) (Fig. 2.1), mortality was most notable around hatching ("egg quality" problems), first feeding, and before family marking (overcrowding problems), in addition to the typical mortality due to water supply problems.

During their second year of freshwater growth (May 82 to May 83), the 2Y80 fish experienced a high mortality (Table 2.1). A well water supplement was used in combination with water recirculation in the spring of 1982, which resulted in high iron level build up in the water.

Iron toxicity became apparent and fungus infections rapidly spread among the weakened fish. Mortality remained high during the following summer and then subsided in the winter (Table 2.1). Yet, some more fish were lost when they were temporarily mixed with similarly sized rainbow trout, probably because of stress.

After individual marking, the initial mortality in the 2Y81 cohort was high, since only 245 fish were received in June 1984 out of the 319 fish marked in November 1983 at the Fraser's Mill Hatchery (Table 2.2). This high mortality is probably linked to the harsh environmental conditions experienced by the fish during the winter at the Fraser's Mill Hatchery (cf. sect. 2.3). It is also possible that some marked fish of this cohort were missed by the hatchery staff when sorting them out from the production fish (cf. sect. 2.3). This initial mortality was found to be independent from precocious maturation (-6). The mortality rate among the precocious mature males (-6) was not significantly different from the mortality rate among non-precocious fish (29.0% versus 23.3% X^2=.9 NS). This mortality was size dependant. The fish that died (mean length 18.8 cm) were significantly smaller than the fish that survived (mean length 20.4 cm) (F ratio=23.3 $p<0.01\%$).

In the 3 cohorts, mortalities were low while the fish were kept in the Dalhousie Aquatron seawater facilities (cf. Chapter I sect. 4.1, Table 2.1 and Table 2.2). Complete data sets were obtained for 58 out of the 63 2Y80 fish marked in August 1983; 229 out of the 238 1Y81 fish marked in August 1983; and 227 out of the 245 2Y81 fish received in June 1984. Mortality during seawater rearing was unrelated to maturation status.

Table 2.1: Mortality rate after individual marking in the 2Y80 and 1Y81 cohorts.

Date of data collection session	Location	2Y80 Number of fish alive	2Y80 Mortality rate (%)	1Y81 Number of fish alive	1Y81 Mortality rate (%)
May 82	IMA Ltd hatchery	569			
			77%		
Oct.82		130			
			48%		
May83		68			
			7%		
Aug.83	Dalhousie Aquatron	63		238	
			5%		3%
Dec.83		60		231	
			3%		1%
June 84		58		229	
			2%		6%
Dec.84		57		216	

Table 2.2: Mortality rate after individual marking in the 2Y81 cohort.

Date of data collection session	Location	2Y81 Number of fish alive	2Y81 Mortality rate (%)
Nov.83	Fraser's Mill hatchery	319	
			23%
June 84	Dalhousie Aquatron	245	
			2%
Nov.84		239	
			4%
May 85		230	
			3%
Dec.85		222	

3.2 Sex ratio of the different cohorts

The exact sex ratio of the 1Y81 cohort is not known. 93 fish are of undertermined sex because they could not be sacrified in December 1984 (Table 2.3 and see sect. 2.1). These 93 fish belonged to a group of 160 fish (93 fish of unknown sex, 20 ♂ and 47 ♀) that never experienced maturation during the experiment. Since males are prone to mature earlier than females, this group of "never mature" fish is likely to be composed of more females than males. Under the assumption that the 67 fish for which the sex is known (20 ♂, 47 ♀) is a representative sample of this entire "never mature" group, then these 93 fish can be estimated to consist of about 28 ♂ and 65 ♀. Under this hypothesis, overall sex ratio of the 1Y81 cohort can be estimated to be around 49% ♂/51% ♀, which is quite similar to the sex ratio observed for the 2Y81 cohort (Table 2.3). Both sex ratio are not significantly different from a 50%/50% sex ratio.

In contrast, sex ratio of the 2Y80 cohort is significantly biased towards male predominance (Table 2.3).

3.3 Maturation patterns

In October 1982, "early" precocious maturation (0+) was checked on all family marked fish of the 1981 year class (future 1Y81 and 2Y81 fish). No precocious mature parr (0+) were found. Similarly, in October 1981, "early" precocious maturation (0+) was not noticed among the family marked fish of the 1980 year class, although maturation was not extensively checked at that time.

Some mature fish were observed at all other possible maturation episodes. Table 2.4 summarises the maturation patterns that were observed for the 3 cohorts.

Table 2.3: Sex ratio of the different cohorts.

Cohort (nb. of fish)	2Y80 (58)	1Y81 (229)	2Y81 (227)
Males (percent. of cohort)	41 ♂ (70.6%)	84+28(1)=112 ♂ (49%)	110 ♂ (48.5%)
Unknown sex fish (estimated nb. of males and females)	/ /	93 (28 ♂, 65 ♀)(1)	/ /
Females (percent. of cohort)	17 ♀ (29.4%)	52+65(1)=117 ♀ (51%)	117 ♀ (51.5%)
Comparison to 50/50 ratio	X2=9.93 1df (p 1%)	X2=0.11 1df (NS)	X2=0.21 1df (NS)

(1): Estimated number of males and females in the unknown sex category (see text).

Table 2.4: Observed maturation patterns among the 3 cohorts.

Cohort	2Y80	1Y81	2Y81
Schematic representation of maturation patterns	S(M1,M2,M3):n (1)	S(M2,M3):n (1)	S(M1,M2,M3):n (1)
Female's maturation patterns	♀(0,0,0):12 fish	♀(0,0):112 fish(2)	♀(0,0,0):74 fish
	♀(0,0,+18):5 fish	♀(0,+18):5 fish	♀(0,0,+18):43 fish
	♂(?,0,0):18 fish	♂(0,0):48 fish(3)	♂(0,0,0):25 fish
	♂(?,0,+18):15fish	♂(0,+18):34 fish	♂(0,0,+18):33 fish
	♂(?,+6,+18):2fish	♂(+6,+18):24 fish	♂(-6,+6,+18):2 fish
Male's maturation patterns	♂(?,+6,0):6fish	♂(+6,0):6 fish	♂(0,+6,0):3 fish
			♂(-6,+6,0):1 fish
			♂(-6,+6,0):1 fish
			♂(-6,0,+18):28 fish
			♂(-6,0,0):18 fish
Total number	58 fish	229 fish	227 fish

(1) S=sex: ?=unknown sex.
M1=maturation status at precocious maturation (-6) episode:
-6=mature, 0=immature, ?=maturation status unknown.

M2=maturation status at post-smolt precocious maturation (+6) episode: +6=mature, 0=immature.

M3=maturation status at grilse maturation (+18) episode:
+18=mature, 0=immature.

n=number of fish showing this maturation pattern.

(2) including the estimated 65 ♀ (see Table 2.3)
(3) including the estimated 28 ♂ (see Table 2.3)

Since individual identification was available at all possible maturation episodes for the 1Y81 and 2Y81 fish, Table 2.4 covers the complete range of maturation patterns that existed for these 2 cohorts. In contrast, Table 2.4 gives only a partial picture of the range of maturation patterns for the 2Y80 fish, since individual identification was available only after the precocious maturation (-6) episode.

Mature females were observed only at the grilse maturation (+18) episodes for the 3 cohorts. Male maturation was observed with varying rates at all possible maturation episodes. A surprisingly wide variety of patterns was observed, going, in the case of the 2Y81 cohort for instance, from males that matured three times consecutively (2 cases) to males that never matured (25 cases). Almost every type of intermediary pattern between these two extremes was observed (Table 2.4).

3.4 Comparison of precocious maturation (-6), post-smolt precocious maturation (+6) , and grilse maturation (+18) between the three cohorts

Fairly high precocious maturation (-6) rates were observed in both the 2Y80 and the 2Y81 cohorts (Table 2.5). The rate in the 2Y80 cohort was significantly higher than in the 2Y81 cohort. However, this appears to be mostly due to the 2Y80 cohort sex ratio imbalance. Both rates are not significantly different when calculated among the male population and not among the entire population.

Post-smolt precocious maturation (+6) was observed in all 3 cohorts (Table 2.6). Whether calculated among the entire population or among the males only, post-smolt precocious maturation (+6) rates of the 2Y80 and 1Y81 fish were not significantly different from one another, but the rate among the 2Y81 fish was significantly lower than either the 2Y80 or

the 1Y81 rates (Table 2.6). Post-smolt maturation (+6) rates (Table 2.6) were lower than either precocious maturation (-6) rates (Table 2.5) or grilse maturation (+18) rates (Table 2.7) in all cohorts.

Overall rates of grilse maturation (+18) were significantly different between the 3 cohorts, the rate observed in the 1Y81 fish being the lowest (Table 2.7). However, when looking at sex specific rates of grilse maturation (+18), it appeared that the cohorts differed mostly by the rate among females, this rate being particularly low among the 1Y81 cohort (Table 2.7), and significantly less than among the 2Y80 and the 2Y81 cohorts. In the 3 cohorts, the rate of grilse maturation (+18) among females was lower than among males. In the 2Y80 cohort, this difference was not significant, but it is probably a consequence of the small size of the cohort.

To summarize, both 2-year-old smolt cohorts (2Y80 and 2Y81) presented similar results: similar rates of precocious maturation (-6) among males, similar rates of grilse maturation (+18) among males and among females, with the exception of the rate of post-smolt precocious maturation (+6) which was significantly less in the 2Y81 cohort. The 1-year-old smolt cohort (1Y81) differed most notably from 2-year-old smolt cohorts by a very low rate of grilse maturation (+18) among females, and also, by the absence of precocious maturation in freshwater, since no fish were "early" precocious mature (0+).

Table 2.5: Comparison of precocious maturation (-6) rate between the 2Y80 and 2Y81 cohorts, calculated among the total population and among the males only. Absolute frequencies are specified between brackets.

Cohort	2Y80	2Y81	Between cohorts comparison
date observed	Oct.82	Nov.83	of rates
Precocious maturation (-6) rate among total population	38.5% (50/130)	21.5% (49/227)	X^2=11.83 1df (p<0.1%)
Precocious maturation (-6) rate among males only	54.5% (50/92(1))	44.5% (49/110)	X2=2.0 1df (NS)

(1) Estimated number of males among the 130 fish of the 2Y80 cohort in October 1982, based on the sex ratio of the 58 fish alive in August 1983 (see Table 2.3).

Table 2.6: Comparison of post-smolt precocious maturation (+6) rates between the three cohorts, calculated among the total population and among the males only. Absolute frequencies are specified between brackets.

Cohort	2Y80	1Y81	2Y81	Between cohorts comparisons
Date observed	Dec.83	Dec.83	Nov.84	of rates (2)
Post-smolt precocious maturation (+6) rate among total population	13.8% (8/58)	13.1% (30/229)	2.6% (6/227)	C1: X^2=18.0 2df (p<0.1%) C2: X^2= 0.0 1df (NS) C3: X^2=10.0 1df (p<1%) C4: X^2=17.4 1df (p<0.1%)
Post-smolt precocious maturation (+6) rate among males only	19.5% (8/41)	26.8% (30/112(1))	5.5% (6/110)	C1: X^2=18.0 2df (p<0.1%) C2: X^2= 0.9 1df (NS) C3: X^2= 5.5 1df (p<5%) C4: X^2=18.5 1df (p<0.1%)

(1): Estimated total number of males in the 1Y81 cohort (see Table 2.3).

(2): C1: Overall comparison between the three cohorts.
C2: Comparison of rates between the 2Y80 and 1Y81 cohorts.
C3: Comparison of rates between the 2Y80 and 2Y81 cohorts. (Yate's corrected X^2)
C4: Comparison of rates between the 1Y81 and 2Y81 cohorts.

Table 2.7: Comparison of grilse maturation (+18) rates between the three cohorts, calculated among the total population and among the males only. Comparison of rates between sexes, within the three cohorts. Absolute frequencies are specified between brackets.

Cohort	2Y80	1Y81	2Y81	Between cohorts comparisons of rates (b)
Date observed	Dec.84	Dec.84	Dec.85	
Grilse maturation (+18) rate among total population	37.9% (22/58)	27.5% (63/229)	46.7% (106/227)	C1: X^2=18.0 2df (p<0.1%) C2: X^2= 2.4 1df (NS) C3: X^2= 1.4 1df (NS) C4: X^2=18.2 1df (p<0.1%)
Grilse maturation (+18) rate among males only	41.5% (17/41)	51.8% (58/112[a])	57.3% (63/110)	C1: X^2= 3.0 2df (NS) C2: / C3: / C4: /
Grilse maturation (+18) rate among females only	29.4% (5/17)	4.2% (5/117[a])	36.8% (43/117)	C1: X^2=37.8 2df (p<0.1%) C2: Fisher's exact p<1% C3: X^2= 0.4 1df (NS) C4: X^2=37.8 1df (p<0.1%)
Within cohorts between sexes rate comparison	X^2=0.3 1df (NS)	X^2=64.8 1df (p<0.1%)	X^2=8.3 1df (p<0.3%)	/

(a): Estimated total number of males and females in the 1Y81 cohort (see Table 2.3).

(b): C1: Overall comparison between the three cohorts.
C2: Comparison of rates between the 2Y80 and 1Y81 cohorts.
C3: Comparison of rates between the 2Y80 and 2Y81 cohorts.
C4: Comparison of rates between the 1Y81 and 2Y81 cohorts.

3.5 Relationships between the different maturation episodes

The relationships between the different maturation episodes were evaluated among the males only since post-smolt precocious maturation (+6) or precocious maturation (-6) was not observed among females.

In the 1Y81 cohort, the rate of grilse maturation (+18) among the males that had been post-smolt precocious mature (+6) was significantly higher than among the males which were not post-smolt precocious mature (80% versus 41.5%) (Table 2.8). This seems to indicate a positive association between both these maturation episodes. For the 2Y80 and the 2Y81 cohorts, the opposite tendency was observed, but differences were non significant, and the small number of post-smolt precocious mature (+6) males in both these cohorts did not allow to draw any meaningful conclusion (Table 2.8).

In contrast to post-smolt precocious maturation (+6), there were no association between precocious maturation (-6) and grilse maturation (+18). The rate of grilse maturation (+18) among precocious males (-6) was not significantly different from the rate among non-precocious males in the 2Y81 cohort (Table 2.9).

There did not appear to be any link between precocious maturation (-6) and post-smolt precocious maturation (+6) in the 2Y81 cohort (Table 2.10). Unfortunately, the number of cases is too low to really draw any meaningfull conclusion. This could not be verified either among the 2Y80 cohort, because of the absence of individual identification at the precocious maturation (-6) episode, or among the 1Y81 cohort, since there were no precocious maturation episode in this cohort (cf. sect. 2.2).

Table 2.8: Independance between grilse maturation (+18) and post-smolt precocious maturation (+6), in the three cohorts. Absolute frequencies are specified between brackets (table compiled for the males only).

Cohort	2Y80	1Y81	2Y81
Grilse maturation (+18) rate among post-smolt precocious males (+6)	25% (2/8)	80% (24/30)	33.5% (2/6)
Grilse maturation (+18) rate among non post-smolt precocious males	45.5% (15/33)	41.5% (34/82(a))	58.5% (61/104)
Within cohort test of independance between post-smolt precocious maturation (+6) and grilse maturation (+18)	X^2=0.4 (b) 1 df (NS)	X^2=13.2 1 df ($p<0.1\%$)	X^2=0.6 (b) 1 df (NS)

(a): Estimated total number of non post-smolt precocious males (see Table 2.3).

(b): Yate's corrected X^2

Table 2.9: Independance between grilse maturation (+18) and precocious maturation (-6), in the 2Y81 cohort. Absolute frequencies are specified between brackets (table compiled for the males only).

Cohort	2Y81
Grilse maturation (+18) rate among precocious mature males (-6)	61% (30/49)
Grilse maturation (+18) rate among non precocious males	54% (33/61)
Test of independance between grilse maturation (+18) and precocious maturation (-6)	X^2=0.6 1 df (NS)

Table 2.10: Independance between post-smolt precocious maturation (+6) and precocious maturation (-6), in the 2Y81 cohort. Absolute frequencies are specified between brackets (table compiled for the males only).

Cohort	2Y81
Post-smolt precocious (+6) maturation rate among precocious (-6) mature males	6.1% (3/49)
Post-smolt precocious (+6) maturation rate among non precocious males	4.9% (3/61)
Test of independance between post-smolt precocious (+6) maturation and precocious maturation (-6)	X^2=0 (a) 1 df (NS)

(a): Yates' corrected X^2

4. Discussion

Unbalanced sex ratios are commonly observed in natural smolt runs and are generally explained by an increased mortality and a delayed smoltification associated with male precocious maturation (Mitans, 1973; Chadwick, 1978; Dalley et al., 1983; Gibson, 1983; Myers, 1984; 1986). Precocious males among hatchery reared salmon do not generally experience an increased mortality and are known to develop into viable smolts, as they did in this present study (Thorpe and Morgan, 1980; Saunders et al., 1982). Nevertheless, Saunders et al. (1982) showed that precocious maturation at age 0+ can prevent smoltification at age 1+, and hence produce unbalanced sex ratio among the 1-year-old and 2-year-old smolts reared in hatcheries. In contrast, under hatchery conditions, precocious maturation at age 1+ does not usually prevent smoltification at age 2+ (Saunders et al., 1982; Naevdal, 1983), and hence would not induce an unbalanced sex ratio. Because precocious maturation at age 0+ was not detected among the 1981 year class fish (1Y81 and 2Y81), the balanced sex ratio of both these cohorts is consistent with these observations.

The predominance of males in the 2Y80 cohort is more surprising. It is thought to be a random sampling effect due to the small size of this cohort, since precocious maturation at age 0+ was not noticed among the 1980 year class fish (2Y80) (cf. sect. 3.3), and since mortality appears sex independent when no maturation is involved (Myers, 1984).

No link was found between maturation and mortality, whether in freshwater or in seawater. The precocious mature males (-6) in the 2Y81 cohort survived as well as the immature fish under the harsh winter

conditions at the Fraser's Mill hatchery following this maturation episode. Similarly, the survival of post-smolt mature males (+6) was as high as that of immature fish in the Dalhousie Aquatron seawater facilities. Naevdal et al. (1978b) noted that the death rates for mature and immature salmon were not as different as claimed by the fish farmers, and Møller et al. (1976) made the same observation about rainbow trout reared in seawater. Thus, there appears to be a considerable contrast between natural populations and populations under cultivation, in respect to maturation causing higher mortality. The low survival of mature parr in natural population has been attributed to high overwintering mortality caused by the reduction in lipid reserves concomitant with precocious maturation (Leyzerovich, 1973; Mitans, 1973; Dalley et al., 1983). Hutchings and Myers (1987) also identified anadromous male agression as contributing significantly to mature parr mortality in natural populations. This could partly explain the aforementioned contrast between natural and hatchery populations, in respect to precocious maturation causing high mortality.

Precocious maturation at age 0+ is not very common and has been observed among males only. It has been reported by Bagliniere and Maisse (1985) among natural populations in Britanny (France) where good growing conditions prevail, and as well among hatchery fish reared under particularly favourable growth conditions (heated water in winter) (Bailey et al., 1980; Saunders et al., 1982). Early hatching and early first feeding is likely to promote male maturation by their first autumn (Saunders et al., 1982; Saunders, 1986). In this study, some heating was provided in the first winter (cf. sect. 2.3). Hatching occurred around April and first feeding around May for both year class fish, but

this was apparently not sufficient to promote "early" precocious maturation (0+). In this study, the 0+ parr (mean length 7.9 cm in Oct. 81 for the 1980 year class, 7.3 cm in Oct. 82 for the 1981 year class) were considerably smaller than the 0+ parr reported in Bailey et al. (1980) (mean length around 15.5 cm in Nov.) or in Bagliniere and Maisse (1985) (mean length around 10.5 cm in Oct.), when 0+ maturation was observed.

Atlantic salmon are known to show a remarkable plasticity in several aspects of their life history (Saunders and Schom, 1985; Saunders, 1986), but the wide variety of maturation patterns observed in this study was nevertheless quite surprising. Male precocious maturation (-6) at age 1+, as reported in the present study, is very common in natural as well as in hatchery populations (Jones, 1959; Leyzerovich, 1973; Mitans, 1973; Sutterlin et al., 1978; Saunders et al., 1982; Dalley et al., 1983; Glebe and Saunders, 1986). Among normally anadromous populations, female precocious maturation in freshwater at age 1+ or older, is much rarer and has seldom been reported (Prouzet, 1981; Bagliniere and Maisse, 1985).

In this study, post-smolt precocious mature (+6) males were found in all 3 cohorts. This maturation episode has been rarely reported in the literature and appears uncommon in natural populations as well as under cultivation conditions (Shearer, 1963; Saunders and Henderson, 1965; Murray, 1968; Naevdal et al., 1975; 1978a; Sutterlin et al., 1978; Lundqvist and Fridberg, 1982). Most post-smolt mature (+6) fish described in these studies were males but Sutterlin et al. (1978) reported mature females as well. Evropeytseva (1960) asserted that precocious sexual developement was incompatible with smoltification.

Large male parr that are often observed in Nordic rivers would be explained by repeated precocious maturation indefinitely postponing the smoltification (Gibson, 1983). Thorpe (1986) stated that there is increasing evidence that smolting and maturing are naturally inhibitory, and that, although maturing does not totally preclude smolting and migration to sea, it may interfere with the successfull completion of smolting or may reduce the probability of survival after the smolt stage. Lundqvist and Fridberg (1982) showed that all male parr precociously mature in fall 1979 and held beyond smoltification in freshwater were mature again in fall 1980. Among similar male precocious parr that were transferred to cages in brackish water, only 7% matured again as post-smolts. Hence, smoltification did seem to greatly inhibit post-smolt maturation (+6) but some fish did smoltify and did mature.

In this study, post-smolt maturation (+6) rates were lower than either precocious maturation (-6) rates or grilse maturation (+18) rates, which would seem to indicate as well some degree of inhibition by the smoltification process. However, the fish that matured as post-smolts did not show any increased mortality during and after the maturation period, and grew well (see Chapter IV sect. 3.4). Saunders and Henderson (1965) made the same observation. The existence of an absolute physiological incompatibility prohibiting smoltification and maturation in the same year is as well doubtful since a closely related salmonid species, the sea trout Salmo trutta, is known to exhibit significant level of post-smolt maturation (+6) in natural populations (Allan and Ritter, 1976; Pratten and Shearer, 1983). Similarly, post-smolt maturation among male rainbow trout reared in sea cages is

not uncommon (Møller et al., 1976; Naevdal et al., 1979b; 1981) Atlantic salmon post-smolt precocious maturation (+6) is probably fairly rare in natural populations, but there is some evidence that it might be more common among intensively cultivated populations than reported in the literature (see Chapter IV sect. 4.7 for a complete discussion of this relatively poorly understood maturation episode).

Grilse maturation (+18) is widespread among farmed salmon, sea ranched salmon and natural populations, throughout the Atlantic salmon geographic range. It has been extensively studied because of its economic impact (Gardner, 1976 and see Proceeding of the International Workshop "Salmonid age at maturity" ed., Meerburg, 1986). The grilse maturation (+18) rates observed in this study are in the range of those observed with similar stocks and under similar cultivation conditions in the Bay of Fundy (Glebe and Saunders, 1986). The observation of grilse maturation (+18) rates being higher among males than females is as well very common (Gardner, 1976; Naevdal et al., 1978a; Naevdal, 1983; Gjerde, 1984).

In this study, a link was observed between post-smolt precocious maturation (+6) and grilse maturation (+18) among the 1Y81 fish. The majority of post-smolt mature males matured again as grilse one year later, and the rate of grilse maturation (+18) was significantly higher among post-smolt mature (+6) males than among males not mature as post-smolt. In freshwater, among natural or hatchery populations, precocious mature males that do not smoltify are generally mature again the following year (Leyzerovich, 1973; Lundqvist and Fridberg, 1982; Gibson, 1983; Myers, 1984). Similarly, in salt water, the rate of maturation as 2 sea-winter salmon (30 months after smoltification) was

higher among fish that had been mature as grilse (+18) than among fish that were immature at the grilse stage (Herbinger and Newkirk, unpublished). Among rainbow trout reared in sea cages, all males but three that were mature as post-smolt were mature again the following year (Naevdal et al. 1979b).

In contrast, there was no link between precocious maturation (-6) and grilse maturation (+18) among the 2Y81 fish. The rate of grilse maturation (+18) was about the same among precocious males (-6) and non precocious males. Larsson and Svensson (1974), Glebe et al. (1980), Gjerde (1984), Glebe and Saunders (1986), concluded as well that precocious maturation in freshwater appeared independent from maturation in the sea.

There seemed to be no link either between precocious maturation (-6) and post-smolt precocious maturation (+6) among the 2Y81 fish, but, as already noted, the number of post-smolt males (+6) in that cohort was too low to be able to state conclusively on the presence or absence of such a relationship. Naevdal (1983) noted that precocious males kept in separate tanks smoltified normally the following spring and did not mature again as post-smolts, but he gave no indication about possible post-smolt precocious maturation among non precocious males.

Therefore, it seems that maturation at age x tends to promote maturation the following year at age x+1, but that smoltification exerts a disrupting influence on this pattern of repeated maturity.

Both 2 year old smolt cohorts presented very similar results, except for the rate of post-smolt precocious maturation (+6) which was significantly less in the 2Y81 cohort as compared to the 2Y80 or the

1Y81 cohort. It is unlikely that this higher incidence of post-smolt precocious maturation (+6) in the 2Y80 and 1Y81 cohorts is due to the short exposure to constant daylight that occurred early in the summer before that maturation episode. This exposure happened at the moment when daylengths are the longest in the natural photoperiod cycle. The exposure was short (2 months and a half) and corrected 4 to 5 months before maturation took place. Manipulations of photoperiodic cycles have been shown to successfully modify (advance or delay) the timing of maturation in several salmonids species (Henderson, 1963; Lam, 1983; Bourlier and Billard, 1984; Bromage et al., 1984; Elliot et al., 1984; Scott et al., 1984; Takashima and Yamada, 1984). However, they do not appear to modify per se the incidence of maturation (Johnson, 1984; McCormick and Naiman, 1984).

The low incidence of post-smolt precocious maturation (+6) in the 2Y81 cohort is probably linked rather with the harsh environmental conditions experienced by these fish during the winter preceding this maturation episode (low temperature, reduced feeding at the Fraser's Mill hatchery), as compared with the 1Y81 and 2Y80 cohorts which experienced milder conditions in the winter preceding their post-smolt precocious maturation (+6) episode (heated water, normal feeding at the IMA Aquatic Farming hatchery).

In this study, the 1-year-old smolt cohort (1Y81) differed most notably from both 2-year-old smolt cohorts (2Y80 and 2Y81) by a significantly lower rate of grilse maturation (+18) among females. Grilse maturation rates are generally higher among 2-year-old smolts than 1-year-old smolts (Ritter, 1975; Gardner, 1976; Ritter and Newbould, 1977; Saunders et al., 1983; Bailey and Saunders, 1984).

However, Naevdal et al. (1979a) and Naevdal (1983) reported the opposite among cage reared salmon in Norway. That sexes might not be equally represented in the different smolt age class in many natural and sea-ranched populations adds further complexity to this problem.

These last two aspects, the lower incidence of post-smolt precocious maturation (+6) among the 2Y81 cohort and of grilse maturation (+18) among females in the 1Y81 cohort will be reexamined fully in Chapter IV, in the light of the findings concerning the links between growth patterns and maturation patterns.

CHAPTER III : FAMILY DIFFERENCES IN THE INCIDENCES OF THE VARIOUS MATURATION EPISODES.

1. Introduction

There is ample evidence that adult maturation (the grilse maturation versus true salmon maturation) and juvenile maturation (precocious maturation) are partially under genetic control (see early references in Gardner, 1976 and later references in Naevdal, 1983; Thorpe et al., 1983; Gjerde, 1984; Glebe and Saunders, 1986; Ridell, 1986; Saunders, 1986). There is also reasonable evidence that part of the genetic variance for age at maturity is additive (Gjerde, 1984; Gjerde and Refstie, 1984) and this supports earlier evidence that adult age at maturity was heritable (Elson, 1973; Piggins, 1974; Ritter and Newbould, 1977). However, the general picture is still confusing. Gjerde and Refstie (1984) found an insignificant non-additive genetic variance for sea age at maturity, while Gjerde (1984) postulated the presence of such non-additive genetic variance. Saunders et al. (1983) demonstrated the presence of genotype-environment interactions for sea age at maturity.

Furthermore, the significance, from a genetic point of view, of the links between growth patterns and maturation patterns (reviewed in Chapter IV), and of the relationships between the different maturation episodes is, as well, largely unresolved.

In this chapter, the variations of incidence of the different maturation episodes between the different families will be investigated. The influence of the parental characteristics on the maturation incidence will be examined, as well as the relationships between the

different maturation episodes.

2. Material and Methods. Stock origin and family creation.

This chapter is concerned with the 1Y81 and 2Y81 fish only (cf. Terminology in Chapter II, sect. 2.2). Family identity was lost for most of the 2Y80 fish because of the marking problem already mentioned in Chapter I, section 2 and Chapter II, section 2.1. Hence, they are not included in this chapter.

Family marking was performed using a combination of adipose clipping, cold branding and jet injection of Alcian Blue in 2 caudal fin locations (1 and 3). Specific details about the family and individual marking techniques are given in Chapter I, section 3. Details about data collection procedures, freshwater and saltwater husbandry, are given in Chapter II, section 2. Some additional details concerning environmental parameters during saltwater rearing will be given in Chapter IV, section 2.

Most of the 1981 year class fish (1Y81 and 2Y81) originated from two distinct mating schemes, with a few fish coming from a third one. All 3 matings were performed in November 1981.

The group No. 1 refers to the fish originating from the first mating scheme, and is composed of 6 families that were created in the Biological Station, St Andrews N.B. (Fig. 3.1).

The group No. 2 refers to the fish originating from the second mating scheme, and is composed of 5 pseudo-families that were created on the sea cage site of the Marine Research Associates Ltd (MRA) entreprise, located in Deer Island, N.B. (Fig. 3.1).

The group No. 3 refers to the fish of a single family that was

created in the Fraser's Mill hatchery, St Andrews N.S. (Fig. 3.1). Because of the very low number of 1-year-old smolts (1Y81) and of 2-year-old smolts (2Y81) produced by the later group/family, it will not be included in the family comparisons. Results concerning this family will be given on an indicative basis.

Tables 3.1 and 3.2 compile the available information on the stock origin and the characteristic of the parents used in these matings, as well as information concerning the sort of families that were created. Figure 3.1 shows the location of freshwater and saltwater rearing stations for both the parents and the fish of this present study, as well as the location of the different river stocks from which the parents originated. One can see from Tables 3.1 and 3.2 that groups 1 and 2 differ mostly by the sea age of the parents used, grilse for group 1, 2-sea-winter salmon for group 2. All families of group 1 (No. 11, 12, 13, 15, 16, 17) were adipose clipped, while all families of group 2 (No. 51, 52, 55, 56, 57) were non-clipped. Hence, in the few cases where family codes could not be read, the fish could still be assigned to group 1 or group 2 (the few fish from family 60/group 3 were non-clipped as well, but no family code losses occured in that family).

The same data treatment procedure that was used in Chapter II, section 2.5, will be used here. Individual identity was available, for the 1Y81 and 2Y81 fish, for all the maturation episodes: i.e. precocious maturation (-6) for the 2Y81 fish; post-smolt precocious maturation (+6) for the 1Y81 and 2Y81 fish, and grilse maturation (+18) for the 1Y81 and 2Y81 fish. Hence, only the fish with complete data sets have been included. (cf. Chapter II, sect. 2.5).

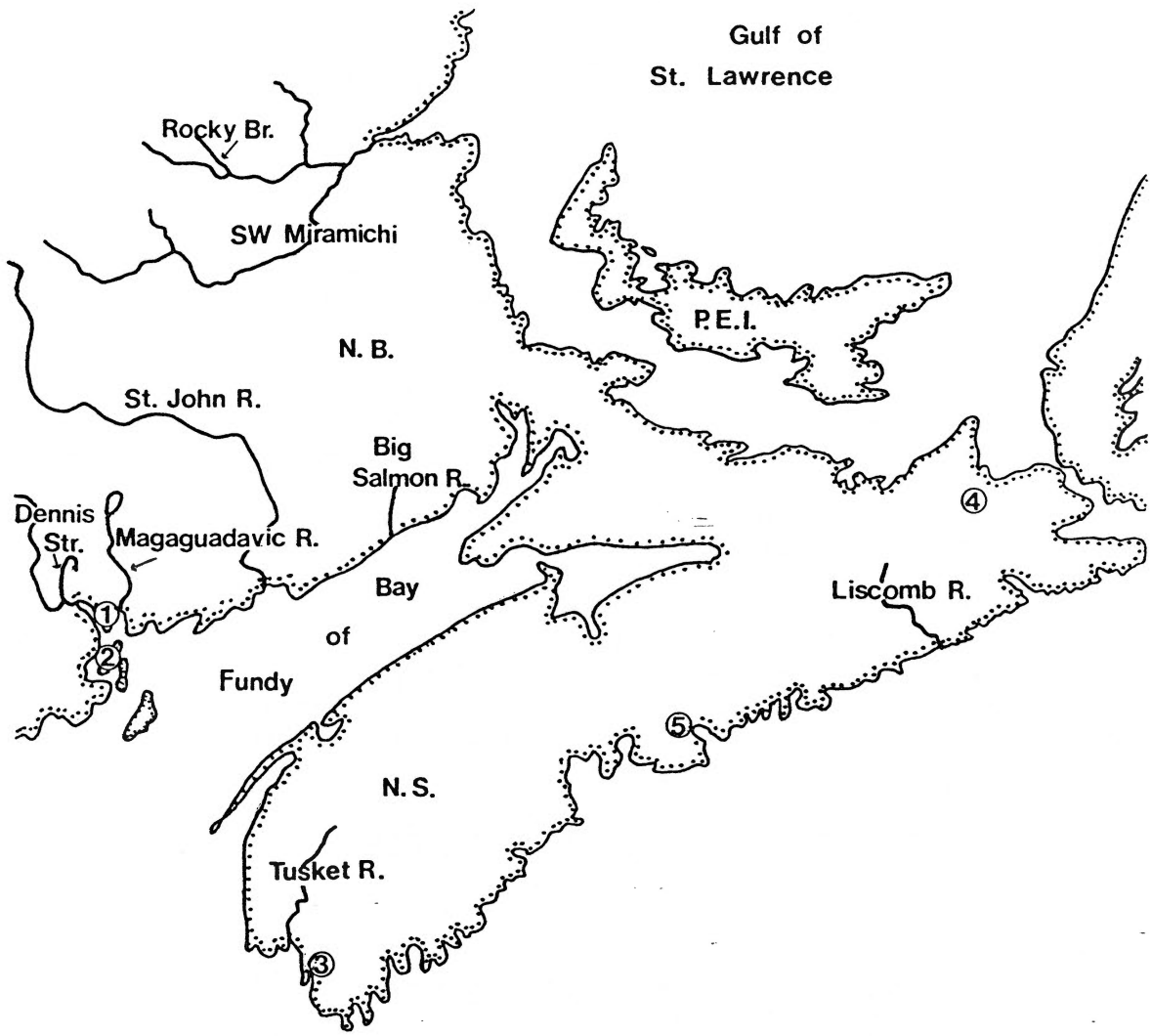

Fig. 3.1: Locations of the parents' river stocks and of the different spawning and rearing places used for both the parents and the fish of this study.

① Biological Station, St. Andrews N.B.

② Marine Research Associates Ltd. (MRA) cage site, Deer Island N.B.

③ IMA Ltd. hatchery, Argyle Head N.S.

④ Fraser's Mill hatchery, St. Andrews N.S.

⑤ Dalhousie University, Halifax N.S.

Table 3.1: Characteristics of the parents used and of the families created.

Group and family code	Family characteristics	Parents characteristics	Parents stock origin
Group 1 (Families 11 12 13 15 16 17)	True full sib families 1♂ x 1♀ matings Family 17 results from the pooling of 2 full sib families	All parents were grilse Some parents were cage reared (MRA) some were sea-ranched. Parents were 1+smolts (1978 year class) or 2+ smolts (1977 year class)	Mixed stock origin from the following: St John R. Big Salmon R. Magaguadavic R. Rocky Bk. Dennis Str.
	See Table 3.2 for specific information		
Group 2 (Families 51 52 55 56 57)	Pseudo-families 2♂ x 3♀ matings Family 57 results from the pooling of 2 pseudo-families	All parents were 2 sea-winter salmon All parents were cage reared (MRA) All parents were 1+ smolts (1977 year class)	Mixed stock origin from the following: Mostly St John R. plus a small contribution from Big Salmon R. and Dennis Str.
Group 3 (Family 60)	True full sib family 1♂ x 1♀ mating	♂ parent was a sea-ranched grilse ♀ parent was a reconditionned kelt (first mature as a grilse)	O: Liscomb R. O: Tricounty Tusket R.

Table 3.2: Specific characteristics of the parents of group 1.

Family code	Male parent characteristics	Female parent characteristics
11	Year class:1977 Smolt age:2+ Sea-ranched grilse 55cm/1.5kg Stock origin (a):BxM or MxM	Year class: ? Smolt age: ? Sea-ranched grilse 62cm/2.3kg Stock origin: ?
12	Year class:1977 Smolt age:2+ Sea-ranched grilse 57cm/1.8kg Stock origin: BxM or MxM	Year class:1977 Smolt age:2+ Sea-ranched grilse 57cm/2.0kg Stock origin: BxB
13	Year class:1977 Smolt age:2+ Sea-ranched grilse 61cm/2.0kg Stock origin: SxS	Year class:1978 Smolt age:1+ Cage reared grilse 62cm/2.8kg Stock origin: (SxS)x(BxD)
15	Year class:1977 Smolt age:2+ Sea-ranched grilse ?cm/ ?kg Stock origin: MxR or BxS	Year class:1978 Smolt age:1+ Cage reared grilse ?cm/ ?kg Stock origin: (BxB)x(?) or (BxB)x(BxB)
16	Year class: ? Smolt age: ? Sea-ranched grilse 63cm/2.3kg Stock origin: ?	Year class:1978 Smolt age:1+ Sea-ranched grilse 59cm/1.8kg Stock origin: mixture
17	Year class:1977 Smolt age:2+ Sea-ranched grilse 55cm/1.5kg Stock origin: RxB or SxS	Year class:1978 Smolt age:1+ Cage reared grilse 60cm/2.6kg Stock origin: ?
	Year class: ? Smolt age: ? Sea-ranched grilse 59cm/1.8kg Stock origin: ?	Year class:1978 Smolt age:1+ Cage reared grilse 56cm/2.2kg Stock origin: ?

(a): Stock origin: Y1xY2. Y1=river stock of the male parent of the particular parent considered. Y2=river stock of the female parent of the particular parent considered. In the cases of the female parent of families 13 and 15, two generation crosses are shown.
S= St John R. stock. B= Big Salmon R. stock. M= Magaguadavic R. stock
R= Rocky Brook stock. D= Dennis Stream stock.

The X2 test was used to compare rates of maturation between families or groups. When more than 20% of the X2 cells had expected frequencies lower than 5, families with low number of fish were pooled. Family pooling was performed within groups. In case it was necessary to pool some families of group 1, then pooling was performed within female parent characteristics, i.e. within cage reared female grilse or within sea-ranched female grilse (Table 3.2). When comparing maturation rates with very low incidence, the exact Fisher's probability was calculated (Schwartz, 1969). Correlation between 2 series of percentages was performed after percentage normalisation through angular transformation (arc sin$\sqrt{p}$). The non parametric Kendall coefficient of concordance W was used to measure the agreement between independant rankings and to test whether ranking patterns were significantly consistent (Siegel, 1956).

3. Results

Among the 2-year-old smolts (2Y81), the 11 families (omitting family 60) had significantly different rates of grilse maturation (+18), ranging from 5.6% in family 51, to 76.2% in family 13 (Table 3.3). Similarly, among the 1-year-old smolts (1Y81), rates of grilse maturation (+18) were also significantly different between families, ranging from 6.7% in family 52, to 61.3% in family 13 (Table 3.3). Furthermore, the 2 series of maturation rates per family, among the 1Y81 and the 2Y81, were significantly correlated ($r = .70$ $p = 0.8\%$). This can be seen in Figure 3.2a,b. Except for the particularly low rate of maturation in family 51 among the 2Y81 fish, there is a generally good concordance between the two percentage series.

Table 3.3: Comparison of grilse maturation (+18) rate between families, among the 2Y81 and the 1Y81 cohorts. Family 60 is excluded from the comparisons.

2Y81 fish

Group	Family	Grilse maturation (+18) rate	Absolute frequencies	Between families comparison
	11	60.0%	9/15	
	12	38.5%	5/13	
1	13	76.2%	16/21	
	15	54.5%	6/11	
	16	53.8%	7/13	
	17	60.0%	6/10	$X2=22.5$ 10 df p=1%
	51	5.6%	1/18	
	52	50.0%	9/18	
2	55	41.2%	7/10	
	56	51.5%	17/33	
	57	44.4%	8/18	
3	60	16.7%	1/6	

1Y81 fish

Group	Family	Grilse maturation (+18) rate	Absolute frequencies	Between families comparison
	11	30.8%	8/26	
	12	6.8%	3/44	
1	13	61.3%	19/31	
	15	42.3%	11/26	
	16	38.9%	7/18	
	17	28.6%	4/14	$X^2=39.8$ 8 df(a) p<0.01%
	51	8.3%	1/12	
	52	6.7%	1/15	
2	55	9.1%	1/11	
	56	21.4%	3/14	
	57	14.3%	1/7	
3	60	33.3%	1/3	

(a) X^2 is calculated after pooling families 51 and 55, and families 56 and 57 because of the small number of fish in these families.

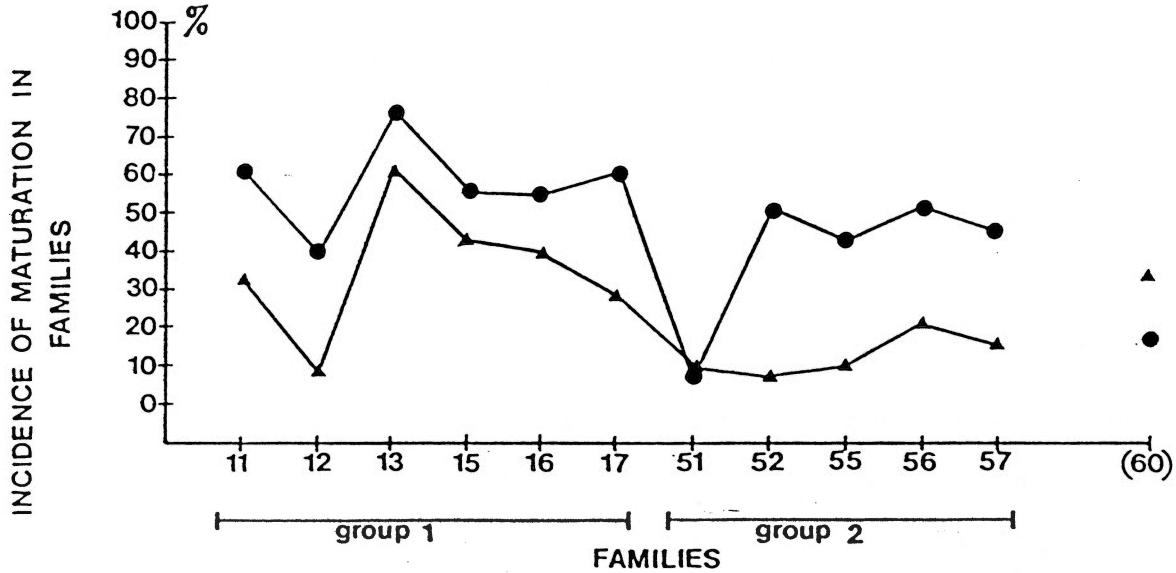

Fig. 3.2 a: Family incidence of grilse maturation among the 1Y81 fish (▲) and the 2Y81 fish (●).

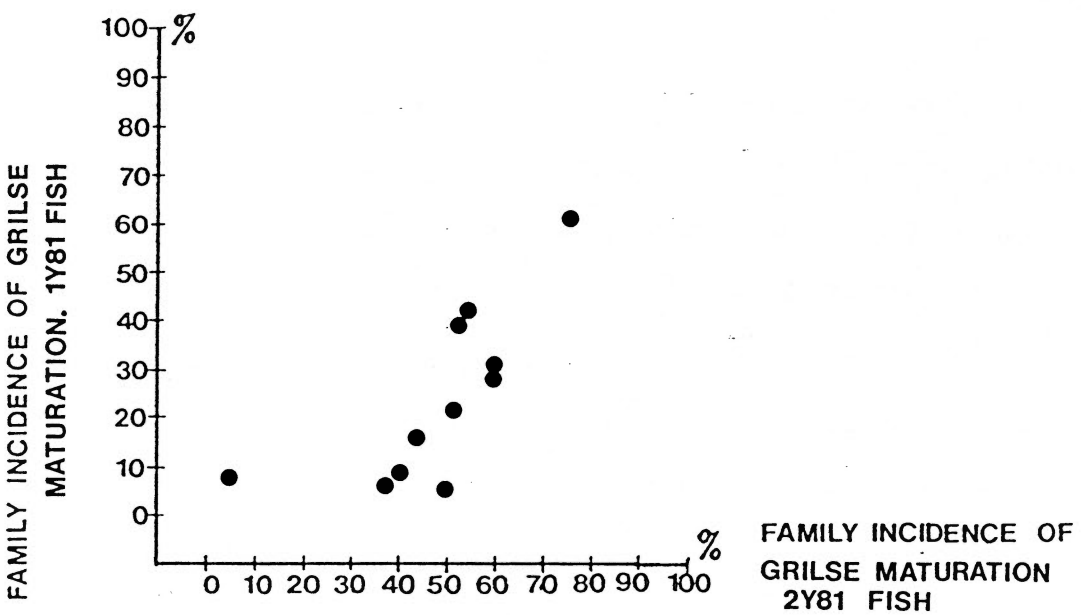

Fig. 3.2 b: Relationships between family incidences of grilse maturation among the 1Y81 and 2Y81 fish.

In all families except in the aforementioned family 51, the rate of grilse maturation (+18) among the 1Y81 cohort is lower than among the 2Y81 cohort.

Since some fish of the 1Y81 cohort are of unknown sex (cf Chapter II, sect. 2.1 and 3.2), it was not possible to compare directly sex specific rates of maturation. However, it is interesting to note that the rare females that matured as grilse among the 1Y81 cohort belonged only to family 13 and 17. These two families had the two highest rates of grilse maturation among females, in the 2Y81 cohort (Table 3.4).

Among the 1-year-old smolts (1Y81), the eleven families (omitting family 60) had significantly different rates of post-smolt precocious maturation (+6), ranging from 0% in family 12 and 55, to 41.9% in family 13 (Table 3.5). Furthermore, among the 1Y81 cohort, the series of post-smolt precocious maturation (+6) rates per family was significantly correlated with the series of grilse maturation (+18) rates per family ($r = .57$ $p = 3.2\%$). Figure 3.3a,b shows that there is a generally fair concordance between the two percentage series, although the concordance is poorer among families of group 2 (family 51 to 57).

The very low occurence of post-smolt precocious mature (+6) fish in the 2Y81 cohort (see Chapter II, sect. 3.4) does not allow any meaningful family statistical comparisons. Yet, it can be noted that post-smolt mature (+6) fish were obtained only in families 11, 13 and 17. These families had the three highest grilse maturation (+18) rates among the 2Y81 fish (Table 3.3).

Table 3.4: Grilse maturation (+18) rates among females for the different families in the 1Y81 and 2Y81 cohorts.

		2Y81 cohort		1Y81 cohort	
Group	Family	Female grilse maturation (+18) rate	Absolute frequencies	Estimated female grilse maturation (+18) rate	Absolute frequencies
	11	60.0%	3/5	0%	
	12	28.6%	2/7	0%	
1	13	69.2%	9/13	23%	3/13(a)
	15	42.9%	3/7	0%	
	16	28.6%	2/7	0%	
	17	80.0%	4/5	33%	2/6(a)
	51	0%	0/10	0%	
	52	37.5%	3/8	0%	
2	55	30.8%	4/13	0%	
	56	50.0%	7/14	0%	
	57	27.3%	3/11	0%	
3	60	0%	0/2	0%	

(a) Estimated total number of females in the family.

Table 3.5: Comparison of post-smolt precocious maturation (+6) rates between families, among the 1Y81 and 2Y81 cohorts. Family 60 is excluded from the statistical comparison.

		1Y81 cohort			2Y81 cohort	
Group	Family	Post-smolt precocious maturation (+6) rate	Absolute frequencies	Between families comparison 1Y81 fish	Post-smolt precocious maturation (+6) rate	Absolute frequencies
	11	11.5%	3/26		13.5%	2/15
	12	0%	0/44		0%	0/13
1	13	41.9%	13/31		4.8%	1/21
	15	11.5%	3/26		0%	0/11
	16	5.6%	1/18		0%	0/13
	17	14.3%	2/14	(a)X^2=30.9 4 df	20.0%	2/10
	51	16.7%	2/12	p<0.01%	0%	0/18
	52	6.7%	1/15		0%	0/18
2	55	0%	0/11		0%	0/17
	56	7.1%	1/14		0%	0/33
	57	28.6%	2/7		0%	0/18
3	60	33.3%	1/3		0%	0/6

(a) X^2 is calculated after pooling together families 11 and 16, families 15 and 17, and families 51 to 57, because of the very low overall maturation rate and because of the small number of fish in these families.

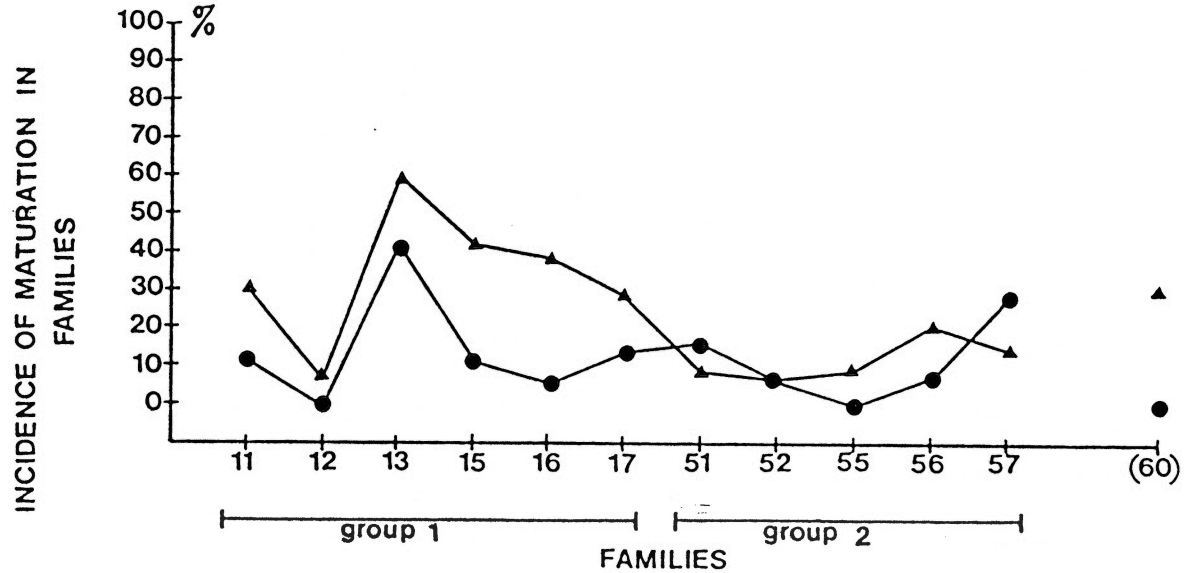

Fig. 3.3 a: Family incidence of post-smolt precocious maturation (●) and grilse maturation (▲) among the 1Y81 fish.

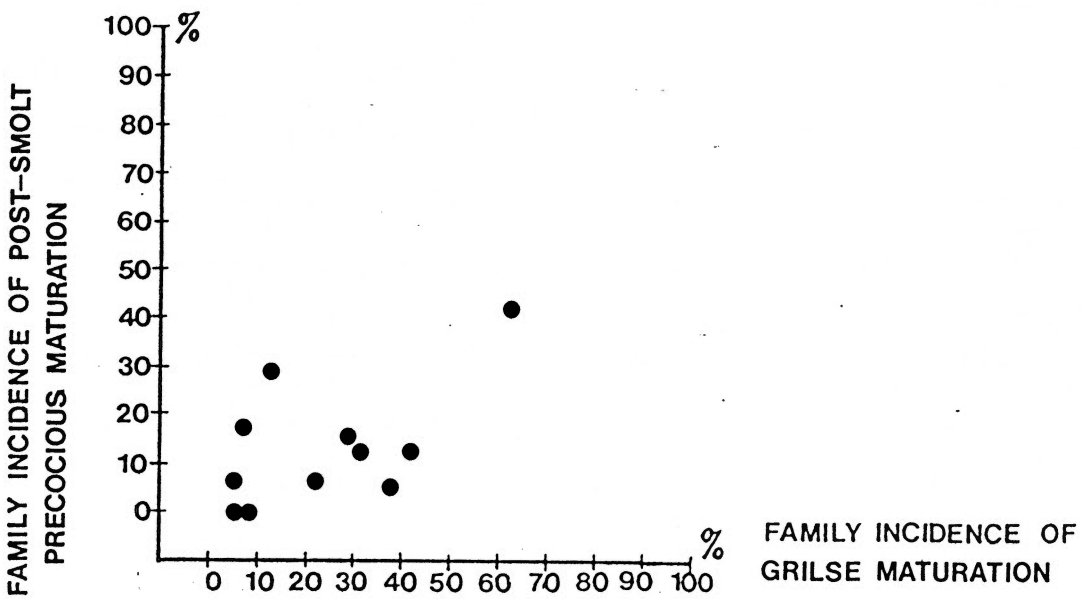

Fig. 3.3 b: Relationships between family incidences of post-smolt precocious maturation and grilse maturation among the 1Y81 fish.

They also had the highest rates of post-smolt precocious maturation (+6) among the families of group 1 in the 1Y81 cohort, although 2 families of group 2 also had comparable rates (Table 3.5).

In contrast with grilse maturation (+18) and post-smolt precocious maturation (+6), the precocious maturation (-6) rates were not significantly different between the 11 families (Table 3.6). Figure 3.4a shows that the rate of precocious maturation was effectively much less variable from family to family than either grilse maturation rates (+18) in the 1Y81 cohort or 2Y81 cohort (Fig. 3.2a), or post-smolt precocious maturation rate (+6) in the 1Y81 cohort (Fig. 3.3a). Yet, this series of precocious maturation (-6) rates per family was significantly correlated with the series of grilse maturation (+18) rates per family in the 2Y81 cohort ($r = .67$ $p = 1.3\%$) (Fig. 3.4b). This indicates that the family differences observed for the rate of precocious maturation (-6), although statistically non significant, were nevertheless consistent in trend with the statistically significant family differences that were observed for grilse maturation (+18).

Overall, grilse maturation (+18), post-smolt precocious maturation (+6) and, to a lesser extent, precocious maturation (-6) appears to be under a strong genetic control which translated into significant variations of the maturation rates between the different families and pseudo-families. Furthermore, the patterns of family differences for the various maturation episodes were quite consistent with one another, as indicated by the significant and positive correlations found between the series of maturation rates per family.

Table 3.6: Comparison of precocious maturation (-6) rates between families, among the 2Y81 cohort. Family 60 is excluded from the statistical comparison.

2Y81 cohort

Group	Family	Precocious maturation (-6) rate	Absolute frequencies	Between families comparison
	11	40.0%	6/15	
	12	30.8%	4/13	
1	13	38.1%	8/21	
	15	18.2%	2/11	
	16	15.4%	2/13	
	17	20.0%	2/10	X^2=14.3
				10 df
	51	5.6%	1/18	NS (16%)
	52	22.2%	4/18	
2	55	11.8%	2/17	
	56	27.3%	9/33	
	57	5.6%	1/18	
3	60	16.7%	1/6	

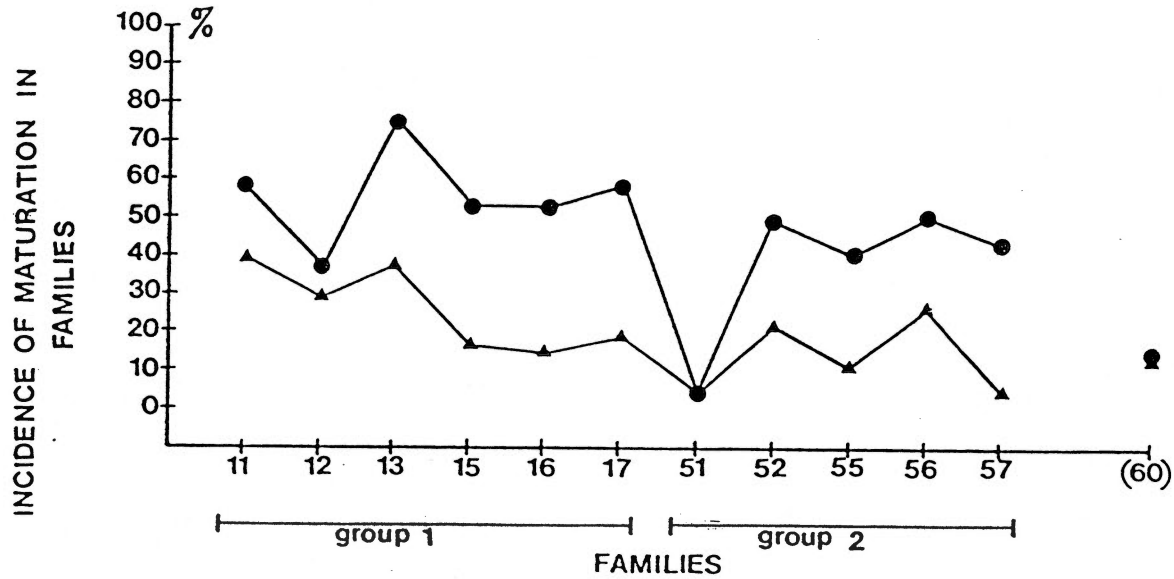

Fig. 3.4 a: Family incidence of precocious maturation (▲) and grilse maturation (●) among the 2Y81 fish.

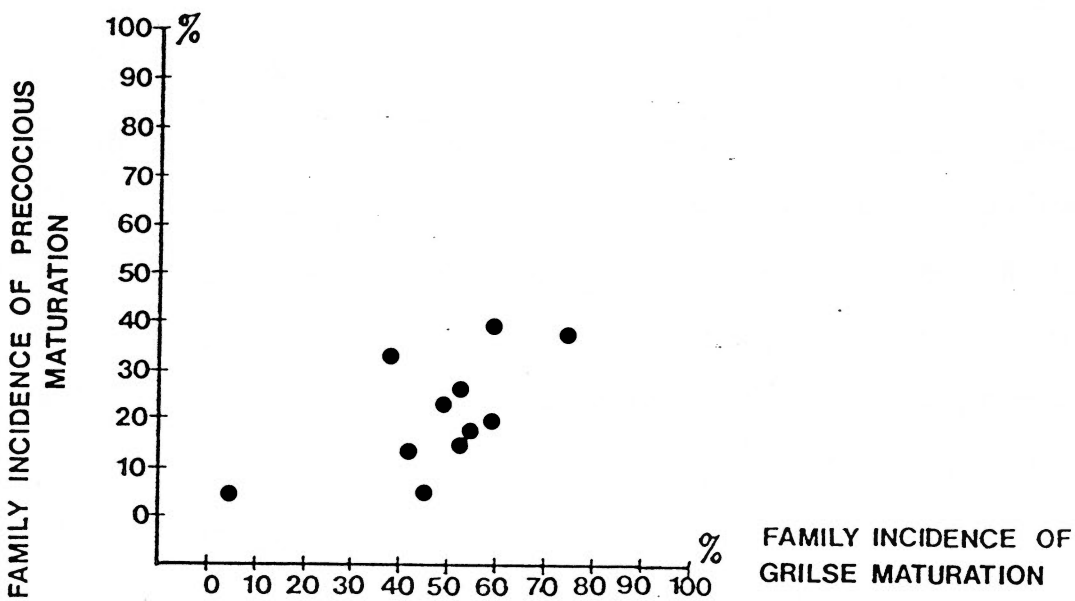

Fig. 3.4 b: Relationships between family incidences of precocious maturation and grilse maturation among the 2Y81 fish.

This consistency is illustrated in Table 3.7. The Kendall concordance coefficient is high (W= .54) and significant, indicating that there is an overall good agreement between the family rankings based on precocious maturation (-6), post-smolt precocious maturation (+6) and grilse maturation (+18). Hence, families with high mean ranks, like family 11 and 13 for example, were characterised by consistently high maturation incidences, whatever the maturation episode considered, while families with low means ranks, like family 55 or 51 for example, were characterised by the opposite.

It is interesting to note that families of group 1 have high mean ranks, except for family 12, while families of group 2 consistently have low mean ranks (Table 3.7). Hence, offsprings from group 1 were generally characterised by higher rates of maturation than offsprings from group 2. This is illustrated in Table 3.8. All maturation episodes had higher incidences among the fish of group 1 than among the fish of group 2, and all these differences were significant, except in the case of post-smolt precocious maturation (+6) among the 1Y81 fish.

Overall, the families of group 2 were quite similar with respect to the incidence of the different maturation episodes, with the already noted exception of family 51 for grilse maturation (+18) rate among the 2Y81 cohort (Tables 3.3, 3.5, 3.6). This is probably a consequence of these "families" being pseudo-families rather than true full-sib families (cf. sect. 2). Since the pseudo-family means are in effect means of the component full-sib families, there should be less variance among the pseudo-family means (Central Limit Theorem).

Table 3.7: Concordance between the family rankings based on precocious maturation (-6) in the 2Y81 cohort, post-smolt precocious maturation (+6) in the 1Y81 cohort and grilse maturation (+18) in the 1Y81 and 2Y81 cohorts.

Group	Family	Mean rank	Kendall concordance coefficient W and significance
	11	8.75	
	12	3.63	
1	13	10.75	
	15	7.38	
	16	5.75	W=0.54
	17	7.63	X2=21.8
			10 df
	51	3.63	p=1.6%
	52	4.25	
2	55	2.88	
	56	6.25	
	57	5.13	

Table 3.8: Comparison of the incidence of the various maturation episodes between group 1 and group 2.

Group	Precocious maturation (-6) rate 2Y81 cohort	Post-smolt precocious maturation (+6) rate 1Y81 cohort	Post-smolt precocious maturation (+6) rate 2Y81 cohort	Grilse maturation (+18) rate 1Y81 cohort	Grilse maturation (+18) rate 2Y81 cohort
Group 1	29.2%	13.5%	6.3%	32.5%	60.4%
Group 2	16.0%	11.1%	0%	14.5%	37.6%
Between groups comparison	X2=5.5 1 df p=2%	X2=0.2 1 df (NS)	Exact Fisher probability p=1.2%	X2=7.6 1 df p=0.6%	X2=11.3 1 df p=0.1%

The families of group 1 were much more dissimilar, but most of the differences were due to families 12 and 13, that is to say the two families with respectively very low and very high incidences of maturation. The remaining families of group 1 (families 11, 15, 16, 17) were intermediate, with relatively similar incidences of the different maturation episodes.

4. Discussion

The results of this study indicated a strong genetic influence on the maturation timing in Atlantic salmon. This compares well to what has generally been reported in the literature.

4.1 Grilse maturation

Significantly different rates of grilse maturation (+18) have been reported between strains (populations) for sea-ranched and cage reared salmon (Naevdal et al., 1978a; 1979a; 1983; Saunders et al., 1983; Bailey and Saunders, 1984; Gjerde and Refstie, 1984) and between families within a strain (Naevdal, 1983). Naevdal et al. (1979a) found a high and significant correlation (r= .81) between the grilse maturation rates of 1-year-old smolts and 2-year-old smolts of the same sib groups. This result is quite similar to that observed in this study, indicating that maturation as grilse seems to be strongly associated with family. However, Naevdal et al. (1979a) observed a higher grilse maturation rate among the 1-year-old smolts than among the 2-year-old smolts for most groups, a result which is quite opposite to what has generally been reported and to what was observed in this study (see Chapter IV for a discussion of the smolt age influence on grilse maturation).

The fact that the few females that matured as grilse among the 1Y81 fish belonged to the 2 families with the highest rates of grilse maturation among females in the 2Y81 cohort indicates that some genetic variability exists probably as well in the commonly reported predominance of males among early maturing fish.

Early breeding studies (Elson, 1973; Piggins, 1974; Ritter and Newbould, 1977) showed that the proportion of grilse was higher among the offspring from grilse parentage than among the offspring from 2-sea-winter salmon parentage, thus indicating a genetic basis to adult age at maturity. This compares well to the results of the present study, where the grilse maturation rate was higher among fish of group 1 (grilse parentage) than among fish of group 2 (true salmon parentage) for both smolt age groups.

The difference observed between group 1 and group 2, in this study, could be due to different stock origin composition. Group 2 was mostly from St John River (S) stock origin (Table 3.1), while group 1 was of a more mixed stock origin (Tables 3.1 and 3.2). Group 1 comprised more Big Salmon River (B) stock contributions to its gene pool than group 2. The Big Salmon River strain has been shown to produce higher proportions of grilse than the St John River strain (Saunders et al., 1983; Bailey and Saunders, 1984). Hence, the differences in maturation rates observed between the two groups could reflect contrasting proportions of Big Salmon River and St John River genes, rather than the sea age at maturity of the particular parents used in each group.

Both groups referred to in this study were of mixed stock origin (Table 3.1), although group 2 is less mixed than group 1. Although the pedigree are too uncertain to be sure, it is unlikely that the lower

grilse maturation rates observed among the fish of group 2, as compared to group 1, reflected this difference in degree of mixing and presumably heterozygosity. Bailey and Saunders (1984) found no evidence of heterosis for adult age at maturity from crosses between the same rivers strains that were used in this study. Similarly, Gjerde and Refstie (1984) found insignificant non-additive genetic variance for this trait among crosses between five Norwegian strains of Atlantic salmon.

The number of full-sib families in this study is small but given the variation observed, it would appear that there were as much genetic differences between families within the groups as there were differences between the groups. Stock origin composition is known with reasonable certainty only in family 12 and 13 (Table 3.2). It is interesting to note that these families showed maturation trends quite opposite to what could be expected from their stock origin compositions. Family 12 had a very high proportion of Big Salmon River genes (50% to 75%) and yet, it was the family of group 1 that showed the lowest rates of maturation, even lower than that of most families of group 2 (mean rank 3.63 in Table 3.7). Family 13 had a low proportion of Big Salmon River genes (12.5%) and a very high proportion of St John River genes (75%) and yet, it was the family showing the highest rates of maturation (mean rank=10.75 in Table 3.7). The stock origin composition of family 13 (75% S, 12.5% B, 12.5% D=Dennis stream) was probably very close to the group 2 stock origin composition (Table 3.1). Yet, family 13 showed consistently very high rates of maturation for all maturation episodes, while all families of group 2 showed consistently the opposite (Tables 3.3, 3.5, 3.6, 3.7).

It therefore appears that the differences in maturation patterns

observed between the group 1 and the group 2 reflected the difference in sea age at maturity of the respective parents used rather than the specific stock origin composition of the two groups.

Gjerde and Gjedrem (1984) estimated heritability for sea age at maturity to be .39 from half-sib correlations, while Gjerde (1984) estimated it from selection experiments at .48 ±.20. Heritabilities estimates for all or none traits are to be taken with caution, since they are dependant upon the incidence of the trait and can vary with estimation procedures (Van Vleck, 1972; Gjerde, 1986; Ridell, 1986). Yet, these studies indicated that the potential to change this trait through selection is good. The parent used in this study had a mixed and partially unknown origin. It is very likely that their parents or grandparents had been selected. Thus, the individuals used may not be a random sample of the river stocks. In any case, the differences shown here indicate a substantial genetic component to the variation in grilse maturation.

4.2 Post-smolt precocious maturation (+6)

Among the 1Y81 fish, the rates of post-smolt precocious (+6) maturation were significantly different between families. Among the 2Y81 fish, the few post-smolt precocious (+6) males belonged to families that had some of the highest post-smolt precocious maturation rates in the 1Y81 cohort. These results indicate that this maturation episode is partly under some genetic control, similarly to grilse maturation.

Very little information can be found in the literature about this maturation episode. Naevdal et al. (1978a) reported varying rates of post-smolt precocious maturation among groups representing 12 Norwegian, 1 Swedish and 2 Canadian rivers. All mature fish were males, like in

the present study. Interestingly, the highest incidence (26% of the total population) was found in the group originating from one of the Canadian rivers, the McDonald River. Post-smolt mature males (+6) were also found among the groups representing 7 other rivers, but with a very low incidence (varying from 1% to 6% of the total population), while in the last 7 rivers, no post-smolt mature fish were found.

4.3 Precocious maturation (-6)

In the present study, varying rates of precocious maturation (-6) were observed for the different families, although these rates were overall not significantly different (p=16%). As noted, the incidence of precocious maturation (-6) was much less variable between families than either the incidence of post-smolt precocious maturation (+6), or grilse maturation (+18). It is probable that this absence of significance reflected the lack of power of the X2 test used, due to the small size of most families and to the lower variability of incidence rather than the real absence of the genetic control on that maturation episode, since conclusive evidence on the heritable nature of this trait can be found in the literature.

Significantly different rates of precocious maturation have been reported between families within strains (Naevdal, 1983). Large variations in the incidence of precocious maturation between the Big Salmon River, St John River, Magaguadavic River, Rocky Brook and Dennis Stream strains, have been documented (Saunders and Sreedharan, 1977; Glebe et al., 1980; Glebe and Saunders, 1986). Thorpe et al. (1983) reported that the incidence of precocious maturation (at age 1+) was significantly higher among the progeny of males 1+ parr than among progeny of adult males, and that the incidence of precocious maturity

was increased 5.4 times and a further 1.7 times over two and three generations respectively, in a selection experiment using mature parr as sires. Similarly, maturing parr (age 0+) were found only among the offspring of precocious males (+0), and not among the offsprings of adult males in a Norwegian selection experiment (Gjerde, 1984).

The significantly higher incidence of precocity (-6) among fish of group 1 as compared to group 2 could reflect the lower mixity of group 2 as compared to group 1, since a strong heterotic effect for incidence ot precocity has been demonsrated in these strains (Saunders and Sreedharan, 1977; Glebe et al., 1980; Glebe and Saunders, 1986). Another explanation could as well be that selecting late maturing parents (group 2) gave a correlated response in reducing the scope of precocity among their offspring. This last possibility is reviewed in the next section.

4.4 Links between the different maturation episodes.

The covariance between precocious maturation in freshwater and later maturation in seawater is still obscure (Naevdal, 1983). Gjerde's results (1984) indicated that maturation as parr might be independently inherited from maturation in the sea. Glebe et al. (1980) found that the highly variable family incidences of maturing parr were not related to parental sea age at maturity. However, Thorpe et al. (1983) criticised this last observation, noting that there was a high probability that the sea run adult males used as sires, for comparison with precocious sires, had themselves matured first as parr, hence, that they would not be qualitatively different. Glebe and Saunders (1986) found a significant correlation between strain incidence of mature parr

and sea-ranched grilse, but they thought that this could be because the strains characterised by a high incidence of precocity also produced larger smolt, which in turn would mature more often as grilse. They found that, with increasing sea age of both parents, the scope for parr maturity within strains was reduced. However, Thorpe's remark is equally valid here, i.e., it is not known whether male parents had been precocious parr and this obscures the interpretation of the results. Lastly, they did not find a significant correlation ($r=0.2$, $P>0.05$ NS) between incidence of mature parr and male grilse within the same family when reared in sea cage, hence concluded that maturation in freshwater and seawater might be independant genetic events.

In Chapter II, section 3.5, grilse maturation of individual fish was found to be independant of precocious maturation among the 2Y81 fish. The probability that an individual fish showed the phenotype grilse appeared independant of whether the fish had shown the phenotype precocious parr or not. However, there seemed to be a significant association betwen these two traits at the family level, as evidenced by the significant correlation ($r=.67$, $p=1.3\%$) between families incidence of precocious maturation (-6) and grilse maturation (+18) among the 2Y81 fish. Precocious maturation (-6) and grilse maturation (+18) do not thus appear to be completely independant genetic events. The absence of a link at the individual fish level (cf Chapter II, section 3.5) probably indicate that some environmental factor might have masked the association between these two traits at the individual phenotypic level.

A significant link between post-smolt precocious maturation (+6) and grilse maturation (+18) was found among the 1Y81 cohort (cf. Chapter II, section 3.5). The probability that an individual fish showed the

phenotype grilse appeared higher if the fish had shown the phenotype post-smolt mature (+6) than if the fish had not. There appeared to be a significant association between these two traits at the family level as well, as evidenced by the significant correlation (r=.57, p=3.2%) between family incidence of both traits. (The observation of a link at the family level cannot be explained simply as a consequence of the presence of a link at the individual level because the incidence of post-smolt precocious maturation (+6) was too low in most families to significantly mask the expression of grilse maturation (+18)). Hence, post-smolt precocious maturation (+6) and grilse maturation (+18) appear to be linked genetic events.

4.5 A tentative synthetic view.

All the different maturation episodes analysed in this study are under some genetic control. Furthermore, they appear to be genetically related to one another, as evidenced by the positive and significant concordance coeficient (Table 3.7, W=.54, p=1.6%), indicating similar trend in family incidence of the different maturation episodes. Hence, the conclusion of Gjerde (1984) and Glebe and Saunders (1986) that precocious maturation and grilse maturation appear independantly inherited does not seem warranted. From the present results, it appears that what is inherited in terms of maturation patterns is not so much a specific age at maturity, but rather a sex specific "facility" to mature in a given environement, at several successive ages. That some maturation episodes are rarer than others probably reflects the fact that the physiological/environmental conditions are less favourable to start maturation for these episodes. However, the families having a higher genetically based "facility" to mature will be generally

characterised by a higher rate of maturation for all maturation episodes, as was the case in the present study. As Saunders (1986) states in his concluding remark,"It is likely that in spite of the demonstrated heritability for age at maturity of Salmo salar, the genetic influence is in the form of a capability with rather wide latitude and flexibility awaiting the appropriate environmental and physiological-biochemical conditions rather than a preset array of biochemical reactions and developement ordained to take place during a given time."

CHAPTER IV. THE LINKS BETWEEN GROWTH PATTERNS AND MATURATION PATTERNS.

1. Introduction

After over 20 years of experimentations, mostly on pond reared brown trout (Salmo trutta), Alm (1959) concluded that fast growth was causally related to earlier attainment of maturity. Thorpe (1986) stated that the positive correlation between growth rate and maturation rate had been shown conclusively for every salmonid species. Numerous papers effectively showed that earlier sea age at maturity was accompanied by higher growth rates in sea cage rearing experiments (see review in Dempson et al., 1986 and Gjerde, 1986). However, the evidence from natural population studies was not so conclusive and there was even an overall tendency to observe opposite results (Dempson et al., 1986). Randall et al. (1986) concluded that there was insufficient evidence to conclude that growth at sea affects sea age at maturity. Maturation is also associated with a reduced growth performance just before and during the spawning season (Tveranger, 1985; Aksnes et al., 1986), which is one of the main reasons for which early maturity is detrimental in cage rearing operations (c.f. General Introduction).

The maturation status can be assessed externally only for a few months before and after maturity. Our knowledge on the growth dynamics associated with a maturation episode is therefore generally restricted to this period. Furthermore, it is generally not possible to assess what might have been the previous maturation history of a fish (e.g. precocious maturation in freshwater among males etc.) Yet, these previous maturation episodes certainly affected the growth dynamics as

well. Hence, the overall picture concerning covariation between growth and maturation is quite sketchy and still obscure. There is no general consensus on whether growth differences exist between grilse and multi-sea-winter salmon or not, or about the exact time during which these differences might take place. Among the authors advocating the presence of a positive correlation between growth rate and maturation rate, there is not even a consensus on the causality issue: Alm (1959) and Thorpe (1986) implied that fast growth was causally related with earlier maturity while Gjerde (1986) suggested the opposite. There is no consensus either on the time at which the "decision" to initiate maturation is taken: Saunders (1986) suggested that this decision was probably made after the smolts entered the sea, whereas Chadwick et al. (1986) and Randall et al. (1986) concluded that this decision was probably made before smoltication, and that environmental factors at sea and growth at sea bore little significance on grilse/multi-sea-winter maturation. Saunders et al. (1983) presented evidence that low winter temperature at a sea cage site greatly reduced the incidence of grilse maturation. However, the evidence from studies of the relation between sea temperature and maturation in natural populations is considerably more contradictory (Scarnecchia, 1983; Martin and Mitchell, 1985; Dempson et al., 1986).

In this study, the use of individually identified fish and the collection of growth data at approximately 6 months intervals allowed the compilation of precise growth curves during 1.5 year of growth in sea water in the 3 cohorts and part of the freshwater growth in the 2Y81 cohort. Among the objectives of this study was to determine if grilse maturation and multi-sea-winter maturation were associated with

different growth patterns and to determine when these growth differences were taking place. Furthermore, since the maturation history of each fish was known (c.f. Chapter II), this allowed an assessment of whether the patterns of growth differences were similar among the males that had been precocious mature (-6), the males that had been post-smolt precocious mature (+6), the males which had not been previously mature and tne females. The use of 2 overwintering temperature regimes allowed as well an assessment of the impact of this environmental factor, on both growth and maturation. A synthetic view of the interactions between growth and maturation is presented and a model of maturation "decision" is proposed and discussed.

2. Material and methods

This section gives details about some of the environmental parameters during the saltwater rearing period in the Dalhousie University Aquatron facilities. Most of the methods have already been described in earlier chapters. Chapter I sections 2 and 3, described the individual and family marking techniques. Chapter III section 2, described the stock origin and family creation of the fish. Chapter II section 2, gave an overview of the experimental design and of the data collection and data selection procedures.

As described in Chapter II section 2.4, all fish (2Y80, 1Y81, 2Y81) were reared in several square tanks (cf. Fig. 2.2 a, b in Chapter II) during the first summer and the following winter in seawater. During the second summer in seawater, they were reared in a 40m3 square net pen (cf. Fig. 2.3 in Chapter II).

From June 1983 to December 1983 (1st summer in seawater for the

2Y80 and 1Y81 cohorts), there were 2 and then 3 tanks available for salmon rearing. From December 1983 to the end of the saltwater rearing in the tanks (May 1985), 6 tanks were available. This resulted in densities varying according to the time and the cohort considered, particularly for the 1Y81 cohort (Fig. 4.1).

In August 1983, the 1Y81 cohort was split into two tanks about one week after the data collection/individual marking session. To avoid an additional stress to the fish it was decided not to reanasthaesize/recount them. The distribution into tank #5 and tank #6 was performed randomly. Densities in these two tanks were evaluated on a visual basis only. This resulted, for this cohort, in a slight imbalance in the number of fish per tank for the first summer in seawater (Fig. 4.1). For the 2Y81 cohort, the initial distribution in June 1984 was performed at the same time as the data collection session, using randomly pre-assigned tank positions. This resulted in a better balance in the fish number per tank (Fig. 4.1).

For the 2Y80 cohort, before the winter period, the distribution between the two overwintering regimes was randomly pre-assigned to all fish to avoid systematic bias. For the 1Y81 cohort, the same system was used. In this cohort, heating was originally planned for the tanks #2 and #6. However, the tank #6 was found to be too far from the heat exchanger and the heating was switched from tank #6 to tank #3 (Fig. 4.2). Hence, in the 1Y81 cohort, the overwintering temperature regime was confounded with 1st summer tank position (Fig. 4.1).

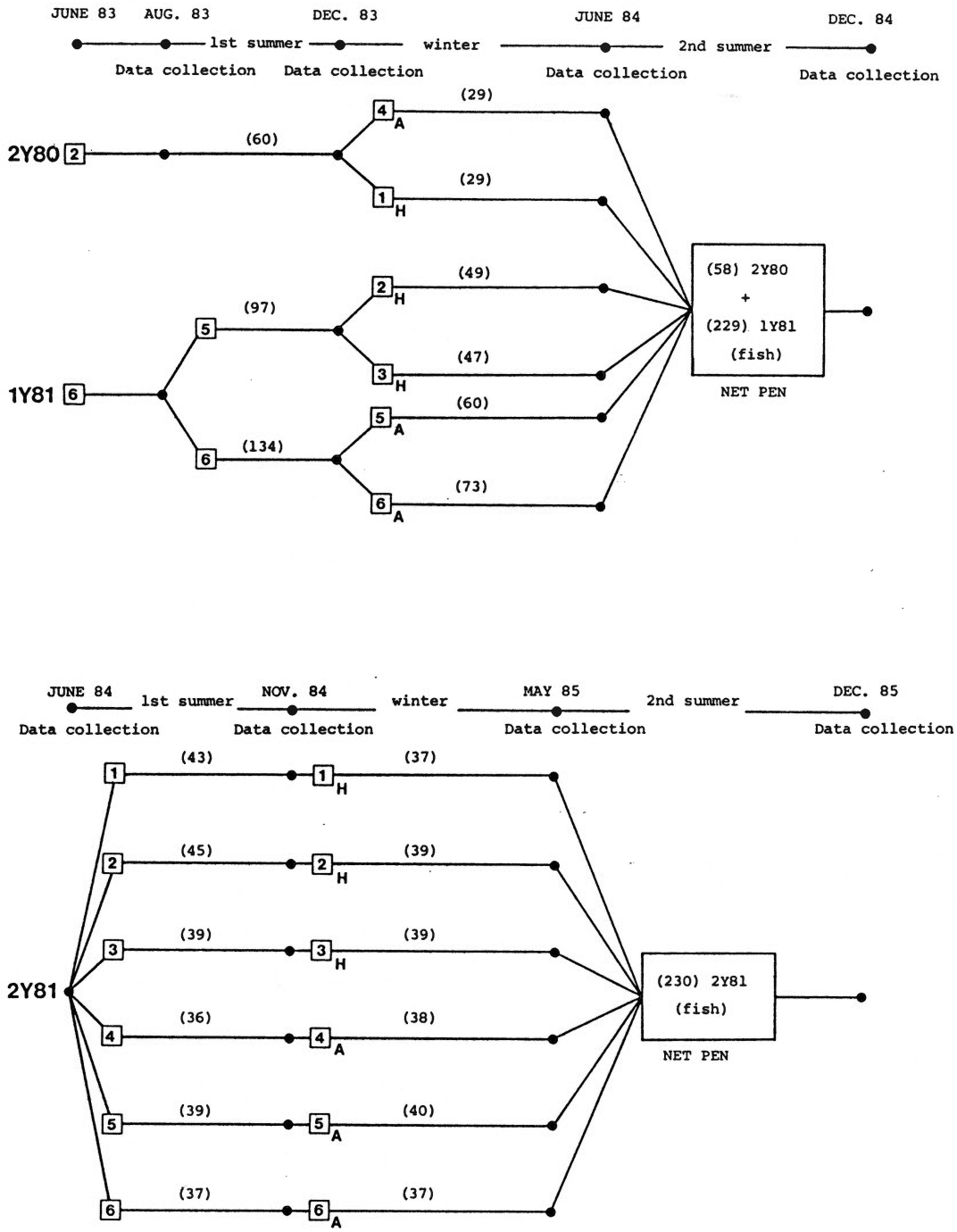

Figure 4.1: Distribution of the fish in the different tanks, during the first summer and the winter in seawater.

□ tanks and their identification numbers
( ) number of fish per tank
A ambiant tank during the winter
H heated tank during the winter

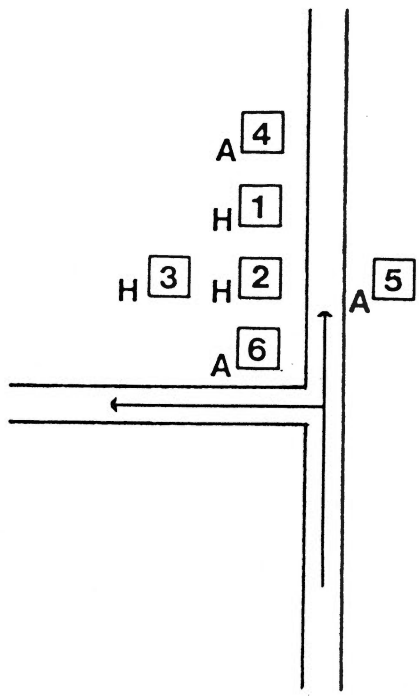

Figure 4.2: Tanks locations with respect to the main alleys.

☐ tanks and their identification numbers

A ambiant tank during the winter

H heated tank during the winter

For the 2Y81 cohort, before the winter period, there was not enough working space to randomly redistribute all the fish between the 6 tanks and, except for a few minor density readjustments, the fish retained the same tank position as in the 1st summer (Fig. 4.1). Hence, in this cohort, the winter tank position was confounded with 1st summer tank position (Fig. 4.1).

During the second summer at sea, all fish shared the same environment being reared together in a 40m3 square net pen floating in the Dalhousie Aquatron pool tank (Fig. 4.1).

As mentioned in Chapter II section 2.4, heating was adjusted so that the warmed seawater temperature varied between 5°C and 6°C during the winter periods. In February 1985 (winter period for the 2Y81 cohort), the ambiant seawater temperature was very cold and the warmed seawater temperature varied between 4°C and 5°C (Fig. 4.3 a,b). On average, the temperature differential between the two overwintering regimes was higher for the second winter (2Y81 cohort) than for the 1st winter (2Y80 and 1Y81 cohorts) (Fig. 4.3 a, b).

The X^2 test was used to compare maturation rates between groups. When comparing maturation rates with very low incidence, the exact Fisher's probability was computed (Schwartz, 1969). Pearson's product moment correlation between maturation rates and weight increments was calculated after percentage normalisation, with angular transformation (arc $\sin\sqrt{p}$). Comparison of variables between 2 large size groups were based on the standard normal deviate Z test (Schwartz, 1969). Comparisons of variables between several groups were performed by one-way analysis of variance.

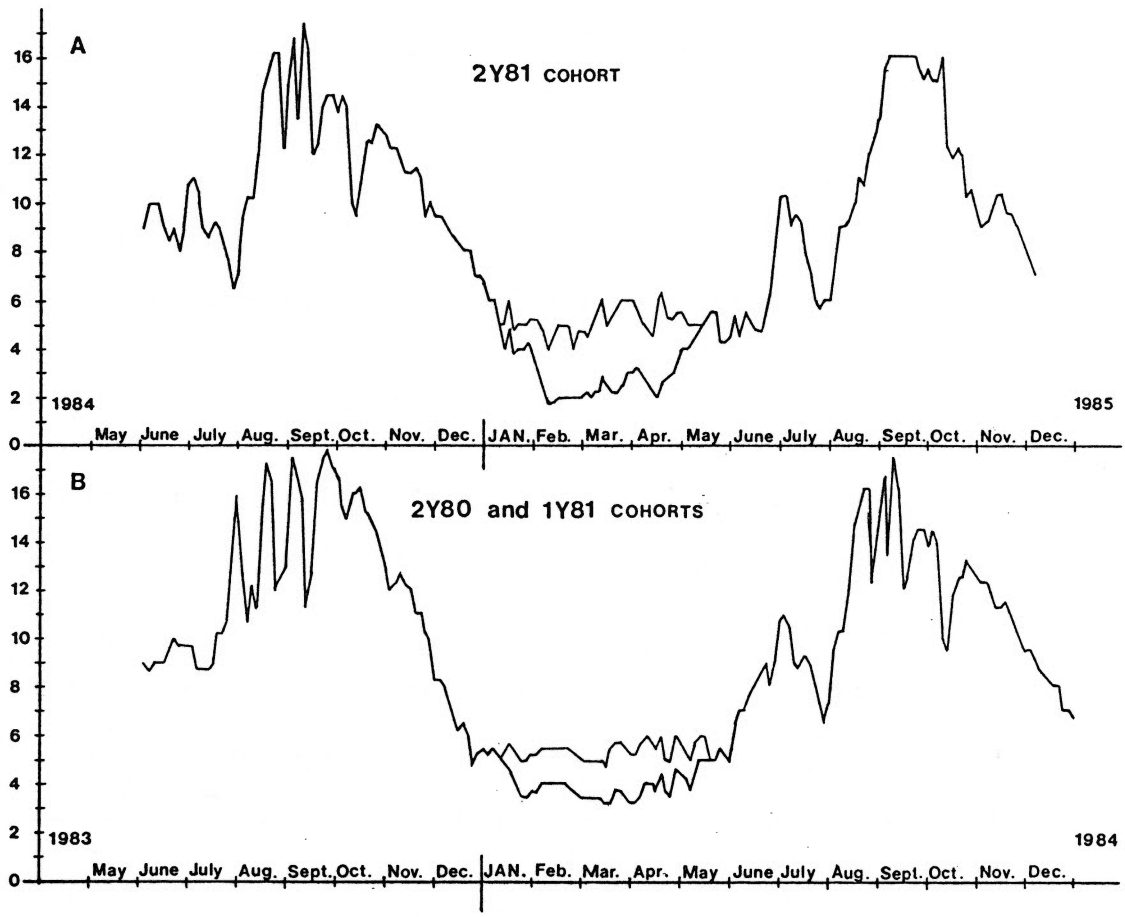

Figure 4.3 A, B: Temperature regimes during the seawater rearing periods for the 2Y81 cohort (A) and the 2Y80 and 1Y81 cohorts (B).

Normality was tested in all samples with the Kolmogorov-Smirnov one sample test (goodness of fit test) (Siegel, 1956; Nie and Hull, 1981). For samples normally distributed, homogeneity of variances was tested with the Bartlett-Box F test (Nie et al., 1975). In all cases where assumptions underlying the use of analysis of variance were violated (i.e. small sample size, nonnormality, heterogeneity of variances) probability statements were based on the Fisher's randomization test (Bradley, 1968; Benson, 1984). This test for group differences requires neither equality of group variances nor normality, because the F ratio reference distribution from which probability statements are formulated is computed from the permutation distribution of the data itself. When sample sizes were small, the method of complete enumeration was used, i.e. all possible data permutations are used to compute the probability. With larger sample sizes, this method of complete enumeration would require prohibitive amount of computation and the method of partial random enumeration was used instead, i.e. a random subset of 1000 permutations was chosen and probability statement was based on this random sample of permutations (Benson, 1984). A priori contrasts based on the t statistic were used to analyse further the nature of the variability. t statistics were based on separate variance estimates, since in many cases, there was reason to believe that the homogeneity of variances assumption had been violated. Analysis of the effects of overwintering temperature regimes and of replicate tanks on growth dynamics during the winter period was performed with a nested analysis of variance, replicate tank effect being nested within overwintering temperature regime effect.

3. Results

"Maiden" generally refers to spawners mature for the first time after smoltification, as opposed to repeat or multiple spawners (Saunders and Schom, 1985). In this study, however, the term "maiden" is used in a slightly different sense, i.e. to characterise the fish that were not precocious mature (-6) and not post-smolt precocious mature (+6). "Multi-sea-winter" refers to the fish that were not mature as grilse, regardless of previous maturation. A maiden grilse is therefore a fish that matured for the first time as a grilse. A maiden multi-sea-winter fish is a fish that never matured during the present experiment and would have matured for the first time as a 2 sea-winter salmon, or as a 3 sea-winter salmon, or maybe even later.

"Growth trajectory" means here the ensemble of growth descriptors available in the different cohorts, i.e. the length, weight and condition factor at the different data collection sessions and the length and weight increments between two consecutive data collection sessions. Condition factor is defined as (100.weight in g/(length in cm)3). The same convention that was used to characterise the maturation patterns in Table 2.2 Chapter II, will be used here.

Given the wide variety of maturation patterns that were observed (cf. Table 2.2 in Chapter II), the following strategy was used to analyse the links between growth patterns and maturation patterns. In the three cohorts, the "growth trajectory" of the maiden multi-sea-winter salmon, i.e. the fish that never matured, was used as a "standard growth trajectory" against which the growth trajectories of the other maturation patterns were compared.

Section 3.1 describes the growth trajectories of the maiden

multi-sea-winter fish, males and females, i.e. the standard growth trajectory in the 3 cohorts. Section 3.2 describes the growth trajectories of the maiden grilse in the 3 cohorts, i.e. the males and females that were mature as grilse but had not matured before. Section 3.3 describes the growth trajectories of the males that were precocious mature (-6) in the 2Y81 cohort. Section 3.4 documents the growth trajectories of the post-smolt precocious mature (+6) males. Section 3.5 analyses the influence of overwintering temperature and the influence of tank effect on the growth dynamics and on the grilse maturation incidence.

3.1 Growth trajectories of the maiden multi-sea-winter fish

In the 2Y81 cohort, these fish are the ♂ (0,0,0) and the ♀ (0,0,0). In the 1Y81 cohort, they are the ♂ (0,0), the ♀ (0,0) and the ? (0,0) since some fish among this maturation type were of unknown sex. In the 2Y80 cohort, they are the ♂ (?,0,0) and the ♀ (0,0,0). Hence, in this last cohort, some of the males may not be truly maiden multi-sea-winter fish since they could have been precocious mature (-6). In the absence of individual identification for this maturation episode, it is unfortunately not possible to differentiate them (cf. Chapter II).

3.1.1 Comparison of growth trajectories between sexes within cohorts. Tables 4.1, 4.2, 4.3.

In the three cohorts, there were no significant differences between males and females for length or weight at the different data collection sessions (26 comparisons), nor for length or weight increments between data collection sessions (20 comparisons) (Tables 4.1, 4.2, 4.3). There was a slight tendency for condition factors to be higher among females than among males, but the differences were small and were only significant in 3 out of 13 comparisons. Hence, it appears that, in the absence of maturation, males and females have very similar growth trajectories.

Table 4.1: Comparison of growth trajectories between sexes among the maiden multi-sea-winter fish, 2Y80 cohort.

Date observed	Variable	♂ (?,0,0) (1) Males 18 cases	♀ (0,0,0) Females 12 cases	Between sexes 1 way anova (2)
Aug. 83	Length (cm)	25.0	25.3	F=0.09 NS
	Weight (g)	169.5	173.5	F=0.05 NS
	Condition factor	1.06	1.05	F=0.19 NS
Dec. 83	Length (cm)	34.6	34.8	F=0.04 NS
	Weight (g)	501.3	501.5	F=0.00 NS
	Condition factor	1.16	1.17	F=0.00 NS
June 84	Length (cm)	37.5	37.8	F=0.06 NS
	Weight (g)	563.4	574.3	F=0.04 NS
	Condition factor	1.04	1.06	F=0.40 NS
Dec. 84	Length (cm)	51.4	50.8	F=0.23 NS
	Weight (g)	1637.4	1592.2	F=0.15 NS
	Condition factor	1.19	1.21	F=0.60 NS
Aug. 83 to Dec. 83	Length increment (cm)	9.6	9.5	F=0.00 NS
	Weight increment (g)	331.6	328.0	F=0.01 NS
Dec. 83 to June 84	Length increment (cm)	2.9	3.0	F=0.02 NS
	Weight increment (g)	62.1	72.8	F=0.10 NS
June 84 to Dec. 85	Length increment (cm)	13.9	12.9	F=3.80 NS
	Weight increment (g)	1074.1	1017.8	F=0.66 NS

(1) Some males might have been precocious mature (-6). See text.
(2) All probability statements based on Fisher's randomization test.

Table 4.2: Comparison of growth trajectories between sexes among the maiden multi-sea-winter fish, 1Y81 cohort.

Date observed	Variable	♂ (0,0) Males 20 cases	? (0,0) unknown 93 cases	♀ (0,0) females 47 cases	Between sexes 1 way anova
	Length (cm)	20.5	20.2	20.1	F=0.32 NS(1)
Aug. 83	Weight (g)	87.7	87.0	87.2	F=0.01 NS
	Condition factor	1.00	1.03	1.06	F=3.21 p=5%
	Length (cm)	28.9	29.2	29.3	F=0.16 NS
Dec. 83	Weight (g)	269.5	274.2	288.4	F=0.97 NS
	Condition factor	1.11	1.09	1.13	F=3.65 p=4% (1)
	Length (cm)	32.4	32.4	32.8	F=0.33 NS
June 84	Weight (g)	338.0	348.9	376.6	F=1.49 NS
	Condition factor	0.97	1.00	1.04	F=7.95 p=1%
	Length (cm)	47.1	47.2	47.4	F=0.10 NS
Dec. 84	Weight (g)	1208.1	1228.1	1268.5	F=0.52 NS
	Condition factor	1.14	1.15	1.17	F=1.18 NS
Aug. 83 to	Length increment (cm)	8.5	9.0	9.2	F=1.09 NS(1)
Dec. 83	Weight increment (g)	181.8	187.3	201.2	F=1.33 NS(1)
Dec. 83 to	Length increment (cm)	3.5	3.2	3.5	F=0.96 NS(1)
June 84	Weight increment (g)	68.5	74.7	88.2	F=1.11 NS
June 84 to	Length increment (cm)	14.6	14.9	14.7	F=0.50 NS
Dec. 84	Weight increment (g)	870.1	876.0	899.3	F=0.31 NS(1)

(1) Probability statements based on Fisher's randomization test.

Table 4.3: Comparison of growth trajectories between sexes among the maiden multi-sea-winter fish, 2Y81 cohort.

Date observed	Variable	♂ (0,0,0) Males 25 cases	♀ (0,0,0) Females 74 cases	Between sexes 1 way anova
	Length (cm)	20.8	20.8	F=0.00 NS(1)
Nov. 83	Weight (g)	101.0	99.6	F=0.04 NS(1)
	Condition factor	1.07	1.09	F=0.86 NS
	Length (cm)	22.7	22.7	F=0.03 NS(1)
June 84	Weight (g)	108.1	104.8	F=0.19 NS(1)
	Condition factor	0.88	0.88	F=0.06 NS
	Length (cm)	35.0	35.2	F=0.11 NS(1)
Nov. 84	Weight (g)	535.4	535.6	F=0.00 NS(1)
	Condition factor	1.21	1.21	F=0.15 NS
	Length (cm)	40.0	40.3	F=0.21 NS(1)
May 85	Weight (g)	710.4	720.0	F=0.05 NS
	Condition factor	1.07	1.08	F=0.31 NS
	Length (cm)	49.9	50.6	F=0.50 NS
Dec. 85	Weight (g)	1330.2	1372.5	F=0.32 NS
	Condition factor	1.03	1.05	F=0.37 NS
Nov. 83 to	Length increment (cm)	1.9	1.9	F=0.01 NS
June 84	Weight increment (g)	6.4	5.1	F=0.19 NS
June 84 to	Length increment (cm)	12.3	12.6	F=0.53 NS(1)
Nov. 84	Weight increment (g)	427.3	432.0	F=0.04 NS(1)
Nov. 84 to	Length increment (cm)	5.0	5.1	F=0.20 NS(1)
May 85	Weight increment (g)	175.0	184.5	F=0.16 NS
May 85 to	Length increment	9.8	10.2	F=0.96 NS
Dec. 85	Weight increment	604.8	643.7	F=0.62 NS

(1) Probability statements based on Fisher's randomization test.

3.1.2 Comparison of the maiden multi-sea-winter fish growth between the three cohorts. Table 4.4, Fig. 4.4.

The strict comparison of growth trajectories between the three cohorts was not possible. The three cohorts differed in mean size at the beginning of the experiments, in environmental conditions (mainly densities and temperature regimes) and also in dates of measurements. Table 4.4 provides, nevertheless, a rough comparison of growth between the three cohorts. In order to correct for the differences in size and in dates of measurement, Table 4.4 compares only the specific rate of increase in weight for the three periods of growth in seawater (1st summer, winter, 2nd summer). The specific rate of increase in weight during the winter before smoltification in the 2Y81 cohort is presented as well.

The maiden multi-sea-winter fish of the 2Y80 and 1Y81 cohorts experienced similar growth for the three periods considered (Table 4.4). Since both cohorts were reared concurrently, hence under the same temperature conditions, and dates of measurement were quite close, this result is not unexpected. However, growth appeared slightly better among the 1Y81 maiden multi-sea-winter fish than among the 2Y80 ones, for the three periods, even though densities were higher among the 1Y81 cohort than among the 2Y80 one for the 1st summer and the following winter in seawater (Fig. 4.1).

During their first summer in seawater, the maiden multi-sea-winter fish of the 2Y81 cohort experienced a somewhat better growth than had the ones of the 2Y80 and 1Y81 cohorts, even though the temperature conditions were not as favourable (Table 4.4).

Table 4.4: Comparison of the specific rate of increase in live weight of the maiden multi-sea-winter fish in the 3 cohorts.

Cohort	2Y80	1Y81	2Y81
Winter before smoltification	/	/	Nov. 83 to June 84
Specific rate of increase in weight [a]	/	/	0.03%
First summer in seawater	Aug. 83 to Dec. 83	Aug. 83 to Dec. 83	June 84 to Nov. 84
Specific rate of increase in weight	0.90%	0.97%	1.07%
Mean degree days available per month	391°C days	391°C days	354°C days
Winter in seawater	Dec. 83 to June 84	Dec. 83 to June 84	Nov. 84 to May 85
Specific rate of increase in weight	0.07%	0.13%	0.17%
Mean degree days available per month	153°C days	153°C days	163°C days
Second summer in seawater	June 84 to Dec. 84	June 84 to Dec. 84	May 85 to Dec. 85
Specific rate of increase in weight	0.57%	0.70%	0.30%
Mean degree days available per month	340°C days	340°C days	292°C days

[a] Specific rate of increase in live weight $= Gw\%\ day^{-1} = \dfrac{\log_e (wt2) - \log_e (wt1)}{t2 - t1}$

$\log_e (wt2)$ = Logarithm of weight at time t2
t2 - t1 = number of days between the two data collection sessions.

This observation is probably linked to the lower fish densities in the 2Y81 cohort during that period (Fig. 4.1). During the following winter, growth was again slightly better among the 2Y81 cohort than it had been among the 2Y80 and 1Y81 cohorts, temperature conditions being similar (Table 4.4). In contrast, growth during the second summer was considerably poorer among the maiden multi-sea-winter fish of the 2Y81 cohort than it had been among the 1Y81 or 2Y80 cohorts. This probably reflects the very poor temperature conditions during this period. During the months of June, July and August 1985, temperatures were between 1°C and 3°C, colder than they were the preceding year during the same months. This can be seen as well from the change in the condition factors with time among the maiden multi-sea-winter fish of the three cohorts (Fig. 4.4). Winter periods were characterised by a decrease of the condition factors while summer periods were generally characterised by the opposite. However, during their second summer in seawater, the maiden multi-sea-winter fish of the 2Y81 cohort experienced a decrease in condition factor, denoting a fairly poor growth performance.

The mean condition factor of the maiden multi-sea-winter fish in the 2Y81 cohort was particularly low (0.88) in June 1984, at the beginning of the first summer in seawater (Fig. 4.4). This is probably a consequence of the harsh environmental conditions experienced by the fish during the preceding winter at the Fraser's Mill hatchery (see Chapter II). The specific rate of increase in weight was only of 0.03%, a very low value compared to the other values reported in Table 4.4.

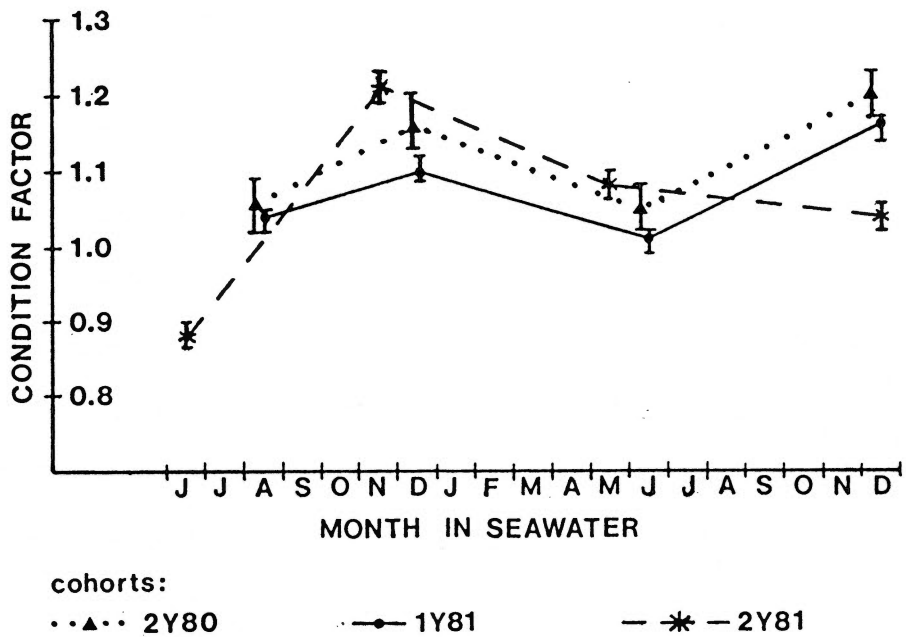

Figure 4.4: Change of condition factor with time, during the saltwater rearing, for the maiden multi-sea-winter salmon, in the three cohorts.

3.2 Growth trajectories of the maiden female grilse and the maiden male grilse

In the 2Y81 cohort, the maiden grilse are the ♂ (0,0,+18) and ♀ (0,0,+18), in the 1Y81 cohort the ♂ (0,+18) and ♀ (0,+18) and in the 2Y80 cohort the ♂ (?,0,+18) and ♀ (0,0,+18). Hence, in this last cohort, some of the males may not be truly maiden grilse since some were probably precocious mature (-6).

Tables 4.5 to 4.14, to be discussed below compare, within each cohort, the growth trajectories of the maiden female grilse and maiden male grilse with the standard growth trajectories (from maiden multi-sea-winter fish), for the different periods. In the three cohorts, the same general pattern can be drawn, although a few differences exist between the cohorts.

3.2.1 Growth during the winter before smoltification. Table 4.5.

Data concerning growth during this period are only available for the 2Y81 cohort (Table 4.5). In November 1983, 7 months before smoltification, no significant differences were found for length, weight and condition factor between the maiden multi-sea-winter fish and the maiden grilse, males and females. From November 1983 to June 1984, there were as well no significant differences for the length and weight increments (Table 4.5).

3.2.2 Growth during the first summer in seawater. Tables 4.6, 4.7, 4.8.

For the 2Y81 cohort, at the smoltification time in June 1984, there were no significant differences for length, weight and condition factor between the 3 maturation types (Table 4.6).

Table 4.5: Comparison of the growth trajectories of the maiden multi-sea-winter fish (standard), the maiden female grilse and the maiden male grilse, in the 2Y81 cohort, during the winter preceding smoltification.

Date observed	Variable	Standard ♂(0,0,0) ♀(0,0,0) 97 cases	♀ (0,0,+18) 43 cases	♂ (0,0,+18) 33 cases	Between maturation patterns comparison (1 way anova)
	Length (cm)	20.8	20.5	20.5	F=0.43 NS
Nov. 83	Weight (g)	100.0	96.9	99.3	F=0.14 NS
	Condition factor	1.09	1.10	1.13	F=2.36 NS
Nov. 83 to	Length increment (cm)	1.9	2.1	2.0	F=0.74 NS(1)
June 84	Weight increment (g)	5.4	9.2	3.5	F=1.93 NS(1)

(1) Probability statements based on Fisher's randomization test.

For the 1Y81 and 2Y80 cohorts, shortly after smoltification, in August 1983, there were as well no significant differences for the same three variables between the 3 maturation types (Tables 4.7, 4.8). Hence, smolt characteristics do not seem to bear any relationship with future grilse maturation status.

Similarly, during the first summer period, there were no significant differences between the 3 maturation types for length and weight increments (Tables 4.6, 4.7, 4.8).

At the end of the first summer period, there were still no significant differences between the 3 maturation types for length, weight and condition factor in the 2Y80 and 1Y81 cohorts (Tables 4.7, 4.8). In the 2Y81 cohort, there were as well no significant differences for length or weight. However, condition factors were slightly but significantly higher among the future male and female grilse than among the fish that would remain immature (Table 4.6).

3.2.3 Growth during the winter in seawater. Tables 4.9, 4.10, 4.11.

The 2Y80 cohort is a bit different with respect to winter growth, and is treated after the 1Y81 and 2Y81 cohorts which show the same pattern.

In the 1Y81 and 2Y81 cohorts, during the winter period, the future grilse (males and females) showed a weight increment considerably higher (very significantly so) than that of the fish that would remain immature (Tables 4.9, 4.10).

Table 4.6: Comparison of the growth trajectories of the maiden multi-sea-winter fish (standard), the maiden female grilse and the maiden male grilse, in the 2Y81 cohort, during the first summer after smoltification.

Date observed	Variable	Standard ♂ (0,0,0) ♀ (0,0,0) 99 cases	♀ (0,0,+18) 43 cases	♂ (0,0,+18) 33 cases	Between maturation patterns comparison (1 way anova)
June 84	Length (cm)	22.7	22.5	22.4	F=0.20 NS
	Weight (g)	105.6	106.1	102.8	F=0.13 NS
	Condition factor	0.88	0.91	0.91	F=2.28 NS
June 84 to Nov. 84	Length increment (cm)	12.5	12.9	13.1	F=1.82 NS(1)
	Weight increment (g)	430.8	462.1	465.9	F=2.20 NS
Nov. 84	Length (cm)	35.2	35.5	35.6	F=0.35 NS
	Weight (g)	535.6	568.2	568.7	F=1.61 NS
	Condition factor	1.21	1.26	1.25	F=6.07 p=0.3%

(1) Probability statements based on Fisher's randomization test.

Table 4.7: Comparison of the growth trajectories of the maiden multi-sea-winter fish (standard), the maiden female grilse and the maiden male grilse, in the 2Y80 cohort, during the first summer after smoltification.

Date observed	Variable	Standard ♂ (?,0,0) ♀ (0,0,0) 30 cases[1]	♀ (0,0,+18) 5 cases	♂ (?,0,+18) 15 cases[1]	Between maturation patterns comparison (1 way anova)[2]
Aug. 83	Length (cm)	25.1	25.4	25.4	F=0.08 NS
	Weight (g)	171.1	180.4	174.3	F=0.10 NS
	Condition factor	1.06	1.06	1.05	F=0.05 NS
Aug. 83 to Dec. 83	Length increment (cm)	9.6	10.7	9.4	F=0.69 NS
	Weight increment (g)	330.1	379.4	329.3	F=0.38 NS
Dec. 83	Length (cm)	34.7	36.1	34.9	F=0.44 NS
	Weight (g)	501.4	559.8	503.7	F=0.36 NS
	Condition factor	1.16	1.15	1.17	F=0.05 NS

[1] Some males might have been precocious mature (-6).
[2] All probability statements based on Fisher's randomization test.

Table 4.8: Comparison of the growth trajectories of the maiden multi-sea-winter fish (standard), the maiden female grilse and the maiden male grilse, in the 1Y81 cohort, during the first summer after smoltification.

Date observed	Variable	Standard ♂(0,0) ♀(0,0) 160 cases	♀ (0,+18) 5 cases	♂ (0,+18) 34 cases	Between maturation patterns comparison (1 way anova)(1)
	Length (cm)	20.2	19.7	19.8	F=0.85 NS
Aug. 83	Weight (g)	87.1	81.5	83.9	F=0.41 NS
	Condition factor	1.04	1.06	1.06	F=1.10 NS
Aug. 83 to	Length increment (cm)	9.0	9.4	9.1	F=0.14 NS
Dec. 83	Weight increment (g)	190.7	197.1	190.7	F=0.03 NS
	Length (cm)	29.2	29.0	28.9	F=0.24 NS
Dec. 83	Weight (g)	277.8	278.6	274.6	F=0.04 NS
	Condition factor	1.10	1.13	1.12	F=1.21 NS

(1) All probability statements based on Fisher's randomization test.

Table 4.9: Comparison of the growth trajectories of the maiden multi-sea-winter fish (standard), the maiden female grilse and the maiden male grilse, in the 2Y81 cohort, during the winter in seawater.

Date observed	Variable	Standard ♂ (0,0,0) ♀ (0,0,0) 99 cases	♀ (0,0,+18) 43 cases	♂ (0,0,+18) 33 cases	Between maturation patterns comparison (1 way anova)
Nov. 84 to May 85	Length increment (cm)	5.1	6.2	6.5	F=19.37 p<0.01%
	Weight increment (g)	182.1	363.8	370.7	F=62.05 p<0.01%
May 85	Length (cm)	40.2	41.7	42.1	F=5.77 p<0.4%
	Weight (g)	717.6	932.0	939.4	F=27.83 p<0.01%
	Condition factor	1.08	1.27	1.25	F=81.95 p<0.01%

Table 4.10: Comparison of the growth trajectories of the maiden multi-sea-winter fish (standard), the maiden female grilse and the maiden male grilse, in the 1Y81 cohort, during the winter in seawater.

Date observed	Variable	Standard ♂ (0,0) ♀ (0,0) 160 cases	♀ (0,+18) 5 cases	♂ (0,+18) 34 cases	Between maturation patterns comparison (1 way anova)(1)
Dec. 83 to June 84	Length increment (cm)	3.3	4.0	3.9	F=2.25 NS
	Weight increment (g)	77.9	165.4	125.1	F=9.14 p=0.5%
June 84	Length (cm)	32.5	33.0	32.7	F=0.12 NS
	Weight (g)	355.7	444.0	399.7	F=3.31 p=4.2%
	Condition factor	1.01	1.22	1.09	F=24.40 p=0.1%

(1) All probability statements based on Fisher's randomization test.

The maiden grilse also showed during this period, a higher length increment than maiden multi-sea-winter fish, but the differences were less pronounced and it was not significant in the 1Y81 cohort (Tables 4.9, 4.10). In the 2Y81 cohort, the maiden female and male grilse showed similar length and weight increments (Table 4.9). In the 1Y81 cohort, the maiden female grilse showed length and weight increments a bit larger than the maiden male grilse (Table 4.10).

At the end of this winter period, as a result of this better growth performance, the future grilse were slightly longer. (significantly so in the 2Y81 cohort, not significantly so in the 1Y81 cohort), and were significantly heavier than the fish that would remain immature. These future grilse, and particularly the females, were characterised by a condition factor considerably higher (very significantly so in both cohorts) compared to the maiden multi-sea-winter fish (Tables 4.9, 4.10).

In the 2Y80 cohort (Table 4.11), the maiden female grilse showed exactly the same pattern that was seen in the 1Y81 and 2Y81 cohorts. However, the future male grilse did not experience a better growth than the future immature fish. Their weight and length increments were of the same order. As a result, in June 84, length, weight and condition factor were quite similar among the future male grilse and among the fish that would remain immature (Table 4.11). The fact that both the groups of "maiden" male grilse and of "maiden" multi-sea-winter male fish are actually heterogeneous, since some of the males were precocious mature (-6), is probably responsible for this difference, particularly because of the relatively small number of fish in both groups.

Table 4.11: Comparison of the growth trajectories of the maiden multi-sea-winter fish (standard), the maiden female grilse and the maiden male grilse, in the 2Y80 cohort, during the winter in seawater.

Date observed	Variable	Standard ♂ (?,0,0) ♀ (0,0,0) 30 cases[1]	♀ (0,0,+18) 5 cases	♂ (?,0,+18) 15 cases[1]	Between maturation patterns comparison (1 way anova)[2]
Dec. 83 to June 84	Length increment (cm)	2.9	3.4	2.9	F=0.22 NS
	Weight increment (g)	66.4	184.4	73.1	F=3.10 NS (5.4%)
June 84	Length (cm)	37.6	39.5	37.8	F=0.65 NS
	Weight (g)	567.7	744.2	576.8	F=2.25 NS
	Condition factor	1.05	1.14	1.05	F=2.20 NS

[1] Some males might have been precocious mature (-6).
[2] All probability statements based on Fisher's randomization test.

3.2.4 Growth during the second summer in seawater. Tables 4.12, 4.13, 4.14.

During this period, in the three cohorts, the maiden female grilse showed length and weight increments considerably lower than the multi-sea-winter fish. The difference was more pronounced in terms of length increments than weight increments. The maturing female grilse showed a length increment around 3 cm lower than that of the immature fish, but their weight increment was only around 160g lower (Tables 4.12, 4.13, 4.14). At the end of this period, the now mature female grilse were smaller than their immature counterparts, showed relatively similar weights and had a much higher condition factor (Tables 4.12, 4.13, 4.14).

It is obvious that these observations of maturing females showing a lower growth during the second summer in seawater is a consequence of the process of gonad development and ripening taking place during this period. Gonadal development is particularly energetically costly for female salmonids. (Thorpe et al., 1982; Tveranger, 1985; Asknes et al., 1986). The lower length increment observed during this period can be seen as a measure of the reduction of somatic growth due to the involment in gonadal growth. In terms of weight increment, the maturation process is less costly because gonadal weight increase compensates partly for the reduced somatic weight increase.

During this same period, the maiden male grilse showed more variable results. In the 2Y80 and 1Y81 cohorts, the maturing males experienced a growth slightly better than their immature counterparts (Tables 4.13, 4.14).

Table 4.12: Comparison of the growth trajectories of the maiden multi-sea-winter fish (standard), the maiden female grilse and the maiden male grilse, in the 2Y81 cohort, during the second summer in seawater.

Date observed	Variable	Standard ♂ (0,0,+18) 94 cases	♀ (0,0,+18) 41 cases	♂ (0,0,+18) 33 cases	Between maturation patterns comparison (1 way anova)
May 85 to Dec. 85	Length increment (cm)	10.5	7.5	8.2	F=39.96 p<0.01%
	Weight increment (g)	633.8	525.9	416.0	F=16.93 p<0.01%
Dec. 85	Length (cm)	50.4	49.3*	50.3*	F=1.54 NS(1)
	Weight (g)	1361.7	1469.5*	1355.4*	F=2.22 NS
	Condition factor	1.04	1.22*	1.06*	F=41.71 p=0.1% (1)

(1) Probability statements based on Fisher's randomization test.
* Denotes maturity at the time considered.

Table 4.13: Comparison of the growth trajectories of the maiden multi-sea-winter fish (standard), the maiden female grilse and the maiden male grilse, in the 1Y81 cohort, during the second summer in seawater.

Date observed	Variable	Standard ♂(0,0) ♀(0,0) 152 cases	♀ (0,+18) 5 cases	♂ (0,+18) 30 cases	Between maturation patterns comparison (1 way anova)(1)
June 84 to Dec. 84	Length increment (cm)	14.8	11.3	15.2	F=11.68 p=0.1%
	Weight increment (g)	881.5	678.6	967.9	F=6.65 p=0.1%
Dec. 84	Length (cm)	47.3	44.3*	47.6*	F=2.37 NS
	Weight (g)	1236.3	1122.6*	1346.1*	F=3.00 NS
	Condition factor	1.16	1.28*	1.23*	F=19.46 p=0.1%

(1) All probability statements based on Fisher's randomization test.
* Denotes maturity at the time considered.

Table 4.14: Comparison of the growth trajectories of the maiden multi-sea-winter fish (standard), the maiden female grilse and the maiden male grilse, in the 2Y80 cohort, during the second summer in seawater.

Date observed	Variable	Standard ♂(?,0,0) ♀(0,0,0) 30 cases[1]	♀ (0,0,+18) 5 cases	♂(?,0,+18) 15 cases[1]	Between maturation patterns comparison (1 way anova)[2]
June 84 to Dec. 84	Length increment (cm)	13.5	10.3	14.4	F=7.86 p=0.3%
	Weight increment (g)	1051.6	871.4	1227.5	F=6.12 p=0.2%
Dec. 84	Length (cm)	51.1	49.8*	52.2*	F=0.94 NS
	Weight (g)	1619.3	1615.6*	1804.3*	F=1.74 NS
	Condition factor	1.20	1.30*	1.26*	F=5.60 p=0.7%

[1] Some males might have been precocious mature (-6).
[2] All probability statements based on Fisher's randomization test.
* Denotes maturity at the time considered.

As a result, in December 1984, the now mature male grilse were slightly longer and heavier than the maiden multi-sea-winter fish. Their condition factor was also higher than that of the immature fish, though not as high as among mature female grilse (Tables 4.13, 4.14). In the 2Y81 cohort, however, the opposite result was observed, the maturing males experiencing a lower growth compared to their immature counterparts (Table 4.12). As a result in this cohort, in November 1985, the now mature male grilse were of about the same length and weight as the maiden multi-sea-winter fish. Their condition factors were not much higher than those of the immature fish, and looked more typical of immature fish than of mature males (Table 4.12). In section 3.1.2, it was noted that the growth performance of the maiden multi-sea-winter fish of the 2Y81 cohort, for the second summer, was quite poor compared to that of the 2Y80 and 1Y81 cohorts. This was attributed to the very poor temperature conditions during that second summer, particularly in June, July and August 1985. It is probable that this growth reduction observed in the maturing males of the 2Y81 cohort, during the second summer in seawater, but not among the maturing males of the 2Y80 and 1Y81 cohorts, is as well linked to the same phenomenon. Gonadal development and maturation are energy costly to males, although much less than in females (Tveranger, 1985; Aksnes et al., 1986). Hence, some degree of somatic growth reduction should have been observed in the maturing males of the three cohorts. However, it was observed that during the winter period (cf. section 3.2.3), future male grilse grew better than the fish that would remain immature. It is probable that the same tendency went on for some time during early summer. Then, later in the season, with increasing involvement in gonadal development,

the reverse tendency probably occurred, translating into somatic growth reduction. In the 2Y80 and 1Y81 cohorts, the good growing conditions prevailing during the second summer probably allowed the future male grilse to experience a strong initial growth advantage over the immature fish which, in turn, tended to mask the reduction in somatic growth that these maturing males were to experience later in the season. In the 2Y81 cohort, in contrast, the poor growing performance during early summer, probably did not allow the future male grilse to accumulate enough growth differential to mask the later reduction in somatic growth accompanying gonadal developement.

It is probable that the same sort of phenomenon takes place among maturing females as well, however in their case, the reduction of somatic growth accompanying gonadal development is probably too strong to be masked under most growing circumstances.

It can be noted that, during the second summer in seawater the maiden multi-sea-winter fish, the maiden female grilse and the maiden male grilse showed, in the 2Y81 cohort, lower length and weight increments compared with their counterparts in the 2Y80 and 1Y81 cohorts, even though these 2Y81 fish were longer and heavier at the beginning of the second summer. These three maturation types showed as well a decrease in condition factor during the second summer in the 2Y81 cohort, while they showed the opposite among the 2Y80 and 1Y81 cohorts. Hence, in the 2Y81 cohort, all the fish showed poor growing performance during the second summer, but the effect of this poor summer was most apparent among the maturing males.

3.2.5 Summary

To summarize the findings, it appears that there were no differences in the growth trajectories of the three maturation types during the winter before smoltification and during the first summer in seawater, just after smoltification. During the winter in seawater, the future grilse, males and females, experienced a better growth, particularly in terms of weight increments, than the fish that were to remain immature. At the end of the winter period, these future grilse were somewhat longer and heavier and had a considerably higher condition factor than the fish that were to remain immature. During the second summer in seawater, the maturing female grilse experienced a somatic growth that was reduced compared to the maiden multi-sea-winter fish. The maturing male grilse experienced a growth that was slightly better than the immature fish, when the growing conditions were good, but they showed a reduced growth compared to the immature fish, when the growing conditions were poor.

3.3 Growth trajectories of the precocious mature (-6) males

No precocious maturation (-6) episode took place in the 1Y81 cohort and, although precocious maturation (-6) did occur in the 2Y80 cohort, the absence of individual identification at that time means that the individual records are incomplete in this cohort (cf. Chapter II). Hence, most of the data presented here (sub-sections 3.3.1 to 3.3.5) were collected in the 2Y81 cohort. Data concerning growth trajectories were collected from the onset of precocious maturation (-6) in November 1983 to the onset of grilse maturation (+18) in December 1985. Hence, these sub-sections analyse the effects of precocious maturation (-6) on growth trajectories <u>after</u> precocious maturation (-6) took place.

In the last sub-section (3.3.6), some data pertaining to the growth trajectories <u>before</u> precocious maturation (-6) or early precocious maturation (0+) took place in the three cohorts are presented.

In the sub-sections 3.3.1 to 3.3.5, the patterns of growth trajectory differences between the precocious mature males (-6) that matured as grilse [$\sigma^{\nearrow}$ (-6,0,+18)] and those that did not mature again as grilse [$\sigma^{\nearrow}$ (-6,0,0)] are compared to the patterns that were observed between the maiden male grilse [$\sigma^{\nearrow}$ (0,0,+18)] and the maiden multi-sea-winter fish [$\sigma^{\nearrow}$ (0,0,0)] (cf. section 3.2). (The 3 males that were precocious mature (-6) and post-smolt precocious mature (+6) are treated in the following section 3.4).

Tables 4.15 to 4.18 present such comparisons between the four maturation types, for the four periods covered from November 1983 to December 1985. For each variable, an overall comparison is presented (1 way anova), as well as a set of three contrasts to analyse more precisely the nature of the variability. Contrasts were performed only

when the overall comparison was significant. Contrasts #1 compare the maiden multi-sea-winter males [♂(0,0,0)] with the maiden male grilse [♂(0,0,+18)]. Hence, contrasts #1 are simply the repetitions of the analysis performed in section 3.2, but this time on males only. Contrasts #2 compare the precocious males maturing again as grilse [♂(-6,0,+18)] with the precocious males that did not mature again as grilse [♂(-6,0,0)]. Hence, contrasts #1 are "between grilse maturation types for nonprecocious males" comparison, while contrasts #2 are "between grilse maturation types for precocious males" comparisons. Contrasts #3 compare the pooled nonprecocious males [♂(0,0,+18) + ♂(0,0,0)] with the pooled precocious males [♂(-6,0,+18) + ♂(-6,0,0)]. Hence, contrasts #3 are "between precocious maturation types" overall comparisons.

3.3.1 Growth during the winter before smoltification. Table 4.15.

Four out of five overall comparisons between the four maturation types showed statistically significant differences (Table 4.15).

In section 3.2.1 (Table 4.5), no differences could be detected during this period between the maiden multi-sea-winter fish [♂(0,0,0) + ♀(0,0,0)], the maiden female grilse [♀(0,0,+18)] and the maiden male grilse [♂(0,0,+18)]. This is confirmed by the contrasts #1, all but one non significant (Table 4.15). The mean condition factor of the maiden male grilse was significantly higher than that of the maiden multi-sea-winter males in November 1983 (Table 4.15), a result which was previously not shown in Table 4.5 (section 3.2.1) where no significant difference for condition factor was detected when males and females were tested together.

Table 4.15: Comparison of the growth trajectories of the maiden multi-sea-winter males (standard), the maiden male grilse, the male grilse that were precocious mature and the multi-sea-winter males that were precocious mature, in the 2Y81 cohort, during the winter before smoltification.

Date observed	Variable	Group 1 Standard (Males only) ♂(0,0,0) 24 cases	Group 2 ♂(0,0,+18) 33 cases	Group 3 ♂(-6,0,+18) 28 cases	Group 4 ♂(-6,0,0) 18 cases	Overall comparison 1 way anova	Contrast 1 Group 1 vs Group 2 (Between grilse maturation types among nonprecocious males)	Contrast 2 Group 3 vs Group 4 (Between grilse maturation types among precocious males)	Contrast 3 Groups 1&2 vs Groups 3&4 (Between precocious maturation types)
Nov. 83	Length (cm)	20.8	20.5	18.8‡	19.2‡	F=5.41 p=0.3%(1)	t=0.48 NS	t=-1.02 NS	t=3.96 p<0.1%
	Weight (g)	101.0	99.3	79.8‡	82.2‡	F=3.02 p=3.2%(1)	t=0.16 NS	t=-0.41 NS	t=3.14 p=0.2%
	Condition factor	1.07	1.13	1.18‡	1.14‡	F=7.19 p<0.1%	t=-2.51 p=1.5%	t=1.52 NS	t=-3.69 p<0.1%
Nov. 83 to June 84	Increment in length (cm)	1.9	2.0	2.4	2.2	F=2.03 NS			
	Increment in weight (g)	6.4	3.5	13.0	13.9	F=3.80 p=1.7%(1)	t=0.73 NS	t=-0.31 NS	t=-3.41 p=0.1%

(1) Probability statements based on Fisher's randomization test.

‡ Denotes maturity at the time considered.

This may be a chance event that carries no specific biological meaning.

None of the contrasts #2 showed statistically significant differences. Hence, among the precocious mature (-6) males, there were no differences in the growth trajectories during this period, between the males that would mature again as grilse (+18) and the ones that would not. This result is exactly similar to that observed among non precocious males (contrasts #1 in Table 4.15, and also Table 4.5 in section 3.2.1).

On the other hand, all contrasts #3 showed significant differences. Hence, it appears that during this period, the overall differences that were detected by the general test were solely attributable to differences between the precocious mature (-6) males and the nonprecocious males, irrespective of the future grilse maturation (+18) status.

In November 1983, the precocious mature (-6) males had a smaller length, a smaller weight and a higher condition factor than the nonprecocious males. These results are not surprising. Mature males generally have a higher condition factor than immature fish (Leyzerovich, 1973; Naevdal, 1983), as was the case with mature grilse (+18) (cf. section 3.2.4) and post-smolt precocious (+6) males (see section 3.4). The fact that these precocious (+6) males are smaller than their immature counterparts probably reflects the fact that precocious maturation (-6) entailed a certain energy cost, which translated into a reduced somatic growth some time before maturation.

From November 1983 to june 1984, the precocious mature (-6) males showed significantly higher weight increments and higher length increments (not significantly so) than the nonprecocious males. This

result is more surprising since mature fish generally show the opposite, i.e. the growth during the winter following maturation is generally reduced, a result generally explained by the lower feeding activity of the fish reabsorbing gonad (Kato, 1975; Smith et al., 1979; personal observation). This observation is quite certainly linked with the particular environmental conditions experienced by the fish during this winter period. As noted in Chapter II section 2.3, the temperature was quite low and the feeding much reduced because of the ice covering the pond in which the fish were reared during this period. It can be seen from Table 4.15 that, even though the precocious mature (-6) males performed better than their immature counterparts, their growth was nevertheless quite low, with a weight increment of only 13 to 14 g in a seven month period. It is probable that during this winter, all fish had a very low feeding activity, irrespective of their precocious maturation (-6) status, because of the ice obstruction. Hence, the nonprecocious males could probably not show a better growth, since their feeding was probably as much reduced as that of the precocious (-6) males. The small but significant "paradoxical" advantage that the precocious (-6) males seemed to have enjoyed over the nonprecocious males, could be linked to the process of gonad reabsorption taking place during this period. Gonad tissues are energy rich and their reabsorption might have provided these males with a small but significant source of energy in this adverse period.

3.3.2 Growth during the first summer in seawater. Table 4.16.

The overall comparisons between the four maturation types showed that in June and November 1984 there existed statistically significant

differences for length and condition factor but not for weight. There were no statistically significant differences for the length and weight increments between June and November 1984 (Table 4.16).

Section 3.2.2 (Tables 4.6 to 4.8) showed that in the 2Y81 cohort, during the first summer in seawater, no differences could be detected among the maiden fish, between those that would mature as grilse (+18) (maiden male and female grilse) and those that would remain immature (maiden multi-sea-winter fish), with the exception of the condition factor which was slightly but significantly higher among the future grilse (+18) in November 1984. The series of contrasts #1 confirm these results among the non precocious males (Table 4.16).

None of contrasts #2 showed statiscally significant differences (Table 4.16). Hence, among the precocious mature (-6) males, no difference could be found in the growth trajectories, during this period, between the fish that would mature again as grilse and the ones that would not. Again, this result mirrors what can be seen among the nonprecocious males (contrasts #1).

All contrasts #3 were significant (Table 4.16), indicating that, again, the overall significant differences detected by the one-way anova were solely attributable to the differences between precocious (-6) and nonprecocious males, irrespective of future grilse maturation (+18) status. However, during this period, the effect of precocious maturation (-6) did not appear to be of a dynamic nature, but rather as a carry over from previous differences. In June 1984, at smoltification time, the previously precocious (-6) males were still significantly smaller than the fish that had not been precocious (Table 4.16).

Table 4.16: Comparison of the growth trajectories of the maiden multi-sea-winter males (standard), the maiden male grilse, the male grilse that were precocious mature and the multi-sea-winter males that were precocious mature, in the 2Y81 cohort, during the first summer in seawater.

Date observed	Variable	Group 1 Standard (Males only) ♂(0,0,0) 25 cases	Group 2 ♂(0,0,+18) 33 cases	Group 3 ♂(-6,0,+18) 28 cases	Group 4 ♂(-6,0,0) 18 cases	Overall comparison 1 way anova	Contrast 1 Group 1 vs Group 2 (Between grilse maturation types among nonprecocious males)	Contrast 2 Group 3 vs Group 4 (Between grilse maturation types among precocious males)	Contrast 3 Groups 1&2 vs Groups 3&4 (Between precocious maturation types)
June 84	Length (cm)	22.7	22.4	21.1	21.4	F=3.34 p=2.5%(1)	t=0.48 NS	t=-0.66 NS	t=3.12 p=0.3%
	Weight (g)	108.1	102.8	92.8	96.2	F=1.31 NS (1)			
	Condition factor	0.88	0.90	0.97	0.97	F=9.26 p=0.1%(1)	t=-0.77 NS	t=0.18 NS	t=-5.64 p<0.1%
June 84 to Nov. 84	Increment in length (cm)	12.3	13.1	12.6	12.7	F=1.06 NS(1)			
	Increment in weight (g)	427.3	465.9	394.6	418.2	F=2.48 NS (1)			
Nov. 84	Length (cm)	35.0	35.6	33.7	34.2	F=2.67 p=4.2(1)	t=-0.63 NS	t=-0.81 NS	t=2.52 p=1.4%
	Weight (g)	535.4	568.7	487.4	514.4	F=2.43 NS(1)			
	Condition factor	1.21	1.25	1.25	1.28	F=2.68 p=5%	t=-2.00 p=5%	t=-1.04 NS	t=-2.04 p=4.5%

(1) Probability statements based on Fisher's randomization test.

Although their length increment had been significantly higher from November 1983 to June 1984, this was not sufficient to compensate for their initial smaller length in November 1983 (Table 4.15). In June 1984, the previously precocious (-6) males had also a smaller mean weight, but not significantly so, since their higher weight increment partly compensated for their initial smaller weight. They were still showing a significantly higher condition factor (Table 4.16).

During the first summer in seawater, from June to November 1984, all four groups showed similar length and weight increments. No statistically significant influence of the previous precocious maturation (-6) status could be detected (Table 4.16).

In November 1984, the previously precocious (-6) males were still characterised by significantly lower length and significantly higher condition factor.

3.3.3 Growth during the winter in seawater. Table 4.17.

The five overall comparisons between the four maturation types showed highly significant differences during this period (Table 4.17). However, when looking at the series of contrasts, the picture emerging is quite different from what was seen during the last two periods.

From November 1984 to May 1985, among the previously maiden fish, the future grilse (+18) showed length and weight increments considerably higher than the fish that would remain immature (first 2 contrasts #1, Table 4.17). The same could be seen among the previously precocious (-6) males, although for the length increment, the difference was not significant (first 2 contrasts #2, Table 4.17).

Table 4.17: Comparison of the growth trajectories of the maiden multi-sea-winter males (standard), the maiden male grilse, the male grilse that were precocious mature and the multi-sea-winter males that were precocious mature, in the 2Y81 cohort, during the winter in seawater.

Date observed	Variable	Group 1 Standard (Males only) ♂(0,0,0) 25 cases	Group 2 ♂(0,0,+18) 33 cases	Group 3 ♂(-6,0,+18) 28 cases	Group 4 ♂(-6,0,0) 18 cases	Overall comparison 1 way anova	Contrast 1 Group 1 vs Group 2 (Between grilse maturation types among nonprecocious males)	Contrast 2 Group 3 vs Group 4 (Between grilse maturation types among precocious males)	Contrast 3 Groups 1&2 vs Groups 3&4 (Between precocious maturation types)
Nov. 84 to May 85	Increment in length (cm)	5.0	6.5	5.8	5.2	F=6.44 p=0.1%(1)	t=-5.04 p<0.1%	t=1.03 NS	t=0.82 NS
	Increment in weight (g)	175.0	370.7	292.9	204.1	F=15.25 p<0.01%	t=-7.65 p<0.1%	t=2.11 p=4.2%	t=0.99 NS
May 85	Length (cm)	40.0	42.1	39.5	39.4	F=4.50 p=0.7%(1)	t=-2.13 p=4.1%	t=0.12 NS	t=2.48 p=1.6%
	Weight (g)	710.4	939.4	780.3	718.4	F=7.99 p=0.1%(1)	t=-4.19 p<0.1%	t=1.08 NS	t=1.90 NS
	Condition factor	1.07	1.25	1.24	1.16	F=21.83 p<0.01%	t=-7.03 p<0.1%	t=2.68 p=1.2%	t=-2.03 p=4.7%

(1) Probability statements based on Fisher's randomization test.

No overall effect of precocious maturation (-6) on the growth performance during the winter period could be detected (first 2 contrasts #3, Table 4.17).

In May 1985, among the nonprecocious males, the future grilse (+18) were significantly heavier and longer and had a significantly higher condition factor than the ones that would remain immature (Table 4.17). Among the precocious (-6) males, the future grilse (+18) had a significantly higher condition factor than the fish that would remain immature, they were longer and heavier as well but not significantly so. Some overall influence of precocious maturation (-6) could still be detected, in that the previously precocious (-6) males were still characterised by a significantly lower mean length and a significantly higher mean condition factor than the fish that were nonprecocious. However, it can be noted that the differences tended to get smaller with elapsed time.

3.3.4 Growth during the second summer in seawater. Table 4.18.

The overall comparisons revealed that between the four maturation types, strong differences existed for growth performance during the second summer (Table 4.18). Exactly the same pattern was seen among the previously precocious (-6) males (contrasts #2) as among the maiden males (contrasts #1). In both cases, the maturing male grilse (+18) showed significantly lower length and weight increments than the males not maturing. No overall effect of precocious maturation (-6) could be detected (contrasts #3).

Table 4.18: Comparison of the growth trajectories of the maiden multi-sea-winter males (standard), the maiden male grilse, the male grilse that were precocious mature and the multi-sea-winter males that were precocious mature, in the 2Y81 cohort, during the second summer in seawater.

Date observed	Variable	Group 1 Standard (Males only) ♂(0,0,0) 24 cases	Group 2 ♂(0,0,+18) 33 cases	Group 3 ♂(-6,0,+18) 28 cases	Group 4 ♂(-6,0,0) 18 cases	Overall comparison 1 way anova	Contrast 1 Group 1 vs Group 2 (Between grilse maturation types among nonprecocious males)	Contrast 2 Group 3 vs Group 4 (Between grilse maturation types among precocious males)	Contrast 3 Groups 1&2 vs Groups 3&4 (Between precocious maturation types)
May 85 to Dec. 85	Increment in length (cm)	9.8	8.2	8.2	10.4	F=9.76 p<0.01%	t=3.40 p=0.1%	t=-3.93 p<0.1%	t=-0.85 NS
	Increment in weight (g)	604.8	416.0	417.1	635.6	F=8.0 p<0.01%	t=3.26 p=0.2%	t=-3.32 p=0.2%	t=-0.36 NS
Dec. 85	Length (cm)	49.9	50.3‡	47.7‡	49.7	F=3.17 p=4.1%(1)	t=-0.29 NS	t=-2.02 p=5%	t=1.92 NS
	Weight (g)	1330.2	1355.4‡	1197.4‡	1354.0	F=1.61 NS			
	Condition factor	1.03	1.06‡	1.08‡	1.08	F=1.80 NS			

(1) Probability statements based on Fisher's randomization test.

‡ Denotes maturity at the time considered.

In December 1985, there was no longer much differences between the four maturation types, since the growth performance during the second summer was exactly the reverse from that observed during the preceding winter. It is surprising to note that there were no significant differences for condition factor between the now mature male grilse (+18) and the still immature multi-sea-winter males among the previously precocious (-6) males and the previously maiden males. This is probably related to the already noted poor growing conditions during this second summer that seemed to have particularly affected the maturing males (cf. section 3.2.4). As previously noted, the overall effect of precocious maturation (-6) tended to fade and could no longer be detected (contrasts #3).

3.3.5 Summary

Among the precocious (-6) males, the pattern of growth trajectory differences between the males that would mature again as grilse [♂ (-6,0,+18)] and the ones that would not [♂ (-6,0,0)], as evidenced by the series of contrasts #2, was surprisingly close to the patterns that had been revealed among the nonprecocious males [♂ (0,0,+18) and ♂ (0,0,0)] (cf. section 3.2 and contrasts #1). No difference could be detected during the winter before smoltification and the first summer in seawater, just after smoltification. During the winter in seawater, the future grilse (+18) experienced a much better growth than the fish that would not mature again as grilse, as characterised by their weight and length increments. During the second summer in seawater, on the contrary, the maturing males showed a reduced growth compared to the males not maturing.

In sections 3.2.4 and 3.2.5, it was noted that the maiden maturing male grilse (+18) showed a much reduced growth during the second summer in seawater compared to the fish not maturing in the 2Y81 cohort, but not in the 2Y80 and 1Y81 cohorts. This difference was assumed to be linked with the very poor growing conditions at the beginning of the second summer for the 2Y81 cohort, which did not allow the maturing males to accumulate enough growth differential in early summer to mask the later somatic growth reduction accompanying gonadal development and maturation. It is quite likely that the same is true of the previously precocious (-6) males. Among them as well, the maturing male grilse [$\sigma^{\prime}$ (-6,0,+18)] performed poorly compared to the males not maturing [$\sigma^{\prime}$ (-6,0,0)], but again, it is probably a consequence of the poor growing conditions during the early second summer in this cohort. Under good growing conditions, the maturing males, whether previously precocious (-6) or not, would probably have shown an overall growth performance, during the second summer, quite similar to that of the nonmaturing males, if not slightly better, as was the case in the 1Y81 and 2Y80 cohorts.

At precocious maturation (-6) time, in November 1983, the precocious (-6) males were smaller and had a higher condition factor than the nonprecocious males. The following winter, these precocious (-6) males showed a growth performance slightly, but significantly better than their immature counterparts, which allowed then to compensate a little bit for their initial smaller size, particularly in term of weight. As noted, it is probable that this better growth performance was indirectly linked to the harsh environmental conditions, particularly the low feeding level during this winter. Later during the

first summer, winter and the second summer in seawater, precocious maturation (-6) did not show a significant effect anymore on the growth dynamics, as evidenced by the nonsignificant contrasts #3 for length and weight increments during these periods. Yet, the effect of previous precocious maturation (-6) could still be detected later, in that these previously precocious (-6) males remained a bit smaller and showed slightly higher condition factor until May 1985, 1.5 year after precocious maturation (-6) took place.

3.3.6 Growth dynamics before precocious maturation (-6). Tables 4.19, 4.20, 4.21.

Since there were no individual identifications available before the onset of precocious maturation (-6) in any of the three cohorts, only indirect evidence of the growth dynamics before precocious maturation (-6) is presented here.

In both the 2Y80 and 2Y81 cohorts, at the time of precocious maturation (-6), the precocious (-6) males had significantly lower length and weight than the nonprecocious fish (Table 4.19). This is probably an indication that precocious maturation (-6) entailed an energy cost and hence, that these maturing precocious males (-6) must have experienced a reduced somatic growth as compared to the fish not maturing, during late summer or early fall, before the precocious maturation (-6) data collection sessions. In both cohorts, the precocious (-6) males had also a significantly higher condition factor than the nonprecocious fish (Table 4.19), a result that was also observed for the other maturation episodes.

Table 4.19: Comparison of the characteristics of the precocious mature males (-6) and the nonprecocious fish at the onset of precocious maturation (-6), in the 2Y81 cohort.

Cohort	Date observed	Variable	Nonprecocious fish (♀ & ♂)	Precocious males	Between precocious maturation types comparison (1 way anova)
2Y80	Oct. 82	Length (cm)	17.4	15.9*	F=15.60 p=0.01%
		Weight (g)	65.0	52.3*	F=9.91 p=0.2%
		Condition factor	1.18	1.21*	F=5.46 p=2.1%
		(Number of cases)	(80)	(50)	
2Y81	Nov. 83	Length (cm)	20.8	19.3*	F=16.76 p=0.01%
		Weight (g)	101.0	83.6*	F=10.27 p=0.1% (1)
		Condition factor	1.10	1.15*	F=11.04 p=0.1% (1)
		(Number of cases)	(176)	(48)	

(1) Probability statements based on Fisher's randomization test.
* Denotes maturity at the time considered.

Hence, the growth dynamics during the summer before precocious maturation (-6) appeared likely to be similar to that observed during the summer before grilse maturation (+18).

Other indirect evidence of the growth dynamics before a precocious maturation episode can be found when looking at the incidence of early precocious maturation (0+) in the 1981 year class fish. As noted in Chapter II section 3.3 (see also Fig. 2.1 for an overview), no early precocious mature (0+) males were found in October 1982 among the fish being family marked, i.e. the fish that would later constitute the 1Y81 and 2Y81 cohorts (Table 4.20). However, such was not the case among the production fish. As explained in Chapter II section 2.3, these production fish were the "surplus" fish taken from the family tanks in May and July 1982, to avoid overcrowding and stunting of the future family marked fish. These fish did not bear any family identification but were adipose clipped according to the source of parent-fish. The fish taken from families 11, 12, 13, 15, 16 and 17 (group 1 in Chapter III) were adipose clipped, while those from families 51, 52, 55, 56 and 57 (group 2 in Chapter III) were not. Among these production fish, early precocious maturation (0+) was noted among a sample of fish from group 1 with a very low rate of occurence, but was not found among a sample of fish from group 2, this difference being significant (Table 4.20). This result is consistent with the trend that was noted in Chapter III Table 3.8, where it was observed that most maturation episodes had significantly higher incidence rates among fish of group 1 than among fish of group 2.

However, among the fish of group 1 alone, the difference between the early precocious maturation (0+) rates among the family marked fish

and among tne production fish was also highly significant (Table 4.20). This result appears to be linked with the difference in the growth dynamics that happened atter the production fish were separated from the future family marked fish (May and early July 1982). These production fish were placed into tanks considerably larger than those where the family fish were retained and hence, they experienced much better growing conditions in terms of density and water flow. As a result, these fish had a growth from May/July to October 1982 considerably better than the family marked fish. In October 1982, the production fish were on average more than twice as heavy as the family marked fish, in both family groups (Table 4.21).

It appears then, that some sort of causal relationships existed between the growth performance from May/July to October 1982 and the early precocious maturation (0+) incidence in October 1982.

Table 4.20: Comparison of incidence of early precocious maturation (0+) between family groups and between production fish and family marked fish, of the year class 1981, in October 1982.

	Group 1[1]	Group 2	Comparison of incidence between groups
Incidence of early prcocious maturation (0+) among family marked fish (Number of mature males/ total populations)	0% (0/1532)	0% (0/1371)	/
Incidence of early precocious maturation (0+) among production fish (Number of mature males/ sample size)	1.8% (7/382)	0% (0/400)	Exact Fisher's probability p=1.4%
Comparison of early precocious maturation (0+) rates between family marked fish and production fish	Exact Fisher's probability p=0.003%	/	

[1] Groups 1 and 2 were defined in Chapter III
Group 1 = families 11, 12, 13, 15, 16 and 17
Group 2 = families 51, 52, 55, 56 and 57

Table 4.21: Comparison of mean weight in October 1982 between the production fish and the family marked fish in Groups 1 and 2.

	Group 1[1]	Group 2
Family marked fish mean weight (g) in Oct. 82 (Standard deviation)	4.3 (1.5)	4.1 (1.6)
(Nbr. of cases in total populations)	(1532)	(1371)
Production fish mean weight (g) in Oct. 82 (Sandard deviation)	9.9 (4.9)	8.5 (5.2)
(Nbr. of cases in samples)	(92)	(92)
Mean weight comparison between family marked fish and production fish	Z=11.02 p<0.0000001%	Z=8.10 p<0.0000001%

[1] Groups 1 and 2 were defined in Chapter III,
Group 1 = families 11, 12, 13, 15, 16 and 17
Group 2 = families 51, 52, 55, 56 and 57

3.4 Growth trajectories of the post-smolt precocious (+6) males.

Post-smolt precocious (+6) males were found in the three cohorts. However, most of the information concerning the growth dynamics associated with this maturation episode will be drawn from the 1Y81 cohort, which is treated first. The absence of precocious maturation (-6) in this cohort simplified the analysis and, furthermore, much more post-smolt precocious males (+6) were found in this cohort (30 cases) than in the two other ones (8 and 6 such males in the 2Y80 and 2Y81 cohorts respectively).

3.4.1 The post-smolt precocious (+6) males in the 1Y81 cohort

The same sort of analysis that was used in section 3.3 to characterise the growth trajectories of the precocious (-6) males is used in this section. The post-smolt precocious (+6) males [$\vec{\sigma}$ (+6,+18) and $\vec{\sigma}$ (+6,0)] are compared to the maiden male grilse [$\vec{\sigma}$ (0,+18)] and the maiden multi-sea-winter males [$\vec{\sigma}$ (0,0)]. It should be noted that only the <u>known</u> males among the maiden multi-sea-winter fish are used here (20 cases). Among the 93 maiden multi-sea-winter fish of unknown sex, it was estimated that about another 28 were males (cf. Chapter II section 3.2), but they could not be included since it was not possible to assign a sex to individual fish in this unknown sex group.

Tables 4.22 to 4.24 present the comparison between the four maturation types [$\vec{\sigma}$ (0,0), $\vec{\sigma}$ (0,+18), $\vec{\sigma}$ (+6,+18), $\vec{\sigma}$ (+6,0)] for the three periods covered from August 1983 to December 1984. For each variable, an overall comparison is presented (one-way anova), as well as a set of three contrasts to characterise more precisely the nature of the variability. The contrasts were performed only when the overall

comparison was significant. Contrasts #1 compare the maiden multi-sea-winter males [♂(0,0)] with the maiden male grilse [♂(0,+18)]. Hence, contrasts #1 are a repetition of the analysis performed in section 3.2 (Tables 4.8, 4.10, 4.13), but this time performed on the males only. Contrasts #2 compare the post-smolt precocious (+6) males that matured again as grilse [♂(+6,+18)] with the ones that did not [♂(+6,0)]. Contrasts #3 compare the pooled nonpost-smolt mature males [♂(0,0) + ♂(0,+18)] with the pooled post-smolt mature males [♂(+6,0) + ♂(+6,+18)]. Hence, contrasts #1 are "between grilse maturation (+18) types for nonpost-smolt mature males" comparisons, contrasts #2 are "between grilse maturation (+18) types for post-smolt mature males (+6)" comparisons and contrasts #3 are "between post-smolt precocious maturation (+6) types" overall comparisons. Contrasts #2 were not very powerful since they compared a group of 24 fish [♂(+6,+18)] with a group of only 6 fish [♂(+6,0)]. Hence, when they yielded probability statements close to the significance level ($5\% < p < 10\%$), these probability statements were specified between brackets after the not significant (NS) statement.

First summer in seawater. Table 4.22.

During this period, overall significant differences between the four maturation types were detected, particularly concerning condition factor and length increments. In section 3.2.2, no significant differences were found during this period for the growth trajectories between the maiden multi-sea-winter fish and the maiden grilse. This can be seen in contrasts #1 which are all nonsignificant except one (Table 4.22).

Table 4.22: Comparison of the growth trajectories of the maiden multi-sea-winter males (standard), the maiden male grilse, the male grilse that were post-smolt precocious mature and the multi-sea-winter males that were post-smolt precocious mature, in the 1Y81 cohort, during the first summer in seawater.

Date observed	Variable	Group 1 Standard (Males only) 0 (0,0) 20 cases	Group 2 0 (0,+18) 34 cases	Group 3 0 (+6,+18) 24 cases	Group 4 0 (+6,0) 6 cases	Overall comparison 1 way anova(1)	Contrast 1 Group 1 vs Group 2 (Between grilse maturation types among maiden males)	Contrast 2 Group 3 vs Group 4 (Between grilse maturation types among post-smolt precocious males)	Contrast 3 Groups 1&2 vs Groups 3&4 (Between post-smolt precocious maturation types)
Aug. 83	Length (cm)	20.5	19.8	19.7	19.3	F=0.95 NS			
	Weight (g)	87.7	83.9	86.8	86.9	F=0.15 NS			
	Condition factor	1.00	1.06	1.12	1.20	F=9.42 p=0.1%	t=-2.42 p=2.1%	t=-1.35 NS	t=-4.09 p=0.3%
Aug. 83 to Dec. 83	Increment in length (cm)	8.5	9.1	7.6	6.2	F=3.71 p=1.5%	t=-1.18 NS	t=1.08 NS	t=2.61 p=2.6%
	Increment in weight (g)	181.8	190.7	173.8	131.0	F=1.67 NS			
Dec. 83	Length (cm)	28.9	28.9	27.3‡	25.5‡	F=3.31 p=3.2%	t=0.10 NS	t=0.79 NS	t=2.16 NS (6.6%)
	Weight (g)	269.5	274.6	260.6‡	217.8‡	F=1.09 NS			
	Condition factor	1.11	1.12	1.22‡	1.25‡	F=8.75 p=0.1%	t=-0.53 NS	t=-0.59 NS	t=-3.61 p=0.6%

(1) Probability statements based on Fisher's randomization test.

‡ Denotes maturity at the time considered.

In August 1983, the condition factor was significantly higher among the maiden male grilse [$\sigma^{\prime}$(0,+18)], a result previously not shown in Table 4.8 (section 3.2.2) when males and females were tested together. It is probable that this result does not carry any specific biological meaning, particularly since the opposite tendency was noted among the post-smolt precocious (+6) males (Table 4.22). All contrasts #2 were not significant (Table 4.22), indicating that among the post-smolt mature (+6) males, no differences could be found in the growth trajectories between the males that would mature again as grilse (+18) and the ones that would not, during the first summer in seawater. This result mirrors what was found among the maiden males and females in the 3 cohorts (cf. section 3.2.5), as well as what was found among the precocious (-6) males in the 2Y81 cohort (cf. section 3.3.3).

Contrasts #3 indicate that most of the differences that were detected by the overall comparisons during this period were attributable to differences between the males that would mature as post-smolt (+6) and the ones that would not, irrespective of the future grilse maturation (+18) status.

In August 1983, the males of the four maturation types had similar mean length and mean weight. However, the condition factor of the future post-smolt mature (+6) males was significantly higher than that of the fish that would not mature as post-smolt, a result which was expected. From August to December 1983, the maturing post-smolt (+6) showed lower length increment (significantly so) and lower weight increment (not significantly so) than the males not maturing. Again, this result was not surprising and reflected the reduction in somatic growth associated with gonadal developement and maturation. In December

1983, the now mature post-smolt precocious (+6) males were characterised by a lower mean length (almost significantly so) and mean weight (not significantly so) and a much higher condition factor (significantly so) as compared with the still immature maiden males.

Winter in seawater. Table 4.23.

From December 1983 to June 1984, length and weight increments were overall significantly different between the four maturation types (Table 4.23). Among the post-smolt precocious (+6) males, the future grilse (+18) showed a significantly higher weight increment than the ones that would not mature as grilse. They also showed a slightly higher length increment but the difference was not significant (contrasts #2, Table 4.23). This mirrors what could be seen among the maiden males (contrasts #1, Table 4.23).

Hence, it appears that among homogeneous groups, grilse maturation (+18) is almost always associated with a better growth during the preceding winter. This was true, among the maiden females in the 3 cohorts (cf. section 3.2.3), the maiden males in the 1Y81 and 2Y81 cohorts (cf. section 3.2.3), the precocious (-6) males in the 2Y81 cohort (cf. section 3.3.3) and here the post-smolt precocious (+6) males in the 1Y81 cohort.

In addition, during this winter period, it can be noted that post-smolt precocious maturation (+6) had an overall significant depressing effect on growth, as evidenced by the contrasts #3 (Table 4.23). The pooled post-smolt mature (+6) males showed significantly lower length and weight increments as compared to the pooled maiden males.

Table 4.23: Comparison of the growth trajectories of the maiden multi-sea-winter males (standard), the maiden male grilse, the male grilse that were post-smolt precocious mature and the multi-sea-winter males that were post-smolt precocious mature, in the 1Y81 cohort, during the winter in seawater.

Date observed	Variable	Group 1 Standard (Males only) ♂(0,0) 20 cases	Group 2 ♂(0,+18) 34 cases	Group 3 ♂(+6,+18) 24 cases	Group 4 ♂(+6,0) 6 cases	Overall comparison 1 way anova(1)	Contrast 1 Group 1 vs Group 2 (Between grilse maturation types among maiden males)	Contrast 2 Group 3 vs Group 4 (Between grilse maturation types among post-smolt precocious males)	Contrast 3 Groups 1&2 vs Groups 3&4 (Between post-smolt precocious maturation types)
Dec. 83 to June 84	Increment in length (cm)	3.5	3.9	3.0	2.3	F=2.76 p=4.5%	t=-0.83 NS	t=1.31 NS	t=2.92 p=0.8%
	Increment in weight (g)	68.5	125.1	80.3	21.8	F=3.37 p=3.4%	t=-2.43 p=1.9%	t=2.98 p=0.6%	t=3.00 p=0.4%
June 85	Length (cm)	32.4	32.7	30.3	27.8	F=4.29 p=0.7%	t=-0.39 NS	t=1.07 NS	t=2.86 p=1.9%
	Weight (g)	338.0	399.7	341.0	239.7	F=2.56 NS			
	Condition factor	0.97	1.09	1.13	1.04	F=6.09 p=0.1%	t=-3.79 p<0.1%	t=2.01 NS (6.7%)	t=-2.07 p=4.8%

(1) Probability statements based on Fisher's randomization test.

In section 3.3.1, it was noted that mature fish generally experience a reduced growth during the winter following maturation, as is the case here, because fish reabsorbing gonad generally show a lower feeding activity.

In June 1984, the pooled previously post-smolt mature (+6) males were still characterised by significantly lower mean length, lower mean weight and significantly higher condition factor, compared to the pooled maiden males (contrasts #3, Table 4.23). Among the previously maiden males, the future grilse (+18) had a significantly higher condition factor, compared to the fish that would not mature as grilse (contrasts #1, Table 4.23). Among the previously post-smolt precocious (+6) males, the same could be seen, the difference being almost significant (contrasts #2, Table 4.23). Among the maiden males and among the previously post-smolt precocious (+6) males, those that would mature as grilse (+18) were characterised by a higher mean length and mean weight, but the differences were not significant (contrasts #1 and #2, Table 4.23).

Second summer in seawater. Table 4.24.

From June to December 1984, length and weight increments were not overall significantly different between the four maturation types. Post-smolt precocious maturation did not show an overall effect on the growth performance (Table 4.24). The maturing male grilse (+18), whether previously post-smolt precocious (+6) or previously maiden, did not show any reduced growth performance as compared with the males non maturing as grilse. This had already been observed in section 3.2.4, and attributed to favourable growing conditions during this period, particularly during the early summer.

Table 4.24: Comparison of the growth trajectories of the maiden multi-sea-winter males (standard), the maiden male grilse, the male grilse that were post-smolt precocious mature and the maiden multi-sea-winter males that were post-smolt precocious mature, in the 1Y81 cohort, during the second summer in seawater.

Date observed	Variable	Group 1 Standard (Males only) $0\bar{0}$(0,0) 20 cases	Group 2 $0\bar{0}$(0,+18) 30 cases	Group 3 $0\bar{0}$(+6,+18) 21 cases	Group 4 $0\bar{0}$(+6,0) 6 cases	Overall comparison 1 way anova[1]	Contrast 1 Group 1 vs Group 2 (Between grilse maturation types among maiden males)	Contrast 2 Group 3 vs Group 4 (Between grilse maturation types among post-smolt precocious males)	Contrast 3 Groups 1&2 vs Groups 3&4 (Between post-smolt precocious maturation types)
June 84 to Dec. 84	Increment in length (cm)	14.6	15.2	14.9	5.8	F=0.58 NS			
	Increment in weight (g)	870.1	967.9	879.0	778.5	F=1.58 NS			
Dec. 84	Length (cm)	47.1	47.6‡	44.5‡	43.5	F=2.78 p=3.7%	t=-0.59 NS	t=0.35 NS	t=2.53 p=2.3%
	Weight (g)	1208.1	1346.1‡	1183.2‡	1018.2	F=2.30 NS			
	Condition factor	1.14	1.23‡	1.28‡	1.20	F=8.63 p=0.1%	t=-3.75 p<0.1%	t=2.32 p=4.1%	t=-2.41 p=2.5%

[1] Probability statements based on Fisher's randomization test.

‡ Denotes maturity at the time considered.

The post-smolt mature (+6) males that did not mature again as grilse [♂ (+6,0)] were the smallest of the four maturation types in June 1984 (Table 4.23). It is interesting to note that, from June to December 1984, they showed a mean weight increment in the range of what could be expected, based on their initial smaller sizes, and compared to the three other groups, but they showed the highest mean length increment of the four groups. It appears that nonrematuring was accompanied by a sort of "increase" of somatic growth.

In December 1984, most of the differences were still attributable to the previous post-smolt precocious maturation (+6) episode. The previously post-smolt mature (+6) males had still a significantly lower mean length and a significantly higher condition factor than the previously maiden males. (contrasts #3, Table 4.24). Among the previously maiden males and among the previously post-smolt precocious (+6) males, the now mature grilse (+18) were characterised by a significantly higher condition factor compared to the fish not mature as grilse (contrasts #1 and #2, Table 4.24).

3.4.2 The post-smolt precocious (+6) males in the 2Y80 cohort

In this cohort, these males were the ♂ (?,+6,+18) (2 cases) and the ♂ (?,+6,0) (6 cases). Hence, some of these males were probably precocious mature (-6) in addition to be post-smolt precocious mature (+6). Tables 4.25 to 4.27 present the comparisons between the four maturation types; ♂ (?,0,0), ♂ (?,0,+18), ♂ (?,+6,+18), ♂ (?,+6,0), for the three periods covered from August 1983 to December 1984. However, given the very low number of post-smolt precocious (+6) males in this cohort, only one type of statistical analysis was performed in these

tables, the comparisons of the pooled post-smolt precocious (+6) males with tne pooled males that were not mature at the post-smolt maturation (+6) episode. These comparisons are equivalent to contrasts #3 in the preceding section. As was the case with contrasts #2 in the last 3 Tables, the probability statements close to the significance level ($5\% < p < 10\%$) are stated between brackets after the not significant statement (NS).

First summer in seawater. Table 4.25.

In August 1983, the future post-smolt precocious (+6) males, compared to the maiden males, were characterised by a significantly higher condition factor (Table 4.25), as was the case in the 1Y81 cohort (cf. Table 4.22). However, they were also characterised by significantly lower length and weight, a result in contrast to what was observed in the 1Y81 cohort (Table 4.22).

From August to December 1983, the maturing post-smolt precocious (+6) males showed significantly lower length and weight increments, as compared to the fish nonmaturing as post-smolt (Table 4.25). This result is similar to what had been observed in the 1Y81 cohort, and was interpreted as reflecting the somatic growth reduction accompanying gonadal development and maturation. In December 1983, the now mature post-smolt precocious (+6) males were characterised by a significantly higher condition factor and significantly lower length and weight, as compared to the males immature at this maturation episodes (Table 4.25).

Table 4.25: Comparison of the growth trajectories of the "maiden" multi-sea-winter males (standard), the "maiden" male grilse, the male grilse that were post-smolt precocious mature and the multi-sea-winter males that were post-smolt precocious mature, in the 2Y80 cohort, during the first summer in seawater.

Date observed	Variable	Group 1 (standard) males only ♂(?,0,0) 18 cases	Group 2 ♂(?,0,+18) 15 cases	Group 3 ♂(?,+6,+18) 2 cases	Group 4 ♂(?,+6,0) 6 cases	Groups 1&2 vs Groups 3&4 comparison [between post-smolt precocious (+6) maturation types] 1 way anova(1)
Aug. 83	Length (cm)	25.0	25.4	22.0	20.9	F=17.50 p=0.1%
	Weight (g)	169.5	174.3	136.8	113.0	F=10.28 p=0.4%
	Condition factor	1.06	1.05	1.27	1.21	F=23.94 p=0.1%
Aug. 83 to Dec. 83	Length increment (cm)	9.6	9.4	7.5	4.7	F=20.20 p=0.2%
	Weight increment (g)	331.6	329.3	218.5	119.2	F=15.10 p=0.2%
Dec. 83	Length (cm)	34.6	34.9	29.5*	25.5*	F=32.44 p=0.1%
	Weight (g)	501.3	503.7	355.0*	232.3*	F=17.78 p=0.1%
	Condition factor	1.16	1.17	1.29*	1.25*	F=5.88 p=1.7%

(1) All probability statements based on Fisher's randomization test.
* Denotes maturity at the time considered.

Winter in seawater. Table 4.26.

From December 1983 to June 1984, the previously post-smolt mature (+6) males showed a poor growth performance, with significantly lower length increment and lower, almost significantly so, weight increment, as compared to the males nonmature as post-smolt (Table 4.26). This is similar to what was observed in the 1Y81 cohort and was attributed to the lower feeding activity of the fish reabsorbing gonad. Among the previously post-smolt mature (+6) males, the 2 fish that would mature again as grilse (+18) did not show a better growth performance than the 6 fish that would not mature again as grilse (Table 4.23), as could have been expected based on previous results (Table 4.23 and section 3.4.1 "winter in seawater"). This was however not very surprising, given the very low number of fish and given the considerable overall variability for weight increment during the winter period, as demonstrated by the fact that the difference between the pooled post-smolt precocious (+6) males and the pooled "maiden" males was large but yet not significant (Table 4.26). Furthermore, it was noted in section 3.2.3 that among the "maiden" males [♂(?,0,0) and ♂(?,0,+18)], not much difference existed for winter growth between the males maturing as grilse (+18) and the ones not maturing as grilse, as it can be seen in Table 4.26. This result, in contrast to what was observed in the other cohorts, was attributed to the heterogeneity of these groups, since some of the males were precocious mature (-6), and to the relatively low number of fish. It is probable that the same is true of the post-smolt precocious (+6) males as well, i.e. the fact that some of them were probably precocious (-6) tended to mask the link between winter growth and grilse maturation (+18) status.

Table 4.26: Comparison of the growth trajectories of the "maiden" multi-sea-winter males (standard), the "maiden" male grilse, the male grilse that were post-smolt precocious mature and the multi-sea-winter males that were post-smolt precocious mature, in the 2Y80 cohort, during the winter in seawater.

Date observed	Variable	Group 1 (standard) males only ♂(?,0,0) 18 cases	Group 2 ♂(?,0,+18) 15 cases	Group 3 ♂(?,+6,+18) 2 cases	Group 4 ♂(?,+6,0) 6 cases	Groups 1&2 vs Groups 3&4 comparison [between post-smolt precocious (+6) maturation types] 1 way anova(1)
Dec. 83 to June 84	Length increment (cm)	2.9	2.9	1.0	1.8	F=4.98 p=2.6%
	Weight increment (g)	62.1	73.1	-21.0	19.7	F=2.77 NS (9.2%)
June 84	Length (cm)	37.5	37.8	30.5	27.3	F=30.67 p=0.1%
	Weight (g)	563.3	576.8	334.0	252.0	F=18.27 p=0.1%
	Condition factor	1.04	1.05	1.06	1.02	F=0.19 NS

(1) All probability statements based on Fisher's randomization test.

In June 1984, the previously post-smolt precocious mature (+6) males were quite significantly smaller and less heavy than the previously "maiden" males. There was as well a significant difference for condition factor between these two pooled groups (Table 4.26). Among both the previously post-smolt precocious (-6) males and "maiden" males, there was a slight tendency for condition factor to be higher among the males that would mature as grilse (+18) than among the males that would not (Table 4.26).

Second summer in seawater. Table 4.27.

From June to December 1984, the previously post-smolt precocious (+6) males showed a similar length increment but a significantly lower weight increment, compared to the fish nonmature as post-smolt (Table 4.27). This is similar to what was observed in the 1Y81 cohort (Table 4.24), although the difference for weight increment was not significant in this last case. The significantly lower weight increment of the previously post-smolt mature (+6) males in the 2Y80 cohort is probably linked with the fact that, in June 1984, they were considerably smaller than the fish non mature as post-smolt (Table 4.26). This was true among the 1Y81 cohort as well, but the difference was much less important (Table 4.23). It is interesting to note that among the previously post-smolt precocious (+6) males, those not maturing again as grilse showed an "increase" of somatic growth, as evidenced by their very high length increment, in spite of their small sizes in June 1984 (Table 4.27). The same was observed in the 1Y81 cohort (Table 4.24).

Table 4.27: Comparison of the growth trajectories of the "maiden" multi-sea-winter males (standard), the "maiden" male grilse, the male grilse that were post-smolt precocious mature and the multi-sea-winter males that were post-smolt precocious mature, in the 2Y80 cohort, during the second summer in seawater.

Date observed	Variable	Group 1 (standard) males only $0^{\nearrow}$(?,0,0) 18 cases	Group 2 $0^{\nearrow}$(?,0,+18) 15 cases	Group 3 $0^{\nearrow}$(?,+6,+18) 2 cases	Group 4 $0^{\nearrow}$(?,+6,0) 5 cases	Groups 1&2 vs Groups 3&4 comparison [between post-smolt precocious (+6) maturation types] 1 way anova(1)
June 84 to Dec. 84	Length increment (cm)	13.9	14.4	10.5	17.2	F=1.21 NS
	Weight increment (g)	1074.1	1227.5	753.0	632.0	F=21.3 p=0.1%
Dec. 84	Length (cm)	51.4	52.2*	41.0*	41.6	F=35.43 p=0.2%
	Weight (g)	1637.4	1804.3*	1087.0*	783.4	F=32.23 p=0.1%
	Condition factor	1.19	1.26*	1.39*	1.08	F=2.06 NS

(1) All probability statements based on Fisher's randomization test.
* Denotes maturity at the time considered.

In December 1984, the previously post-smolt mature (+6) males were still considerably smaller and less heavy than the previously "maiden" males, but their condition factor was not significantly different (Table 4.27), as was already the case in June 1984 (Table 4.26). Among both pooled groups, the now mature male grilse (+18) showed a higher condition factor than the multi-sea-winter males.

3.4.3 The post-smolt precocious (+6) males in the 2Y81 cohort

In this cohort, these post-smolt precocious (+6) males were the $\sigma^{\uparrow}$ (0,+6,0) (3 cases), $\sigma^{\uparrow}$(-6,+6,+18) (2 cases) and the $\sigma^{\uparrow}$(-6,+6,0) (1 case). Given these very low numbers, only one type of statistical comparisons is performed in this section, the comparison of the pooled post-smolt precocious (+6) males with the pooled males that were nonpost-smolt precocious, as was the case in the preceding section. The same convention, concerning probability statements close to the significance level, is used again in this section.

The pooled group of the post-smolt precocious mature (+6) males consisted of three different maturation types [$\sigma^{\uparrow}$(0,+6,0), $\sigma^{\uparrow}$(-6,+6,0), $\sigma^{\uparrow}$(-6,+6,+18)]. The pooled group of males nonmature as post-smolt consisted of four different maturation types [$\sigma^{\uparrow}$(0,0,0), $\sigma^{\uparrow}$(0,0,+18), $\sigma^{\uparrow}$(-6,0,0)] and $\sigma^{\uparrow}$(-6,0,+18)]. In order to facilitate the presentation of the results, some regrouping of the different maturation types has been performed:

1. Tables 4.28 and 4.29 present the growth trajectories during the winter before smoltification and during the first summer in seawater. For both periods, no significant differences in the growth trajectories were found between the

males that would mature as grilse (+18) and the males that would not, and this among both the "maiden" males (cf. sections 3.2.1 and 3.2.2) and among the precocious males (-6) (cf. sections 3.3.1 and 3.3.2). Regrouping was performed accordingly.

2. Tables 4.30 and 4.31 present the growth trajectories during the winter in seawater and the second summer in seawater. During these periods, there were significant differences in the growth trajectories between the males not maturing as grilse and the males maturing as grilse (+18), but on the other hand, the previous precocious maturation (-6) status did not affect the growth dynamics anymore (cf. sections 3.3.3 and 3.3.4). Regrouping was performed accordingly.

Winter period before smoltification. Table 4.28

In November 1983, the future post-smolt mature (+6) males were significantly longer, significantly heavier, and they had a significantly lower condition factor, as compared to the males that would not mature as post-smolt. This appeared to be true whether the males were precocious mature (-6) or not (Table 4.28). From November 1983 to June 1984, all males showed similar length increments, but the weight increments of the future post-smolt mature (+6) males were significantly larger than those of the males not maturing as post-smolt. Again, this appeared to be true independently of previous precocious maturation (-6) status (Table 4.28).

Table 4.28: Comparison of the growth trajectories of the post-smolt precocious males [precocious (-6) and nonprecocious] and of the males that were not post-smolt precocious mature, in the 2Y81 cohort, during the winter before smoltification. Regrouping was performed according to precocious maturation (-6) and post-smolt precocious maturation (+6) but independantly of grilse maturation status (+18).

Date observed	Variable	Group 1 (nonprecocious) ♂(0,0,0) ♂(0,0,+18) 57 cases	Group 2 (precocious) ♂(-6,0,0) ♂(-6,0,+18) 46 cases	Group 3 (nonprecocious) ♂(0,+6,0) 3 cases	Group 4 (precocious) ♂(-6,+6,+18) ♂(-6,+6,0) 2 cases	Groups 1&2 vs Groups 3&4 comparison [between post-smolt precocious (+6) maturation types] 1 way anova(1)
Nov. 83	Length (cm)	20.6	19.0*	27.4	26.0*	F=47.75 p=0.1%
	Weight (g)	100.0	80.8*	212.7	149.0*	F=37.11 p=0.1%
	Condition factor	1.10	1.16*	1.03	0.83*	F=17.38 p=0.1%
Nov. 83 to June 84	Length increment (cm)	1.9	2.3	2.4	1.9	F=0.08 NS
	Weight increment (g)	4.7	13.4	39.3	38.0	F=15.72 p=0.2%

(1) All probability statements based on Fisher's randomization test.
* Denotes maturity at the time considered.

Hence, it seems that post-smolt precocious maturation (+6) was associated with good growth during the winter preceding this maturation episode, just as grilse maturation (+18) seemed associated with good growth duing the preceding winter.

First summer in seawater. Table 4.29.

At smoltification time, in June 1984, the future post-smolt mature (+6) males were still significantly longer and heavier, as compared to the males not maturing as post-smolt. However, there was no longer a significant difference in the condition factor attributable to future post-smolt precocious maturation (+6) status (Table 4.29).

From June to November 1984, the maturing post-smolt (+6) males showed significantly lower length increments and lower weight increments (not significantly so) compared to their nonmaturing counterparts (Table 4.29). This is similar to what had been observed in the 2 other cohorts (Tables 4.22 and 4.25) and was interpreted as denoting the somatic cost of maturation.

In November 1984, the now mature post-smolt (+6) males were still a bit larger, but much of the size differences had disappeared because of their poorer growth performance: there were no longer significant differences for length or weight or condition factor between the mature post-smolt (+6) males and the males immature at this episode.

Winter in seawater. Table 4.30.

From November 1984 to May 1985, the previously mature post-smolt (+6) males showed significantly lower length increments and lower weight increments (not significantly so) (Table 4.30). This had been observed in the two other cohorts as well (Tables 4.23, 4.26).

Table 4.29: Comparison of the growth trajectories of the post-smolt precocious males [precocious (-6) and nonprecocious] and of the males that were not post-smolt precocious mature, in the 2Y81 cohort, during the first summer in seawater. Regrouping was performed according to precocious maturation (-6) and post-smolt precocious maturation (+6) but independantly of grilse maturation status (+18).

Date observed	Variable	Group 1 (nonprecocious) ♂(0,0,0) ♂(0,0,+18) 58 cases	Group 2 (precocious) ♂(-6,0,0) ♂(-6,0,+18) 46 cases	Group 3 (nonprecocious) ♂(0,+6,0) 3 cases	Group 4 (precocious) ♂(-6,+6,+18) ♂(-6,+6,0) 3 cases	Groups 1&2 vs Groups 3&4 comparison [between post-smolt precocious (+6) maturation types] 1 way anova(1)
June 84	Length (cm)	22.6	21.3	29.8	25.6	F=35.49 p=0.1%
	Weight (g)	105.1	94.1	252.0	157.0	F=53.80 p=0.1%
	Condition factor	0.89	0.97	0.93	0.92	F=0.00 NS
June 84 to Nov. 84	Length increment (cm)	12.8	12.6	5.10	11.10	F=28.60 p=0.1%
	Weight increment (g)	449.3	403.8	237.7	479.0	F=2.32 NS
Nov. 84	Length (cm)	35.3	33.90	34.9*	36.7*	F=0.98 NS
	Weight (g)	554.3	498.0	489.7*	636.0*	F=0.41 NS
	Condition factor	1.23	1.26	1.14*	1.26*	F=1.39 NS

(1) All probability statements based on Fisher's randomization test.
* Denotes maturity at the time considered.

Table 4.30: Comparison of the growth trajectories of the post-smolt precocious males and of the males that were not post-smolt precocious mature, in the 2Y81 cohort, during the winter in seawater. Regrouping was performed according to post-smolt precocious maturation (+6) and grilse maturation (+18) but independantly of precocious maturation (-6) status.

Date observed	Variable	Group 1 (MSW[1] males) ♂(0,0,0) ♂(-6,0,0) 47 cases	Group 2 (male grilse) ♂(0,0,+18) ♂(-6,0,+18) 61 cases	Group 3 (MSW males) ♂(0,+6,0) ♂(-6,+6,0) 4 cases	Group 4 (male grilse) ♂(-6,+6,+18) 2 cases	Groups 1&2 vs Groups 3&4 comparison [between post-smolt precocious (+6) maturation types] 1 way anova[2]
Nov. 84 to May 85	Length increment (cm)	5.1	6.2	4.2	4.3	F=5.24 p=2.7%
	Weight increment (g)	187.2	335.0	191.5	206.0	F=1.75 NS
May 85	Length (cm)	39.7	40.9	40.3	39.50	F=0.07 NS
	Weight (g)	713.8	866.4	753.8	770.0	F=0.23 NS
	Condition factor	1.11	1.24	1.14	1.26	F=0.02 NS

(1) MSW = multi-sea-winter fish.
(2) All probability statements based on Fisher's randomization test.

Among the previously post-smolt mature (+6) males, not much difference could be detected between the growth performance of tnose that would mature again as grilse, and of those that would not, but this was not surprising, given the very low number of fish (Table 4.30).

In May 1985, there were no significant differences for length, weight or condition factor between the previously post-smolt mature (+6) males and the fish that had not been post-smolt mature (Table 4.30).

Second summer in seawater. Table 4.31.

From May to December 1985, length and weight increments were significantly higher among the previously post-smolt mature (+6) males, as compared to the males that had not been post-smolt mature (Table 4.31). This is probably partly a consequence of the previously post-smolt mature males not maturing again as grilse that showed a sort of somatic growth "increase" as it had been observed in the two other cohorts.

In December 1985, the previously post-smolt mature (+6) males were longer (not significantly so), heavier (almost significantly so) and had a slightly higher condition factor (not significantly so), as compared to the males that were not mature as post-smolt.

3.4.4 Summary

In the 1Y81 cohort, among the post-smolt precocious (+6) males, the pattern of growth trajectory differences between the males that would mature again as grilse [♂(+6,+18)] and the ones that would not [♂(+6,0)] was quite similar to what had been observed among the maiden fish, and the precocious males (-6) (cf. sections 3.2.5 and 3.3.5).

Table 4.31: Comparison of the growth trajectories of the post-smolt precocious males and of the males that were not post-smolt precocious mature, in the 2Y81 cohort, during the second summer in seawater. Regrouping was performed according to post-smolt precocious maturation (+6) and grilse maturation (+18) but independantly of precocious maturation (-6) status.

Date observed	Variable	Group 1 (MSW[1] males) ♂(0,0,0) ♂(-6,0,0) 42 cases	Group 2 (male grilse) ♂(0,0,+18) ♂(-6,0,+18) 61 cases	Group 3 (MSW males) ♂(0,+6,0) ♂(-6,+6,0) 4 cases	Group 4 (male grilse) ♂(-6,+6,+18) 2 cases	Groups 1&2 vs Groups 3&4 comparison [between post-smolt precocious (+6) maturation types] 1 way anova[2]
May 85 to Dec. 85	Length increment (cm)	10.0	8.2	11.0	11.3	F=10.86 p=0.1%
	Weight increment (g)	618.0	416.5	775.8	830.5	F=9.26 p=0.5%
Dec. 85	Length (cm)	49.9	49.1*	52.2	50.8*	F=2.28 NS
	Weight (g)	1340.4	1282.9*	1529.5	1600.5*	F=3.37 NS (6.4%)
	Condition factor	1.05	1.07*	1.05	1.22*	F=1.01 NS

(1) MSW = multi-sea-winter fish.
(2) All probability statements based on Fisher's randomization test.
* Denotes maturity at the time considered.

No difference could be detected during the first summer in seawater. During the winter in seawater, the future grilse (+18) experienced a significantly better growth than the fish that would not mature again as grilse. During the second summer of growth, no striking difference could be detected, although the males not maturing as grilse appeared to show an "increase" of somatic growth, as evidenced by a large length increment. Among the previously post-smolt mature (+6) males, those maturing again as grilse (+18) did not show a somatic growth reduction as compared to those not maturing as grilse. This is similar to what had been observed among the maiden males in that cohort (cf. section 3.2.5), and was attributed to the good growth condition during this summer, masking the somatic growth reduction accompanying gonadal development. In this cohort, the overall effect of post-smolt precocious maturation (+6) was similar to what had been observed about precocious maturation (-6) in the 2Y81 cohort. In August 1983, all males were about the same size, but from August to December 1983, the maturing post-smolt precocious (+6) males showed a reduced growth compared to the maiden males. In December 1983, these now mature post-smolt males were smaller and had a higher condition factor, compared to their immature counterparts. During the following winter, the post-smolt males reabsorbing gonad showed a reduced growth, so that in June 1984, they were still smaller and had still a higher condition factor, compared to the previously maiden males. During the second summer in seawater, post-smolt precocious maturation (+6) did not show anymore a significant effect on the growth dynamics. In December 1984, the previously post-smolt precocious mature (+6) males were still smaller and still characterised by a higher condition factor.

Information concerning the growth trajectories during the winter preceding smoltification was only available in the 2Y81 cohort. Despite the very low number of post-smolt mature (+6) males in this cohort, it was apparent that post-smolt precocious maturation (+6) was associated with a good growing performance during this period, and this independantly of precocious maturation status (-6). As already noted, this appears to be very similar to the repeatedly noted association of grilse maturation (+18) with good growing performance during the winter in seawater.

There were not enough cases in the 2Y80 and 2Y81 cohorts to meaningfully compare growth trajectories between the post-smolt precocious (+6) males maturing again as grilse (+18) and the ones not maturing again as grilse. The overall effect of post-smolt precocious maturation (+6) could nevertheless be assessed in these two cohorts, and the findings were quite similar to what had been observed in the 1Y81 cohort. A few differences between the three cohorts were present, but these were mostly initial size differences or consequences of these initial size differences. Around smoltification time, compared to the males not maturing as post-smolt, the post-smolt precocious (+6) males were significantly smaller in the 2Y80 cohort, significantly larger in the 2Y81 cohort and not significantly different in the 1Y81 cohort. This indicates that smolt size probably bears little direct significance for post-smolt precocious maturation (+6). The probable causes of these initial size differences between the 3 cohorts will be discussed in section 4.7.

3.5 Influence of overwintering temperature regimes and tank effect on the growth dynamics and grilse maturation incidences (+18)

This section analyses the effects of environmental factors (tank location during the first summer in seawater, tank location during the winter in seawater, overwintering temperature regimes) on subsequent grilse maturation (+18) rates in the three cohorts, as well as the effects of these factors on the growth dynamics.

In the 1Y81 cohort, first summer tank location was confounded with overwintering temperature regimes, and in the 2Y81 cohort, it was confounded with winter tank location (cf. section 2). Hence, it was not possible to treat independantly the tank and related effects during these two periods on subsequent grilse maturation rates. However, it was possible to analyse the effects of these factors on the growth dynamics during those two periods and to draw tentative conclusions about links between growth performance and subsequent maturation rates.

3.5.1 Winter periods. Tables 4.32, 4.33, Fig. 4.5, Fig. 4.6.

In the 3 cohorts, there was no detectable overall effect of the overwintering temperature regimes on subsequent grilse maturation (+18) rates (Table 4.32). On the other hand, half of the comparisons between replicate tanks within overwintering temperature regimes were significant, indicating that there existed some other environmental factors associated with the tanks which significantly influenced subsequent maturation rates. These factors seemed to be linked with the growth dynamics during this period.

Table 4.32: Comparison of the rate of grilse maturation (+18) between overwintering temperature regimes, and between replicate tanks within overwintering temperature regimes.

Cohort	2Y80		1Y81				2Y81					
Overwintering temperature regime	Heated	Ambiant	Heated		Ambiant		Heated			Ambiant		
Rate of grilse maturation in the regime	34.5%	41.4%	28.1%		27.1%		50%			43.2%		
(Absolute frequencies)	(10/29)	(12/29)	(27/96)		(36/133)		(58/116)			(48/111)		
Between overwintering temperature regimes comparison (X^2 test)	X^2=0.3 1df NS		X^2=0.0 1df NS				X^2=1.0 1df NS					
Tank number	1	4	2	3	5	6	1	2	3	4	5	6
Rate of grilse maturation per tank	/		16.3%	40.4%	25.0%	28.8%	46.2%	46.2%	57.9%	29.7%	29.7%	70.3%
(Absolute frequencies)			(8/49)	(19/47)	(15/60)	(21/73)	(18/39)	(18/39)	(22/38)	(11/37)	(11/37)	(26/37)
Within overwintering regime, between replicate tanks comparison (X^2 test)	/		X^2=6.9 1df p=1%		X^2=0.2 1df NS		X^2=1.4 2df NS			X^2=16.5 2df p<0.1%		

A positive and significant correlation (Pearson correlation coefficient r=0.64, p=1.3%, n=12) was observed between the rates of grilse maturation (+18) (after angular normalisation) and the mean weight increments in the different tanks during the winter periods (Fig. 4.5). Furthermore, similar correlations were observed when only the 2Y81 cohort data (Pearson correlation coefficient r= 0.60 p= 10.3% n= 6) or the 1Y81 cohort data (Pearson correlation coefficient r=0.78, p=11%, n=4) were included. Both these correlations were not significant at the 5% level, but this is probably a consequence of the very low number of points in each case. The observation of these similar "within cohort correlations" confirmed however that the overall correlation was not an artefact due to the relatively higher grilse maturation (+18) rate and winter growth of the 2Y81 fish. As can be seen in Fig. 4.6, there was as well a significant correlation (Pearson correlation coefficient r=0.96 p=0.001% n=12) between the winter weight increment of the multi-sea-winter salmon and of the grilse in the different tanks. In the tanks characterised by good overal growth, both the multi-sea-winter fish and the grilse grew well, while in the tanks characterised by poor overall growth, the opposite could be seen.

The analysis of the overwintering temperature regimes effects and of the tank effects on the growth dynamics during the winter, in the 3 conorts, showed results quite parallel (Table 4.33) to what had been observed about tne effect of these factors on grilse maturation rates (+18).

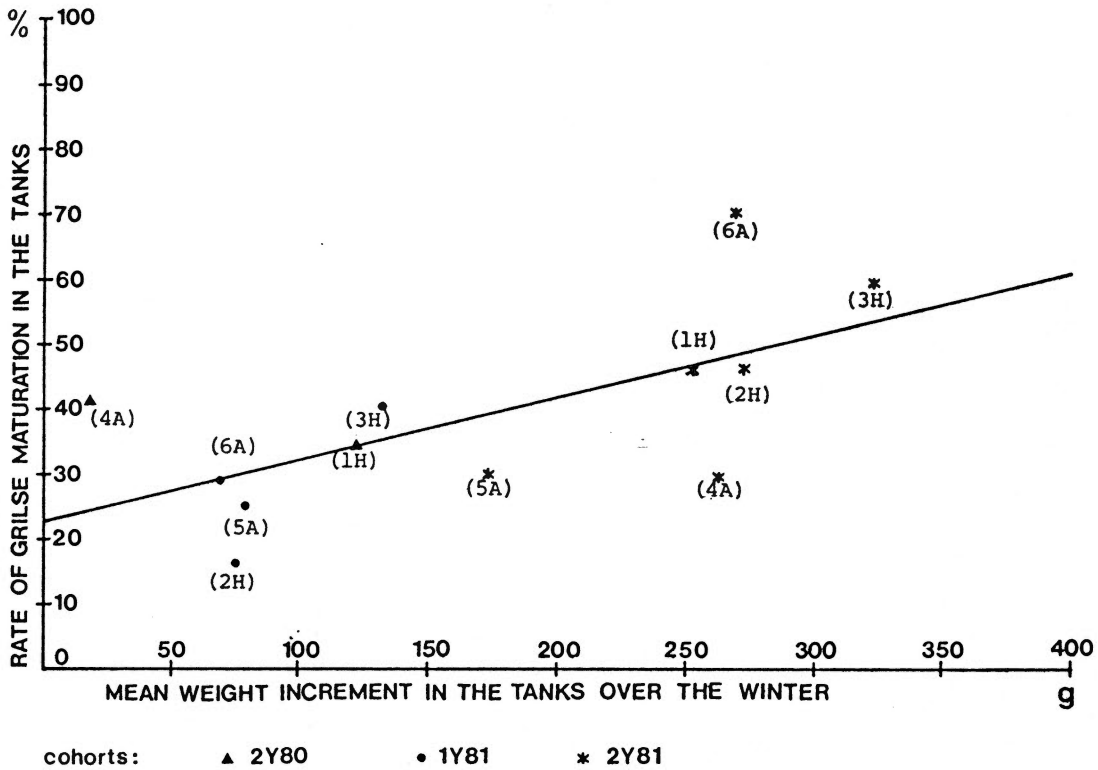

Figure 4.5: Correlation between the rate of grilse maturation in the different winter tanks and the mean weight increment in the same tanks, over the winter period.

(Into brackets: tank identification number and overwintering regime A: ambiant, H: heated)

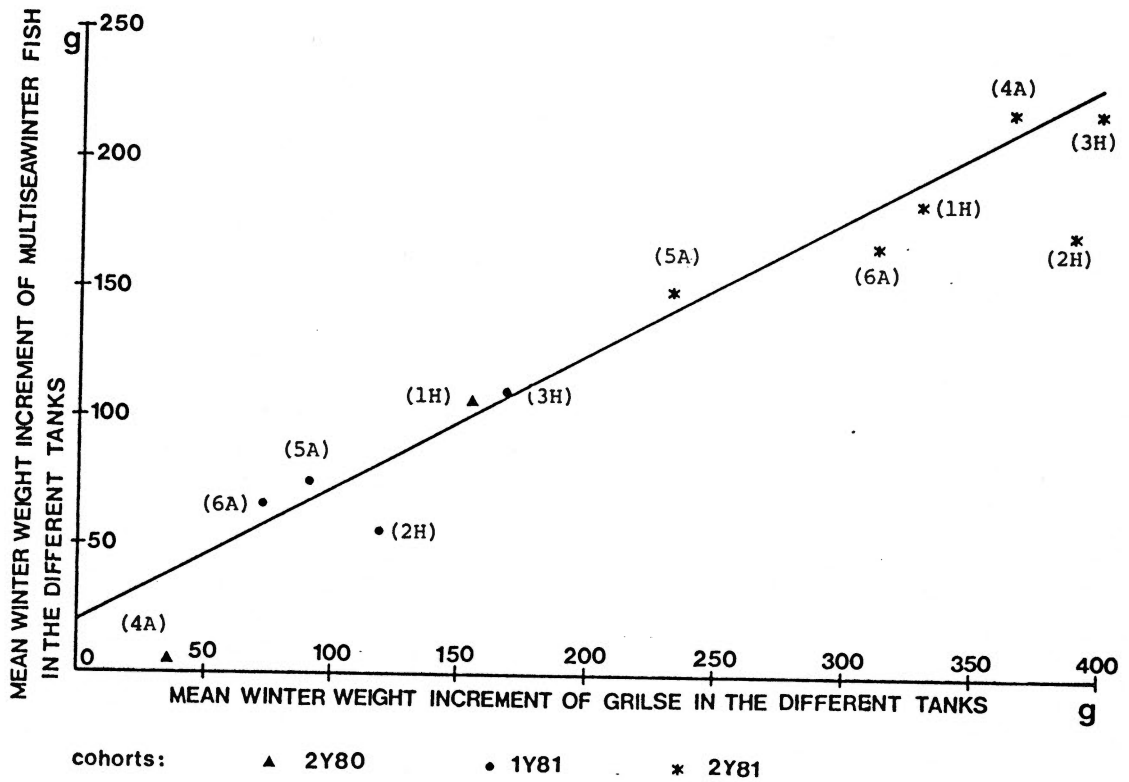

Figure 4.6: Correlation between the mean winter weight increment of the multi-sea-winter salmon and of the grilse, in the different tanks.

(Into brackets: tank identification number and overwintering regime A: ambiant, H: heated)

Table 4.33: Comparison of the winter weight increment between overwintering temperature regimes, and between replicate tanks within overwintering temperature regimes, in the 3 cohorts.

Cohort	Overwintering temperature regime	Tank number	Number of fish	Mean weight increment (g) in the tank	Mean weight increment (g) in the regime
2Y81	Heated	1	(39)	252.0	282.6
		2	(39)	273.7	
		3	(38)	323.3	
	Ambiant	4	(37)	263.9	235.8
		5	(37)	173.9	
		6	(37)	269.5	
1Y81	Heated	2	(49)	75.1	103.6
		3	(47)	133.3	
	Ambiant	5	(60)	78.3	72.6
		6	(73)	68.0	

NESTED ANALYSIS OF VARIANCE

Source of variation	DF	Mean square	F ratio	Significance
Between regimes	1	124481.8	1.58	NS
Between tank replicates nested within temperature regimes (error 1)	4	78956.3	4.29	p=0.2%
Within cells	221	18388.1		
Between regimes	1	53512.2	1.26	NS
Between tank replicates nested within temperature regimes (error 1)	2	42451.6	8.46	p=0.03%
Within cells	225	5017.9		

Cohort	Overwintering temperature regime	Tank number	Number of fish	Mean weight increment (g) in the tank	Mean weight increment (g) in the regime
2Y80	Heated	1	(29)	123.3	123.3
	Ambiant	1	(29)	17.5	17.5

ANALYSIS OF VARIANCE

Source of variation	DF	Mean square	F ratio	Significance
Between groups	1	162392.4	20.88	p<0.001%
Within groups	56	7776.1		

In the 1Y81 and 2Y81 cohorts, there were significant differences for winter mean weight increment between replicate tanks within overwintering temperature regimes, but no significant differences between overwintering temperature regimes. In the 2Y80 cohort, the overwintering temperature regimes had a significant impact on the winter mean weight increments. However, in this cohort, there was only one tank per temperature regime and thus, overwintering temperature regimes effects were confounded with tank effects.

It therefore appeared that the previously mentioned environmental factors associated with tanks affected both the winter growth dynamics and subsequent grilse maturation rates (+18) in a parallel manner, and tended to mask the effect of overwintering temperature regimes on maturation rates and winter growth. The nature of these environmental factors is quite puzzling. Among the heated tanks, tank #3 was characterised by a good winter growth and a high grilse maturation rate (+18), in both the 1Y81 and 2Y81 cohorts (Tables 4.32, 4.33). This could be due to the position of this tank (Fig. 4.2) since it was the most remote from the alleys and therefore the least prone to disturbance by passerbys. Yet, this tank was not characterised by a higher growth during the first summer for the 2Y81 fish (Table 4.34). Among ambient tanks, in the 2Y81 cohort, tank #6 was characterised by an average winter growth and a high rate of grilse maturation (+18). This tank was, in contrast to tank #3, the most prone to disturbance by passerbys (fig. 4.2).

3.5.2 First summer in seawater. Table 4.34.

There did not seem to be any link between the growth performance in the first summer, in the different tanks, and the subsequent maturation rates according to tank locations. In the 1Y81 cohort, first summer mean weight increments were significantly different between the 2 tanks used, probably because of the different fish densities, but this did not translate into different rates of grilse maturation (+18) (Table 4.34). In the 2Y81 cohort, the opposite was observed: the first summer growth performance was not significantly different between the 6 tanks used, and yet, significantly different rates of grilse maturation (+18) were observed (Table 4.34).

3.5.3 Summary

These observations confirm indirectly what was observed in the preceding sections, i.e. that there is a strong link between the growth performance during the winter in seawater and the subsequent grilse maturation rates (+18), but that the growth dynamics during the first summer in seawater bear little significance on the subsequent grilse maturation rates (cf. sections 3.2.5, 3.3.5, 3.4.4). It also appears that the overwintering temperature does not have any direct influence on maturation as grilse (+18).

There is as well some indirect evidence that the decision to undertake maturation is not taken before the winter period. The rate of grilse maturation (+18) among the 1Y81 fish overwintering in tank #2 was significantly different from that among the fish overwintering in tank #3 (Table 4.32).

Table 4.34: Comparison of weight increments during the first summer in seawater, between the different tanks, and comparison of grilse maturation rates between the different first summer tanks, in the 1Y81 and 2Y81 cohorts.

Cohort	Tank number	Number of fish in tank	Rate of grilse maturation (+18) in the tank	Comparison of maturation rate between tanks	Mean weight increment (g) during the 1st summer	Comparison of mean weight increment between tanks (1 way anova)
1Y81	5	(97)	28.1%	X^2=0.0 1df NS	211.3	F=30.6 p<0.01%
	6	(134)	27.1%		170.3	
2Y81	1	(45)	45.5%	X^2=19.7 5df p=0.1%	443.2	F=1.9 NS
	2	(39)	44.7%		455.3	
	3	(36)	54.3%		401.9	
	4	(43)	31.6%		409.8	
	5	(39)	30.6%		432.8	
	6	(37)	75.0%		460.3	

Yet the fish shared the same environment during the first summer (tank #5) and were randomly assigned to tanks #2 and #3, only in December 1983 (cf. Fig. 4.1). Similarly, since the fish shared the same environment during the second summer in seawater (cf. Fig. 4.1), and since overwintering locations significantly affected the rate of grilse maturation (+18) (Table 4.32), it can be inferred that the decision to mature is either taken during the winter periods or is strongly linked with biological events occuring during the winter periods.

4. Discussion

4.1 General summary of the findings of the present study on growth and maturation patterns

From the preceding sections 3.2, 3.3, 3.4 and 3.5, it appeared that grilse maturation (+18) was consistently associated with the following patterns of growth: the growth dynamics during the winter before smoltification and during the first summer after smoltification did not seem to bear any relationship with the future grilse maturation (+18) status; during the winter in seawater, the future grilse (+18) showed a significantly better growth performance than the fish that would not mature as grilse; during the second summer in seawater, the opposite was generally seen, although maturing male grilse (+18) did not consistantly showed a growth reduction, compared to the males not maturing.

Post-smolt precocious maturation (+6) seemed as well to be associated with a very similar pattern: during the winter preceding this maturation episode (winter before smoltification), the future post-smolt mature (+6) males showed a significantly better growth performance than the fish that would not mature as post-smolt, and during the following summer (first summer in seawater) the opposite could be seen.

Only indirect evidences of the growth dynamics before precocious maturation (-6) were available, but they appeared as well to be consistant with the existence of a similar pattern. During the summer preceding this maturation episode, the maturing precocious (-6) males seemed to show a reduced growth compared to the fish not maturing, but early precocious maturation (0+) also appeared to be associated with the presence of an environment allowing an early good growth.

The growth during the winter following post-smolt precocious

maturation (+6) in the 3 cohorts was reduced. This was not obvious in the case of growth after precocious maturation (-6) in the 2Y81 cohort, probably because the harsh environmental conditions during this period did not allow the fish to experience much growth, regardless of precocious maturation (-6) status.

Hence, it appears that maturations are associated with complex patterns of variations in the fish growth, but that these patterns are fairly similar for the different maturation episodes. It should be stressed that the obervation of these patterns was possible only because each fish was individually identified for the complete length of the experiment and because growth data were collected every 6 months or so. Had it not been the case, these patterns would have been considerably or even totally obscured.

The use of individual identification allowed the separation of the males from the females, and among the males, the separation of the precocious males (-6), the post-smolt precocious males (+6) and the maiden males. The patterns of growth associated with grilse maturation were qualitatively similar across these groups but there were nevertheless some quantitative differences. For example, in the 1Y81 cohort, the mean winter weight increment of the future grilse (+18) was significantly higher than that of the multi-sea-winter fish, among both the maiden males (125.1g vs 68.5g in Table 4.23) and the post-smolt precocious males (+6) (80.3g vs 21.8g in Table 4.23). Yet, without individual identification, this relationship between winter weight increment and grilse maturation (+18) would have been obscured, because the winter weight increment of the maiden males <u>not maturing</u> as grilse (68.5g) was very close to that of the post-smolt precocious (+6) males

maturing as grilse (+18) (80.3g). The use of individual identification also allowed the calculation of individual weight and length increments, which was a much more precise and powerful way to characterise the growth during a period, rather than relying on the length or weight at a specific time as an indication of growth. For example, grilse maturation (+18) was systematically associated with higher weight increments during the winter in seawater. As a result, the future grilse were heavier than the future multi-sea-winter fish in May or June, at the end of the winter periods. However, the differences were much more important (higher F ratio) in terms of weight increment rather than or weight in spring (Tables 4.9, 4.10, 4.11, 4.17, 4.23), because the variance in winter weight increment explained only a small part of the variance of the weight at the end of the winter periods. Furthermore, the patterns of growth associated with grilse maturation (+18) during the second summer in seawater was generally opposite to that observed during the winter in seawater, so that the length or weight at the time of grilse maturation (+18) was not very informative. For example, in December 1984 and 85, there were no longer significant differences for length or weight between the maiden multi-sea-winter fish, the maiden male grilse and the maiden female grilse in the 3 cohorts (Tables 4.12, 4.13, 4.14).

Few of the published studies on maturity in salmonids have used individually identified fish. The literature data on relationships between the growth and size of salmonids and age at maturity are rather contradictory (Gardner, 1976; Kazakov, 1981), but in many cases, the conflicting results and conclusions that have been reported seem to be explained, at least partly, by the inability to collect precise growth

trajectories, and by erroneous generalisations of findings at one time of the growth cycle to the ensemble of the growth cycle.

The following sections offer a review of the results that have been reported on growth and maturation, first in reared salmonids populations and then in natural salmonids populations.

4.2 Growth patterns and maturation patterns in reared salmonids populations

Maturation status can easily be assessed for a few months before and after maturity so that the growth patterns associated with maturation during this period (from a few months before to a few months after maturity) have been well documented. There is a good agreement between what has been reported and the findings of the present study.

4.2.1 Growth after a maturation episode

A reduced growth performance after a maturation episode was reported by Kato (1975), Burger (1985) and by McKay et al. (1986), for freshwater reared rainbow trout, and by Møller et al. (1976), Naevdal et al. (1979b) and Tveranger (1985) for sea-cage reared rainbow trout. The same was reported for Atlantic salmon after precocious maturation (Leyzerovich, 1973) and after grilse maturation (Naevdal et al., 1978b). In contrast, Naevdal (1983) reported no obvious difference between precocious parr and nonmature parr, for growth from November (time at which precocious maturation was assessed) to May/June the following spring. The lower growth performance of the mature fish, compared to the immature ones, during and after the spawning period, has generally been attributed to the lower feeding activity of the mature fish (Kato, 1975; Naevdal et al., 1978b; Smith et al., 1979; Tveranger, 1985),

although Leyzerovich (1973) also suggested that the gradual resorption of the sexual products required additional energy expenditure. However, the observation that the precocious males (-6) showed a slightly but significantly higher weight increment, compared to the immature, during the following winter under conditions of near starvation (c.f. section 3.3.1, Table 4.15) seems to contradict Leyzerovich (1973) hypothesis. In this study, the post-smolt mature (+6) males appeared effectively to show a lower feeding activity during the winter period following this maturation episode. Naevdal et al. (1978b) used individually identified fish and noted that there was a considerable variability in the growth performance following the grilse maturation (+18) episode, particularly among the males. This was assumed to reflect the observation that some mature fish start to eat soon after spawning while others start later or not at all. This is similar to what was observed in the present study. In the 3 cohorts, post-smolt mature (+6) males showed in general a reduced growth performance during the winter in seawater, but among them some males showed a growth performance as good, if not better, as that of most of the fish not mature as post-smolt.

4.2.2 Growth during the last months before a maturation episode

A reduced growth performance of the maturing fish during the last months before maturity has also been widely reported. Leyzerovich (1973) noted that the Atlantic salmon precocious maturation was associated with a lower growth in the late summer and fall so that these dwarf males were smaller at the time of maturity (late fall), compared to the sexually immature juvenile, even though these dwarf males were larger at the beginning of the summer. Leyzerovich stated that the large energy expenditure necessary for the process of gonads maturation

in these dwarf males was covered during the summer by feeding and the use of inner reserves, along with the process of growth. However, from the end of the summer, as feeding rate and assimilation of the food declined, the energy was being increasingly diverted from somatic to gonadal growth. Saunders and Sreedharan (1977) also observed that the growth of maturing precocious males (aged both 0+ and 1+) was reduced, compared to that of immature males and females, from August to November. Bailey et al. (1980) noted that once precocious maturation was initiated, energy previously used for somatic growth was diverted into gonadal development, which reduced the growth rate of maturing males and allowed immature individuals to become relatively larger. Saunders et al. (1982) followed the growth of individually identified juvenile Atlantic salmon from July to November. The maturing precocious parr grew at a similar rate relative to the immature parr until late August, after which the immature grew faster. Lundqvist and Fridberg (1982) noted that the growth of the precocious maturing males held in freshwater started to slow down in mid-July. The same could be noted on a few post-smolt precocious maturing males held in brackish water pens. Tveranger (1985) observed that, in large seacage reared rainbow trout, the growth of maturing males and females stagnated just before the spawning period. Maturing females spent much more energy on gonadal growth than males and they showed a depressed growth earlier than the maturing males. Asknes et al. (1986) observed a very similar pattern among sea cage reared Atlantic salmon before the 2-sea-winter maturation episode. The gutted weight of the immature fish increased regularly from June to December. The maturing males also gained gutted weight, but relatively less as maturation proceeded. The maturing females

gutted weight increased until July but decreased afterwards. In June, the maturing males and females were about 1kg heavier than the immature fish, but the immature fish gutted weight overpassed that of the maturing females in September and that of the maturing males in December.

These observations are quite similar to what was observed in the present study. It appears probable that among the males, the relative energy cost of gonadal development and maturation decreases with increasing size (corresponding to increasing age at maturity). Hence, male maturation at small sizes, i.e. precocious maturation, post-smolt precocious maturation, can probably be expected to almost always induce a reduction in somatic growth in the last months before maturity. On the other hand, the somatic growth reduction associated with male maturation at large size, i.e. grilse, 2-sea-winter, 3-sea-winter maturations etc., might be much less conspicuous, particularly if the growing conditions are good. Tveranger (1985) noted that in large sea cage reared rainbow trout, the maturing males seemed to have consumed enough food during the period of gonadal maturation so that their energy demand was satisfied for this purpose, thus enabling them to store surplus energy intake as fat in the musculature. The maturing females, in contrast, seemed to have spent heavy supplies of the added nutrients in the gonads formation during the later part of gonadal maturation. It is probable that among females the relative energy cost of gonad development and maturation remains relatively constant with increasing size, because the amount of sexual products produced by salmonids females increases with the size of the females (Glebe et al., 1979; Gjerde, 1986).

4.2.3 Growth up until 4-6 months before a maturation episode

There is an overall good agreement between the results of the present study and those from cage rearing studies, particularly concerning growth and maturation in sea cages. Naevdal et al. (1983), Gjerde and Refstie (1984), Aksnes et al. (1986) and Gjerde (1986), all reported a very similar pattern in cage reared Atlantic salmon: about 4 months before the 2-sea-winter maturation episode, the maturing males were significantly heavier than the maturing females, themselves significantly heavier than the immature fish. The same was reported 4 months before the 3-sea-winter and 4-sea-winter maturation episodes (Gjerde, 1984). This is also in agreement with Gjerde and Gjedrem (1984) who reported a negative phenotypic correlation between body weight (measured 4 months before maturity) and age at maturity. Simpson and Thorpe (1976) reported that among cage reared salmon, grilse were apparently recruited from the larger members of the population. Naevdal (1983) noted that incidence of grilse maturation seemed to depend on the growth rate of the fish. Fish of the same families and strains were reared in two different environments and in all groups, the incidence of grilse maturation was higher in the environment in which overall growth rate was higher. These observations are quite similar to what was observed in the present study, and indicate that maturation in the seawater phase is associated with an early good growth. Studies on reared rainbow trout showed similar results as well. Kato (1975), Naevdal et al. (1979b), McKay et al. (1986) and Siitonen (1986) reported that larger rainbow trout tended to mature earlier than smaller fish. The same was reported for several forms of brown trout (Salmo trutta) reared in freshwater ponds (Alm, 1959). Most of these studies on salmon

reported that maturing males were significantly heavier than maturing females, 4 months before maturity, while in the present study, a slightly opposite tendency was noted, 6-7 months before maturity (c.f. section 3.2.3). This probably indicates that, as previously noted, maturing females experience a stronger and earlier growth reduction at the approach of maturation.

Naevdal et al. (1983) reported that the effect of maturation was much less evident on lengths than on weights. Six months before maturity there was no significant difference for length between the maturing fish and the immature fish in 2 of the 4 year classes comparisons, while all year classes comparisons for weight were significant. They also noted that, in nearly all groups, condition factors were higher for maturing than for immature fish of both sexes. The same difference in condition factors was reported by Simpson and Thorpe (1976) and by Aksnes et al. (1986). These observations are again quite similar to what was observed in the present study. At the end of the winter period, there were more differences (higher F ratio) in terms of weight rather than of length in the 3 cohorts. Condition factors were considerably higher among future grilse than among multi-sea-winter fish (c.f. sections 3.2.3 and 3.3.3). It is interesting to note that in all cohorts, the mean condition factor at the end of the winter period was the most informative variable (highest F ratio) of all, relative to future grilse maturation status. Yet, as noted by Naevdal et al. (1983), the differences cannot be due to gonad weight at this stage because the gonads are just starting to develop and represent only a negligible fraction of the total weight. This difference in condition factor reflects thus real differences in body proportions between

maturing and immature fish.

In this study, the higher weight of the future grilse at the end of the winter period was shown to result exclusively from a better winter growth performance. There were no initial size differences nor differences for the growth performance during the winter before smoltification and in the first summer at sea, in the 3 cohorts. Naevdal (1983) showed similar results concerning grilse incidence among 14 strains reared at two fish farms, A and S, which differed mainly by the food and feeding schedules used. The fish at farm A had a markedly higher growth rate during the first summer, while the fish at farm S grew better throughout the next winter and early spring. The fish of farm A were then transferred to farm S for the second summer at sea and in September, the mean length of both batches were similar. However, the condition factors of the fish kept in all the time in farm S were higher and, in most strains, incidence of grilse was higher among the fish reared at farm S. This confirms the observation of the present study, that maturation as grilse seemed to be associated with a good winter growth performance, while growth during the first summer bears little significance on it (c.f. section 3.5). However, on a study of individually identified rainbow trout reared in sea cages, Naevdal et al. (1979b) reported that the fish maturing in their third year were larger than their immature counterparts in the spring, 6 months before maturation, but that this difference could be traced back in one of the year class to the preceding fall, one year before maturation. This result contrasts with the results of the present study where no differences for size were detectable at the end of the first summer, one year before grilse maturation.

Gjerde and Refstie (1984) also reported that before the 2-sea-winter maturation episode, immature males were significantly heavier than immature females. Naevdal et al. (1983) reported similar results on average, in a group of commercially reared salmon, but noted that the effect of sex was not clear in a group of experimental fish. In the present study however, in the absence of maturation (maiden multi-sea-winter fish) absolutely no differences were detected between the males and females growth trajectories, from 6 months before to 18 months after smoltification (c.f. section 3.1.1). In Gjerde and Reftsie (1984) study, the sex of the immature fish was determined at slaughter upon visual examination of the gonads. Their statement is considerably obscured by the fact that sex could not be determined in a large number of immature fish, which were therefore classified as "neuter". 51.6% of the fish in their study were immature. Of these, 58% were classified as females, 38% as "neuter" and only 4% were positively identified as males. The sex ratio of the maturing fish was 47% males and 53% females. It would then appear most probable that the "neuter" fish were mostly if not all males, in which case the reworked mean weight of the immature males appears quite similar to that of the immature females (Table I, in Gjerde and Reftsie, 1984).

Post-smolt precocious maturation (+6) appeared associated with a better growth during the previous winter (winter before smoltification) (c.f. section 3.4.3) in a very similar way to what was observed for grilse maturation (+18). As was noted in Chapter II, very little information, other than anecdotic, have been published on this maturation episode. However, it appears that when the information was available, this maturation was always associated with a particularly

good growth before smoltification. Sutterlin et al. (1978) described an experiment in which an accelerated rearing regime to produce large 1+ smolt resulted in an appreciable proportion of both males and females maturing as post-smolt. The fish were maintained in warm brackish water from October (10 months post-hatching) to the following spring when the fish were transferred in full seawater. They grew from a mean weight of 20g in October to 115g in June. Piggins and Mills (1985) reported that undersized 1+ smolt (12cm) reared another year in freshwater, reached sometimes very large sizes as 2+ smolt (25.0 - 42.0 cm). These "giant" smolt gave a very poor return when released for sea-ranching but, interestingly, 8 out of 9 of the recovered adults from these smolt were post-smolt coming back on the river after only 3-4 months at sea. Ridell (1986) reported similar results from Coho salmon (Oncorhynchus kisutch). A family of Coho salmon that demonstrated a remarkable freshwater growth rate, reached after 1 year a mean smolt weight of 320g (versus 10/20 g in most natural populations). Subsequently, more than half of the family matured as post-smolt.

Many authors have shown that precocious maturation in hatchery reared populations was as well associated with an early good growth. The future precocious males were larger than immature juveniles in the spring and early summer, before both early precocious maturation (0+) and precocious maturation at age 1+ (Leyzerovich, 1973). Glebe et al. (1978) noted that incidence of precocious males was higher in the high growth years. Bailey et al. (1980) suggested that the male parr that mature precociously may be initially among the faster growing individuals in the population. Murphy (1980, cited in Thorpe et al. 1983) found that maturing precocious males were the larger members

of a sibling population in April-June, but that the immature fish overtook them in size from August onwards. Lundqvist (1980) reported as well that maturing 1+ males were heavier than immature fish in August. However, Saunders and Sreedharan (1977) found that mature males were already smaller than immature fish in August, and Saunders et al. (1982) found no differences for size in July. As previously discussed, precocious maturation is associated with a decreased growth from early summer onwards. It appears probable that the future precocious males are larger in late winter and early spring than the immature fish, but the relative difference is probably variable, depending on previous growth conditions. These conflicting results reported for size differences in July/August may simply reflect that, in some experiments, maturing males were much larger than immature fish in spring, so that even with the following growth reduction, they were still larger in July/August, while in other experiments, the maturing males might have been only slightly larger in spring so that with the following growth reduction, they were already smaller in August, compared to the immature fish. Leyzerovich (1973) noted that the condition factors were higher among maturing precocious males than among immature juveniles from the spring before maturation and remained so until a few months after the spawning season. The same could be seen in August before precocious maturation, in Lundqvist (1980), and from September onwards, in Saunders et al. (1982).

4.3 Growth pattern and maturation pattern in natural populations

The growth reduction during the last months before maturation and during the winter after maturation has been observed in natural populations as well. Myers et al. (1986) calculated the reduction of

early growth associated with precocious maturation to be around 8% on average, on the Little Codroy River, Nfld. Dalley et al. (1983) reported as well that the growth of precocious parr was slowed down by maturation, in several Newfoundland rivers. Allen et al. (1972) noted that grilse were smaller at the time of capture in the river (late summer, early fall) than multi-sea-winter fish of the same smolt class still feeding at sea and which had been captured at the same date around Greenland. Their data also suggested a similar difference between 2-sea-winter and 3-sea-winter salmon and they concluded that growth during the migration at sea was reduced at the approach of maturity.

The fact that maturation is associated with an early good growth has also been reported in natural populations, at least concerning precocious and apparently post-smolt precocious maturations. Schieffer (1971, cited in Thorpe et al., 1983) hypothesized that fast growth rates led to high percentages of precocious males in several Quebec North Shore rivers. Dalley et al. (1983) concluded from age-specific length examination that faster growing males were becoming precocious. Bagliniere and Maisse (1985) reported that precocious maturation at age 0+ and 1+ appeared linked to favourable growth conditions in some Brittany rivers (France). They noted that maturing 1+ males were apparently recruited from the larger individuals and maintained their size advantages until the fall and even sometimes until the end of the winter following precocious maturation. Post-smolt precocious fish appear extremely rare in natural populations and very little information is available on them. Shearer (1963) examined the scales of 2 such fish and noted that both fish had migrated as exceptionally large smolt, hence that they had had a very good growth before smoltification. Utoh

(1976, 1977) showed that precocious males at age 0+ in Masu salmon (Oncorhynchus masou) were recruited among the largest members of a river population, and the size differences between the maturing males and the immature fish could be detected as early as June. He also found that the incidence of early precocious maturation (0+) was higher in years of higher growth.

In contrast, evidence of the relationships between early growth rate at sea and maturation at sea (grilse, 2-sea-winter, 3-sea-winter etc. maturations) among wild stocks is considerably more contradictory. There are no direct data available for these sorts of studies, so the evidence presented below comes from scales studies. Most of these studies have compared grilse and multi-sea-winter fish for the back calculated length at the end of the first sea-winter annulus (as recorded by the scales) and/or the length increment between smoltification (as recorded by the scales) and the end of the first sea-winter annulus.

Earlier scales studies of the Ministry of Agriculture and Fisheries for Scotland were summarized by Gardner (1976, Table VII) and showed no systematic differences in growth rates of the different maturation classes. Out of the 14 such studies listed, 10 suggested that grilse had smaller length increment from smoltification to the end of the first sea-winter and were smaller at the end of the first sea-winter, compared to the 2-sea-winter salmon, while the remaining 4 studies suggested the opposite. The differences, whether in one direction or another, were generally small: for example, differences between grilse and 2-sea-winter salmon for length back calculated at the end of 1-sea-winter were 1cm or less in 7 of these 14 studies. On the

contrary, for sockeye salmon (Oncorhychnus merka) Foester (1968) showed, among fish of the same freshwater age, a very consistant pattern. At the end of the first sea-winter, the back calculated lengths of the 1-sea-winter fish were on average larger than that of the 2-sea-winter, themselves larger than that of the 3-sea-winter. These larger lengths were due to larger length increments, during both the first summer and the first winter at sea and were not linked to smolt sizes or growth in freshwater. A similar pattern was evident at the end of the second sea-winter between the fish maturing as 2-sea-winter or as 3-sea-winter. In contrast, no consistant pattern of relationships between growth and age at maturity was revealed in the extensive study of the North Esk salmon populations (Shearer, 1973, cited in Gardner, 1976). Shaffer and Elson (1975) proposed that mean age at maturity was positively correlated with marine growth rate after the grilse stage, the slower growing fish maturing earlier. However, Myers and Hutchings (1987) reanalysed their data and found that this positive correlation was spurious. Dempson et al. (1986) compared the growth during the first sea year, as calculated from counting the number of circuli (rings) laid between the last freshwater annulus and the first annulus in the sea zone, between grilse and 2-sea-winter salmon. They concluded that grilse had generally less or the same number of circuli in the first sea year than had the 2-sea-winter salmon, the differences being not always significant from year to year.

Naevdal et al. (1983) suggested that the discrepancies between the results from cage reared populations and from natural populations might reflect differences between natural and artificial environments, particularly concerning feeding regimes. Dempson et al. (1986)

concluded that the extrapolation of results from sea cage studies to natural populations might be invalid. The absence of growth differences between the grilse and the 2-sea-winter salmon in natural populations could result from these fish having different migration routes at sea, hence being in different environments, while in sea cage studies all fish share the same artificial environment. Conversely, these discrepancies might simply reflect the inability of the scales reading technique to detect, in natural populations, differences in the growth of grilse and 2-sea-winter fish similar to those seen in cage reared populations, for the following reasons:

1) Many of the scales studies compared mixtures of year classes, sexes and smolt age classes, which could considerably obscure the interpretation of the results. Some studies (eg. Foerster, 1968; Dempson et al.,1986) offered a better control by comparing length within year classes, within smolt age classes and even sometimes within sexes. However, even in the best case, the males would still represent a mixture of previously precocious parr and previously immature parr, which could again obscure the results.

2) Scale reading provides growth data in terms of length, not in terms of weight. As was previously discussed, there was much less difference between the grilse and the multi-sea-winter fish in terms of length than or weight. This problem is further compounded by the fact that scale reading provides only a rough approximation of length at different times, and is potentially subject to numerous operator errors (Jones, 1959). Great accuracy is not possible when dealing

with scales. For example, the change over from river to sea-ring, which would correspond to smoltification is not always clear cut (Jones, 1959). The method might therefore be not precise enough to detect small differences in length or length increments, in the order of the ones detected in the present study.

3) Lastly, but most importantly, I would suggest that the use of scale reading techniques to detect differences in back calculated length or length increment between grilse and 2-sea-winter salmon might be inappropriate, because of a problem in the technique itself that might automatically nullify or even invert any real differences. The scale reading techniques are based on the observation that the circuli (rings) of a scale can be seen to be grouped in alternate annuli (bands) of widely spaced (open) circuli, and less widely spaced and less numerous (narrow) circuli. It has long been accepted that the annuli of open circuli represent periods of fast growth, while annuli of narrow circuli represent periods of slow growth. These periods have been loosely termed "summer growth" and "winter growth" respectively, but the correspondance with these seasons is only rough (Jones 1959). The succession of the summer and winter annuli does not constitute an absolute time scale, but rather a relative one representing the variation of growth that an individual fish experienced. For example, Jones (1959) noted that in Britain, the freshwater "winter" annuli corresponded approximately to the October to March season, but

there was some variation from year to year in any one river, and that there was a tendency for the formation of "summer" annuli to begin earlier in the more southerly rivers. Hence, the exact time at which the last circulus of the first sea-winter annulus is laid down is most probably variable between individual fish and furthermore, this variation in time is certainly related to the individual growth rate of the fish during this period. If we assume that the differences in growth patterns between the grilse and the 2-sea-winter salmon are similar in natural populations to what is observed in cage reared populations, then we might expect that the grilse, which show a faster growth during the winter and early summer, are laying the last circulus of the first sea winter annulus earlier, on an absolute time scale, than the 2-sea-winter salmon. Therefore, when comparing the back calculated length at the end of the first sea-winter annulus of the grilse with that of the 2-sea-winter salmon, we might be comparing, for example, the length of the grilse in May to that of the 2-sea-winter salmon in June. This would understandly lead to the sort of inconsistencies that are found at large in scale reading studies.

Overall, the results that have been reported in the literature concerning growth patterns associated with maturation are quite consistent, once replaced on a proper time scale, with what was observed in the present study. Many contradictions are only superficial and result from the fact that a maturation episode is generally accompanied

by a better growth early and by a poorer growth later, which results in a complicated variation of the relative size of the maturing fish, compared to the immature fish. The major remaining source of contradictions is the absence of clear growth patterns associated with maturation at sea in the wild populations. As previously discussed, this could be a consequence of the inability of the scale reading technique to detect growth differences between the grilse and the multi-sea-winter fish, similar to that observed in the present study and in other cage rearing experiments. Studies of precocious maturation in wild stocks have used scales data as well, but they were complemented by extensive direct samplings of the fish in the rivers which allowed a much more precise quantification of growth patterns associated with this maturation episode. It is interesting to note that the results reported in these cases are consistent with what was observed in hatchery reared populations. The next section discusses causality between growth and maturation.

4.4 Causality

The observations that maturing fish showed a reduced growth during the last months before maturity and during the winter following maturation are evidently consequences of the process of maturation itself. As already discussed, this growth reduction appears caused by: 1) An increasing diversion of energy from somatic to gonadal growth, as evidenced by a growth reduction during the summer before maturation generally more intense in terms of length increment rather than of weight increment. This energy diversion probably starts from early summer but is mostly evident by late summer, the females probably showing a stronger and earlier energy diversion compared to the males.

2) A diminution of the energy intake, starting probably around early fall, as the feeding activity of the maturing/mature fish decreases considerably around maturity and during the winter following it.

On the contrary, during the winter preceding maturation, the fish that would mature showed a better growth than the fish that would not.

This better growth performance was more important in terms of weight increment rather than of length increment. It therefore appears that the fish that would mature the following fall were accumulating energy during this period, likely to cover part of the energetic expenses that would later come with the process of gonadal development and maturation. This better growth performance of the future mature fish could be interpreted either as a direct or indirect consequence, or as a direct or indirect cause of maturation. Gjerde (1986) stated that the large differences in body weight observed between maturing and immature fish, 4-5 months prior to maturity, might largely be caused by sex hormones accelerating the growth rate. Male steroid hormones (androgens), including 11-ketotestosterone, a natural male sex hormone in salmonids, have indeed been showed to have anabolising effects on growth in several fish (Jalabert et al., 1982). However, the effect of oestrogens on fish growth is much less clear and most of the published results reported either no effect, or even detrimental effects on growth (Jalabert et al., 1982). If the hypothesis of Gjerde (1986) is nevertheless correct, this implies that the salmon initiate the maturation cycle (maturation decision), probably early in the winter, some 8-10 months before maturity. Once this maturation decision is initiated, the increasing level of circulating sex hormones would lead to a surge of growth of the maturing fish, compared to the immature fish

during the winter and early summer, until the growth reduction associated with the final stage of gonadal development, starting in late summer. No differences of growth patterns were observed, before the winter in seawater, between the grilse and the multi-sea-winter fish in the present study. Therefore, accepting the hypothesis of Gjerde (1986) would mean that growth is in no way causally related to maturation. The complex variation of growth that is associated with maturity, as observed in the present study and reported in many others, would be strictly consequences of the maturation cycle.

Alternatively, the better winter growth performance of the future mature fish could be interpretated as causally related to the initiation of the maturation process. Although the essentially observational nature of this study does not allow ones to conclude definitely in favour of one or the other of those two possibilities, there were some indications that winter growth performance was related to maturation in a causal way, rather than as a consequence of maturation. For example (c.f. section 3.3.6), the higher incidence of early precocious maturation (0+) among the production fish appeared caused by the considerably better growth that these fish had, compared to the family marked fish. In section 3.5.3, it was noted that there was a significant correlation between the rate of grilse maturation in the different winter tanks and the mean winter weight increment in the same tanks. There was as well a significant correlation between the mean winter weight increment of the immature multi-sea-winter fish and the mean winter weight increment of the maturing grilse in these tanks, which indicates that the better winter growth performance in some tanks,

compared to others, was not a consequence of the higher rate of maturation in these tanks. It therefore appeared that some unknown environmental factors associated with the tanks affected the fish growth rate and created some variation between tanks for mean winter weight increment, which in turn, somehow caused variation in the incidence of grilse maturation.

Furthermore, many studies have shown that varying incidence of maturation can be obtained by manipulation of the fish growth rate. This would not be observed if the hypothesis of Gjerde (1986) was correct, since this hypothesis would imply that the variations in growth are strictly consequences of the maturation cycle. Kato (1975, 1978) reported that higher percentages of mature fish were observed in the groups reared on large amount of food, for both rainbow trout and Kokanee salmon (Oncorhynchus nerka). Similar results were obtained with brook trout (Salvelinus fontinalis) (McCormick and Maiman, 1984). Burger (1985) reported that when different growth regimes for underyearling rainbow trout were initiated in July, this led to some variation between the different groups for final weight in December, but not for the incidence of precocious maturation. However, when the different growth regimes were initiated earlier (in April), this led to much stronger differences for final weight and also to significant differences in the incidence of precocity, the highest incidence being observed in the groups showing the highest growth. Burger (1985) concluded that maturation appeared to be caused by an initial rapid growth and that there could be a specific time "window" during which fast growth initiated maturation. Sutterlin and MacLean (1984) mentionned that, in a dwarf landlocked form of Atlantic salmon, a large

proportion of the males and females can be induced to spawn one year earlier than usual by keeping the fish in warmed water during the winter. Although they did not specifically mentionned it, the fish under the warmed regimes appeared to have a better growth during the winter than the fish kept under natural temperature regimes. Sutterlin et al. (1978) concluded as well that the peculiar rearing regimes that they used to produce large 1+ smolt was probably responsible for the high incidence of post-smolt precocious maturity. Growth during the winter before smoltification was particularly strong in that experiment. Saunders et al. (1982) accelerated hatching and early growth of Atlantic salmon by using heated water in the winter and found that a proportion of the rapidly growing males matured as 0+, a result generally not seen when ambiant temperature is used. This appears similar to what was observed in the present study (section 3.3.6). Lastly, as previously discussed, accepting Gjerde's hypothesis would mean that maturation is initiated probably around early winter. Korsgaard et al. (1986) studied the vitelogenic response to estradiol treatment in Atlantic salmon post-smolt. They showed that no vitellogenic response could be elicited if the salmon were kept at 3°C during the treatment, while a response could be elicited if the fish were kept at 10°C. The response was dependent on the temperature at the time of treatment, but not on previous month temperature regimes. This response inhibition by low temperature indicates that the initiation of maturation is probably not taking place during the winter months but could be taken in early spring.

It therefore appears that the better winter growth performance showed by the fish that would mature the following fall is not <u>simply</u> a

consequence of the maturation cycle, but is rather somehow causally related to the initiation of the maturation process. Yet, it cannot be completely ruled out that once the better growth of some fish directly or indirectly caused the initiation of maturation, a further growth differentiation between the maturing and immature fish might occur because of a growth accelerating effect due to a higher level of circulating sex hormones in the maturing fish, as hypothesized by Gjerde (1986).

The following section offers an hypothetic model for the mechanism of maturation "triggering" and its links to winter growth performance.

4.5 An hypothetic model of maturation triggering

I would propose that the "decision" to initiate maturation, whatever the maturation episode, is taken by individual fish in early spring (April/May) and that the timing of this decision is regulated by the photoperiod (Henderson, 1963; Lundqvist, 1980; Lam, 1983; Bourlier and Billard, 1984; Bromage et al., 1984; Elliot et al., 1984; Johnson, 1984; McCormick and Naiman, 1984; Scott et al., 1984; Takashima and Yamada, 1984). I would propose that the decision to initiate maturation is based on the amount of energy stored in the fish, in the form of lipid in the flesh and fat tissue accumulated in the abdominal cavity. If the amount of energy stores is over a certain genetically determined sex specific threshold level, the fish will initiate maturation. These energy reserves will then be tapped to cover the energy expenses necessary for gonadal development and maturation (Leyzerovich, 1973; Saunders et al., 1982; Tveranger, 1985; Asknes et al., 1986). I would further propose that the major contributing factor to the level of energy reserves in early spring is the winter growth performance and

particularly the winter weight increment. In the present study, it was clear that during summer periods, most fish showed important somatic growth and were able in addition to store some energy reserves, as characterised by the typical increase in mean condition factors showed by most groups during summer periods. On the contrary, during winter periods, most fish showed a reduced somatic growth and a decrease in mean condition factor. This probably indicates that during winter periods, many fish do not get enough energy intake from feeding and revert to a catabolic state and use up some of the energy reserves they accumulated the previous summer, in order to cover their basic metabolic energy demands and for their reduced somatic growth. At the end of the winter, these fish have a low level of energy stores and do not initiate maturation. However, the fish that show a higher level of energy intake from feeding (the fish showing a higher winter weight increment) maintain their level of energy reserves, or even increase it and, at the end of the winter period, these fish initiate maturation. This would explain the quite systematic observation in the present study, of the fish that would mature the following fall showing a better winter weight increment and being characterised by much higher condition factors at the end of the winter period, compared to the immature fish. As noted by Naevdal et al. (1983), these higher condition factors in early spring cannot be explained by gonad weight differences between maturing and immature fish. It probably reflects differences in the level of fat tissues accumulated in the abdominal cavity around viscera.

I would also propose that females demand a higher level of energy stores to initiate maturation, compared to males. This could be seen in that, at the end of the winter periods, the maiden female grilse had

higher condition factors than the maiden male grilse in the 3 cohorts. Maiden female grilse had also shown better winter weight increments than the maiden male grilse, in 2 of the 3 cohorts (Tables 4.9, 4.19, 4.11). This could be linked with the already noted fact that the energy cost of maturation is higher among females than among males.

Lastly, I would propose that the minimum level of energy stores necessary to initiate maturation in early spring is genetically fixed, i.e. that it may be variable between stocks and between families within stocks. This point will be fully discussed in Chapter V.

As can be seen in Fig. 4.7, the overall distribution of condition factor in the spring preceding the grilse maturation (+18) episode is unimodal in the 3 cohorts. The future grilse (+18) show in general higher condition factors compared to the future multi-sea-winter fish, although this tendency is not very pronounced in the 2Y80 cohort. There is a considerable variance for condition factor in spring, in both the future grilse (+18) and the future multi-sea-winter fish and the two distributions broadly overlap in the 3 cohorts. This is probably partly due to the fact that each cohort is a mixture of males and females of various genetic backgrounds.

In the present study, weight increment during the winter in seawater did not appear to be linked with size at the beginning of the winter, or with previous growth performance (during first summer at sea, or during the winter before smoltification), which would explain why grilse maturation appeared independant from the growth trajectories during these periods.

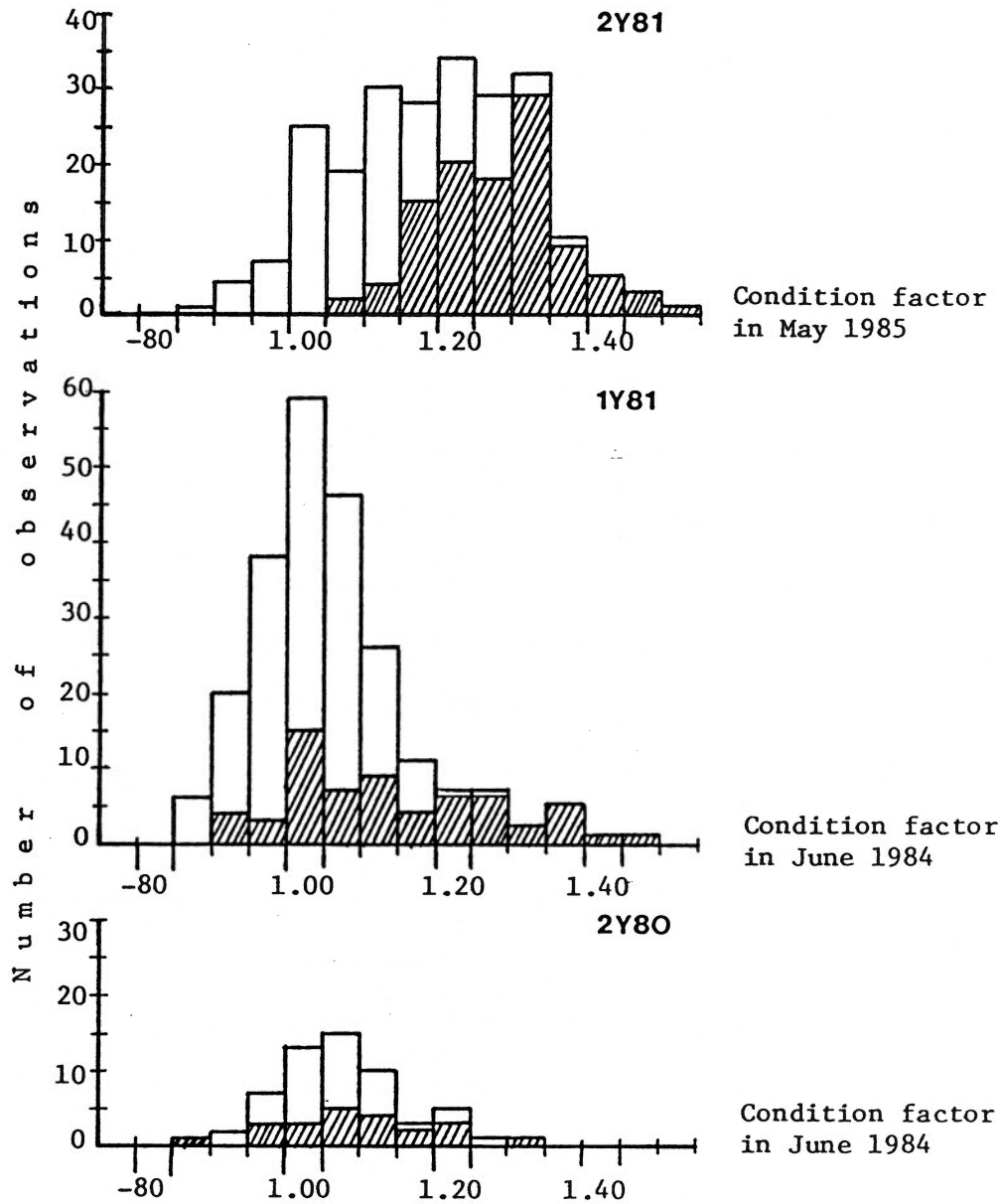

Figure 4.7:
Distribution of the condition factor in the spring preceding the grilse maturation (+18) episode in the 3 cohorts.

Open histogram: total population

Shaded histogram: fish maturing as grilse (+18)

However, it is probable that the fish showing higher level of energy stores at the beginning of the winter (higher condition factor) have a higher probability to have a higher level of energy stores remaining at the end of the winter period, even though their winter growth performance might not be better on average. This would explain why there was a slight tendency to observe higher condition factors among the future grilse in some groups, already at the end of the first summer in seawater. It is probable as well that under some conditions, winter growth performance could be related to other growth characteristics earlier in the cycle. For example, in a competitive environment, larger fish could have an advantage over smaller fish for winter feeding in seawater. In this case, it would appear that maturation as grilse was associated as well with larger smolt sizes, or with better growth during the first summer in seawater. However, these relationships would be only indirect consequences of larger smolt sizes allowing a better winter growth, itself causing higher maturation incidence. From the present study, it appears probable that smolt sizes or growth performance during the first summer at sea have no <u>direct</u> effect per se on the incidence of grilse maturation.

In the next section, the main findings in Chapter II concerning grilse maturation (the low rate of grilse maturation (+18) among the females in the 1Y81 cohort, the presence of a link between post-smolt precocious maturation (+6) and grilse maturation (+18) in the 1Y81 cohort, and the absence of a link between precocious maturation (-6) and grilse maturation (+18) in the 2Y81 cohort) are analysed under the perspective of this proposed causal mechanism linking winter growth

performance with maturation.

4.6 Grilse maturation (+18) and weight increments during the winter in seawater

The term "homogeneous" that is going to be used here refers to fish that showed the same patterns of maturation before the grilse maturation (+18) episode, e.g.: females ♀ (0,0,0) + ♀ (0,0,+18), nonprecocious males ♂ (0,0,0) + ♂ (0,0,+18), precocious males ♂ (-6,0,0) + ♂ (-6,0,18), etc.

Fig. 4.8 synthesized the individual information concerning the relation between winter weight increment and grilse maturation by plotting, for homogeneous groups in the three cohorts, the rate of grilse maturation (+18) on the different classes of winter weight increments. In the 1Y81 cohort, this was done after having randomly assigned a sex to individual fish in the group of 93 maiden multi-sea-winter fish of unknown sex ? (0,0). Random sex assignment was performed so that the sex ratio of this unknown sex group approximated that estimated in Chapter II (28 ♂/65 ♀). Since no significant differences between sexes, for winter growth performance among maiden multi-sea-winter fish in the three cohorts, were detected in section 3.1.1, this random assigning of sex was not likely to have introduced significant biases. This operation was done to remove the following biases: sex was known mostly for the fish that had matured, which had therefore showed higher winter weight increments.

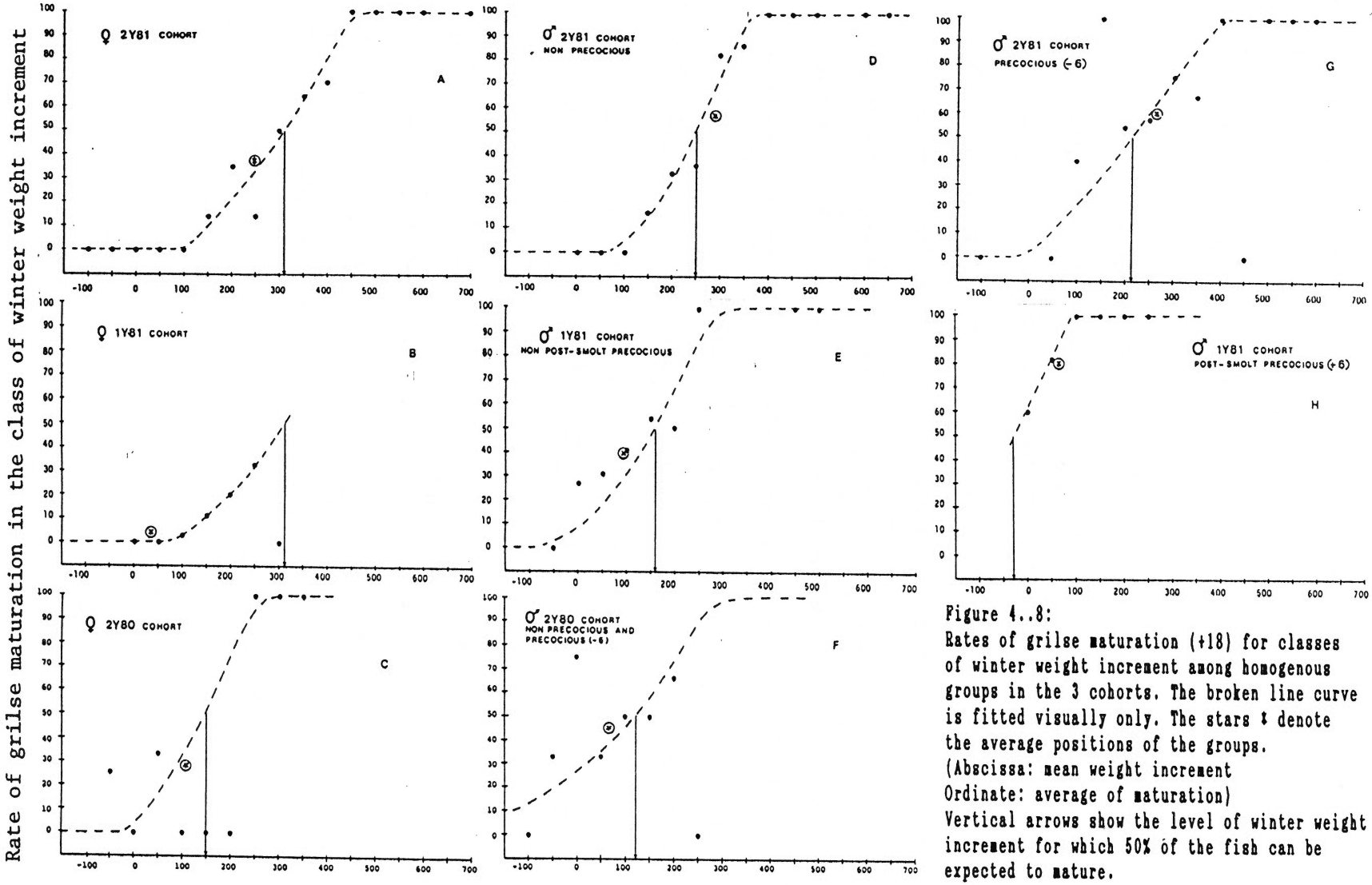

Figure 4..8:
Rates of grilse maturation (+18) for classes of winter weight increment among homogenous groups in the 3 cohorts. The broken line curve is fitted visually only. The stars ⚹ denote the average positions of the groups.
(Abscissa: mean weight increment
Ordinate: average of maturation)
Vertical arrows show the level of winter weight increment for which 50% of the fish can be expected to mature.

In most groups, the pattern of the plotted points approximated reasonably S shaped curves (fitted visually only), and this even though some weight increment classes were represented by very few individuals. In the 2Y80 cohort, particularly among the males, the patterns were not very clear, but this was probably a consequence of the low number of fish in this cohort, and also of the fact that no clear link was found between winter growth performance and grilse maturation (18) among the males in this cohort (cf. section 3.2.3). The S shape of these curves seemed to indicate that the decision to mature as grilse (+18) taken by individual fish was indeed quite dependant on the level of winter weight increment realised by the fish. In general, none of the fish that had showed a poor winter weight increment matured, while on the contrary, all fish that had showed a very large winter weight increment matured. Between both extremes, there was a fairly large zone in which an increasing proportion of fish matured with increasingly large winter weight increments. In order to make comparisons between the different cohorts and between the different groups, the winter weight increment levels for which 50% of the fish could be expected to mature as grilse (50% levels) were estimated from the curves in each group. These 50% levels should not be mistaken for the mean winter weight increment of a group: the latter represents the realised winter growth while the former is only an estimation of the level of winter growth at which 50% of the group would have matured, given the proposed causal mechanism linking winter growth and maturation.

It can be noted that in the three cohorts, these 50% levels were higher among the female groups (Fig. 4.8 A,B,C) than among any of the male groups (Fig. 4.8 D to H). This therefore appeared to confirm that

females were on average more demanding than males in terms of minimum level of winter growth to undertake maturation. The curves and the estimated 50% levels among the females in the 1Y81 and 2Y81 cohorts were positionned very similarly (Fig. 4.8 A,B). The significantly lower rate of grilse maturation (+18) observed among the females of the 1Y81 cohort, as compared to the 2Y81 cohort (cf. Table 2.5 in Chapter II) appeared thus to be mostly attributable to the poor winter growth performance of the 1Y81 females (mean winter weight increment $\simeq$ 85g), compared to that of the 2Y81 females (mean winter weight increment $\simeq$ 250g). With such low winter weight increment in the 1Y81 cohort, few females could maintain a level of energy stores that would be sufficient to initiate maturation in spring. On the other hand, the curve and the 50% level among the females of the 2Y80 cohort (Fig. 4.8 C) appeared much shifted towards lower levels of winter weight increment, as compared to either the 1Y81 or the 2Y81 females (Fig. 4.8 A,B). The females in the 2Y80 cohort seemed thus to be much less demanding in terms of minimum winter growth performance to undertake maturation than the females of the 1Y81 and 2Y81 cohorts. This appears to explain why the females in the 2Y80 cohort were characterised by a significantly higher rate of grilse maturation (+18), compared to the 1Y81 cohort females (cf. Table 2.5 in Chapter II), even though they did not show a much better winter growth performance (mean winter weight increment $\simeq$ 106g). Among the "maiden" males as well, those of the 2Y80 cohort seemed to be characterised by lower 50% level (Fig. 4.8 F), as compared to the maiden males of the 1Y81 or 2Y81 cohorts (Fig. 4.8 D,E). However, since the S shaped pattern was not very clear in this group which, furthermore, was not really homogeneous, the analysis of these

2Y80 males was not pursued further. The fact that both the males and females of the 2Y80 cohort appeared less demanding in terms of winter weight increment, compared to similar groups of the 1Y81 and 2Y81 cohorts, could be due to their different genetic origins.

The curve and the 50% level of the maiden males in the 1Y81 cohort (Fig. 4.8 E) was shifted towards lower levels of winter weight increment, compared to that of similar males in the 2Y81 cohort (Fig. 4.8 D). Hence, even though the 1Y81 maiden males showed a much poorer winter growth performance (mean winter weight increment $\simeq$ 94g), compared to the 2Y81 maiden males (mean winter weight increment $\simeq$ 286g), their rate of grilse maturation (40%) was not considerably lower than that of the 2Y81 maiden males (57%). The fact that the 1Y81 maiden males appeared less demanding than the 2Y81 maiden males could be due to different proportion of the genetic origin in the two cohorts. The 1Y81 cohort was composed of 72% group 1, 28% group 2, while the 2Y81 cohort was composed of 43% group 1 and 57% group 2. In Chapter III, group 1 was shown to have significantly higher incidence of all maturation episodes compared to group 2.

Among the 2Y81 males, the curve and the 50% level of the previously precocious (-6) males and that of the maiden males were positioned similarly (Fig. 4.8 D,G), the precocious (-6) males appearing very slightly less demanding than the maiden males. Their winter weight increments were as well quite similar (cf. 2 first contrasts #3 in Table 4.17), both groups being therefore not surprisingly characterised by very similar grilse maturation rates (+18) (60% among previously precocious (-6) males, 57% among the nonprecocious males). The observation that precocious males appeared slightly less demanding in

terms of winter weight increment, compared to the maiden males, could be due to their slightly higher mean condition factor at the beginning of the winter period (Table 4.16). It therefore appears that the independance between precocious maturation (-6) and grilse maturation (+18) noted in Chapter II, is due to the fact that precocious maturation (-6) has only a minor influence on the dynamics of events (energy level, winter growth performance, threshold level for maturation decision) that will lead to the grilse maturation (+18) decision, 1 year to 1 1/2 year later.

On the other hand, among the 1Y81 males, the curve and the 50% level of the previously post-smolt precocious (+6) males (Fig. 4.8 H) was quite considerably shifted towards very low levels of winter growth, compared to that of the maiden males (Fig. 4.8 E). This group was actually the only one with a 50% level located below the 0 g mark for winter weight increment. This indicates that, in this group, only the fish showing a very poor growth performance could be expected not to mature again as grilse (+18). Hence, in this cohort, even though the previously post-smolt precocious (+6) males showed a significantly lower winter mean weight increment, compared to the maiden males (2 first contrasts #3 in Table 4.23), they nevertheless showed a significantly higher incidence of grilse maturation (+18) (80% versus 41.6% respectively).

The high rematuration rate of the post-smolt precocious (+6) males could be due to the higher level of circulating sex hormones that these males probably still show at the end of the winter period, which could have a promoting effect on the grilse maturation decision. However, this would not explain the link between winter growth performance and

rematuration as grilse, which was apparent in these males as well. I would therefore like to suggest an alternative hypothesis to explain why post-smolt precocious (+6) males apparently require a considerably lower winter weight increment to remature as grilse (+18). At the beginning of the winter period, the mature post-smolt precocious (+6) males were characterised by considerably higher condition factors than the maiden males (Table 4.22). Their subsequent winter growth performance was reduced, but most of the post-smolt (+6) males showing a mediocre winter growth performance were nevertheless apparently able not to experience a too drastic drop in mean condition factor, so that in June, these post-smolt (+6) still had the highest mean condition factor of the four groups compared in Table 4.23. With a mean winter weight increment of only about 80g, the post-smolt males rematuring as grilse [♂(+6,+18)] showed a mean condition factor in June of 1.13, while with a considerably better growth performance (about 125g), the previously maiden males maturing as grilse [♂(0,+18)] showed a mean condition factor of only 1.09 (Table 4.23). Only the few post-smolt (+6) males that showed a particularly poor winter growth performance experienced a drastic drop in mean condition factor and these did not remature (Table 4.23). This hypothesis therefore simply states that post-smolt precocious (+6) males require much lower winter weight increments, compared to maiden males, because they have a considerable head start at the beginning of the winter period, as can be seen in their much higher condition factors. However, it should be noted that these higher condition factors of the mature post-smolt (+6) at the beginning of the winter is not due to the presence of large fat reserves in the abdominal cavity, but rather to the presence of large testes. At maturity time,

mature fish have indeed been shown to be characterised by low fat content in the muscles and the viscera, for both precocious maturation (Leyzerovich, 1973; Mitans, 1973; Saunders et al., 1982) and maturation at sea (Tveranger, 1985; Aksnes et al., 1986). This hypothesis thus implies that the reabsorption of the gonad material provides the post-smolt mature (+6) males with a consequent additional source of energy during the winter following this maturation episode. This additional source of energy, added to the energy intake from feeding, even if reduced, would therefore be sufficient for most of these males to reconstitute their energy stores and reinitiate maturation at the end of the winter period. As was discussed in section 4.2.1, there was indeed some indications that precocious mature males (-6) were able to obtain some energy from the process of gonads reabsorption.

Since the proposed mechanism for maturation decision is the same for all maturation episodes, and since mature fish are characterised by higher condition factors for all maturation episodes as well, the postulated hypothesis to explain the high rematuration rate of post-smolt mature (+6) males would presumably apply to all maturation episodes as well. This appears to be the case since, as it was discussed in Chapter II, there were indications in the literature that maturation at age x tends to promote maturation at age x+1.

The next section reviews some characteristics of post-smolt precocious maturation (+6) both within and between cohorts, in the light of the proposed mechanism linking the growth performance during the winter preceding smoltification with the incidence of post-smolt precocious maturation (+6). It offers in addition a general discussion

on this poorly understood maturation episode.

4.7 Post-smolt precocious maturation (+6) and weight increments during the winter before smoltification

Individual data were available only in the 2Y81 cohort in which very few cases of post-smolt precocious (+6) males were recorded. However, for this maturation episode as well, there seemed to exist the same sort of mechanism linking the winter weight increment with subsequent incidences of maturation. Three out of the five post-smolt mature (+6) males showed the 3 highest weight increments of all males (Fig. 4.9).

It appears that the significantly lower rate of post-smolt precocious maturation (+6) in the 2Y81 cohort, compared to the 2Y80 or 1Y81 cohorts which was noted in Chapter II, was a consequence of the very poor growth performance of the 2Y81 cohort during the winter preceding smoltification (Table 4.35), due to the adverse environmental conditions at the Fraser's Mill Hatchery (cf. Chapter II). It also appears that size per se did not bear any relationships with future post-smolt precocious maturation (+6), since the 2Y81 fish were considerably larger than the 2Y80 or 1Y81 fish (Table 4.35), and yet showed a lowest incidence of post-smolt precocious maturation (+6).

It was noted in section 3.4.4 that there were considerable contrasts between the 3 cohorts, for the smolt size of the future post-smolt (+6) males relative to the smolt size of the nonpost-smolt males. In August 1983, 2 months after smoltification, the future post-smolt males were significantly smaller compared to the nonpost-smolt males in the 2Y80 cohort, but there was no significant size difference in the 1Y81 cohort (Table 4.22, 4.25).

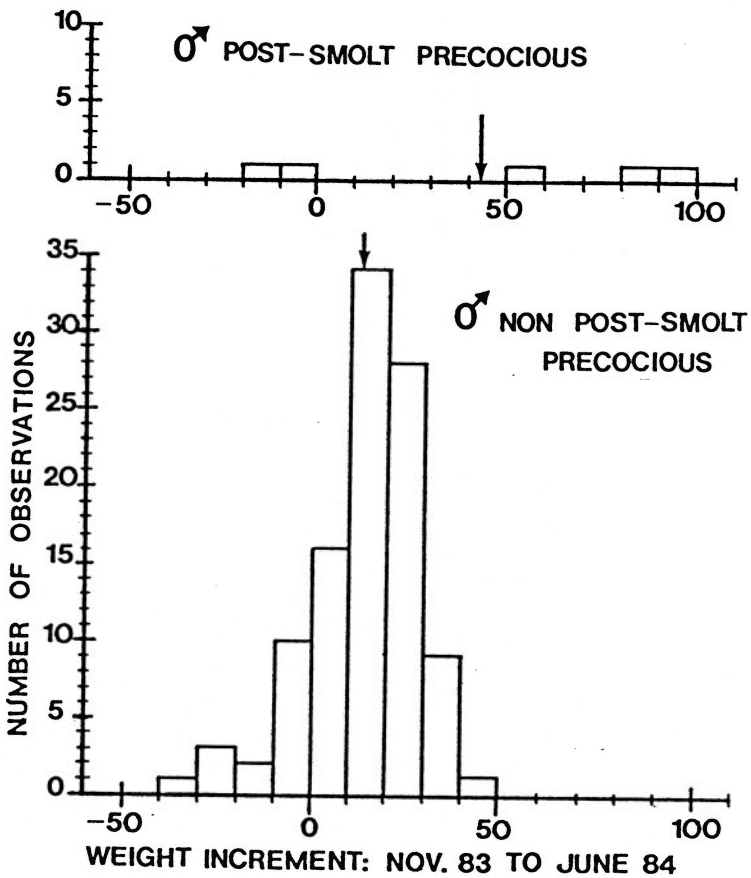

Figure 4.9: Distribution of the weight increment during the winter before smoltification, for the males maturing as post-smolts (upper graph) and the males not maturing as post-smolts (lower graph).

The down arrow denotes the mean weight increment.

Table 4.35: Mean weight increment during the winter before smoltification and subsequent incidence of post-smolt precocious maturation (+6) among males in the 3 cohorts.

Cohort	2Y80	1Y81	2Y81
Date measured	Oct. 82 to May 83	Oct. 82 to May 83	Nov. 83 to June 84
Mean initial weight/mean final weight	59.3g to 92.7g	6.7g (1) to 31.0g	97.3g to 105.6g
Mean weight increment during the winter before smoltification	33.4g	24.3g	8.3g
Rate of post-smolt precocious maturation (+6) among males	19.5%	26.8%	5.5%

(1) Estimated mean weight of the 1Y81 parr in October 1982.

On the contrary, in the 2Y81 cohort, in June 1984 at smoltification time, the future post-smolt (+6) males were significantly larger than the nonpost-smolt males (Table 4.29). These post-smolt males in the 2Y81 cohort were already larger at the beginning of the winter before smoltification (Table 4.28). The poor growth performance of the 2Y81 fish during the winter before smoltification resulted in only a few fish showing a winter weight increment sufficient to initiate post-smolt precocious maturation (+6). Furthermore, it is quite likely that large fish had an important competitive advantage during this winter period where feeding was much reduced, which probably explained why these few future post-smolt (+6) males were also considerably larger. On the contrary, environmental conditions during the winter before smoltification were quite favourable (feeding ad libidum, warmed water) for the 1Y81 fish (c.f. Chapter II, section 2.3). It is probable that there were no specific competitive advantages associated with larger size, which explained why no significant differences for size were detected in August in the 1Y81 cohort. The future post-smolt (+6) males were probably slightly larger in June compared to nonpost-smolt males, since the model of maturation decision proposed here predicts that these future post-smolt males must have showed a better winter growth performance. However, since growth is reduced afterwards, it is not surprising to observe no more difference in August.

The situation in the 2Y80 cohort is more surprising. Since the environmental conditions experienced by these fish during the winter before smoltification were similar to that experienced by the 1Y81 fish (c.f. Chapter II, section 2.3), one could expect to observe similar results. Yet, the post-smolt (+6) males were considerably smaller in

August, compared to the non post-smolt and the size difference was so important that it is most probable that they were already smaller in June (Table 4.25). There was however a major difference between the 1Y81 and the 2Y80 cohorts: at the beginning of the winter before smoltification, no males were mature in the 1Y81 cohort (0% incidence of early precocious maturation 0+, c.f. Chapter II), while 54.5% of the males were precocious mature (-6) in the 2Y80 cohort (c.f. Table 2.5, Chapter II). These precocious (-6) males were smaller than their immature counterparts, at the beginning of the winter before smoltification (Table 4.19) and the size difference probably increased during the winter, as was discussed in section 4.2.1. Following the last point discussed in section 4.6, I would suggest that most of the post-smolt (+6) males in the 2Y80 cohort were precocious (-6) males rematuring as post-smolt (+6), which explained their smaller size at the time of smoltification. This cannot be verified since, as already mentionned, no individual identification was available for the precocious maturation episode (-6) in the 2Y80 cohort. However, it is interesting to note that a similar problem would have been encountered in the 1Y81 cohort concerning the size of the future grilse at the end of the winter in seawater, if no individual identification for post-smolt precocious maturation (+6) had been available. The future grilse would have appeared <u>smaller</u> than the multi-sea-winter fish, simply because they comprised a large number of smaller rematuring post-smolt mature (+6) males. This confirms as well that individual identification of the fish is indeed practically necessary to understand the quite complex pattern of interaction between growth and maturation.

The post-smolt precocious maturation (+6) episode does not appear

different from other maturation epsiodes, in respect to its interaction with growth, nor did it appear different in respect to its relation with mortality (c.f. Chapter II). Yet, as was discussed in Chapter II, there are very few published reports on this maturation episode, and it appears thus fairly uncommon in natural and in cultivated populations. The mechanism proposed here for the initiation of post-smolt precocious maturation (+6) cannot explain this apparent rarity: if post-smolt precocious maturation (+6) is initiated simply when the salmon show a good growth performance during the winter before smoltification, then, post-smolt precocious maturation (+6) should be observed quite frequently, in both reared and natural populations. Evropeytseva (1960) and Thorpe (1986) have stated that maturation and smoltification are mutually inhibitory and physiologically incompatible. As discussed in Chapter II, the existence of an absolute physiological incompatibility between both phenomena is doubtful, and the great similarities observed in this chapter between this maturation episode and the two other "normal" maturation episodes seem to indicate that the post-smolt (+6) males were not physiologically abnormal or abherant. Yet, Lunqvist and Fridberg (1982) provided evidence that smoltification seems to inhibit, to a large extent, maturation as post-smolt and the same could be seen in this study in that the rate of post-smolt precocious maturation (+6) was considerably lower than either precocious maturation (-6) rate or grilse maturation (+18) rate in the 3 cohorts. The few other references on this maturation epsiode in cultivated populations also reported low rate of occurences, in the order of 10% (Saunders and Henderson, 1965; Sutterlin et al., 1978; Lundqvist and Fridberg, 1982). In the model of maturation decision proposed here, the decision is postulated to be

taken in April/May. Smoltification generally occurs in May/June. Both decisions are thus probably taking place around the same period. Smoltification requires also energy expenditure and is accompanied by a depletion of the same lipid stores that are used for gonadal development and maturation (Saunders, 1979; Wedemeyer et al., 1980; Sheridan et al., 1983).

I would therefore suggest that in wild populations, the fish that have the size and the energy stores sufficient to initiate maturation and/or smoltification will initiate one or the other, but almost never both together, not because of a physiological barrier preventing it, but probably rather because it would represent a too large energy expenditure. Evropeytseva (1960) noted that among pond reared juvenile salmon, many individuals that had reached a size apparently sufficient to smoltify did not do so and remained in freshwater. Upon examination, a large proportion of these were maturing males, which had "chosen" to initiate maturation and postponed smoltification. This situation appears quite frequent in many nordic rivers where large repeatedly maturing male parr are observed and where females compose the majority of the migrating smolts (Mitans, 1973; Dalley et al., 1983; Gibson, 1983; Chadwick et al., 1986). I would suggest that the alternative strategy, i.e. some fish initiating smoltification and postponing maturation, exists as well. In Brittanny rivers (France), very good growing conditions prevail, even during the winter, and most fish migrate as 1-year-old or 2-year-old smolt. Precocious maturation at age 1+ is variable between years but can have very high rates of occurence. Furthermore, mature males at age 0+ and precocious mature females are also reported (Prouzet, 1981; Baglinière and Maisse, 1985). Scale

studies indicated that the few older maturing male and female parr found in these rivers could have migrated as smolt earlier, suggesting that they had postponed smoltification to initiate maturation. However, the majority of the males migrated normally as 1+ or 2+ smolt. Given the particularly good growing conditions during the winter, it is probable that many of these males had, in early spring, a level of energy store sufficient to initiate maturation, but that they postponed it and smoltified instead.

In cultivated populations however, the situation is different. The environmental cues that the fish might use to resolve the conflicting choice between smoltification and maturation might not be present or adequate. This could lead a small number of fish to initiate both maturation and smoltification. Furthermore, in cultivated populations, the fish are not given the choice to smoltify or to mature. The fish appearing smolt like (a decision generally based on size and silvery colouration criteria) are transferred automatically to seawater rearing facilities. It is therefore probable that smoltification is "imposed" on a certain number of fish that had initiated maturation and which would have remained in freshwater under natural conditions. I would suggest that most of these fish are then able to stop the maturation process but that some are carrying on both smoltification and maturation and are found to be post-smolt mature fish the following fall. This would explain why the incidence of post-smolt maturation is relatively low. Accelerated freshwater rearing regimes with warmed water during the winter are being increasingly used to produce younger smolt. It is probable that this nearly always leads to at least a small proportion of these fish maturing as post-smolt. I would suggest three reasons for

which these post-smolt mature fish are not commonly reported in cultivated populations:

1) It is not a common practice in most aquaculture operations to collect data 6 months after smoltification.

2) These post-smolt mature fish are particularly unconspicuous and difficult to detect (pers. obs.; Saunders and Henderson, 1965; Sutterlin et al., 1978).

3) Even when discovered, many workers assume that they are uninteresting abherant artefacts (Naevdal et al., 1975; Dr Y. Harrache, pers. comm.).

Yet, it was apparent in this study that this maturation episode had important consequences, since most of these post-smolt (+6) males rematured as grilse (+18). Furthermore, they showed a fairly poor overall growth in seawater because of the 2 consecutive growth reductions associated with maturation. The frequency and importance of this poorly understood maturation episode are thus certainly underestimated.

4.8 Comparison of the model of maturation decision proposed in this study with other models in the literature

In an extensive study of the Baltic salmon natural populations, Thurow (1966), proposed a very similar hypothesis to explain the separation between 2-sea-winter and 3-sea-winter salmon. He noted that in late fall, salmon after their second summer at sea and salmon after their third summer at sea had very similar levels of fat contents, in the order of 14 to 15 percent of body weight. However, during the winter, salmon in their second winter at sea suffered on average a considerable deterioration in condition so that the fat contents fell to an average of 6.5% of body weight. In contrast, the salmon in their

third winter at sea did not use much of their fat supplies which fell only to about 12%, presumably because they were able to feed better. Thurow was in addition able to show that each year, the "spawners" (the fish that would spawn the following fall) were mixed with the "feeders" (the fish that would not spawn the following fall) on the feeding group, until April/May, after which the spawners were leaving the feeding groups to migrate back to their rivers. He therefore hypothesized that the salmon that were able to keep a favourable growth during their second winter at sea so that in early spring, they still had a fat content in the order of 12% of body weight, would migrate from the feeding ground in April/May to spawn as 2-sea-winter salmon. The other fish, having a fat content too low at the end of their second winter at sea, would then postpone maturation and remain on the feeding ground to spend a third winter at sea. At the end of their third winter at sea, their level of fat contents would then be sufficient in general for them to initiate maturation and spawn as 3-sea-winter salmon. It is probable that the better winter growth performance of the salmon in their third winter at sea compared to the salmon in their second winter at sea, is due to their larger size, giving them a competitive advantage in a period where the food resource is quite scarce.

The model I proposed in section 4.5 is also similar to that formulated by Thorpe (1986) who "proposed that: salmon are physiologically aware of their growth-rate through their rate of acquisition of surplus energy, and hormone kinetics associated with its storage: that, provided this rate is above a genetically determined level on the early spring when the fish are sensitive to photoperiodic stimulation of their gonadotrophic hormone systems, gonadal maturation

will be triggered and reallocation of energy resources to induce maturation will be set in train." The main difference between Thorpe's model and the one proposed here is that, in Thorpe's model, maturation would be triggered if the fish growth rate in early spring is above a certain value while here, I propose that the important variable is not so much the growth rate per se, but rather the amount of surplus energy stored that the fish can invest in the maturation process.

Many authors have proposed threshold size mechanisms to explain maturation initiation (Bailey et al., 1980; McCormick and Naiman, 1984; Myers et al., 1986; Siitonen, 1986). This proposed mechanism was based on the observation that maturing fish are generally larger in spring than immature fish. I would suggest that the larger size of the maturing fish in spring is not due to any causal mechanism linking size and maturation, but can be explained as an indirect consequence of the mechanism proposed here: since the fish that will initiate maturation are the fish having the highest energy reserves in early spring, and since the energy reserves are linked with the winter growth performance, the maturing fish will effectively be on average larger in spring and early summer. In the present study however, these differences in sizes were in some groups very slight or even nonexistent (Table 4.17, 4.23), which seems to indicate that size per se is not causally related to maturation.

Saunders et al. (1983) hypothesized that low sea temperature during the winter at salmon cage sites (Bay of Fundy) explained the low incidence of grilse among cage-reared smolts, as compared to sea-ranched smolt of the same stocks and hatchery rearing history. Scarnecchia

(1983) showed that, among Icelandic stocks of Atlantic salmon, females in stocks south of the thermal gradients separating Atlantic and Artic/Polar waters tend to return as grilse, while females north of this gradient tend to return as multi-sea-winter salmon. On the contrary, Martin and Mitchell (185) suggested that lower temperature increases the number of returning grilse and reduces the number of returning multi-sea-winter salmon in a Scottish wild population study. Dempson et al. (1986) found no evidence that ocean temperature influences sea age at maturity, both among and within populations.

In the present study, no influence of overwintering temperature regime on the rate of grilse maturation (+18) could be detected. It appears that some other environmental factors masked the effect of overwintering temperature regime, on both the winter growth performance and maturation in a parallel manner: there were significant differences for the winter weight increment and for incidence of grilse maturation between replicate tanks within temperature regime, but no significant differences between temperature regimes. However, whether heated or ambient, the tanks in which the fish showed a good winter growth performance showed high rates of grilse maturation. This indicates that winter temperature has no <u>direct</u> influence on maturation. It is however probable that winter temperature has, in general, an <u>indirect</u> influence on maturation, through the influence of temperature on winter growth, athough this was not apparent in the present study.

I would therefore suggest that the hypothesis of Saunders et al. (1983) is partially correct, not because low winter sea temperature in the Bay of Fundy directly inhibited maturation as grilse, but because this low temperature probably reduced the winter growth performance of

these fish so that in spring their levels of energy stores were too low to initiate maturation. In the original data used by Saunders et al. (1983), it was noted that during the winter months, food consumption fell dramatically and growth in weight was slightly negative for part of this period (Sutterlin et al., 1981).

Again, the evidence from wild stocks studies is considerably more contradictory (Scarnecchia, 1983; Martin and Mitchell, 1985; Dempson et al., 1986). It is probable that one of the problems with wild salmon stocks studies is that our knowledge of salmon and grilse migration routes at sea is very restricted and is practically nil for the crucial winter months. Dempson et al. (1986) also pointed out that traditional statistical analysis to treat such time series problems are completely inadequate and misleading. Martin and Mitchell (1985) noted that the choice of temperature data series was difficult, since the few unbroken series were not particularly well placed to reflect the areas that are presumably occupied by grilse and salmon. Furthermore, it is quite probable that wild stocks of salmon at sea vary their migration routes according to the local circumstances encountered (food supplies, temperature, etc.). Martin and Mitchell (1985) suggested that the contradiction between their results and those of Saunders et al. (1983) and Scarnecchia (1983) could be apparent only, and could result from the salmon, in the two later studies, being forced to endure cold winter sea temperature, while the Scottish salmon of their study were free to avoid such conditions. Dempson et al. (1986) results are not truly in contradiction with the model proposed in the present study. Their between river stocks comparison used the sea temperature collected in July/August, close to the specific river mouths. Since this is neither

the critical time, nor the critical place where the maturation decision is taken, according to the model proposed here, the absence of a significant effect of sea temperature is not surprising. Similarly, for their within population study, the temperature series used were yearly mean sea surface temperatures collected in Booth Bay Harbour (Maine), St. Andrews (N.B.) and Grimsey Island (Iceland). Again, it is probable that these yearly mean sea temperatures do not describe adequately the critical winter temperatures that the fish might have encountered on their migration route. Furthermore, as already stated, it is likely that salmon are modifying their migration route to avoid local unfavourable conditions, which could certainly attenuate the effect of local sea winter temperatures on winter growth, hence on maturation.

Much literature has dealt with the possible influence of smolt age on sea age at maturity, but results are overall rather confusing. With natural populations, earlier works showed that in many rivers, older smolt tended to mature earlier than younger smolts. Yet, many river populations did not follow this pattern (c.f. review in Gardner, 1976). Many of these studies did not address relationships between sex and smolt age. Yet, there is evidence that in some rivers, females are more predominent among younger smolt age classes, and males among older smolt age classes. Given the tendency for males to mature earlier than females, the relationships between smolt age and sea age at maturity could be mostly an effect of unequal sex distribution. Recently, Bielak and Power (1986) examined 20 Quebec North Shore rivers and concluded that there is strong evidence for the independance of sex and river age, and of river age and sea age. They also suggested that the focus of future investigations shift from river age per se as an important

regulator of sea age at maturity.

In sea ranching experiments, 2-year-old smolts generally produced proportionately more grilse than the 1-year-old smolts (Ritter, 1975; Ritter and Newbould, 1977; Saunders et al., 1983; Bailey and Saunders, 1984). However, Ritter et al. (1986) concluded that sex ratio and size differences can be expected to account for much, and perhaps all, of the differences in sea age at maturity displayed by 1-year-old and 2-year-old smolts.

In contrast to most reported results and to the results of the present study, higher incidences of grilse were found among 1-year-old smolts rather than among the 2-year-old ones, in Norwegian cage-reared salmon (Naevdal et al., 1979a).

As was shown in section 4.7, the higher grilse maturation (+18) rate among the 2Y81 fish, compared to the 1Y81 fish, appeared due to their much better winter growth. The results reported by Naevdal et al. (1979a) might simply reflect that the opposite situation prevailed in their experiment. In this study, within each cohort, smolt sizes did not bear any relationship with maturation as grilse. However, in natural populations or sea-ranched populations, larger smolt might have a competitive advantage for growth during the migration at sea, particularly during the winter period when food supply is scarce. Under these conditions, older smolts might be characterised by higher rates of grilse maturation, simply because they are generally larger and would thus show on average a better growth performance during the winter at sea.

Chadwick et al. (1986) and Randall et al. (1986) proposed that sea age at maturity was determined before the fish migrated to sea, hence

that environmental factors and growth during the migration at sea bore little influence on sea age at maturity. This position appears untenable since there are convincing evidences showing that environmental factors at sea (sensus largo) affected the rate or grilse maturation in sea cage (Naevdal, 1983; Saunders et al., 1983; Gjerde, 1986); also in this study, the rate of grilse maturation (+18) was significantly different between the different winter tanks used in the 1Y81 and the 2Y81 cohorts. Furthermore, the two arguments underlying the statement of Chadwick et al. (1986) and Randall et al. (1986) do not appear entirely robust. Chadwick et al. (1986) compared the ovarian developement in female smolt samples from 7 Canadian rivers characterised by different mean parent sea ages. They found that ovarian development was inversely correlated with mean sea age of the parent. Hence, ovarian development was most advanced in smolt from grilse rivers, and least advanced in smolt from 3-sea-winter populations, which seemed to support the idea that sea age at maturity was already determined before the smoltification. However, in the samples they used, mean sea age of the parents was also inversely correlated with mean smolt age, so that the ovarian development was correlated with smolt age. Therefore, these observations could simply reflect that older female smolts have more advanced ovarian development and that older smolts tend to mature earlier, as discussed in the preceding section. The second argument presented, both by Chadwick et al. (1986) and Randall et al. (1986) was that in many rivers, the ratio of grilse to multi-sea-winter salmon is relatively stable from year to year, since the number of returning multi-sea-winter salmon, in any one year, could be predicted from the number of grilse that returned the

preceding year. If the ratio remains constant, it is then unlikely that sea age is determined by factors in the marine environment. This argument does not appear entirely convincing. Upon examination of the data provided by Chadwick et al. (1986), their statement that the ratio of grilse/2-sea-winter salmon is constant from year to year does not appear warranted. The significant correlation found between the number of grilse returning in year n and the number of 2-sea-winter salmon returning in year n+1 is not due to the constancy of that ratio but appears rather due to the large year to year variability in the total number of returning adults, which is most probably due to a large year to year variability of the smolt output. Hence, if the smolt output in year n-1 is low, the number of returning grilse in year n and of 2-sea-winter salmon in year n+1 will be low, while if smolt output in year n-1 is large, the converse will be observed. This will impose a correlation between the number of grilse returning in year n and the salmon returning in year n+1, even if the relative ratio grilse/multi-sea-winter fish varies from year to year. Since the year to year smolt output is obviously dependant of the previous year to year return of adult fish, both the time series of grilse return and 2-sea-winter salmon return are most likely autocorrelated. The use of standard statistical methods on such time series problems, such as the simple correlation used in Chadwick et al. (1986), might be appropriate for simple management purpose, but they are obviously inadequate for drawing conclusions about the mechanism of determination of sea age at maturity, as Dempson et al. (1986) pointed out for similar problems.

CHAPTER V. SOURCES OF FAMILY VARIABILITY FOR MATURATION INCIDENCE.

1. Introduction

In Chapter III, it was noted that there was large differences among families in the incidence of the various maturation episodes. Furthermore, there was a significant concordance between the family rankings based on the incidence of the various maturation episodes, some families being characterised by high rates of maturation for all maturation episodes, while some other families were characterised by the opposite. Chapter IV analysed the covariation between growth and maturation and a model of maturation decision was proposed. This model assumed that an individual fish would initiate maturation in early spring if its level of energy storage was over a specific threshold level. It was also shown that, among groups having the same previous maturation history, this level of energy storage was mostly dependant on the growth performance during the winter and, to a lesser extent, on the level of energy storage at the beginning of the winter period.

This chapter analyses, given the model proposed in Chapter IV, what might be the sources of the between family variability for maturation rates and what might cause the concordance between the different maturation episodes for family rankings.

2. Material and methods.

As was the case in Chapter III, this chapter is concerned with the 1Y81 and 2Y81 cohorts only. The 2Y80 cohort is not treated here, since the family identities were lost because of marking problems (c.f. Chapter I, section 2 and Chapter III, section 2.1). Family 60 is

not included either, as was also the case in Chapter III, because of the very low number of fish.

Five maturation episodes were covered in the present study: post-smolt maturation (+6) and grilse maturation (+18), in both the 1Y81 and 2Y81 cohorts, and precocious maturation (-6) in the 2Y81 cohort. Given the rather low number of fish in each family, it was not possible to do an indepth analysis of the mechanisms of maturation for each family, similar to what was done in Chapter IV. In the light of the findings of Chapter IV, the following strategy has been used instead:

1. The mean condition factors per family in spring have been assumed to represent reasonable estimates of mean levels of energy stores per family in spring (Naevdal et al., 1981; Chapter IV, section 4).

2. For each maturation episode, the extent of the between family variability for mean level of energy stores in the previous spring (as characterised by mean condition factor) was investigated, as well as the correlation between mean family condition factor in spring and mean family incidence of maturation the following fall.

3. The sources of between family variability for mean condition factor in spring was investigated, particularly in terms of growth dynamics.

Most of the material and data collection pocedures have already been described in earlier chapters (c.f. Chapter II, section 2 for an overview). The following section gives some details about the collection of mean length, weight and condition factor per family, in October 1982 and April 1983, for the 1981 year class, at the I.M.A. Aquatic Farming hatchery. This was only superficially covered in

Chapter II, section 2.3. No individual data were available at these times, since the 1Y81 fish were individually marked only in August 1983 and the 2Y81 fish in November 1983. However, all fish were family marked in October 1982 (c.f. Fig. 2.1 in Chapter II). At that time, mean length and mean weight were estimated in each family, and the same was done again in April 1983. It is therefore possible to estimate mean growth parameters per family during this period, once the following approximations are taken into account.

- In each family, some fish smoltified in June 1983 (1Y81 fish) while others did not until 1 year later (2Y81 fish). Since fish were not individually identified, it is unfortunately not possible to differentiate the future 1Y81 and 2Y81 fish in October 1982 and April 1983. However, as it was briefly mentionned in Chapter II, section 2.3, at the time of family marking in October 1982, the fish were graded by size. In each family, the fish weighing between 2g and 5g were pooled in tank A, while all fish weighing more than 5g were pooled in tank D. On average, the fish put in tank D represented the 20% largest individuals, the remaining 80% smaller fish being pooled in tank A. The fish in tank D experienced better growth, from October 1982 to the following spring, because of the lower crowding. These fish being larger in October 1982 were considerably larger in spring than the fish kept in tank A. Around 80% of the fish kept in tank D smoltified as 1-year-old smolts (1Y81) in June 1983, while only around 15-20 % of the fish kept in tank A did. In October 1982 and April 1983, mean length and mean weight were estimated for each family in both tanks. The family growth parameters collected in tank D and tank A will therefore be assumed to represent reasonable estimations of the family growth

parameters of the 1Y81 fish and the 2Y81 fish respectively.

- The second necessary approximation concerns the estimation of mean condition factor per family, in October 1982 and April 1983. This was estimated as the condition factor based on the mean length and the mean weight in each family sample, which tended to produce slight overestimations, compared to the true mean condition factor. This was verified on 13 families from both the 1Y81 and the 2Y81 cohorts, at different data collection sessions, after individual marking. The families were chosen to represent both average and extremely high or low mean condition factors. The condition factors based on the mean length and mean weight were all but one overestimated, compared to the true mean condition factor. The overestimation was on average 0.02 units ($\simeq$ 2%) and ranged from 0.00 to 0.04 on the 13 samples chosen. It was therefore assumed that this way of estimating mean condition factors per family would not introduce large biases. It should be noted however, that the between family statistical comparisons of mean condition factor in October 1982 and in April 1983 were not possible, because no estimates of within family variance were available. The same was true of the between family comparison of mean weight increment from October 1982 to April 1983.

Comparison of variables between several groups were performed by one-way analysis of variance. Normality was tested with Kolmogorov-Smirnov one sample test (Siegel, 1956; Nie and Hull, 1981). Homogeneity of variances was tested with the Bartlett-Box F test (Nie et al., 1975). When assumptions underlying the use of analysis of variance were violated, the probability statements were based on the Fisher's randomization test (c.f. Chapter IV, section 2, Bradley, 1968; Benson,

1984). Correlations involving percentages were performed after percentage normalisation through angular transformation (arc sin $\sqrt{p}$). The non parametric Kendall coefficient of concordance W was used to measure the agreement between independant rankings and to test whether ranking patterns were significantly consistent (Siegel, 1956).

3. Results.

3.1 Mean condition factor per family in spring and incidence of maturation per family.

In the spring (June 1984) preceding the grilse maturation (+18) episode, in the 1Y81 cohort, there were highly significant differences between families in mean condition factor (Fig. 5.1, A). The same could be seen in the springs (June 1984, May 1985) preceding both post-smolt precocious maturation (+6) and grilse maturation (+18) episodes in the 2Y81 cohort (Fig. 5.1, C,D). In April 1983, there were as well large variations between families for mean condition factor, in both the 1Y81 and the 2Y81 cohorts (Fig. 5.1, B,E), but it was not possible to verify if these differences were statistically significant (cf section 2).

In addition, in the 2Y81 cohort, there were significant positive correlations between the mean family condition factor in spring and the family incidence of maturation the following fall, for all 3 maturation episodes (Fig. 5.1, C,D,E). In the 1Y81 cohort, similar positive correlations could be observed (Fig. 5.1, A,B), although they were weaker and not significant at the 5% level ($p=6.2\%$ and $p=8.7\%$).

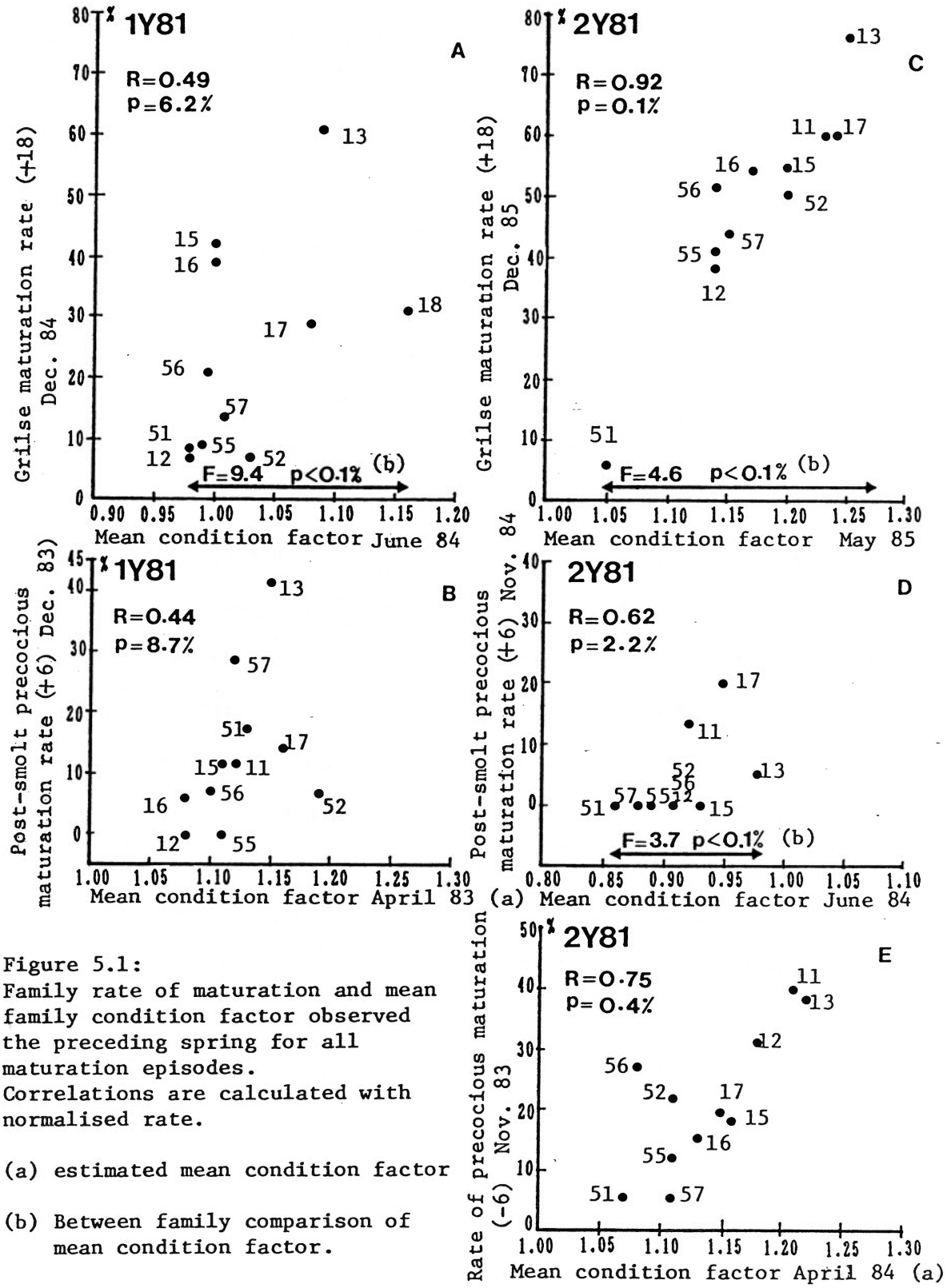

Figure 5.1:
Family rate of maturation and mean family condition factor observed the preceding spring for all maturation episodes.
Correlations are calculated with normalised rate.

(a) estimated mean condition factor

(b) Between family comparison of mean condition factor.

Probability statements are based on Fisher's randomization test.

This indicates that a large part of the between family variability for the incidence of maturation that was observed in Chapter III, section 3, for the 5 maturation episodes, was actually due to large between family variability for average level of energy stores in spring. Hence, for any one maturation episode, some families, like family 13 for example, showed higher incidences of maturation because they had, on average, higher levels of energy stores the preceding spring, so that a higher proportion of the fish in these families could initiate maturation.

There was as well a significant concordance between the family rankings based on the 5 series of mean family condition factor in the spring before the 5 maturation episodes (Table 5.1). Hence, some families, like families 13 and 17, were systematically characterised by high condition factor in spring, while some other families, like families 51 or 55, were systematically characterised by the opposite. The mean family ranks based on the 5 series of condition factor in spring corresponded fairly closely to those based on the 5 series of maturation incidence (Table 5.1). Thus, this concordance, based on the condition factor in spring, appears to explain the concordance between family rankings based on incidence of maturation for the 5 maturation episodes (c.f. Chapter III, section 3).

In Chapter IV, section 4.5, it was suggested that there could be differences between strains and/or families for the minimum level of energy stores in spring necessary to initiate maturation. The mean ranks based on condition factor in spring were slightly higher compared to those based on maturation incidence for families 52 and 17, and slightly lower for families 16, 51 and 56 (Table 5.1).

Table 5.1: Concordance between the family rankings based on mean condition factor in the spring preceding 5 maturation episodes and concordance between family rankings based on incidence of maturation for the same 5 maturation episodes.

Family	Mean rank	Kendall concordance coefficient W and significance	Mean rank	Kendall concordance coefficient W and significance
	Based on family mean condition factor in the spring preceding the 5 maturation episodes covered in this study		based on family incidence of maturation, for the 5 maturation episodes covered in this study	
11	8.9		9.0	
12	4.2		3.8	
13	10.3	W=0.65	10.4	W=0.55
15	6.7	X^2=32.3	6.8	X^2=27.6
16	4.4	10 df	5.5	10 df
17	9.3		8.3	
51	2.5	p=0.04%	3.8	p=0.2%
52	7.3		4.3	
55	3.5		3.2	
56	4.0		5.9	
57	4.9		5.0	

This could indicate that among the 11 families covered in this study, families 52 and 17 required slightly higher levels of energy stores in spring to initiate maturation, while on the contrary families 16, 51 and 56 required slightly lower levels of energy in spring. However, these differences were not very pronounced. Upon specific examination of each maturation episode (Fig. 5.1), no family appeared to be characterised by large and systematic deviations in the relationships between mean condition factor in spring and incidence of maturation the following fall. Therefore, in the present study, differences between families for minimum level of energy stores necessary to initiate maturation did not appear to be a major source of between family variability for incidence of maturation or of concordance between the different maturation episodes for family rankings.

3.2 Sources of family differences for mean condition factor in spring.

Winter weight increment was suggested as the main factor contributing to the level of energy stores in spring, among individual fish (c.f. Chapter IV, section 4.3).

In the 1Y81 cohort, during the winter in seawater, there were significant differences between families for mean winter weight increment (Table 5.2). In the 2Y81 cohort, there was some variability between families for mean winter weight increment during the winter in seawater, but it was not significant at the 5% level (p=7%). However, the two series of mean weight increment per family during the winter in seawater were significantly positively correlated (Fig.5.2), indicating that some families were indeed characterised by better growing capabilities during winter in seawater, compared to others.

Table 5.2: Mean weight increment per family during the five winters preceding the 5 maturation episodes and concordance between family rankings.

Winter period and cohort	Mean winter weight increment (g) per family											Between family comparision 1 way anova
	11	12	13	15	16	17	51	52	55	56	57	
Winter in seawater 1Y81 Dec. 83 - June 84	137	79	86	48	105	101	62	54	48	123	70	F=3.42 p=0.1% (1)
Winter in seawater 2Y81 Nov. 84 - May 85	334	249	252	243	266	343	198	301	210	246	277	F=1.74 NS (7%)
Winter before smoltification 2Y81 Nov. 83 - June 84	16.3	11.0	10.7	7.7	5.0	9.4	8.5	5.8	5.8	9.1	7.4	F=0.62 NS (1)
Winter before smoltification 1Y81 Oct. 82 - April 83	19.3	18.1	12.4	12.2	13.9	10.0	15.3	13.6	14.2	12.0	8.3	/
1st winter in freshwater 2Y81 Oct. 82 - April 83	6.4	8.0	6.3	5.4	5.7	3.7	5.1	4.7	5.7	4.5	4.1	/
Mean ranks	10.4	8.4	7.4	3.8	6.1	6.0	4.8	4.5	4.3	6.1	4.2	
Concordance between the different mean winter weight increment for family rankings				W=0.38 X^2=19.0		10 df		p=4%				

(1) Probability statements based on Fisher's randomization test.

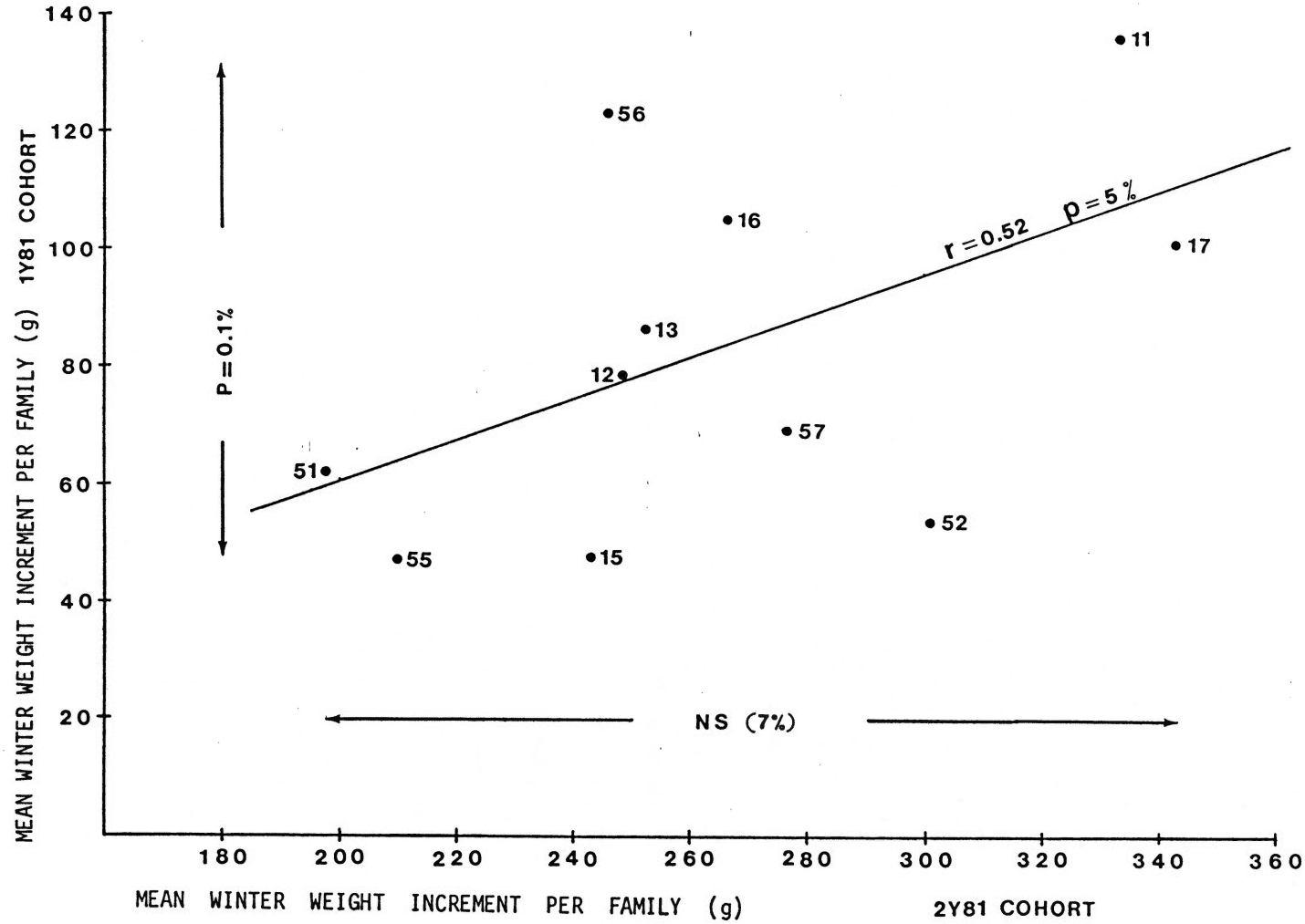

Figure 5.2: Correlation between mean winter weight increment per family in the 1Y81 and 2Y81 cohorts.

During the winter before smoltification in the 2Y81 cohort, there were no significant differences between families for mean winter weight increment (Table 5.2), all families showing fairly poor growth performances during this harsh winter at the Fraser's Mill hatchery (c.f. Chapter II, section 2.3). During the winter before smoltification, in the 1Y81 cohort, (Oct. 82-April 83 at the I.M.A. Aquatic Farming hatchery, c.f. section 2) there appeared to be some variability between families for mean weight increment (Table 5.2), but it was not possible to verify if it was statistically significant (cf section 2). This was not possible, either for growth per family among the future 2Y81 fish during the same period (Table 5.2).

Overall, there was a significant concordance between the different winter growth performances for family rankings with some families, like family 11, showing systematically a very high winter weight increment and some others, like families 15 or 57 for instance, showing systematically the opposite (Table 5.2). These consistent between family differences for winter growth performance appeared to be responsible for at least a part of the family variability for mean condition factor in spring. Before the grilse maturation (+18) episode, in both the 1Y81 and the 2Y81 cohorts, there was a significant positive correlation between mean winter weight increment per family and mean condition factor in spring per family (Table 5.3). The same could be seen before the precocious maturation (-6) in the 2Y81 cohort. However, before the post-smolt precocious maturation episode in both cohorts, the correlations were non-significant, and in the 1Y81 cohort, there was even a tendency to observe a negative correlation.

Table 5.3: Correlation between the mean winter weight increment per family and the mean condition factor in spring per family.

Cohort	Relevant maturation episode	Date of measurement for winter weight increment	Date of measurement for condition factor in spring	Correlation between mean winter weight increment per family and mean condition factor in spring per family
1Y81	Grilse maturation (+18)	Dec. 83 - June 84	June 84	r=0.59 n=11 p=2.9%
2Y81	Grilse Maturation (+18)	Nov.84 - May 85	May 85	r=0.73 n=11 p=0.6%
2Y81	Post-smolt precocious maturation (+6)	Nov. 83 - June 84	June 84	r=0.38 n=11 NS (12.5%)
1Y81	Post-smolt precocious maturation (+6)	Oct. 82 - April 83	April 83	r=-0.31 n=11 NS (17.5%)
2Y81	Precocious maturation (-6)	Oct. 82 - April 83	April 83	r=0.58 n=11 p=3%

It therefore appeared, that differences between families for growth capabilities during winter periods were probably responsible for only a part of the variability between families for incidence of maturation, and that some other sources of variability between families existed as well. This could be seen, for example, in that family mean ranks based on winter growth performance (Table 5.3) did not correspond closely to those based on mean condition factors in spring, or based on incidence of maturation (Table 5.2). Also, incidence of grilse maturation (+18) per family was significantly correlated with mean weight increment per family during the winter in seawater in the 2Y81 conort (Fig. 5.3, A). In the 1Y81 conort, there was a similar tendency, but the correlation was much weaker and not significant at the 5% level (Fig. 5.3, B). However, in both cases, there were similar deviations for some families. Family 13, and to a lesser extend, family 15, were characterised by incidence of grilse maturation (+18) much higher than what could have been expected from their winter growth performances. The opposite could be seen in family 51 and to a lesser extend, in family 12. It is interesting to note that, in both cohorts, families 12 and 13 were characterised by very similar mean weight increments during the winter in seawater and yet, they snowed very different mean condition factors in spring and very different grilse maturation (+18) incidences (Fig. 5.3, A,B).

The other factor identified in Chapter IV as contributing to the level of energy stores in spring among individual fish, was the level of energy stores at the beginning of the winter period (as characterised by the condition factor in fall).

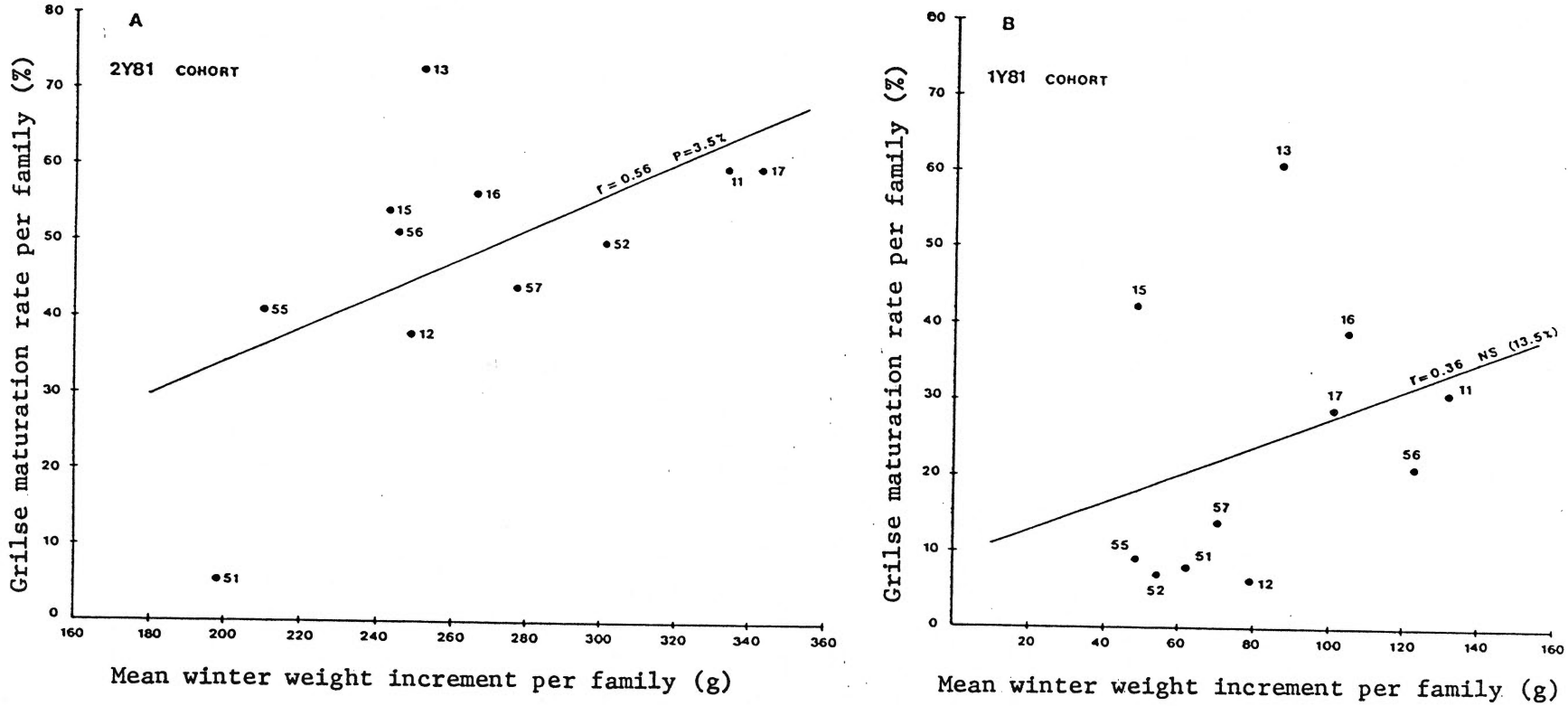

Figure 5.3: Correlations between the grilse maturation rate per family, in the 2Y81 (A) and the 1Y81 (B) cohorts. Correlations are calculated with normalised rates.

In both cohorts, before the grilse maturation (+18) and the post-smolt precocious maturation (+6) episodes, there were highly significant positive correlations between the mean condition factor per family at the beginning of the winter season (in fall) and the mean condition factor per family at the end of the winter season (in spring) (Table 5.4). This indicates that a large part of the variability between families for levels of energy stores in spring was a carry over from variability between families already present at the beginning of the winter period. This indicates as well that the contribution from variability between families for winter growth performance to the variability betwen families for levels of energy stores in spring was probably minor in those four cases.

In contrast, before the precocious maturation (-6) in the 2Y81 cohort, there was no correlation between mean family condition factors in fall and in spring (Table 5.4), so that it appears that the variability between families for mean condition factors in spring in this last case, was mostly due to variability between families for winter growth performance.

As it can be seen in Table 5.5, the fact that much of the variability between families for mean condition factors in spring was already present in fall appeared to be part of a very general feature. At all data collection sessions in the 1Y81 cohort, and at all but one in the 2Y81 cohort, there were highly significant differences between families for mean condition factors. Furthermore, there was a highly significant concordance for family rankings between the series of condition factors collected at 13 different data collection sessions on both cohorts.

Table 5.4: Correlation between mean condition factor per family in fall and mean condition factor per family the following spring.

Cohort	Relevant maturation episode	Date of measurement for condition factor in fall	Date of measurement for condition factor in spring	Correlation between mean condition factor per family in fall and mean condition factor per family in spring
1Y81	Grilse maturation (+18)	Dec. 83	June 84	r=0.88 n=11 p=0.1%
2Y81	Grilse Maturation (+18)	Nov. 84	May 85	r=0.80 n=11 p=0.2%
2Y81	Post-smolt precocious maturation (+6)	Nov. 83	June 84	r=0.87 n=11 p=0.1%
1Y81	Post-smolt precocious maturation (+6)	Oct. 82	April 83	r=0.72 n=11 p=0.6%
2Y81	Precocious maturation (-6)	Oct. 82	April 83	r=0.08 n=11 NS

Table 5.5: Comparison between families of mean condition factor at all data collection sessions in the 1Y81 and 2Y81 cohorts. Concordance between family rankings based on mean condition factor at all data collection sessions (including October 1982 and April 1983).

Cohort	Date	Mean condition factor per family											Between family comparison	
		11	12	13	15	16	17	51	52	55	56	57	1 way anova	
1Y81	Oct. 82	1.15	0.98	1.14	1.14	1.05	1.19	1.14	1.16	1.16	1.11	1.15	/	
2Y81	Oct. 82	1.16	0.94	1.22	1.07	1.07	1.38	1.09	1.08	1.11	1.08	1.08	/	
1Y81	April 83	1.12	1.08	1.15	1.11	1.08	1.16	1.13	1.19	1.11	1.11	1.12	/	
2Y81	April 83	1.21	1.18	1.22	1.16	1.13	1.15	1.07	1.11	1.11	1.08	1.11	/	
	Aug. 83	1.10	0.99	1.09	1.07	1.02	1.10	1.06	1.10	1.11	1.01	1.04	F=5.94	p<0.1% (1)
	Dec. 83	1.20	1.10	1.18	1.11	1.09	1.18	1.08	1.15	1.07	1.04	1.11	F=6.99	p<0.1% (1)
1Y81	June 84	1.16	0.98	1.09	1.00	1.00	1.09	0.98	1.03	0.99	1.00	1.01	F=9.42	p<0.1% (1)
	Dec. 84	1.19	1.17	1.23	1.16	1.19	1.19	1.14	1.24	1.14	1.15	1.19	F=2.96	p=0.4%
Number of cases per family		(26)	(44)	(31)	(26)	(18)	(14)	(12)	(15)	(11)	(14)	(7)		
	Nov. 83	1.09	1.10	1.14	1.11	1.09	1.13	1.06	1.12	1.09	1.11	1.10	F=1.03	NS (1)
	June 84	0.92	0.91	0.98	0.93	0.89	0.95	0.86	0.91	0.89	0.91	0.88	F=3.67	p<0.1% (1)
2Y81	Nov. 84	1.23	1.22	1.29	1.23	1.20	1.28	1.19	1.27	1.23	1.22	1.22	F=2.52	p=0.8%
	May 85	1.23	1.14	1.25	1.20	1.17	1.24	1.05	1.20	1.14	1.14	1.15	F=4.58	p<0.01%
	Dec. 85	1.12	1.10	1.14	1.09	1.11	1.18	1.04	1.10	1.10	1.05	1.04	F=2.31	p=1.4%
Number of cases per family		(15)	(13)	(21)	(11)	(13)	(10)	(18)	(18)	(17)	(33)	(18)		
Mean ranks		8.3	3.8	9.6	5.9	4.2	9.7	2.3	7.9	5.0	3.7	5.1		

Kendall concordance coefficient W and significance W=0.56 X^2=72.9 10 df p<0.01%

(1) Probability statements based on Fisher's randomization test.

Some families, e.g. families 11, 13, 17 and 52, had relatively higher condition factors at almost all data collection sessions, while some other families, e.g. families 12, 51 and 56, were characterised by the opposite. This tendency could be detected as early as October 1982 and April 1983, 11 and 17 months after spawning. This observation explains several apparent inconsistencies. For example family 13 had higher incidences of maturation, as compared to family 12, even though both families showed similar winter weight increments.

These consistent family differences for mean condition factor were not an indirect consequence of among families differences in rates of maturation. When only the maiden multi-sea-winter fish were used (the fish that never matured), there were still significant differences among families for mean condition factors at all data collection sessions in the 1Y81 cohort, and there was also a significant concordance for family rankings based on the condition factors collected at different times (Table 5.6). The mean family ranks calculated on these 1Y81 maiden multi-sea-winter fish were in reasonable agreement with those presented in Table 5.5.

Among the 2Y81 maiden multi-sea-winter fish, there were generally no significant differences among families for mean condition factor at the different data collection sessions, but this was obviously a consequence of the very low number of such fish in more than half of the families (Table 5.6). This is why these data were not included when computing the Kendall concordance coefficient and family mean ranks in Table 5.6.

Table 5.6: Comparison between families of mean condition factor at all data collection sessions in the 1Y81 and 2Y81 cohorts, for the maiden multi-sea-winter fish only. All probability statements are based on the Fisher's randomization test. Concordance between family rankings based on mean condition factor at all data collection sessions in the 1Y81 fish.

Cohort	Date	Mean condition factor per family, Maiden multi-sea-winter fish only											Between family comparison	
		11	12	13	15	16	17	51	52	55	56	57		
	Aug. 83	1.07	0.99	1.07	1.07	1.01	1.09	1.01	1.08	1.12	0.99	1.02	F=5.47	p<0.1%
1Y81	Dec. 83	1.19	1.10	1.15	1.08	1.07	1.19	1.03	1.12	1.08	1.03	1.11	F=6.26	p<0.1%
	June 84	1.08	0.98	1.04	0.97	0.98	1.08	0.95	1.02	0.99	0.97	1.01	F=6.45	p<0.1%
	Dec. 84	1.16	1.16	1.18	1.11	1.16	1.17	1.10	1.23	1.13	1.12	1.18	F=4.22	p<0.1%
Number of cases per family		(17)	(41)	(12)	(15)	(11)	(9)	(9)	(13)	(10)	(11)	(5)		
Mean ranks		8.5	4.5	8.6	4.0	4.3	9.8	1.8	9.0	6.4	2.1	7.1		
Kendall concordance coefficient and significance (1Y81 fish only)				W=0.74 X^2=29.7		10 df		p=0.1%						
	Nov. 83	1.04	1.10	1.15	1.12	1.10	1.10	1.06	1.11	1.07	1.08	1.08	F=0.80	NS
	June 84	0.89	0.92	0.96	0.97	0.88	0.86	0.85	0.95	0.89	0.87	0.87	F=2.85	p=1.2%
2Y81	Nov. 84	1.20	1.20	1.26	1.24	1.17	1.24	1.17	1.30	1.20	1.20	1.20	F=1.41	NS
	May 85	1.08	1.13	1.11	1.17	1.05	1.17	1.03	1.14	1.07	1.07	1.07	F=1.77	NS(8%)
	Dec. 85	1.10	1.09	1.05	1.16	1.07	1.08	1.03	1.10	1.06	1.01	0.99	F=1.50	NS
Number of cases per family		(3)	(6)	(4)	(4)	(5)	(2)	(16)	(7)	(10)	(11)	(10)		

4. Discussion.

The fact that fast growth rate was somehow causally related to the attainment of earlier age at maturity, but that there were also large differences between families or between stocks for incidence of maturation has been noted by several authors (Kato, 1975; Burger, 1985). Alm (1959) studied two forms of brown trouts, a small sized form (Salmo trutta fario) and a large sized form (Salmo trutta ferox or lacustris). He stated that, in the two forms, fast growth rate led to earlier maturity. However, he also noted that there was a considerable difference between the two forms, in that the small form was reaching maturity at an earlier age and a smaller size, as compared to the large form. He assumed that this difference for average age and size at maturity was genetically determined. Siitonen (1986) noted that maturation seemed strongly correlated with fish size in rainbow trout, the heavier fish maturing first, but he also noted that there were differences between stocks; the mean weight of the mature fish in one stock was similar to that of the immature fish of another stock, yet both stocks were characterised by similar incidences of maturation. Similarly, Dalley et al. (1983) studied Atlantic salmon precocious maturation in several natural populations (in several distinct ponds and rivers). He concluded that within a particular population, the faster growing parr may be most likely to exhibit precocious maturation. However, there were large differences between populations, some of them showing high growth rate and low percent precocity, while some others showed low growth rate and high percent precocity.

With the families used in the present study, two sources of variability (one major and one minor) between families for incidence of

maturation and of concordance between the 5 maturation episodes for family ranking were identified. There were as well some indications that a third minor source might exist as well.

1. The major source that was identified was that there were large differences between families for mean condition factor, at all times. Some families were systematically characterised by relatively higher condition factors, while others were characterised by the opposite. This situation was prevalent at all times, and was also the case specifically in spring. The families characterised in general by high condition factors were therefore characterised by higher levels of energy stores in spring and consequently by higher rates of maturation, for all maturation episodes.

2. The other identified source was that there appeared to be systematic differences between families for winter growth capabilities, which also led to some variability between families for mean condition factors in spring. However, this source appeared to be of a more minor importance, as compared to the first one discussed. This could be seen in the fact that mean family ranks based on winter growth performance (Table 5.2) did not match very well those based on mean condition factors in spring, or based on maturation incidence (Table 5.1).

3. Lastly, there were some indications that there might be some differences between families for the minimum level of energy stores in spring necessary to initiate maturation.

The presence of large and systematic differences between families for mean condition factors at all times, indicates that there are probably large differences between families for the allocation of surplus energy (surplus energy being the energy that is still available,

after the basic metabolic demands have been satisfied). Families characterised by low condition factors, like families 51 and 56 for example, probably allocate most of their surplus energy into somatic growth and do not appear to maintain large energy reserves. On the contrary, families characterised by high condition factors, like families 13 and 17 for example, appear to allocate a larger part of the surplus energy to the maintenance of energy reserves. Naevdal et al. (1976) found heritabilities for condition factors ranging from 0.04 to 0.81 in Atlantic salmon. Naevdal et al. (1981) also found estimates of heritabilities for condition factors significantly greater than zero, in rainbow trout and they concluded that "body shape which may represent both varying fat content, and real height/length differences, seems to be affected by additive genetic factors." McKay et al. (1986) found that, in rainbow trout, heritabilities for condition factors were generally higher than for size traits and they also detected a moderate influence of non-additive genetic effects for this trait. In contrast to these results and those of the present study, Refstie and Steine (1978), Gunnes and Gjedrem (1978), for Atlantic salmon, and Gunnes and Gjedrem (1981) for rainbow trout, found small heritabilities for condition factors and they concluded that the combination of weight and length used to calculate this condition factor had little genetic basis.

Thorpe et al. (1983) suggested that "genetic selection for rapid growth and late maturation within stocks of Atlantic salmon are incompatible objectives, since late maturation will be coupled genetically with lower growth rate." Gjerde and Gjedrem (1984) and Gjerde (1986) reported highly negative genetic correlations between body weight measured 4 months before maturity and age at maturity in Atlantic

salmon. As it can be seen on Figure 5.3, selecting the families showing low incidences of grilse maturation in both cohorts, would have effectively resulted in selecting some of the families showing the lowest winter growth capabilities (Fig. 5.2 and Table 5.2). However, it should be noted that selecting for late age at maturity should result in selecting indirectly for low winter growth specifically, and not for growth in general, as implied by Thorpe's statement. As the winter growth represents only a small part of the total growth, the negative impact of this correlated response to selection for late age at maturity would probably be reduced. Furthermore, it appears possible to "uncouple" selection for late age at maturity from selection for low winter growth. As previously noted, most of the variability between family for incidence of maturation was due to family differences in the relative allocation of surplus energy into the formation of energy reserves. Selecting for families that do not maintain large energy reserves, but rather invest most of their energy surplus into somatic growth, should result in selecting for lower incidence of maturation without necessarily selecting for low winter growth. For example, family 12 showed some of the best winter growth performances (Table 5.2) and yet showed in average very low incidences of maturation (Table 5.1), because it was one of the families characterised by low condition factors at all times (Table 5.5).

Lastly, there were some indications that there might be differences between families for the minimum level of energy stores in spring necessary to initiate maturation. Such differences might be an important source of variability for maturation incidence between different river stocks. In natural populations, the energy reserves

available in spring, are not only used to cover the energetic cost of gonadal developement and maturation, but as well to cover the energetic cost of the migration back to the spawning area, since salmon do not feed in the river (Idler and Clemens, 1959; Randall et al., 1986). Since rivers differ by many characteristics such as length, discharge, difficulty in the obstacles to upstream migration, etc., one could expect differences between rivers for the total energetic cost of reproduction. River length and discharge have been shown to be important covariates of sea age at maturity in several natural populations (Power, 1981; Scarnecchia, 1983). Thus, differences among river stocks for minimum level of energy stores in spring necessary to initiate maturation might be adaptations to local river environment. This might as well explain the observation that the age at first maturity of several full-sib families reared in sea cages correlated well with the life histories of the different river populations from which the full-sib families originated (Naevdal et al., 1978a). Selecting for high minimum level of energy stores in spring necessary to initiate maturation should result in selecting for lower incidence of maturation and should allow, in addition, the possibility to select for high growth in the same time.

GENERAL CONCLUSION.

The possibilities of reduction or even suppression of maturation to avoid its negative consequences in the salmonid aquaculture context have generated much interest in the last decade. This was mainly approached along two lines: the production of sterile populations and the production of all female populations, as females are generally characterised by a lower grilse maturation incidence and no incidence of precocious maturation (c.f. Chapter II, section 4).

Sterile populations can be obtained through interspecific hybridization, egg irridiation, induced polyploidy, hormonal treatment or auto-immune castration (Johnstone et al., 1978; Laird et al., 1978; Chevassus et al., 1979 a; 1979 b; Ellis, 1981). All female populations can be obtained through hormonal treatment, gynogenesis, or a combination of chromosomal manipulation and sex steroid treatment (Purdom, 1969; Schreck, 1974; Nagy et al., 1978; Chevassus et al., 1979 a; 1979 b; Hunter and Donaldson, 1983).

Several of these techniques have serious biological or economical shortcomings (poor market image of hormones treated animals or of interspecific hybrids, increased inbreeding of gynogenetic fish, etc.) and will probably not be used on a large scale in commercial aquaculture (Chevassus et al., 1979 a; 1979 b).

In contrast, induced polyploidy and combination of chromosomal manipulation and sex steroid treatment appear more promising and the mass production of all female triploid sterile eggs is already a commercial reality in rainbow trout (Ingram, 1987).

However, all these techniques of manipulation of maturation have

three common shortcomings: 1) they are relatively expensive; 2) they are complex and would generally require the fish farmer to obtain treated eggs or smolt from a specialised source; 3) the fish farmer cannot generally use the animals produced in his/her own fish farm as the broodstock for the next generations, because they are generally sterile. Therefore, the selection of stocks for a specific fish farm environment would not be possible, unless some complex schemes of separation between production and broodstock fish were put into place.

I would therefore like to propose an alternative technique of environmental manipulation of maturation. Based on the results of the present study (c.f. Chapter IV), starving cage reared salmon during the first winter in seawater should result in a lower incidence of grilse maturation. As the salmon would be forced to use their energy stores to cover their basic metabolic demands over the winter, most fish would probably not have in spring levels of energy stores sufficient to initiate maturation. Similarly, starving salmon during their second winter at sea should lower the incidence of 2-sea-winter maturation. This maturation delaying method would be simple, inexpensive and would not preclude site specific selection, as the fish farmer could easily obtain broodstock from his/her own stock by reversing the operation, i.e. feeding the fish in winter. This method would have however the obvious disadvantage of a nil winter growth. This would probably not be a major shortcoming as: 1) winter growth represents only a small portion of the total growth, at least under environmental conditions similar to those of the present study (the situation in Europe might be different as winter conditions are less extreme); 2) this winter growth loss would be partly compensated by a reduction of summer growth losses due to

maturation; 3) starving the fish during the winter would decrease feeding and labour costs.

However, this technique should probably be considered only as a temporary measure to alleviate early maturation problems in cage reared salmon. On the long term, genetic manipulation of the age at first maturity appears a much more promising way to deal with early maturation problems (c.f. Chapter III, section 4; Chapter V, section 4). Møller (1981, pers. comm. cited in Saunders at al., 1983) reported that early maturation problems had been largely solved through stock selection in Norway, the world's largest cage reared salmon producer. Chapter V, section 4 discussed several ways of selecting for late age at maturity that would not produce negative correlated response for growth. Optimising selection schemes, selecting for instance for both high growth rate and late age at maturity would however require the monitoring of growth during sea winter, either on stock, family or individual basis. This might prove to be difficult. The collection of precise growth data on sea cage sites is generally difficult, particularly around the winter. In the case of a sea ranching operation, it is impossible. I would therefore propose two suggestions to circumvent this problem:

- Upon finding a satisfactory standardizing technique, scale reading could provide a very convenient way to back-calculate growth parameters for potential broodstock fish.
- Alternatively, it might be possible to carry on a part of the selection program in freshwater at the parr stage, even before the fish are transferred to sea cages. For example, selecting for families or strains showing both high winter growth in freshwater and low incidence

of precocious maturation should also result in selecting for late age at maturity in sea cages, since the sources of family variability for incidence of maturation appeared to be the same for precocious maturation and grilse maturation (c.f. Chapter V). Selecting then the individuals showing the best growth performances in sea cages (e.g. highest slaughter weight) among the families or strains pre-selected in freshwater, should overall result in selecting for high growth rate and late age at maturity.

I would like to conclude the present study with two remarks concerning the notion of age at first maturity.

Smoltification has often been conceptualised as a transition between the "juvenile" freshwater stage and the "adult" sea going stage. Anadromous salmon rarely spawn more than once in natural populations, probably because of the high natural and fishing mortalities. Hence, maturation appears to be of a discrete nature and salmon appear to fall into convenient nonoverlapping categories for age at spawning: the grilse, the 2-sea-winter salmon, the 3-sea-winter salmon, etc., while "juvenile" maturation (precocious parr) is treated as yet another unrelated phenomenon. This is a convenient but probably misleading conception. From the results of the present study, the various classes of age at maturity that are observed are simply consequences of the same annually recurrent dynamic mechanism of maturation initiation. There does not appear to be any inherent difference between "precocious" maturation, grilse maturation or 2-sea-winter maturation, etc. This situation appears similar to that of the smoltification, where the annually recurrent dynamic mechanism of smoltification "decision" results in various smolt age classes.

Among anadromous spawners, there is a considerable variability for the season of ascent of the river, even within salmon of the same age at first maturity. This variability was partly responsible for the early adoption of a classification based on the number of winter(s) spent at sea, as this was the simplest "common denominator" and as this could easily be seen in the salmon scales. Hence, grilse which are mature 1.5 years after smoltification are 1-sea-winter fish, salmon that are mature after 2.5 years are 2-sea-winter fish and so forth. The fact that such a classification based on the number of winter(s) spent at sea is the easiest and most satisfactory way to classify the different groups of age at first maturity is not a coincidence but a very logical consequence of the mechanism of maturation decision proposed in this study. Among individual fish, the growth performance during the winter in seawater was identified as the single most important parameter contributing to the level of energy stores in spring, itself directly linked to the decision to mature as grilse or not (c.f. Chapter IV, section 4.5).

Therefore, a particular 1-sea-winter fish is so simply because this particular fish had a growth performance during its first winter at sea that was good enough, given the genetic background of this fish, to initiate maturation. A particular 2-sea-winter fish is so because the winter growth performance of this fish during its first sea winter was not good enough for this fish to initiate maturation, but this condition was attained after the second sea winter, and so forth.

To sum up, a n-sea-winter fish is so simply because its various winter growth performance(s) during its first (n-1) sea-winter(s) at sea were not good enough for this fish to initiate maturation, but the

growth performance of this fish during the nth winter at sea was good enough for it to initiate maturation.

There is often hidden wisdom in old customs.

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