Control of puberty in farmed fish

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Abstract

Puberty comprises the transition from an immature juvenile to a mature adult state of the reproductive system, i.e. the individual becomes capable of reproducing sexually for the first time, which implies functional competence of the brain-pituitary-gonad (BPG) axis. Early puberty is a major problem in many farmed fish species due to negative effects on growth performance, flesh composition, external appearance, behaviour, health, welfare and survival, as well as possible genetic impact on wild populations. Late puberty can also be a problem for broodstock management in some species, while some species completely fail to enter puberty under farming conditions. Age and size at puberty varies between and within species and strains, and are modulated by genetic and environmental factors. Puberty onset is controlled by activation of the BPG axis, and a range of internal and external factors are hypothesized to stimulate and/or modulate this activation such as growth, adiposity, feed intake, photoperiod, temperature and social factors. For example, there is a positive correlation between rapid growth and early puberty in fish. Age at puberty can be controlled by selective breeding or control of photoperiod, feeding or temperature. Monosex stocks can exploit sex dimorphic growth patterns and sterility can be achieved by triploidisation. However, all these techniques have limitations under commercial farming conditions. Further knowledge is needed on both basic and applied aspects of puberty control to refine existing methods and to develop new methods that are efficient in terms of production and acceptable in terms of fish welfare and sustainability.

Key words: Puberty control; fish farming; brain-pituitary-gonad axis; environmental conditions; genetics; growth; adiposity; sterility; triploids.

1. Introduction

Puberty in fish is the developmental period during which an individual becomes capable of reproducing sexually for the first time, and implies a functional competence of the brain-pituitary-gonad (BPG) axis (Schulz and Goos, 1999; Zanuy et al., 2001; Okuzawa, 2002; Patiño and Sullivan, 2002; Schulz and Miura, 2002; Weltzien et al., 2004; Jalabert, 2005; Dufour and Rousseau, 2007). Puberty starts some time after sex differentiation and is associated with the initiation of germ cell maturation and full functional differentiation of the germ cell-supporting somatic cells of the gonads, and culminates in the first spermiation and sperm hydration or ovulation (Okuzawa, 2002).

Early puberty is a major problem in farmed fish, such as in salmonids (McClure et al., 2007), sea basses (Felip et al., 2008), flatfishes (Weltzien et al., 2003a), cod fishes (Karlsen et al., 2006a), tilapias (Longalong et al., 1999), sea breams (Gines et al., 2003; 2004) and perches (Shewmon et al., 2007). Puberty adversely affects growth, feed utilization, health and welfare. Early puberty can also increase the risk for negative genetic effects of escapees on wild stocks (Bahri-Sfar et al., 2005; Naylor et al., 2005; Hindar et al., 2006; Skaala et al., 2006) or after spawning in sea cages (Jørstad et al., 2008).

Although methods exist to delay puberty in commercial farming, mainly by selective breeding (Gjedrem, 2000), photoperiod control (Bromage et al., 2001), monosex stocks (Devlin and Nagahama, 2002) and induced triploidy (Benfey, 1999), major limitations still exist in the commercial use of these methods. Breeding programs usually take multiple generations to significantly reduce the problems with early puberty, they are costly, and they are not always fully efficient in every species (e.g. Kolstad et al., 2006). Photoperiod protocols to delay puberty have yet to be developed in some species like Atlantic halibut (Norberg et al., 2001), and there are unpredictable outcomes of the photoperiod treatments between different sites and years, e.g. in farming of Atlantic salmon and Atlantic cod where such techniques are commonly in use (Hansen et al., 2000; Taranger et al., 2006). This may, in turn, be related to other factors also impacting on the control of puberty, such as growth rate, feeding and adiposity/energy homeostasis of the fish (Taranger et al., 1999; Oppedal et al., 2003). Production of monosex stocks are not yet possible in some species (e.g. the European sea bass; Piferrer et al., 2005; Guiguen et al., this volume), and sterility induced by triploidisation may compromise fish welfare and production performance (Benfey, 2001; Felip et al., 2001c; Hulata, 2001)

On the other hand, in some species, a delay, or complete failure of, rather than a precocious puberty causes problems under farming conditions, e.g. in European eel (Dufour et al., 2003; van Ginneken et al., 2007), hence preventing reproduction and closure of the life-cycle in culture. Moreover, in species such as groupers, tunas or sturgeons it can take many years until puberty starts, increasing costs and risks since potential broodstock has to be maintained for prolonged periods of time in farm facilities until maturation. In such cases, an advancement of puberty to harvest eggs (i.e. for caviar) or for reproduction, will improve the costs-efficiency of the fish farms. Thus, puberty control implies both techniques to delay/arrest and to advance/induce puberty. This control must be species-specific considering the great variety of reproductive patterns among species.

To fully control age and size of onset and completion of puberty in fish farming, we need to understand the underlying mechanisms triggering puberty, as well as the impact of various internal and external factors that govern and modulate this process. Commencement of puberty in teleosts is linked to genetic factors (Gjerde et al., 1994), metabolic signals e.g. related to energy stores (Campbell et al., 2006; Thorpe, 2007) and environmental inputs (e.g. Bromage et al., 2001; Drinkwater, 2002).

Although the precise involvement of factors that initiate puberty are generally not well known in fish, the integrative signals derived from these internal and external factors stimulate the release of the hypothalamic neurohormone gonadotropin-releasing hormone (Gnrh), which stimulates the production and/or release of pituitary gonadotropins, in turn regulating downstream targets, such as sex steroid and germ cell production in the gonads (Schulz and Goos, 1999; Zanuy et al., 2001; Okuzawa, 2002; Patiño and Sullivan, 2002; Schulz and Miura, 2002; Swanson et al., 2003; Weltzien et al., 2004; Jalabert, 2005; Yaron and Sivan, 2006; Dufour and Rousseau, 2007).

Objectives and scope of the paper:

1. Provide definitions and concepts about puberty in fishes.
2. Review in short our knowledge about puberty related problems in fish farming.
3. Provide information about variability in age and size at puberty of farmed fish, including differences between sexes (using some selected species as examples; Atlantic salmon, European sea bass, Atlantic cod, Atlantic halibut) and the underlying patterns of gametogenesis prior to and during puberty.
4. Review mechanisms underlying puberty onset and completion in fishes.
5. Review impact of internal (e.g. genetic, energy homeostasis) and external (e.g. photoperiod and temperature) factors on age and size at puberty.
6. Review the status of different techniques (selective breeding, environmental control, sterility models) to control puberty (delay/arrest or promote/induce) in fish farming using some selected species as examples.
7. Identify gaps in knowledge and perspectives for new approaches (e.g. new sterility models).

2. Definitions of puberty

Puberty is the developmental period comprising the transition from an immature juvenile to a mature adult state of the reproductive system, i.e. the stage of development during which an individual becomes capable of reproducing sexually, implying functional competence of the brain-pituitary-gonad (BPG) axis. Adult vertebrates produce gametes, the cellular basis of fertility, and have the somatic and behavioural competence to competitively function as mating partner and/or parent. These are long-term and demanding tasks in many respects, requiring the integrative regulation of different life processes, such as extracting energy from the environment, regulation of growth and energy metabolism, development of secondary sexual characters, reproductive behaviour and so forth. It is therefore not surprising that the two main functions of the gonads – to produce fertile gametes and hormones – are orchestrated by the endocrine system, typically involved in coordinating complex developmental and physiological processes. We can discern two types of regulatory input in this context. Of primary relevance is the BPG axis with its feedback systems, regulating both pubertal development and the maintenance of adult reproductive capacity. Secondly, other systems such as those regulating growth and energy metabolism, the immune system, or the brain-pituitary-thyroid axis that is involved in the functional differentiation of many cell/tissue types, provide permissive rather than direct regulatory signals.

The control of puberty and reproduction in general by the BPG axis offers several evolutionary advantages. For example, the reproductive system usually is silenced until an individual's somatic development has proceeded sufficiently to permit investing into pubertal development. Through the dependency on sex steroids, the start of germ cell development is integrated with the development towards reproductive competence in general, and allows for the evolutionary mechanism of sexual selection to have an impact (Clutton-Brock, 2007; Siller, 2001). Hence, puberty is characterised by the concomitant activation of the two main

functions of the gonad, the production of germ cells and the synthesis of reproductive hormones, in particular sex steroids, themselves required for supporting different aspects of germ cell development in both females (e.g. estrogens and vitellogenesis; Lubensz et al.; this volume) and males (e.g. androgens and spermatogenesis; Schulz et al.; this volume), and reproductive competence in general.

The first successful reproduction or, alternatively, the production of the first batch of fertile gametes (spermiation and sperm hydration in males; ovulation in females) can be considered as end point of puberty (Okuzawa, 2002). The start of puberty, however, seems more difficult to define. Genetic models in mammals show that loss of the androgen receptor (De Gendt et al., 2004), of the receptor for luteinising hormone (Lhr)(Pakarainen et al., 2005) of the β-subunit of luteinising hormone (Lh) (Kumar, 2007), of the Gnrh receptor (de Roux et al., 1999), or the loss of a critical input to the Gnrh-producing neurones via the Kiss/Gpr54 system (de Roux et al., 2003; Seminara et al., 2003), all block entry into puberty. Loss of follicle stimulating hormone (Fsh) function resulted in follicle development being blocked completely while spermatogenesis was still possible, although compromised as regards number and motility of the spermatozoa produced (Huhtaniemi and Aittomaki, 1998), and with species-specific differences of the graveness of the phenotype which can reach infertility in primates (Themmen and Huhtaniemi, 2000). Recent studies in channel catfish and zebrafish reported that up-regulation of pituitary *fshβ* and ovarian *fshr* gene expression started prior to vitellogenesis, coinciding with the accumulation of cortical alveoli, and continued through vitellogenesis (Kumar and Trant, 2001; Kwok et al. 2005; So et al., 2005). Moreover, Campbell et al. (2006) found evidence suggesting that Fsh signalling is important during the accumulation of cortical alveoli in oocytes in the early stages of puberty of coho salmon females.

Taken together, there is convincing evidence that regulatory input from outside the gonads is required to trigger pubertal development. Early experiments based on the surgical removal of the pituitary in fish, allow drawing a similar conclusion. In particular rapid proliferation of spermatogonia in males (Billard, 1969; Dobson and Dodd, 1977; Khan et al., 1986) and the entry into the lipid droplet stage of oocyte development (Sundararaj et al., 1972) are the first stages requiring pituitary input in fish. The requirement for the gonadotropin-stimulated production of androgens for the initiation of spermatogenesis is in line with the observation that 11-ketotestosterone (11KT) is able to stimulate rapid spermatogonial proliferation in eel testis tissue fragments in vitro (Miura et al., 1991), in juvenile African catfish in vivo (Cavaco et al., 1998), and is in line with concomitantly elevated plasma 11KT levels and spermatogonial proliferation in naturally maturing Atlantic salmon in vivo (Schulz, Andersson, Taranger; unpublished). Moreover, in male Chinook salmon increases in pituitary Fsh and plasma 11KT levels were found during the transition from spermatogonia A to spermatogonia B (Campbell et al., 2003), and recent studies in Japanese eel (Ohta et al., 2007) and African catfish (Garcia-Lopez et al., 2008) suggested that Fsh can directly stimulate Leydig cells, since they express the fshr gene.

In coho salmon females, significant increases in plasma estradiol-17β (E2) and Fsh levels (Campbell et al., 2006) accompany the entry into the first pituitary-dependent stage of ovarian development, the lipid droplet stage (Sundararaj et al., 1972). However, Campbell et al. (2006) also reported that Fsh and E2 levels increased already at the cortical alveoli stage in coho salmon going into puberty, and Manning et al. (2008) found the first endocrine signs of puberty as an increase in plasma E2 levels in yellowtail flounder.

We therefore propose to consider the transition to the first wave of rapid spermatogonial proliferation, or to the first batch of oocytes accumulating cortical alveoli, as the start of puberty, which – in both sexes – may be regulated by Fsh. Recent work indicated that oogonial proliferation and entry into meiosis may also be sensitive to steroid hormones

(Miura et al., 2007), but work in this direction has just started and the regulatory input in these early stages has not been investigated yet.

3. Variability in age and size at puberty

3.1 Plasticity in age and size at puberty

There is considerable phenotypic and genotypic variation in both age and size at puberty in fish species that is used in farming, e.g. in Nile tilapia (Duponchelle and Panfili, 1998; Longalong et al., 1999)**,** Atlantic salmon (Saunders et al., 1983; Wild et al., 1994; Hutchings and Jones, 1998; Taranger et al., 1998), rainbow trout (Kause et al., 2003; Taylor et al., 2008), Arctic char (Duston et al., 2003), brook trout (Kennedy et al., 2003), coho salmon (Vollestad et al., 2004), sea bass (Rodriguez et al., 2001b), sea bream (Matic-Skoko et al., 2007), turbot (Imsland et al., 1997) Atlantic halibut (Imsland (Imsland and Jonassen, 2005), bluefin tuna (Fromentin and Powers, 2005), Atlantic cod (Olsen et al., 2005; Karlsen et al. 2006), haddock (Davie et al., 2007a), channel catfish (Shephard and Jackson 2005), Eurasian perch; (Migaud et al., 2006) and sole (Mollet et al., 2007). This variation is found both between and within strains/populations (Myers et al., 1986; Fleming, 1996; Damsgard et al., 1999; Jonsson and Jonsson, 2004; L'Abee-Lund et al., 2004; Grover, 2005; Morita et al., 2005). The Atlantic salmon is one of the most extensively studied species in this regards, and has been found to display a remarkable variation in life-history traits such as age and size at puberty, and including differences between and within populations as well as between year-classes (Hutchings and Jones, 1998; Garcia de Leaniz et al., 2007).

Many studies on age and size at puberty are based on examination of natural populations, or studies of release of offspring of wild populations into natural environments (e.g. Hutchings and Jones, 1998; Heino and Godo, 2002; Dieckmann and Heino, 2007; Jonsson and Jonsson, 2007; Dominguez-Petit et al., 2008; Ottersen, 2008), and it is difficult to establish to which extent the variation in age and size at puberty is of genotypic or phenotypic origin (Morita et al., 2005; Kuparinen and Merila, 2007; Marshall and McAdam, 2007). On the other hand, a range of experimental studies have demonstrated large phenotypic variation in age and size at puberty (Bromage et al., 2001; Thorpe, 2007), and also a significant genetic variation in age and size at puberty both between and within strains and families (Gjerde et al., 1994; Wild et al., 1994). However, the relative importance of phenotypic and genotypic variation in age and size at maturity has been much debated, and is complicated by the interaction with growth history/growth patterns, which may explain why there appears to be no fixed size or age thresholds for puberty in those species that have been most closely studied such as salmonids (Morita and Fukuwaka, 2006).

The relation between environmental conditions and changes in age and size at puberty can be described in terms of reactions norms (Stearns, 1992). Life history models predicts that age at puberty is delayed when growth conditions become less favourable (Stearns and Koella, 1986; Stearns, 2000; Hutchings and Fraser, 2008; Piche et al., 2008), while the effects on size at puberty (i.e. decrease or increase) depends on a range of factors such as mortality patterns and increase of fecundity and offspring quality with increasing body size of parents (Fig. 1). In several heavily exploited fish populations both age and size at puberty has been reduced over time (Chen and Mello, 1999; Engelhard and Heino, 2004; Hutchings, 2005; Olsen et al., 2005), which may reflect phenotypic plasticity response to increased growth rates as the population declines, or genetic changes due to size selective fishing, reducing both age at size at maturation in long-term exploited stocks (Chen and Mello, 1999; Heino and Godo, 2002; Engelhard and Heino, 2004; Dieckmann and Heino, 2007). In some pacific salmon populations, however growth rate reductions have resulted in delayed puberty as well as smaller size at puberty, possibly due to concomitant changes in mortality patterns (Morita and

Fukuwaka, 2007). The relationship between growth, body size and age at puberty is also complicated by frequency dependent fitness of different reproductive strategies such as mature salmon freshwater parr or salmon "jacks" adopting a "sneaking" spawning strategy competing with large salmon males returning from seawater that apply a "fighting" spawning strategy (Hutchings and Myers, 1994; Esteve, 2005).

Different relationships between body size and reproductive success in males and females are also the predicted reasons for sexually dimorphic growth, and differences between the sexes in age and size at puberty. In many species of farmed fish, male growth typically levels off at a smaller size and age compared to females (e.g. sea bass, halibut etc.), most probably because female fecundity and offspring "quality"/survival gain more by increasing body size than in males. However, this is again complicated by frequency dependent alternative mating strategies such as in salmonids where "sneaking" strategies in freshwater as mature parr can have an optimal size window (e.g. Aubin-Horth et al., 2006).

In fish farming, growth conditions and feed availability is normally improved compared to the situation in natural ecosystems, and hence both age and size at puberty are often reduced compared to wild fish from the same strains (Svåsand et al., 1996). Thus, the phenotypic responses to improved growth conditions and feed availability, often with associated higher adiposity and energy stores, are probably the major causes of the early puberty commonly observed in many farmed fish species (Fig. 1). This also poses a challenge to selective breeding programs, because such phenotypic responses can mask genetic variability in age and size at maturation, and make it more difficult to select for late maturity. On the other hand, some species like the European eel do not reach puberty under farming conditions, most likely due to lack of appropriate environmental stimuli and/or lack of appropriate behaviours such as long term swimming (Dufour et al., 2005; Van Ginneken et al., 2005; 2007; van Ginneken and Maes, 2005; Sebert et al., 2008; Weltzien et al., 2008).

Atlantic salmon

The Atlantic salmon (*Salmon salar*) show a stunning variability in age and size at puberty, both between and within strains, and also between years/environmental conditions (Hutchings and Jones, 1998; Garcia de Leaniz et al., 2007; Thorpe, 2007). Similar variations in life-history strategies are also seen in other salmonids used in fish farming such as rainbow/steelhead trout (Kause et al., 2003; Tipping et al., 2003; Thrower et al., 2004; Thrower and Joyce, 2006; Sharpe et al., 2007) or coho salmon (Vollestad et al., 2004; Snover et al., 2005, 2006; Wattersi and Bessey, 2008). This large variability in life-history strategies is believed to be an adaptation to the local conditions in the native river environments where they spawn and have their juvenile development, as well as conditions in the sea including likelihood of marine growth and survival. Some salmon populations remain in fresh water throughout life, whereas others have smaller or larger anadromous components, migrate to seawater following parr-smolt transformation (smoltification), and live in the marine environment for one or more years before returning to their native rivers to spawn.

The combinations of different smolt ages and sea age at maturity, with resident parts of the population consisting mainly of males maturing at a small body size as "dwarf" males, give rise to an impressive variety of life-history patterns in terms of age and size at puberty, both within and between populations. Experimental evidence shows a large phenotypic variability in these life-history patterns. Within a certain strain or population, variability in feed availability and water temperature will modulate growth rate and consequently age and size at puberty (cf. Thorpe, 2007). However, there are also clear genetic differences both between and within strains (Garcia de Leaniz et al., 2007) that can be exploited in selective breeding programs to delay puberty (Gjedrem, 2000). The importance of various proximate

and ultimate factors in determining variability in life-history event such as age at maturity has recently been modelled in salmonids (Mangel and Satterthwaite, 2008).

In salmon farming, the parr-smolt transformation normally takes place in one-year old fish (i.e. at 18 months of age), or even as underyearling smolts following photo-thermal manipulations (Berge et al., 1995; Duston and Saunders, 1995). The main problem with early puberty in farmed salmon is at the "grilse" stage, i.e. after 1.5 years in seawater and at a body size typically from 2 to 5 kg. Moreover, some farmed salmon reach puberty as "jacks" after only a few months in seawater and at a body size of around 0.5 kg. Also, male parr that become sexually mature precociously in freshwater prior to the parr-smolt transformation (typically at 10-30g) can represent a problem, both due to negative interference with the smoltification process, and due to loss of growth (Whalen and Parrish, 1999).

Atlantic salmon often display sexually dimorphic growth. This can both be a consequence of different age at puberty between sexes, and may further be affected by a pubertal growth spurt that commonly take place in sexually maturing individuals in the marine phase during spring prior to spawning. Males normally have a much higher proportion of parr maturation, and typically also have a higher proportion of both jacks and grilse compared to females. Salmon females often can take an intermediary position and reach puberty after two winters in seawater, whereas some males delay maturity to 3 years or more in seawater, and grow very big before reaching puberty.

Atlantic cod

Atlantic cod (*Gadus morhua*) is distributed in eastern and western parts of the Atlantic Ocean, with a polar and temperate distribution. The different stocks inhabit waters with temperatures ranging from -1 to 20°C, though usually found in waters with temperatures between 1 and 12°C. The spawning period for most stocks is between January and April (Brander, 2005). Growth and age of puberty varies between stocks, and is affected by prey availability and temperature in their habitat (Drinkwater, 2002). It has been shown that age at puberty is affected such that a lower bottom temperature in their habitat increases age of puberty by approximately 1 year when the temperature is decreased by 2°C (Drinkwater, 2002). The northeast Arctic cod stock usually spawns at an age between 4 and 8 years (Bergstad et al., 1987; Jørgensen, 1989), while Norwegian coastal cod recruits to the spawning stock 3 years and older (Berg and Albert, 2003). In farming, these strain differences are more or less lost, as all tested stocks spawn at an age of 2 years under normal growing conditions, reaching a body weight of around 1.5 to 2 kg at spawning (Godø and Moksness, 1987; Svåsand et al., 1996, Hansen et al., 2001; Karlsen et al., 2006a; Taranger et al., 2006). Some males mature even at 1 year of age with a mean weight of <300 g, while no females have been observed to mature at 1 year of age. The reduced age at puberty in farmed cod is probably due to the favourable food availability, leading to much faster growth and larger energy stores compared to in wild populations, most notably seen as a higher liver index in farmed compared to wild cod (Karlsen et al., 2006a, b). Under farming conditions, a sex-dependent growth difference has occasionally been observed, with females being slightly larger than males (Kolstad et al., 2006; Solberg and Willumsen, 2008).

Atlantic halibut

The Atlantic halibut (*Hippoglossus hippoglossus*) is distributed in parts of the Arctic Ocean and in the northern part of the Atlantic Ocean. Sexually mature animals congregate for spawning in winter, on well-defined deepwater spawning grounds. The spawning period for Atlantic halibut varies with geographical region, from December to March in the most northern parts of Norway, with peak spawning in January/February, while the spawning period in more southern regions such as the Iceland/Faroes/North Sea area and the Nova

Scotia/Gulf of St Lawrence/Newfoundland banks area extends into early spring (Haug, 1990).

Atlantic halibut show a distinct, sex specific growth pattern and age at sexual maturation, males reaching puberty at a younger age and smaller size than females (Jakupstova and Haug, 1988), at about 80 cm body length in males, compared to 110-120 cm in females (Methven et al., 1992). The reproductive strategy behind this dimorphism is a trade-off between body size, age at maturity and fecundity expressed as number of eggs spawned. The halibut is periodic spawner that release large numbers of pelagic, transparent eggs. There is no parental care and survival of offspring is mainly secured by quantity rather than quality. As a consequence, females need to attain a large body size to produce a high number of eggs. Accordingly, females mature at a very large size compared to male halibut and to other flatfishes; wild halibut males typically mature at a size around 1.7 kg and at 4-5 years of age, while mature females around 18 kg and 7-8 years of age (Jakupsstovu and Haug, 1988). In aquaculture, accelerated growth of juvenile fish commonly result in an advancement of age at puberty so that male halibut mature at 2 - 3 years and at a similar body size as wild males (Norberg et al., 2001), while females mature at around 5-6 years and at a body size of around 8 kg. Farmed female halibut show significantly higher growth at least from one year of age compared to males (Norberg et al, 1999), and the females generally reach the desired market size before puberty, making this species particularly suited for all-female production.

European sea bass

The European sea bass (*Dicentrarchus labrax*) is a gonochoristic perciform fish in which puberty of females occur at three years of age while in males puberty is attained at two years of age (Carrillo et al. 1995, Saillant et al., 2003). Under intensive culture conditions, sea bass exhibits a high rate of growth and as a consequence around the 20-30% of the male population mature precociously. These fish are larger than the non-precocious ones and reproduce at the first year of life, before attaining market size. However, at the second annual cycle, precocious males grow up to 18% less in weight and 5% less in fork length than the non precocious fish (Felip et al., 2008a). Moreover, males in general exhibit 20-40% less body weight at harvest time than females (around 18-22 months of age), likely induced by their earlier onset of puberty which diverts energy towards gonadogenesis and breeding behaviour instead of somatic growth (Carrillo et al., 1995; Saillant et al., 2001). In addition, under aquaculture conditions there are often a high percentage of males, reaching 70-90% of the total population (Carrillo et al., 1995; Gorshkov et al., 1999). According to these considerations, mono-sex culture (females) has been proposed as a likely solution to improve production of sea bass in terms of sexual dimorphism in growth and to alleviate the disadvantage of skewed proportion rates to males in cultivated populations.

3.2 Patterns of gonadal growth and development prior to and during puberty

Atlantic salmon

Atlantic salmon females have a group-synchronous oocyte development, with one leading cohort of oocytes entering into secondary oocyte growth as marked by the formation of cortical alveoli and later perinuclear oil drops. Secondary oocyte growth commences normally at least one year before spawning in parallel with increasing plasma E2 levels (Chadwick et al., 1987; Taranger et al., 1999; King and Pankhurst, 2003). The leading oocyte cohort enters true vitellogenesis around winter solstice, approx 10 months prior to spawning, and accumulates yolk during spring, summer and early autumn in parallel with a massive increase in oocyte diameter and gonad size. After completion of vitellogenesis and oocyte growth, final oocyte maturation resumes approx one week before ovulation that normally takes place between late autumn and early winter depending on strain and environmental conditions such

as water temperature (Heggberget, 1988a,b; Taranger and Hansen, 1993). The eggs are ovulated in a single batch, and can remain in the body cavity for around one week prior to egg deposition (spawning) and fertilization. The gonadosomatic index (GSI) increases from typically < 0.3% at the smolt stage to around 20-25% just prior to ovulation. Recruitment into vitellogenesis appears to take place earlier in the season in females that mature at a higher age (e.g. comparing salmon maturing after either one or two years in seawater), allowing for larger egg size and/or fecundity in older females. In parallel, salmon males typically have a GSI of < 0.1% at the smolt stage, which increases rapidly from winter/spring prior to spawning to a maximum of around 5-10% in the beginning of the spawning period. The rapid testis growth takes place after the initiation of rapid spermatogonial (type B) proliferation in parallel with increasing plasma sex steroid levels in late winter/early spring depending on strain, age and environmental conditions (Hunt et al., 1982; Youngson et al., 1988; Youngson and McLay, 1989; McLay et al., 1992; Stead et al., 1999). It appears that onset of puberty is marked by the rapid spermatogonial proliferation and increase in gonad size can commence earlier in the season in older and larger males, in a similar fashion as in females. The large investments in gametogenesis and reproductive behaviour in combination with ceased feeding from the summer months, lead to a marked depletion of lipids, proteins and astaxanthin (red pigment) from the muscle tissue in sexually mature salmon (Aksnes et al., 1986). However, both males and females can survive following spawning and remature in later seasons.

Atlantic cod

The repeat spawning, group-synchronous Atlantic cod spawns mainly between January and April depending on the stock and water temperature, but some stocks spawn during summer and autumn (Brander, 2005). Females release egg portions every 2 or 3 days, and in captivity they may spawn 17-19 batches during their spawning period (Kjesbu, 1989). Prior to the first spawning season, the ovary remains immature and contains only small transparent previtellogenic oocytes less than 250 μm until about October (Dahle et al., 2003). One month later most females have commenced formation of cortical alveoli and yolk sequestration. As vitellogenesis proceeds during late autumn and early winter, the size of the oocytes increases to above 800 μm prior to hydration (Kjesbu, 1991). The GSI increases from less than 1% in the beginning of October to about 5 % in December. A rapid growth starts in January until a maximum is reached just prior to spawning of about 15%. Some females may have much larger GSI. The proliferation of spermatogonia starts in August, followed by meiosis and spermiogenesis from October (Dahle et al., 2003; Almeida et al., 2008a). Free spermatozoa are observed from December onwards (Dahle et al., 2003; Almeida et al., 2008a). The males are therefore prepared for spawning at least 1 month prior to females. The GSI increases from below 2% in October, to about 4% in November and reaching a maximum of about 12% in January. Cod drains energy from liver and muscle during the spawning period to supply energy both for the incorporation of yolk during the development of new batches of eggs (Kjesbu and Kryvi, 1993), and for behaviour.

The presence of cortical alveoli and yolk granules observed in mid-November indicates that these females will spawn the following season (Saborido-Rey and Junquera, 1998). It is possible to distinguish maturing females based on the appearance of circum-nuclear ring (Woodhead and Woodhead, 1965), which appears in summer during primary oocyte growth. Spermatogenesis occurs synchronously within cysts formed by Sertoli cells; different cysts often develop asynchronously (Dahle et al., 2003; Almeida et al., 2008a). In males there is a gradient in development within the testis lobes, where undifferentiated spermatogonia are found in the periphery of the lobes, and the more advanced germ cells closer to the collecting duct (Almeida et al., 2008a).

Atlantic halibut

Female halibut are group-synchronous spawners, releasing multiple batches of large, pelagic eggs approximately every 72-80 h over a period of three to six weeks (Norberg et al. 1991). The cortical alveoli stage appears to commence one year before spawning, while the first histological evidence of vitellogenic oocytes was found five months before first ovulation (Riple, 2000). Plasma levels of E2 and vitellogenin (VTG) increase from August/September, indicating that the onset of vitellogenesis occurs around five months before spawning (Methven et al., 1992). Concurrent with the increase in plasma VTG and E2, the major vitelline envelope proteins were also detected (Hyllner et al., 1994). During the spawning period, plasma VTG and E2 fluctuate, indicating a cyclic synthesis, release and uptake of VTG into the oocytes before final maturation (Methven et al., 1992). While pituitary gene expression of the gonadotropins, *fsh* and *lh*, appears to be high through all stages of ovarian development except just prior to ovulation, ovarian expression of the gonadotropin receptors, *fshr* and *lhr*, show a temporally differentiated expression pattern. The *fshr* is highly expressed in ovarian follicles during primary growth and vitellogenesis. During this period, *lhr* expression is very low, while it is highly expressed in follicles undergoing final maturation (Kobayashi et al., 2008b)

The germinal compartment in Atlantic halibut testis appears to be organized in branching lobules of the unrestricted spermatogonial type based on the localization of spermatocysts containing all germ cell developmental stages throughout the germinal compartment (Weltzien et al., 2002). The reproductive cycle of male Atlantic halibut is characterized by distinct seasonal variations in absolute and relative testicular size and developmental stage, and by fluctuations in plasma levels of T and 11KT associated with different phases of reproductive activity. The growth phase culminates in the formation of mature spermatozoa (spermiogenesis) at the initiation of the spawning period in January (Norberg et al., 2001). During the spawning period, which usually lasts until March/April, the GSI and plasma androgen levels soon begin to decrease, reaching regressed levels by April/May. Thus, spermatogenesis in halibut can be divided into three phases (Norberg et al., 2001; Weltzien et al., 2002, 2004). First, an initial phase with low levels of circulating T and 11KT, spermatogonial proliferation and meiosis marked by the formation of spermatocytes. Second, a phase with increasing T and 11KT levels, and with haploid germ cells including spermatozoa present in the testis. Third, a phase with low T and 11KT levels and a regressing testis with Sertoli cells displaying signs of phagocytotic activity. In terms of absolute measures, the GSI in male halibut remains below 0.1% until the appearance of spermatids (Weltzien et al., 2002), and increase to maximum levels of about 3% at spawning. 11KT normally occurs in higher quantities than T, generally with levels at least 4-fold higher during all stages of spermatogenesis (Methven et al., 1992; Weltzien et al., 2002). Plasma T and 11KT stay below 0.1 and 1.0 ng ml^{-1}, respectively, in male halibut until the appearance of spermatids in the testis, whereas maximum levels of 1-2 and 4-5 ng ml^{-1}, respectively, are reached at spawning. Increasing plasma levels of T and 11KT are associated with increasing testicular mass throughout the reproductive cycle. A slight elevation of androgen levels is apparent in males one year before first maturation, showing that halibut, like several other species, undergo a so-called dummy-run with increased steroid-production a year before puberty. It is believed that this gradual increase in androgen levels is necessary for the onset of puberty (Weltzien et al., 2003a). At the pituitary level, gene expression of both gonadotropins are apparent both in juvenile, early maturing, and maturing male halibut (Weltzien et al., 2003b,c).

European sea bass

Sea bass show a group-synchronous mode of gonadal development. In females, successive clutches of germ cells that will mature and be spawned in a given season are recruited from a population of vitellogenic oocytes (Alvariño et al., 1992), and a similar situation is observed in the male. Consequently, different types of ovarian follicles or testicular cysts may appear at certain periods of the sexual cycle. However, only one type dominates and defines the gonadal stage at a given period of the reproductive cycle (Begtashi et al., 2004; Rodríguez et al., 2001b).

The hormonal regulation of female gonadogenesis has been described by Asturiano et al. (2000, 2002) showing that vitellogenic oocytes can be recruited into maturation in four consecutive waves, and individual females can produce up to four consecutive spawns at around bi-weekly intervals during the reproductive period (mid January-mid March) (Mylonas et al., 2003). During this period no regression of the gonads was observed until the last spawning was completed. During the post-spawning period (May-June) the next generation of the germinal cells starts its development. Thus, different periods of gonadal activity are very well established; resting, early, mid and late vitellogenesis and spermatogenesis, maturation-ovulation, spermiogenesis-spermiation and finally ovarian and testicular regression.

These patterns of gonadogenesis observed in adult fish have also been confirmed in pubertal fish (Rodríguez et al., 2001b; Begtashi et al., 2004; Carrillo et al., 2008c) in parallel with a high increase in plasma sex steroids during spermatogenesis and vitellogenesis, remaining elevated throughout most of the maturation period, particularly in females (Rodríguez et al., 2000; Rodríguez et al., 2001a, 2004, 2005, Carrillo et al., 2008a, Rocha et al., 2008). The profile of E2 plasma levels observed in pubertal females was similar to the one in adult sea bass (Prat et al., 1990; Mañanós et al., 1997; Asturiano et al., 2000), with a single annual peak at late vitellogenesis (December) and constantly high levels during the whole maturation and ovulation period. The maintenance of constantly high E2 levels during the entire maturation and ovulation stage may be required for a prolongation of the vitellogenic process, as vitellogenic oocytes are also present during this stage.

Recently, expression studies on *fshr* mRNA levels in fish entering puberty showed up-regulation of this receptor at early stages of gonadal development (Rocha et al., 2008). Increased expression was also observed during the spermiation period in males and the maturation-ovulation period in females, suggesting that this receptor may also be involved in the control of these late processes. Increases in sea bass ovarian *lhr* mRNA levels were only observed when post-vitellogenesis began (December). At this stage, *fshr* mRNA levels were already at their maximum. During the maturation-ovulation period, expression levels of both receptors remained elevated, returning to their basal levels only after spawning. The observed high expression level of *fshr* during maturation could be connected with oocyte growth and is explained by the reproductive strategy of this species. As mentioned earlier, sea bass ovary exhibits a group-synchronous type of development and contains clutches of oocyte populations at various stages of secondary growth that are successively recruited (Mayer et al., 1990a; Asturiano et al., 2000). Therefore, the expression of any gene measured at the ovary level reflects the average of the existing follicles, including that of growing oocytes that would still express *fshr*.

11KT is considered to play an important role in stimulating spermatogenesis in several fish species (Schulz and Miura, 2002). In pubertal male sea bass, 11KT levels rise during mid spermatogenesis, and drop once spermiation begins (Rodriguez et al., 2000; 2001a; 2004; 2005; Carrillo et al., 2008c, Rocha et al., 2008). Similarly, sea bass plasma Lh levels showed an increase during spermatogenesis reaching the highest levels during spermiation which is in agreement with the expression profiles of sea bass *lhβ* (Mateos et al., 2003) and *lhr* (Rocha et

al., 2008). Finally, the study of the hormonal regulation of the early events of gametogenesis in sea bass has revealed the rhythmic nature of the synthesis and release of hormones. Pubertal sea bass going to maturation showed daily rhythms of pituitary sbGnrh content negatively correlated with plasma Lh daily rhythms, which as well exhibited nocturnal peaks (Bayarri et al., 2004). These daily rhythms were drastically suppressed by exposure to an inhibitory photoperiod (continuous light), fully arresting maturation (Bayarri et al., 2008).

4 Consequences of puberty

Onset of puberty can have large consequences for important production parameters in fish farming such as appetite, growth rate, feed conversion efficiency, flesh quality traits, external appearance, agonistic behaviours, health, welfare and survival rates.

Growth and somatic weight

Puberty results in direction of resources and energy from somatic growth and maintenance to gonad growth, production of gametes, and reproductive behaviour. In many species, feed intake will also be markedly reduced or stop completely prior to and/or during the spawning period (Kadri et al., 1996). As a consequence, somatic growth will decrease prior to and during the spawning period. However, the timing and magnitude of the growth decrease and/or loss of somatic weight depends on the reproductive effort in terms of gamete production and reproductive behaviour (Hendry and Beall, 2004), including the development of secondary sex characteristics as most typically seen in salmonids males (Naesje et al., 1988; Järvi, 1990). Some species like Atlantic salmon and several of the Pacific salmon species more or less exhaust their body reserves completely during spawning migration, gametogenesis and spawning, and suffer high or total mortality post spawning, at least on their native spawning grounds in rivers. Other species like the Atlantic cod, with only subtle secondary sex characteristics (Engen and Folstad, 1999) will normally survive the spawning season, but the loss in somatic weight can be more than 30% during a single spawning season (Karlsen et al., 1995; Fordham and Trippel, 1999). There can be some compensatory growth following completion of the spawning season, e.g. in Atlantic cod (Pedersen and Jobling, 1989), that will narrow but not remove the difference between previously mature and immature individuals (Taranger et al., 2006).

Pubertal growth spurt

Onset of puberty can also initially have positive effects on appetite and somatic growth. Individuals that enter puberty early are commonly the larger individuals within a population or a sibling group (e.g. Skilbrei 1989). In addition, in the early stages of puberty, somatic growth rates are often observed to be higher than in immature individuals. This is typically seen in Atlantic salmon, where maturing individuals often display higher growth rates from January to June in parallel with increased plasma sex steroid levels and start/resumption of gametogenesis (Hunt et al., 1982; Youngson et al., 1988; Skilbrei, 1989; McLay et al., 1992). Thereafter, feeding ceases in maturing individuals in early summer (Kadri et al., 1996), and hence somatic weight starts to decrease in parallel with the rapid gonadal growth in summer and autumn when Atlantic salmon approaches spawning. As a consequence, sexually maturing salmon are typically much larger than immature siblings in early summer, in part because the maturing fish were initially larger the winter before spawning, but mainly as a consequence of the puberty induced growth spurt from January to early summer. It has also been demonstrated that this growth increase following onset of the early stage of pubertal development is associated with increased appetite and feed intake (Kadri et al., 1996). Under farming conditions this pubertal growth spurt may be exploited to maximize growth and feed intake. However, in the case of Atlantic salmon, harvest should be shortly after the cessation

of the growth spurt, as both body weight and flesh quality will start to become negatively affected at the end of the summer (Aksnes et al., 1986).

Feed conversion efficiency

Puberty results in reallocation of energy from somatic growth to gametogenesis and reproductive related behaviours such as migrations and/or agonistic behaviour prior to and during the spawning period (e.g. Jonsson et al., 1991; Kjesbu et al., 1991; Karlsen et al., 1995; Hinch and Rand, 1998; Healey et al., 2003; Jonsson and Jonsson, 2003; Hendry and Beall, 2004). Moreover, the appetite is often reduced prior to and during large parts of the spawning season (Kadri et al., 1995; 1996; Tveiten et al., 1996; Fordham and Trippel, 1999; Skjæraasen et al., 2004). As a consequence the feed conversion efficiency will be markedly negatively affected (e.g. Stead et al., 1999). In addition, the weight loss with spawning will result in longer time to reach harvest size, and thereby larger expenditures to basal metabolism due to longer production time. Hence, the total amount of feed needed to reach as certain body size will increase if the fish is allowed to go through one or more spawning seasons before harvest, and thereby negatively affect the sustainability of the fish farming in terms of feed resource use.

Increased aggression/agonistic behaviour

Sexual maturation can impact on agonistic behaviour as typically seen in salmonids (Järvi, 1990; Fleming, 1996). Salmon can adopt different mating strategies and tactics depending on age and size at maturity (Fleming, 1996; Thorpe, 2007). Salmon males mature either directly in freshwater as parr ("dwarf males"), after return from seawater following a few months as "jacks", after one sea winter as "grilse", or after 2 or more sea winters as "hooknose". Depending on size, age and competitors they may behave as dominant (fighting) or as subordinate (sneaking) males. Secondary sex characteristics such as hook on the jaw, bright skin colouration and other changes in body shape are regarded as display of status (Tchernavin, 1944; Järvi, 1990). The "hooknose" males usually establish a size-based hierarchy, where the larger individuals are found closer to females (Järvi, 1990) and these usually also fertilize more eggs than the sneakers.

The combined efforts in gametogenesis, development of secondary sex characteristics and reproduction related behaviours drain heavily on the energy reserves in salmonids. In Atlantic salmon the cost of reproduction in both sexes have been calculated to around 59% measured as expended energy reserves (Fleming, 1998), and larger salmon expend more than smaller. There is an intense male-male competition for access to females. While females usually spend less than a week on the spawning grounds, males may spend a month (Webb and Hawkins, 1989). In addition, nesting females may have mate choice where they direct their aggression towards males (Fleming et al., 1997).

A contrasting spawning strategy is seen in the broadcast spawner Atlantic cod, where females release eggs into the surroundings, without any parental care. However, in spite of this, cod has a complex mating system where males court females using both display and sound (Brawn, 1961; Hutchings et al., 1999; Finstad and Nordeide, 2004; Rowe and Hutchings, 2006). Male cod have a territorial behaviour close to and during spawning (Brawn, 1961). Brawn (1961) observed that one large male occupied half the tank, and excluded other males by fast aggressive approaches, threat displays and sound production (Brawn, 1961). Reproductive success increases with male body length and number of agonistic interactions (Rowe et al., 2008). Courtship starts with a female approaching a male, and after a complex behaviour ends with the ventral mount, where the male and female swims belly to belly and releases eggs and sperm. The mating pair may be joined by "satellite males" that swim amongst the eggs and release sperm in an attempt to fertilise the eggs in competition with the

dominant male (Hutchings et al., 1999; Rakitin et al., 2001; Bekkevold et al., 2002). In the wild there is a vertical separation of mature males and females (Morgan and Trippel, 1996), and there are considerable vertical movements (Brawn, 1961; Rose, 1993; Hutchings et al., 1999; Lawson and Rose, 2000), where males assemble lower in the water column and females sink slowly down to this assembly. Spawning behaviour is likely to involve female choice (Hutchings et al., 1999; Rowe et al., 2007). The most aggressive agonistic male-male behaviour occurs in the lower parts of the water column, while most courtship behaviour appears in the upper part of the water column.

Increased disease susceptibility, health and welfare problems

Onset of puberty and sexual maturation can have an impact on the immune system of the fish (Maule et al., 1996; Suzuki, 1997; Hou et al., 1999; Cuesta et al., 2007), and consequently on disease susceptibility and the overall health status. This may in part be due to the immunomodulatory role of hormones such as sex steroids, cortisol and growth hormone that change in association with reproduction (Harris and Bird, 2000; Law et al., 2001; Yada and Nakanishi, 2002; McQuillan et al., 2003). This problem can be further aggravated by agonistic behaviours (see above), resulting in skin damages and in increased risk for secondary infections and parasite infections (Skarstein et al., 2001). Onset of sexual maturation can also lead to other changes in physiological homeostasis, e.g. in salmonids where sexual maturation compromise their hypo-osmoregulatory ability (Makino et al., 2007), and hence can result in dehydration and ultimately mortality if they are maintained in sea water throughout the reproductive season. Mortality has also been noted in farmed female cod that are unable to release their eggs following sexual maturation in sea cages (Ø. Karlsen, B. Norberg, G.L. Taranger, unpublished results). Thus, early sexual maturation (i.e. before the fish reach the desired marketable size) can also represent a welfare problem in fish farming due to compromised health, problems with maintaining homeostasis, spawning failure and related problems, as well as damages caused by aggressive behaviour.

Increased risk of genetic impact on wild stocks

Early puberty can also increase the risk of genetic impact of fish farming on wild stocks. In Atlantic salmon farming, it is assumed that sexually mature individuals will have a much higher likelihood to enter a nearby river and spawn upon escape from the fish farm, whereas fish that are immature at escape will more probably leave the coast to enter the feeding ground in the ocean and have a much lower likelihood to survive until they return to a river to spawn (Hansen, 2006). This is also seen in sea ranched triploid salmon that show lower return rates to freshwater from the marine environment than diploid salmon, probably due to the lower incidence of gonadal development seen in triploid salmon (Cotter et al., 2000). It has also been documented recently, that farmed Atlantic cod that are naturally spawning in sea cages give rise to surviving larvae and juveniles in the nearby coastal areas (Jørstad et al., 2008). This could also represent a risk for unwanted introgression of farmed genotypes into wild fish populations.

Atlantic salmon

A range of studies has investigated the impact of puberty on growth in Atlantic salmon, (e.g. Skilbrei, 1989) as discussed above. The general pattern is initially a growth promoting effect of puberty, typically seen in the winter, spring and early summer before spawning, and thereafter a decline in body weight during late summer/autumn when feeding ceases (Kadri et al., 1995, 1996) and energy is mobilized for rapid gonadal growth, development of secondary sexual characters, and reproduction-related behaviour (Aksnes et al., 1986). This has also profound effects on the fillet composition; initially the higher growth rate in pubertal fish can

lead to higher lipid stores than in immature fish, while the fillet is depleted for lipids, proteins and pigments (astaxhanthin) during the later stages of maturation. However, the magnitude and seasonal timing of the pubertal growth spurt, the loss of body weight and the associated changes in fillet composition can vary between strains with different seasonal timing of spawning, and between the highly divergent life-histories found in size and age at maturity in salmonids. The muscle fat content in maturing fish is higher than in immature during summer (Aksnes et al., 1986; Kadri et al., 1996), while in the period September-November the muscle lipid and protein content of maturing Atlantic salmon decreases. At spawning the lipid content were found to be about 3 % lower, and protein content about 4% lower (Aksnes et al., 1986). During the maturation the carotenoids originally deposited in the muscle are shifted to the gonads and skin, and consequently the muscle loses its red colour. The flesh quality is not different between mature and immature salmon until October; thereafter the flavour decreased in maturing fish, and the muscle texture becomes softer in mature salmon.

Atlantic cod

There is no, or only a minor sex dependent growth difference between male and female Atlantic cod prior to maturation. Male Atlantic cod have only subtle secondary sexual characteristics, such as increased length of the pelvic fins and larger drumming muscles (Engen and Folstad, 1999; Skjæraasen et al., 2006), which probably do not drain excessive energy. Closer to the spawning season starting in February, the females are usually slightly larger, mainly due to an enlarged liver compared to the males (Karlsen et al., 1995; Dahle et al., 2003), and in addition they have larger maximum GSI and continue gonad growth longer than males. Since cod reduce/stop feeding due to a loss of appetite approximately 1 month prior to spawning, and during ¾ of the individuals' spawning season (Fordham and Trippel, 1999; Skjæraasen et al., 2004), energy used for maintenance, behaviour and gonad development is fuelled by stored energy in muscle and liver (Dambergs, 1964; Krivobok and Tokareva, 1973; Black and Love, 1986; Kjesbu et al., 1991). Spawning therefore results in a major weight loss of 30-35% (Karlsen et al., 1995; Lambert and Dutil, 2000; Dahle et al., 2003), and the round weight measured in January is usually not regained until June (Karlsen et al., 2006b; Taranger et al., 2006) even though cod show a compensatory growth after spawning (Pedersen and Jobling, 1989). The actual losses depend on the diet, considering that the GSI is positively related to the dietary lipid content (Karlsen et al., 2006b). The mortality during spawning varies, but in captivity there seems to be a higher female mortality during spawning due to problems with irregular spawners in cod. Females in poor condition do not reduce their investment in reproduction, which increases the risk of mortality (Lambert and Dutil, 2000)

During maturation the cod drains energy from the muscle, which then contains less protein and more water (Kjesbu et al., 1991; Karlsen et al., 2006b), in particular at the end of the spawning season. The actual values for dry matter and protein content again depend on the diet (Karlsen et al., 2006b). Traditional quality assessment, using a trained sensory panel and texture analyses, did not reveal any differences between the spawning and the immature groups in June after the spawning season (Hemre et al., 2004).

Atlantic halibut

Somatic growth is strongly affected by maturation in Atlantic halibut (Norberg et al., 2001; Weltzien et al., 2003a). Maturing males tend to have very low, or even negative growth rates, and do not recruit new muscle fibres for growth, apparently directing all surplus energy into testes development and/or reproductive behaviour (Norberg et al., 2001; Weltzien et al., 2003a; Hagen et al., 2006). Information on the interplay between growth and puberty, and how this is regulated is scarce in this species. However, high Gh plasma levels were

demonstrated in mature male Atlantic halibut during annual cycles compared with mature females (Einarsdottir et al., 2002). This sex difference could indicate that the Gh levels are inversely correlated to growth in this species. Weltzien et al. (2003a) showed that Igf1 levels were correlated to growth during the period of slow growth in winter/spring in male Atlantic halibut, but not at other times of year, and there were no clear differences between immature and mature fish. In apparent contrast, Imsland et al. (2008) found a correlation between growth rates and plasma IGF-1 both in September and in March in juvenile halibut of both sexes. However, this correlation was stronger in March than in September, while growth rates were lower. Maturation results in significant changes in muscle texture and flesh quality in male Atlantic halibut (Roth et al., 2007). This was suggested to be caused by the slower growth of mature males, where no new muscle fibres are recruited (Hagen et al., 2006).

European sea bass

Most farmed sea bass populations show skewed sex ratios, with 74% or more males. Many of them (around 20-30%) reach puberty at one year of age (Carrillo et al., 1995). Although precocious males are significantly larger than the non-precocious ones during their first year of life (Begtashi et al., 2004), they show lower growth rates than their non-precocious counterparts during their second year (Felip et al., 2006) resulting in considerable economic losses to the fish farmer. A "critical" size and/or energetic status seem necessary for the appearance of precocious males, and individuals below these thresholds remain immature until the next reproductive season. Most male sea bass reach puberty in the second year of life by the time when they reach marketable size (400-500 g), and the growth depressing effect of puberty is more pronounced than in males maturing in their 1st year of life. Finally, growth cessation is observed at the end of the third annual cycle when also the females attain puberty. Thus, the reduction of the growth rate associated with puberty becomes progressively more marked with age in sea bass, partly due to increasing investments into maturation with age. Moreover, under intensive culture conditions a high proportion of the females can also reach puberty at two years of age (precocious females; Zanuy and Carrillo, unpublished results), which will affect somatic growth negatively in a similar way as in precociously mature male fish.

5 Internal and external determinants of puberty

5.1 Genetic factors and puberty

A range of studies, in particular in salmonids, have demonstrated the importance of genetic impact on age at puberty in fishes (e.g. Nilsson, 1992; Crandell and Gall, 1993; Hankin et al., 1993; Gjerde et al., 1994; Silverstein and Hershberger, 1995; Longalong et al., 1999; Su et al., 1999; Martyniuk et al., 2003). As an example, in farmed Atlantic salmon, large genetic differences were found both between strains and families with regard to the age of maturity (e.g. Nævdal, 1983; Gjerde and Gjedrem, 1984; Herbinger and Newkirk, 1990); the heritability of this trait was estimated to 0.48 by Gjerde (1984), and more recently to 0.15 by Gjedrem (2000). Strong response to selection for late maturity was also found in rainbow trout (Kause et al., 2003; 2005; Martinez et al., 2006; Ritola et al., 2007).

However, several studies have also shown genotype-by-environment interactions (GEI) on age at puberty, explaining a significant portion of the observed phenotypic variation (Saunders et al., 1983; Heath et al., 1994; Wild et al., 1994). This GEI can be described as genetically determined "reaction norms" defining how age and size at puberty change in response to changes in growth and environmental conditions (cf. Dieckmann and Heino, 2007; Hutchings and Fraser, 2008; Piche et al., 2008). Thus, in most species and strains, the inherited trait is not a fixed age and/or size at puberty, but an adaptive response that is

believed to maximize reproductive success and fitness as growth and mortality patterns change in natural populations (Stearns, 1992).

Moreover, genetic factors may have an indirect effect on age at maturity through other heritable traits, such as growth rate, size-at-age and energy stores. A range of studies, e.g. in salmonids, have demonstrated large genetic variation in muscle fat content (Gjerde and Schaeffer, 1989; Rye and Gjerde, 1996) and growth (Gjerde et al., 1994; Friars et al., 1995). Thus, genetic background may have indirect effect on age-at-puberty through its influence on these parameters. On the other hand, there are Atlantic salmon families that display high growth and late age at maturity (Gjerde et al., 1994), allowing for simultaneous selection of fast growing and late puberty (Gjedrem, 2000). Moreover in experimental studies with wild Atlantic salmon populations, strains with high age and size at puberty also display higher growth during the first year in seawater compared to strains with earlier maturity (Jonsson and Jonsson, 2007), suggesting that genetic factors for high growth rate and early puberty are not necessarily positively correlated.

5.2 Correlation between feeding, growth, energy allocation, adiposity and puberty

As in all vertebrates, puberty in fish occurs when individuals have reached a certain combination of age and size, and most likely also, have accumulated sufficient energy reserves (generally in the form of body fat) to meet the nutritional and energetic requirements of maturation. This is supported by evidence indicating a strong relationship between body growth rates and age of puberty in salmonids (e.g. McCormick and Naiman, 1984; Skilbrei, 1989; Rowe and Thorpe, 1990a,b; Thorpe et al., 1990; Silverstein and Shimma, 1994; Friedland and Haas, 1996; Friedland et al., 1996; Kadri et al., 1996; Duston and Saunders, 1999; Thorpe, 2004, 2007). In this context, it has been suggested that the onset of puberty in fish is linked to absolute levels or rates of accumulation of lipid stores (Rowe et al., 1991; Silverstein et al., 1997, 1998; Shearer and Swanson, 2000; Shearer et al., 2006). However, this relationship between growth/adiposity and onset of puberty is often complicated due to large plasticity in life-history strategies both within and between populations (Hutchings and Jones, 1998), and is further influenced by environmental signals (Taranger et al., 1999).

High growth rate and/or lipid storage under farming conditions often results in earlier onset of puberty than their wild counterparts as discussed above (cf. Thorpe, 2007). The interactions between the brain and peripheral signals which regulate appetite, growth, adiposity, and how they affect onset of puberty, have been studied extensively in mammals including the role of leptin (e.g. Zieba et al., 2005). By contrast, information of this type is very limited for fish. Adiposity appears to exert a negative feedback on appetite in fish (Shearer et al., 1997a,b; Silverstein et al., 1999; Johansen et al., 2001, 2002; Jobling et al., 2002). Based on this, and similar results in mammals, a lipostatic model was hypothesized for fish (Johansen et al., 2002), suggesting that adipose tissue participates in the regulation of feed intake through negative feedback signals to the brain. However, the mechanisms for such negative feedback are not yet known in fish, nor the precise impact of energy homeostasis and related endocrine signalling on puberty (see below for discussion of potential roles of leptin and ghrelin).

5.3 Impact of environmental factors

In fish species with marked seasonality of breeding activity, the reproductive cycle is controlled and synchronized by annual environmental variations in relation to local climatic and feed availability conditions. A range of environmental factors such as photoperiod, water temperature, rainfall, food availability, water quality and water level have been shown to synchronize the reproductive cycle with the seasonal cycle (reviews; Sumpter, 1990; Bromage et al., 2001). However, in temperate regions, photoperiod and/or temperature variations are

the main cues controlling the fish reproductive cycle. Such environmental cues and factors can be classified as proximate and ultimate factors. Proximate factors provide seasonal cues for reproduction whereas ultimate factors determine the optimal reproductive timing (often a combination of temperature conditions and optimal prey/feed availability for the offspring.

As an example, in the Atlantic salmon, winter water temperature can be considered as an ultimate factor determining the timing of spawning. This is again related to the timing of egg and larval development in the river, since number of day-degrees from fertilization to hatching and first feeding appears to be fairly constant across salmon populations, and hence the timing of gravel emergence and first feed intake that should take place at the optimal time in the spring which depends on when appropriate prey are available. The salmon then use photoperiod as a proximate cue to enable initiation and completion of sexual maturation and spawning at the appropriate time in the autumn/early winter. Different river populations of salmon show an adaption in spawning time associated with winter temperature with earlier spawning in winter-cold rivers enabling sufficient numbers of day-degrees for optimal hatching- and emergence-time next spring (Heggberget, 1988a,b). Thus, spawning time appears to be an inherited trait adapted to the average winter temperature conditions and/or optimal timing of emergence and first feeding of the offspring.

However, water temperature may also act as a proximate factor, probably fine-tuning timing of spawning between years, as high water temperature can arrest or delay ovulation and spermiation in Atlantic salmon (Taranger and Hansen, 1993; Taranger et al., 2003; King and Pankhurst, 2004; Vikingstad et al., 2008), whereas cold water can advance and/or allow spawning (Taranger and Hansen, 1993; Taranger et al., 2003; King et al., 2007; Vikingstad et al., 2008). A similar situation has been observed in the sea bass, a winter spawning marine fish (Carrillo et al., 1993; 1995)

5.3.1 Photoperiod

Photoperiod is regarded as a key environmental factor for initiation and completion of puberty in fish species living at moderate to high latitudes, ensuring the appropriate seasonal timing of reproduction according to favourable conditions for the offspring (Bromage et al., 2001). In salmonids, a decreasing proportion of fish were able to initiate or complete puberty within a given year when the seasonal timing of spawning was progressively advanced by photoperiod manipulations (e.g. Taranger et al., 1998; Bromage et al. 2001; Duston et al., 2003; Taylor et al., 2008). Based on a range of studies, it was suggested that photoperiod treatment act via entrainment of circannual endogenous rhythms controlling a "gating" mechanisms or a "critical time window" during which puberty is allowed to commence or continue depending on the physiological state of the animal (e.g. body size, adiposity and/or stage of gonadal development) or being postponed to the next reproductive season if the animal failed to exceed genetically determined developmental thresholds (Fig. 2; McCormick and Naiman, 1984; Thorpe, 1986, 2004, 2007; Duston and Bromage, 1987, 1988, 1991; Duston and Saunders, 1999; Randall and Bromage, 1998; Taranger et al., 1999; Bromage et al., 2001; Oppedal et al., 2006).

The role of different constant and changing photoperiods on entrainment of the seasonal timing of reproduction has also been extensively studied in salmonids and some perciforms, in particular in rainbow trout and sea bass, suggesting that the direction of change in photoperiod is more important than the absolute day-length, and that exposure to long days at a specific time period of the year in an otherwise short day regime is very effective in entraining the reproductive cycle (e.g. Bromage and Duston, 1986; Duston and Bromage, 1987, 1988; Carrillo et al., 1993, 1995; Randall and Bromage, 1998, Randall et al., 1988; 1998). Moreover, the role of the pineal and melatonin in transducing the photic information on the seasonal entrainment of physiological processes such as reproduction and

smoltification has been extensively studied in salmonids (Randall et al., 1995; Porter et al., 1996; Mazurais et al., 1999). While advancing photoperiods can reduce the proportion of salmonids entering into puberty in a given year, e.g. by a change from short to long days in winter or early spring (Randall et al., 1988; Taranger et al., 1998), prolonged exposure to long days or continuous light, or exposure to long days or continuous light after summer solstice can have the opposite effect by increasing the proportion of fish recruiting into puberty (Duncan et al., 1999; Oppedal et al., 2006).

It has been demonstrated that continuous light (24L:0D or LL) or long day treatments can inhibit or delay onset of puberty in several fish species (Fig. 2). In European sea bass, constant long days of short duration (i.e. 1-2 months) applied in a regime with otherwise constant short days can advance spawning time if applied before summer solstice, whereas constant long days applied after summer solstice delay spawning, providing solid evidence that reproduction can be entrained by the photoperiod in this species (Carrillo et al., 1993, 1995). Moreover, LL treatments applied over the entire reproductive cycle (12 months), during the pre-gametogenesis (4 months), or during the gametogenesis (6 months) were all effective in reducing the number of early maturing males in sea bass (Begtashi et al., 2004; Felip et al., 2008a). Similar effects were observed in grey mullet (O'Donovan-Lockard et al., 1990), Atlantic cod (Hansen et al., 2001; Davie et al., 2003; Karlsen et al., 2006a; Davie et al., 2007b), Eurasian perch (Migaud et al., 2006) and haddock (Davie et al., 2007a). However, in the Atlantic cod, the inhibitory effect of LL depends on the timing of its initial application (Hansen et al., 2001; Davie et al., 2003). Interestingly, in grey mullet, both continuous light and continuous darkness inhibits gonad development (O'Donovan-Lockard et al., 1990).

Recently, it was also demonstrated that application of constant long days can inhibit the onset of the reproductive cycle in Eurasian perch. Eurasian perch maintained at a constant and long photoperiod (17L:7D) from the juvenile stage (2g) did not respond to a water temperature decrease, while both males and females showed normal gonad development under a similar temperature decrease when combined with a one, four or eight hour photoperiod decrease (Abdulfatah et al., 2007). Such inhibitory effects of constant and long photoperiods has also been observed in yellow perch (*Perca flavescens*) under a 14L:10D photoperiod (Shewmon et al., 2007). These results are in line with previous studies that suggested that a photoperiod decrease is necessary for induction of the reproductive cycle in other perciform species (Zanuy et al., 1986, 1995; Mañanós et al., 1997; Wang et al., 2006). By contrast, Migaud et al. (2003, 2004) observed only a partial inhibition of reproduction in female Eurasian perch when a constant photoperiod (16L:8D) was applied from mid-July. However, the fish were introduced into tanks mid-June and were subjected to a natural photoperiod during the corresponding one month long acclimatization phase. Therefore over this time period, the fish received a one hour photoperiod decrease which may have been sufficient to trigger reproductive development.

The observed inhibitory effects of constant photoperiods may also depend on the photophase duration (e.g. O'Donovan-Lockard et al., 1990). Total inhibition of reproduction was observed under a constant long photoperiod (17L:7D), while only a partial inhibition was observed when a shorter constant photoperiod (12L:12D) was applied (Migaud et al., 2002, 2004). On the other hand, in sea bass there is evidence that the direction of change of the photoperiod (i.e. from long to short) is more important than the absolute values of the photoperiod decrease in determining the onset of gonadal recrudescence (Carrillo et al., 1993, 1995).

Moreover, in three species of mid-spring/early summer spawners, barbel (*Barbus barbus*), tench (*Tinca tinca*) and chub (*Leuciscus cephalus*), Poncin et al. (1987) showed that a photoperiod decrease inhibited pubertal development, suggesting some species specific responses to photoperiod changes. Also a recent study on Eurasian perch demonstrated that a

3-hour photoperiod increase from 13L:11D to 16L:8D applied two weeks before the application of an efficient inductive program inhibited onset of the reproductive cycle (Fontaine et al., 2006). These results indicate that the photoperiod history before the application of a certain photo-thermal inductive program is a major factor in the induction of the pubertal development.

5.3.2 Temperature

Water temperature plays an important role in teleost fish because it can modulate all physiological processes and endocrine regulations. Temperature can potentially affect puberty by modulating the rate of gametogenesis, or allow or inhibit gametogenesis to proceed beyond certain stages and/or being completed, e.g. as indicated in European sea bass (Prat et al., 1999, Zanuy et al., 1986; Mañanós et al., 1997a). Moreover, water temperature can also affect onset of puberty indirectly by its effects on somatic growth and energy storing as discussed above.

Although temperature appears to play a minor role in the proximate control of the reproductive cycle of salmonids (e.g. Bromage et al., 2001; Davies and Bromage, 2002), it is often considered as key-factor in cyprinids (Peter and Yu, 1997). Also in percids and moronids, a decrease of temperature was found to induce the reproductive cycle (Dabrowski et al., 1996; Prat et al., 1999; Migaud et al., 2002; Clark et al., 2005). However, this positive response of temperature could depend on the constant photoperiod applied in these studies, as suggested by contradictory results obtained in Eurasian perch (Migaud et al., 2002; Abdulfatah et al., 2007). On the other hand, in Eurasian and yellow perch, almost all data suggest that gonadal recrudescence occurs only when temperature decreases after, or at the same time as the decrease of photoperiod, and in Eurasian perch the amplitude of the initial temperature decrease was found to play an important role for the induction of reproductive development (Dabrowski et al., 1996; Ciereszko et al., 1997; Migaud et al., 2002, 2004; Shewmon et al., 2007; Wang et al., 2006, 2008).

Moreover, a series of studies demonstrate that maturation and/or ovulation can be inhibited when temperature exceed a certain threshold; i.e. ≥ 6ºC for Atlantic halibut (Brown et al., 1995); ≥ 8ºC for Arctic charr (Gillet 1991); ≥10ºC for Pacific herring (Hay, 1986); ≥ 12ºC for Atlantic salmon (Taranger and Hansen, 1993); ≥ 15ºC for white sturgeon and rainbow trout (Pankhurst et al., 1996; Webb et al., 1999); ≥ 17 ºC for sea bass (Zanuy et al., 1986) and ≥ 28 ºC for grass carp (Glasser et al., 2004). All of these results suggest that temperature can act as a permissive factor, particularly during the final stages of gonadal maturation and at spawning.

5.3.3 Other factors (salinity, raining period, swimming exercise, social factors…)

Other types of control of reproduction (environmental or not) in fish obviously exist, but they have been far less studied. The case of the eels, *Anguilla spp.* is particular since these species have a very long life cycle from 8 to 20 years (van Ginneken and Maes, 2005). They reproduce only once after a long migration and the control of reproduction in these species is far from clear, although a period of prolonged swimming might be a physiological stimulus necessary for the onset of puberty in the European eel (Palstra et al., 2007; Sebert et al., 2007; van Ginneken et al., 2007a). Moreover, other factors like salinity (Saunders et al., 1994), water level/raining periods (Duarte et al., 2007) or social communication, e.g. by pheromones (Burnard et al., 2008), may also be of importance for puberty onset and/or completion in some fish species. As an example it has been shown that sexually mature European eels stimulate gonadal development in neighbouring males, which may be due to chemical communication (Huertas et al., 2006; 2007, 2008).

6 Neuroendocrine control of puberty

6.1. Activation of BPG axis during puberty

Reproductive competence is acquired during puberty. Hallmark events include enhanced gonadotropin secretion, and complete gonadal maturation and functioning (Ojeda et al., 2006). Prior to the full activation of the pituitary and gonads, a series of developmental and neuroendocrine events paves the way to full activation of the Gnrh system. This neuroendocrine system is dynamically integrating central, peripheral, and environmental information, which then reaches the pituitary via Gnrh neurons (Ojeda and Skinner, 2005; Ojeda et al., 2006).

The onset of puberty in vertebrates is marked by a (re-) activation of hypophysiotropic Gnrh neurons that stimulate pituitary gonadotropin release, triggering pubertal development of the gonads. Until recently, it has not been known what controls the activation of Gnrh neurons. However, pharmacological and clinical data obtained in mammals, strongly suggest that kisspeptins, the peptide products of the *kiss-1* gene, and their receptor (Gpr54) constitute an essential gatekeeper of Gnrh functions, allowing the integration of central and peripheral inputs (Tena-Sempere, 2006; Roa et al., 2008).

Recently, the cloning of *gpr54* and *kiss-1* sequences, and the anatomical distribution of *kiss-1* mRNA expressing neurones in the brain have been identified in several teleosts (Carrillo et al., 2008c; Elizur 2008, Felip et al., 2008b,c; Kah et al., 2008; Mechaly et al., 2008; Nocillado and Elizur, 2008). These studies support the notion that the Kiss-1/Gpr54 system is well-conserved in vertebrate evolution, not only in adults but also during pubertal development, as suggested by changes in *kiss* gene expression during puberty in fathead minnow males and females (Filby et al., 2008). Moreover, *kiss* mRNA expressing neurons in the preoptic area and the mediobasal hypothalamus were sensitive to steroid treatment in medaka (Kanda et al., 2008). It has also been proved in sea bass that two *kiss-1*-like genes exist in this species. Both genes show a marked expression in the brain and gonadal tissues of pubertal sea bass. Functional activity of the two *kiss-1*-like genes has been examined in vivo and the results show that both Kisspeptins stimulated Lh and Fsh secretion, although Kiss2 induces a stronger response than Kiss1 (Felip et al., 2008b). Likewise, two *gpr54* (*kiss1r*) genes have been characterized in sea bass, and their tissue expression analysis revealed that both are mainly expressed in brain, pituitary and testis (Carrillo et al., 2008c). Although more information on the physiological effects of Kiss1/Kiss2 in fish, notably on Gnrh neurons and gonadotropin release is needed, it is expected that future studies will point to a high conservation of the Kiss/Gpr54 system between fish and mammals (Nocillado and Elizur, 2008), possibly representing an integration of various internal (e.g. sex steroid feedback and nutritional homeostasis signalling) and external factors (e.g. photoperiod) on puberty onset in fishes.

The Gnrh system has been extensively investigated during puberty in sea bass. Rodríguez et al. (2000b) reported high to moderate levels of Gnrh1 and Gnrh3 in the pituitary at the onset of puberty. Later, three different *gnrh* cDNAs were characterized in the brain of sea bass: *gnrh1* (*sbgnrh*), *gnrh2* (*cgnrh-II*), and *gnrh3* (*sgnrh*) (González-Martínez et al., 2001, 2002a,b, 2004a,b), of which Gnrh1 and 3 are considered as the main hypophysiotropic isoforms. In addition, five *gnrh* receptors have been cloned and characterized in sea bass, all of them being functional and all showing highest binding affinity for Gnrh2. However, only one of these receptors (dlGnrhr-II.1a), which is strongly expressed by the pituitary Lh cells and also by some Fsh cells, showed affinity for Gnrh1 and Gnrh3 (Kah et al., 2007). Interestingly, it was previously demonstrated that the expression of this receptor increases as the sea bass enters puberty (González-Martínez et al., 2004a). Recently, Molés et al. (2007) showed that pituitary *dlgnrhr-II.1a* gene expression increased in parallel with the brain *gnrh1*

mRNA levels during sex differentiation and the anticipated puberty period. Collectively, these data suggest that Gnrh1 and dlGnrhr-II.1a are most relevant for the onset of puberty in sea bass.

Long-term Gnrha release delivery systems also induce long-term release of Lh in male sea bass (Mañanós et al., 2002). Pretreatment of immature adult sea bass with T and E2 followed by injections of Gnrha stimulated *lhβ* and *gpα* subunit mRNA, but not *fshβ* gene expression (Mateos et al., 2002). However, a peak of pituitary *fshβ* gene expression was observed during sex differentiation, simultaneously with the aforementioned peak in brain (Molés et al., 2007). Taken together, this opens the possibility that activation of the brain Gnrh system triggers both, sex differentiation and the onset of puberty in sea bass, possibly via Fsh, while increased expression of *lhβ* subunit may be more prominent at later stages of development.

In addition to the stimulatory control by Gnrh, anatomical and physiological investigations have shown that gonadotropes can be subjected to an inhibitory control by dopamine. Pioneer works by Richard E. Peter and co-workers identified dopamine as the main inhibitor of ovulation and spermiation in goldfish (Peter et al., 1978; Chang and Peter, 1983; Kah et al., 1987). Following the initial discovery in goldfish, the inhibitory role of dopamine was confirmed in various adult teleosts, including other cyprinids (Lin et al., 1988), silurids (De Leeuw et al., 1986), salmonids (Saligaut et al., 1999), and some percomorphs (Yaron et al., 2003; Aizen et al., 2005). Dopamine inhibits both basal and Gnrh-stimulated Lh expression and release in these species, for instance through down-regulation of Gnrh receptor levels (receptor binding activity, De Leeuw et al. 1989; receptor mRNA expression (Levavi-Sivan et al., 2004), and intracellular signalling pathways of gonadotropes following binding of Gnrh (reviews; Peter et al., 1986; Yaron et al., 2003).

While the role of dopamine in the regulation of ovulation and spermiation has been established in adults in a certain number of teleost species, there is no evidence for a similar inhibitory role at the beginning of puberty in most teleosts. Indeed, the observation in many species that E2 increases the inhibitory tone during vitellogenesis, suggests that dopamine inhibition is an adult-specific control of the last steps of gametogenesis. Accordingly, results obtained in juvenile striped bass, indicate that dopamine is not involved in the control of puberty in this species, since the dopamine antagonist pimozide did not affect the changes in pituitary or plasma Lh levels induced by T and/or Gnrha (Holland et al. 1998). Similar results were obtained in another percomorph fish, where Gnrha alone induced precocious puberty, and no further effect was observed using a dopamine antagonist (Kumakura et al., 2003). In rainbow trout precocious puberty could be induced using a combination of Gnrha and steroids (Crim and Evans, 1983); a dopamine antagonist was not required. On the other hand, dopamine might play an inhibitory role in the control of puberty in the spadefish, where Marcano et al. (1995) found a decrease in dopaminergic metabolism in hypothalamus at the initiation of puberty, although a causal link has not been established yet.

Functional evidence for a role of dopamine in the inhibitory control of puberty was first provided in the European eel, a species with a unique life cycle including a long-lasting juvenile stage during the continental period. Dopamine plays a key role in the inhibitory control of eel puberty onset: In female (prepubertal) silver eel, only a triple treatment with Gnrha, pimozide and steroid (T or E2) is able to trigger an increase in Lh synthesis and release, and subsequent vitellogenin production (Dufour et al., 1988; Vidal et al., 2004). Preventing silver eel from completing their downstream migration towards the ocean will keep them in pubertal arrest. This shows that one or several environmental cues encountered during the migration route are necessary to release the dopaminergic lock on puberty. Recent studies demonstrated that melatonin regulates the activity of the eel dopaminergic system, revealing a new pathway for the integration of environmental effects on the gonadotropic axis

(Sebert et al., 2008b). For details on the nature of dopamine inhibition on eel puberty, including physiology, anatomy, and regulation by internal and environmental factors, see recent works by (Dufour et al., 2003; 2005; Vidal et al., 2004; Pasqualini et al., 2004; 2009; Weltzien et al., 2005a,b; 2006; Aroua et al., 2007; Sébert et al., 2007; 2008a,b).

Comparative studies in eel and striped bass, using similar experimental conditions, highlighted the specific strength of the dopaminergic inhibition of puberty in eel, as compared to its apparent lack of involvement in the striped bass (Holland et al., 1998b; Vidal et al., 2004). Recently, Aizen et al. (2005) provided evidence that dopamine inhibition may be involved in the early stages of vitellogenesis in grey mullet, indicating that puberty can be under dopaminergic control in various teleost species.

Regarding gonadotropin participation, the relative importance of Fsh or Lh has been studied in a range of teleost species during initiation and completion of puberty, most notably by studying gene expression of *fshβ* and *lhβ* subunits in the pituitary (Sohn et al., 1998a,b; 1999; 2001; Gomez et al., 1999; Hassin et al., 1999; 2000; Jackson et al., 1999; Melamed et al., 2000; Kajimura et al., 2001a,b; Yaron et al., 2001; 2003; Mateos et al., 2002a; Ishii et al., 2003; Mateos et al., 2003; Onuma et al., 2003; Weltzien et al., 2003b,c; Kumar and Trant, 2004; Meiri et al., 2004; Schmitz et al., 2005; Choi et al., 2005).

Among the teleosts, homologous immunoassays for both Fsh and Lh have until recently only been developed for salmonids such as chum salmon (Suzuki et al., 1988), coho salmon (Swanson et al., 1991) and rainbow trout (Fsh and Lh; Govoroun et al., 1998, Fsh; Santos et al., 2001), while ontogeny and quantification of Fsh in non-salmonids have relied on the expression levels of *gth* subunit genes in the pituitary. Lh immunoassays have been developed for tilapia (Bogomolnaya et al., 1989), European eel (Dufour et al., 1983), hybrid striped bass (Mañanós et al., 1997b), red sea bream (Tanaka et al., 1993), silver carp (Kobayashi et al., 1985), goldfish (Kah et al., 1989), African catfish (Koide et al., 1992) and European sea bass (Mateos et al., 2006). Recently, homologous ELISAs were developed for both Fsh and Lh in tilapia using recombinant gonadotropins (Aizen et al., 2007).

Taken together, the expression data of gonadotropin subunits and plasma gonadotropin studies suggest that Fsh is mainly involved in gametogenesis in both sexes, whereas Lh is mainly involved in final maturation and ovulation and spermiation and sperm hydration. However, the relative importance of Fsh and Lh in gametogenesis and spawning can differ between species, e.g. Lh levels may be elevated also at stages before spawning in perciforms (Swanson et al., 2003; Yaron et al., 2003, Yaron and Sivan, 2006). On the other hand, studies focusing on puberty onset suggest that Fsh signalling is more important in the early stages of puberty, most notably associated with rapid spermatogonial proliferation in males and secondary oocyte growth including vitellogenesis and zonagenesis in females (e.g. Hassin et al., 1999; Campbell et al., 2006; Manning et al., 2008; Felip et al., 2008; Moles et al., 2007; 2008; see also the discussion on gonadotropin receptor expression sites).

The two gonadotropin receptors, Fshr and Lhr have been characterized in several teleost groups including *Salmoniformes* (Oba et al., 1999a,b; Maugars and Schmitz, 2006; Andersson et al., submitted), *Gadiformes* (Mittelholzer et al., 2009), *Cypriniformes* (Basu and Bhattacharya, 2002; Laan et al., 2002; Kwok et al., 2005), *Siluriformes* (Bogerd et al., 2001; Kumar et al., 2001a, b; Vischer and Bogerd, 2003) *Pleuronectiformes* (Kobayashi et al., 2008a,b), *Anguilliformes* (Jeng et al., 2007; Kazeto et al., 2008), and *Perciformes* (Oba et al., 2001; Wong et al., 2004; Rocha et al., 2007, 2008). The hormone binding specificity of the gonadotropin receptors studied in zebrafish (Kwok et al., 2005; So et al., 2005), channel catfish (Kumar et al. 2001), Japanese eel (Kazeto et al., 2008), and African catfish (Bogerd et al., 2001; Vischer and Bogerd, 2003; Vischer et al., 2003), have indicated that Fshrs show a preference for Fsh but also respond to high (e.g. ovulatory) concentrations of Lh, while Lhrs specifically respond to Lh. Recently, pharmacological studies showed also that the Atlantic

salmon follow this pattern (Andersson et al., submitted), which is in agreement with earlier ligand binding data from coho salmon gonad tissue (Yan et al., 1992; Miwa et al., 1994). However, in amago salmon (Oba et al., 1999a,b), rainbow trout (Sambroni et al., 2007) and Atlantic halibut (Kobayashi et al., 2008b), receptor activation studies suggested that the Lhr, but not the Fshr responded to both gonadotropins, indicating some species differences.

The *fshr* and *lhr* show different expression profiles during the seasonal reproductive cycle and pubertal development in amago salmon (Oba et al., 2000) and channel catfish (Kumar and Trant, 2001). In the gonads of channel catfish, both *fshr* and *lhr* transcripts are expressed in a stable fashion, except for an increase of *lhr* during spawning, and of *fshr* during a 2–3 months long post-spawning period. In amago salmon and tilapia, the *fshr* is highly expressed early in the reproductive cycle, whereas the *lhr* reaches its maximum expression level around spawning (Hirai et al., 2000; Oba et al., 2000). Studies in Nile tilapia, zebrafish and Atlantic cod indicate that *fshr* expression is associated predominantly with vitellogenesis, while the *lhr* is mainly up-regulated during final oocyte maturation and ovulation (Hirai et al., 2002; Kwok et al., 2005; Mittelholzer et al., 2009). Also, Luckenbach et al. (2008) found that ovarian *fshr* expression increased significantly already at the cortical alveoli stage in female coho salmon. Furthermore, in Japanese eel, ovarian *fshr* mRNA level was significantly higher than that of *lhr* in immature previtellogenic female eels (Jeng et al., 2007). These data suggest that Fsh signalling is most important during pubertal onset. This notion is further strengthened by the observations in male fish that Fsh and 11KT plasma levels increases in association with rapid spermatogonial proliferation (Campbell et al., 2003; Moles et al., 2007, 2008), and that in Japanese eel (Ohta et al., 2007) and African catfish (Garcia-Lopez et al., 2008), Fsh is potent stimulator of androgen production, mediated by Fshr expression by Leydig cells.

Pubertal activation of steroidogenesis in gonads

In most species, precocious puberty is a problem that is particularly prominent in males. Moreover, in males the causal relationship between Fsh-stimulated androgen production and the shift from the slow proliferation of A type spermatogonia to the rapid proliferation of B type spermatogonia has been demonstrated. The following section will therefore focus on the pubertal activation of steroidogenesis in gonads only in males.

11KT is the major androgen produced in the testicles of teleost fish, it stimulates the Sertoli cells to produce growth factors and promotes spermatogonial proliferation leading to meiosis and later stages of spermatogenesis (Miura et al., 1991). It has also been suggested that the 11KT may have a positive feedback on *sbgnrh* expression levels in the brain of some teleosts (Okuzawa, 2002). In sea bass, various lines of evidence show that 11KT is likely to trigger the onset of puberty (Rodriguez et al., 2005). In prepubertal males, 11KT induced spermatogenesis and exogenous 11KT (not T) administered to LL (continuous light) exposed fish rescued active spermiogenesis and induced increases of pituitary *lhβ* gene expression and pituitary and plasma Lh levels (Carrillo et al., 2007).

The juvenile testis of a number of fish species is characterised by a rather high production of androgens per weight unit (Schulz and Blüm, 1990; Consten et al., 2001): specific androgen release (i.e. release per weight unit) decreases with the start of pubertal testis growth, to increase again when approaching adulthood. We assume that immature testes show a high specific androgen release because Leydig cell density is relatively high before but becomes "diluted" after germ cell numbers increase following the start of spermatogenesis. This phenomenon has been studied in African catfish. In this species, the Lhr shows a constitutive activity, but still is clearly sensitive to Lh (Vischer and Bogerd, 2003). Leydig cells in the juvenile catfish testis already show all ultrastructural signs of fully active steroidogenic cells (Cavaco et al., 1999). Interestingly, Leydig cells produce a

biologically inactive androgen, 11β-hydroxyandrostenedione (OHA), which is released into the blood and converted to 11KT in the liver (Mayer et al., 1990; Cavaco et al., 1997), the main androgen in adult male fish (Borg, 1994). At the start of puberty, two things happen concomitantly. Rapid testis growth starts reflecting mainly an increase in germ cell number, thereby reducing the OHA release per mg of tissue (Schulz et al., 1996). However, also Leydig cells proliferate during rapid testis growth (Schulz et al., 2005), which may explain the increase in total testicular androgen output and increasing plasma androgen levels that typically accompany puberty (Schulz et al., 1994). Another level of regulation is exerted via androgen-mediated inhibition of the steroidogenic capacity of the testis (Cavaco et al., 1999), reducing the number of mitochondria and the cell surface in Leydig cells along with a reduced capacity to produce androgens via an impairment of the 17-20 lyase activity. Both T and 11KT exert these effects in juveniles, while during pubertal maturation, the inhibitory effects of 11KT, but not T, fade out (Schulz et al., 2008), which might be a mechanism to allow increased production of 11KT, the main androgen, without compromising Leydig cell function. The molecular basis for this observation remains to be elucidated.

Also in rainbow trout (Schulz and Blüm, 1990), specific androgen release was highest in juveniles. While initially the two main 11-oxygenated androgens released, 11KT and 11β-hydroxytestosterone (OHT), were produced in similar amounts (with 11KT > OHT), OHT was exceeding the release of 11KT when maximum GSI levels were present during full spermatogenesis. This reverted back to 11KT being the main androgen released in spawning animals, before the post-spawning associated reduction in androgen release started. This suggests that testicular expression of the enzyme responsible for the conversion of OHT -> 11KT, 11β-hydroxysteroiddehydrogenase, would increase specifically when approaching the spawning season. Indeed, (Kusakabe et al., 2003) described an increase in the expression of this enzyme when the GSI levels started to decrease from maximum levels towards the spawning season. On the ultrastructural level, trout Leydig cells were present before the start of spermatogenesis but full functional maturity developed slowly and was attained in mature males (Loir et al., 1995). Enzyme histochemical approaches also suggested a gradual development of Leydig cell functionality (van den Hurk et al., 1978). The main changes in testicular expression of genes associated with steroidogenesis as well as expression of gonadotropin receptors were recorded when the first spermatozoa were observed in the testis (Kusakabe et al., 2006), suggesting that the initial steps of puberty, i.e. the switch to rapid spermatogonial proliferation may depend on changes in the plasma levels of gonadotropins.

Consten et al. (2001) showed that immature carp testes produced mainly 11-ketandrostenedione (OA), which switched to 11KT during puberty. This suggested that 17β-hydroxysteroid dehydrogenase activity might be limiting 11KT production in the immature testis. In another cyprinid species, the zebrafish, the adult testis produces relatively high amounts of OA as well, and it has been suggested that expression of a testicular 17β-hydroxysteroid dehydrogenase isoform may increase during zebrafish puberty (de Waal et al., 2008). This enzyme activity is also present in blood cells of several species (Schulz, 1986; Mayer et al., 1990) but depends, of course, on the provision of substrate, probably from the testis.

Taken together, it appears that puberty-associated testis growth, including a certain proliferation also of Leydig cells as well as their functional differentiation (e.g. increase in expression of key-enzymes), form the basis for the increased testicular androgen production, and hence increasing circulating androgen levels that accompany male puberty. Depending on the species, the regulatory input triggering these changes is either Fsh alone (e.g. salmonids, eel, sea bass), or Fsh and Lh (e.g. Nile tilapia; see previous section on gonadotropins and their receptors). Steroid-mediated inhibitory effects may prevent Leydig cell hyperactivity at initial

stages of puberty, while the selective loss of 11KT-mediated inhibition may allow the specific increase of the production of this androgen.

Gonadal feedback to brain and pituitary

Castrating juvenile African catfish did not change the amount of the hypophysiotropic (catfish) GnrhI while treatment with T or E2, but not with 11KT, did increase GnrhI content in the pituitary (Dubois et al., 2001; Dubois et al., 2002). Also the number of GnrhI producing neurones increased under T treatment, prematurely reaching, but not surpassing, adult levels (Dubois et al., 2001). This suggests that (i) a predetermined but partially dormant number of GnrhI neurones exists before puberty and can be awakened by T treatment in terms of GnrhI synthesis, and that (ii) the status quo levels of GnrhI do not depend on the presence of the juvenile gonads. However, increased pituitary GnrhI levels can also, at least in part, be explained by an accumulation of GnrhI, possibly reflecting a steroid-mediated inhibition of GnrhI release. In this context, it is interesting to note that the amount of Lh in the pituitary decreases within 2 weeks after castration of 10 week old catfish and can be rescued by treatment with T (and E2 but not 11KT) (Cavaco, 2005). This shows that removal of aromatiseable androgens were responsible for the decrease in Lh. Since also in castrated fish the Lh amount increased above start control levels to a certain degree, a gonad-independent pathway stimulating Lh synthesis might exist, possibly involving a Gnrh-mediated effect. However, plasma Lh levels had not increased 2 weeks after castration in juvenile catfish while T treatment did reduce plasma Lh levels (Cavaco et al., 2001a), suggesting that the juvenile gonad does not produce sufficient amounts of steroids to exert a negative feedback on Lh release.

In gonad-intact, immature Atlantic salmon male parr, the response to T treatment depended on the dose, low doses being stimulatory, high doses being inhibitory to gonad growth and plasma sex steroid levels (Berglund et al., 1995a). However, these long-term experiments were not designed to investigate short-term effects on the initiation of puberty. Using gonad-intact juvenile male African catfish, 11KT treatment stimulated gonad growth and spermatogenesis, probably via a direct stimulatory action on the testis. Interestingly, however, co-treatment with 11KT and T abolished the stimulatory effect of 11KT on spermatogenesis (Cavaco et al., 2001b). It appears that gonadal steroids are required on the one hand to promote the functional development of the Gnrh neurones and the build-up of pituitary Lh stores, while they suppress testicular steroidogenesis or 11KT-stimulated spermatogenesis. Under these circumstances, a signal from outside of the pituitary-gonad feedback system on the Gnrh/gonadotroph may have to break the deadlock. Future studies will have to show if the Kiss1-producing neurones play this role and activate the reproductive system in prepubertal fish, as has been shown for the initiation of puberty in mammals, and as has been suggested for fathead minnow (Filby et al. 2008) and zebrafish (Biran et al., 2008). In this case, expression of Kiss and/or of its cognate receptor Gpr54 are possible targets of the steroid feedback that would then be conveyed to the Gnrh neurones, and eventually to the pituitary, as has been reported for some mammalian species (Ojeda et al., 2006; Ojeda et al., 2008).

After unilateral ovaryectomy of rainbow trout (Tyler et al., 1997), a drop of plasma E2 but a rise of plasma Fsh levels was recorded, which was associated with recruiting an additional batch of follicles into maturation. It would be interesting to examine if this recruitment activated oocytes before or after they entered the lipid vesicle stage, the hypothesis being that the first pituitary-dependent stage (i.e. lipid vesicle stage) would have been the one induced by the rising Fsh levels.

6.2. Growth and adiposity related endocrine factors

The relationship between body weight and fertility that integrates body weight and food intake as puberty initiating factors has been known for decades in mammals. However, only recently, peripheral signals and neuroendocrine networks that integrate energy balance and reproduction are being identified (Fernandez-Fernandez et al., 2006).

Cloning of mammalian leptin in 1994 was a major breakthrough to understand the mechanisms underlying reproduction and metabolism. Leptin secreted by white adipose tissue, is considered as a satiety factor in the regulation of body weight in mammals. Leptin has also a role in the control of reproduction by its action in the hypothalamus involving Gnrh release, which in turn, regulates pulsatile Lh secretion, suggesting that leptin may play a permissive role in the onset of puberty in mammals (Tena-Sempere and Barreiro, 2002). In teleost fish, leptin characterization is very recent, i.e. in puffer fish (Kurokawa et al., 2005; Yacobovitz et al., 2008) and in rainbow trout (Murashita et al., 2008). Physiological evidences for involvement of leptin in the regulation of the reproductive function in teleosts came from observations that mammalian leptin stimulated the release of luteinizing hormone (Peyon et al., 2001) and somatolactin (Peyon et al., 2003) in sea bass, and that high concentration of human leptin stimulated in vitro release of pituitary Fsh and Lh in female rainbow trout (Weil et al., 2003). In the ayu (Nagasaka et al., 2006) a clear correlation between Ir-Leptin values, rising levels of E2 and an increase of prolactin secretion at maturity was found. The recent availability of recombinant leptin (Kurokawa et al., 2005; Yacobovitz et al., 2008; Murashita et al., 2008) in some teleost species will help to enlighten the likely participation of this hormone in the control of puberty in fish.

Ghrelin, a hormone secreted by the stomach as signal of energy insufficiency, has been proposed as functional antagonist of the effects of leptin on energy balance in fishes (Kaiya et al., 2003), and the role of ghrelin in non-mammalian vertebrates has recently been reviewed by Kaiya et al. (2008). Ghrelin links food intake and the Gh-Igf1 system by stimulating Gh-secretion (Kaiya et al., 2003, 2008). Ghrelin has been identified in several teleosts including goldfish (Unniappan et al., 2002), eel (Kaiya et al., 2003b), Mozambique tilapia (Kaiya et al., 2003c), Nile tilapia (Parhar et al., 2003), rainbow trout (Kaiya et al., 2003a), channel catfish (Kaiya et al., 2005), sea bream (Yeung et al., 2006), European sea bass (Terova et al., 2008) and zebrafish cf. (Olsson et al., 2008). Moreover, Ghrelin receptor (Ghsr) has been found in two teleost species; black sea bream (Chan and Cheng, 2004; Chan et al., 2004) and a pufferfish (Palyha et al., 2000). Ghrelin was found to stimulate food intake in goldfish (Unniappan et al., 2002; Unniappan et al., 2004; Unniappan and Peter, 2005; Matsuda et al., 2006a; Matsuda et al., 2006b), Mozambique tilapia (Riley et al., 2005) and rainbow trout (Shepherd et al., 2007). By contrast, (Jonsson et al., 2007) found no effect of trout ghrelin on food intake in two-year-old rainbow trout. Ghrelin may also have direct effects on the reproductive axis as ghrelin was found to stimulate Lh release and *lhβ* mRNA expression in pituitary cells in goldfish (Unniappan and Peter, 2004), indicating direct actions of ghrelin on goldfish gonadotrophs. This suggests that ghrelin may have an important role in regulating appetite and growth, and potentially affecting puberty onset in fish, either by direct effects on the reproductive axis – or indirectly via controlling appetite and/or energy storage.

There is also evidence for a role of the growth hormone/insulin like growth factor 1 (Gh-Igf1) system in control of gonadal growth and development in fish, either by direct action of Gh or Igf1 on the gonads, or indirectly by effects on the gonadotropes (cf. Le Gac et al., 1993; Björnsson et al., 1994, 2002; Björnsson, 1997; Jalabert et al., 2000). Gh receptor has been identified in gonads of several teleosts (e.g. Gomez et al., 1999; Kajimura et al., 2004), and Gh has been shown to stimulate or modulate gonadal steroid production (Young et al., 1983; Singh et al., 1988; van der Kraak et al., 1990; Le Gac et al., 1992; Singh and Thomas, 1993). Igf1r is expressed in gonads, and there is locally produced Igf1 (Gray et al., 1990;

Sakamoto and Hirano, 1991; Yao et al., 1991; Gutierrez et al., 1993; Gomez et al., 1999; Gioacchini et al., 2005). Igf1 and Igf2 has been shown to increase during oocyte maturation in rainbow trout (Bobe et al., 2003; 2004), and the Igf binding proteins in oocytes are modulated by stimulation of 17,20βP and gonadotropins (Kamangar et al., 2006).

Igf1 has direct effect in the gonads (e.g. Le Gac et al., 1993; Kagawa et al., 1994; Weber and Sullivan, 2000; Weber et al., 2007). Moreover, plasma Igf1 levels can modulate hypothalamic Gnrh release and subsequent pituitary gonadotropin secretion (Huang et al., 1999; Baker et al., 2000; Schmitz, 2003), providing a possible link between the growth and reproductive axes. Recently, Furukuma et al. (2008) showed that Igf1 stimulated gonadotropin subunit expression in a dose-dependent manner in primary pituitary cells early in gametogenesis in masu salmon males, but not in the later stages. In females, Igf1 also stimulated release of Fsh and Lh early in gametogenesis, but did not stimulate gonadotropin subunit expression at any stage. These results suggest that Igf1 directly stimulates synthesis and/or release of Gth early in gametogenesis in masu salmon, possibly acting as a metabolic signal that triggers the onset of puberty, but apparently with some gender specific effects.

The pituitary hormone somatolactin (Sl) may also affect reproductive function in fish. Sl levels were found to increase in parallel with final gonadal growth in salmonids (Rand-Weaver et al., 1992; Rand-Weaver and Swanson, 1993), and were higher in mature rainbow trout and chinook salmon than in immature individuals (Rand-Weaver and Swanson, 1993; Rand-Weaver et al., 1995). Moreover, *sl* mRNA expression was enhanced by sexual maturation in chum salmon (Taniyama et al., 1999), and both *slα* and slβ transcripts were found to increase in pituitaries before and during spawning in Atlantic salmon females and the SL receptor was highly expressed in the ovaries (Benedet et al., 2008). Also, the somatolactotrophs were found to be activated in sexually maturing and spawning sockeye, chum and Chinook salmon (Olivereau and Rand-Weaver, 1994a,b). By contrast, Kakizawa et al. (1995), found no correlation between plasma Sl and final gonadal maturation. Sl has been suggested to act during early oogenesis (Campbell et al., 2006), gonadal maturation (Rand-Weaver et al., 1992) and gonadal steroid biosynthesis (Planas et al., 1992). It has also been proposed to act as a facilitator of oocyte maturation through its regulation of lipid metabolism (Fukada et al., 2005; Fukamachi et al., 2005). However, the exact functions of Sl in reproduction are still not known in fishes (cf. Benedet et al., 2008).

7. Techniques for puberty control in fish farming

7.1. Selective breeding

Selective breeding programs can be effective in delaying age at maturity in farmed fish and thereby also increase body size at puberty (Gjedrem, 2000). Selecting strains with genetically high age and size at puberty has been, successfully applied in Atlantic salmon farming, and these traits have been further improved after several generations of selective breeding based on family selection, individual selection or combinations of these two approaches (Gjerde, 1984; 1986; Gjøen and Bentsen, 1997; Gjedrem, 2000). However, improvements of feed, feeding protocols and other husbandry conditions in fish farming results in rapid improvement of growth performance that to some extent can counteract the results of the breeding programs on age at puberty, due to the strong phenotypic link between growth rate and early puberty.

There is considerable genetic variation in age at maturity or puberty in farmed fish species. In Atlantic salmon (*Salmo salar*) heritability (h^2) estimates range from 0.15 to 0.48 (Glebe and Saunders, 1983; Gjerde, 1984; Wild et al., 1994; Gjerde et al., 1994; O'Flynn et al., 1994; Gjedrem, 2000), while in rainbow trout (*Oncorhynchus mykiss*) the estimates range from 0.12 to 0.35 (Gjerde and Schaeffer, 1989; Crandell and Gall, 1993, Kause et al., 2003), and in Atlantic cod (*Gadus morhua*) h^2 was estimated to 0.21 (Kolstad et al., 2006). However,

there are also reports on genetic correlations between growth (i.e. body weight at age) and early puberty in Atlantic salmon (Gjerde, 1984; Wild et al., 1984; Glebe and Saunders, 1986; Gjerde et al., 1994) and Atlantic cod (Kolstad et al., 2006). Such genetic correlations must be taken into consideration in selective breeding programs to avoid simultaneous selection of rapid somatic growth and early puberty.

In spite of the large potential to delay puberty in farmed fish by selective breeding, this technique has only been adopted in the breeding programmes for a limited number of farmed fish species so far. The status of selective breeding in farmed fish and shellfish species in Europe has recently been reviewed in the project Aquabreeding (http://www.aquabreeding.eu). Currently there are more than 30 different selective breeding programmes fish species in Europe. These programs include mainly rainbow trout, Atlantic salmon, Common carp, brown trout, turbot, Gilthead sea bream and European sea bass. However, only a few of these programmes, mainly for salmonids, have included age at maturity as one of the selection criteria so far.

7.2. Feeding control

A clear link between feeding and age at puberty is seen in several experimental studies, in particular in salmonids (Thorpe et al., 1990; Silverstein et al., 1997b; Silverstein et al., 1998b; Duston and Saunders, 1999; Shearer and Swanson, 2000a; Shearer et al., 2006). Restricted feeding reduces growth rate, can reduce energy stores and adiposity (Shearer et al., 1997a; Shearer et al., 2006), and can delay age at puberty, and therefore it has been suggested that lipid stores, or rate of lipid deposition, are important factors in determining age at first maturity in salmonids (Rowe and Thorpe, 1990b; Rowe et al., 1991; Herbinger and Friars, 1992; Berglund et al., 1995b; Hopkins and Unwin, 1997; Duston and Saunders, 1999; Shearer and Swanson, 2000a; Shearer et al., 2006). Cod depend upon reserves of protein and lipid for gonad maturation (Dambergs, 1964; Kjesbu et al., 1991; Kjesbu and Holm, 1994), and it has been postulated that the age at which sexual maturity is initiated in gadoids may be dependent upon lipid reserves (Eliassen and Vahl, 1982). Periodic starvation during the autumn before puberty (Karlsen et al., 1995), or restricted feeding (starved every second week) from January a year prior to puberty (Kjesbu and Holm, 1994) did not reduce relative fecundity nor age at, puberty. Increasing the energy expenditure by exercising Atlantic cod 7 months prior to spawning did not influence age at puberty (Karlsen et al., 2006). Studies indicate that this approach is only/mostly effective when applied on fish with limited energy reserves and or small body size (Silverstein et al., 1998b; Shearer et al., 2006), and the lack of any response in cod could be due to that farmed cod have much larger livers (energy stores) than their wild counterparts, and therefore is little sensitive to dietary manipulations unless these are extreme. In addition, growth control by restricted feeding during the first year of life may be more efficient in terms of puberty control (Herbinger and Friars, 1992; Silverstein et al., 1998b; Shearer et al., 2006).

Feed ration may also affect reproductive investments (Bagenal, 1969; Luquet and Watanabe, 1986; Kjesbu et al., 1991), and similarly may feed composition, such as lowering the dietary lipid content, which will result in lower gonadosomatic index in Atlantic cod (Karlsen et al., 2006b). The feed composition may also have an effect on age at puberty, as the dietary content of energy and/or protein affects growth and energy stores (Einen and Roem, 1997; Karlsen et al., 2006b). However, prolonged periods of restricted feeding have also severe negative effects on growth and condition (Karlsen et al., 1995), and can negatively affect fish health (Damsgård et al., 2004) and lead to higher incidence of agonistic behaviours (Magnusson, 1962; Symons, 1968) and resulting damages, e.g. as a consequence of fin biting (Turnbull et al., 1998; Hatlen et al., 2006; Noble et al., 2007, 2008). In addition, reduced growth normally results in longer production time to harvestable size, hence having negative

effects on the economy and sustainability of fish farming. It has been hypothesizes, and partially shown, that restricted feeding in shorter time periods that are believed to be critical 'decision' periods can delay age at puberty, with minor effects on the overall growth rate due to compensatory growth during full feeding subsequent to the feed deprivation period (Thorpe et al., 1990). These negative factors limits the applicability of overall restricted feeding as a way to reduced incidence of early puberty in farmed fish, and may thus not be suitable for practical aquaculture purposes.

7.3. Photoperiod control

Photoperiod control of the reproductive process has been successfully applied to broodstock to alter the phase of the annual sexual cycles and hence the spawning time in a range of fish species (e.g. Carrillo et al., 1993; Bromage et al., 2001). The process of puberty could be considered as a particular (the first) case of the cyclic reproductive events in the lifespan of the fish. Consequently it was expected that environmental manipulation altering spawning time in adults may also be effective in altering the onset of puberty in juvenile fish, such as seen in rainbow trout (Duston and Bromage, 1988; Randal et al., 2001; Bromage et al., 2001).

A range of studies demonstrate that photoperiod manipulation can be an effective tool to delay or advance puberty in farmed fish, e.g. Atlantic salmon (Oppedal et al., 2006), rainbow trout (Taylor et al., 2008), Chinook salmon (Unwin et al., 2005), pink salmon (Beacham and Murray, 1993; Beacham et al., 1994), Arctic charr (Duston et al., 2003), brook trout (Holcombe et al., 2000), Atlantic cod (Hansen et al. 2001), haddock (Davie et al., 2007a), channel catfish (Kelly and Kohler, 1996), striped trumpeter (Morehead et al., 2000), yellowtail (Mushiake et al., 1994; Mushiake et al., 1998; Hamada and Mushiake, 2006), European sea bass (Begtashi et al., 2004; Rodriguez et al., 2005), striped bass (Clark et al., 2005), black sea bass (Howell et al., 2003) Gilthead sea bream (Kissil et al., 2001; Gines et al., 2003, 2004), Atlantic halibut (Norberg et al. 2001), turbot (Imsland et al., 2003; Imsland and Jonassen, 2003), Senegalensis sole (Garcia-Lopez et al., 2006), Eurasian perch (Migaud et al., 2003; Migaud et al., 2006), yellow perch (Ciereszko et al., 1997; Shewmon et al., 2007) and Nile tilapia (Biswas et al., 2005; Rad et al., 2006).

However, the effectiveness of photoperiod protocols differs among species and appears also to be modulated by other factors such as age, feeding, body size and adiposity of the fish (Taranger et al., 1999; Oppedal et al., 2006; Taylor et al., 2008). Moreover, full photoperiod control can be difficult to achieve in outdoor rearing systems such as sea cages (Oppedal et al., 1997; Porter et al., 1999; Taranger et al., 2006b), and improved lighting technologies and approaches are needed to implement such techniques at lower cost and with more predictable outcomes in commercial farming situations.

Atlantic salmon

A range of studies demonstrated the effects of photoperiod on age at puberty in Atlantic salmon (Hansen et al., 1992, Kråkenes et al., 1991; Duston and Saunders, 1992; Oppedal et al., 1997; 1999; 2003; 2006; Porter et al., 1999; Taranger et al., 1995; 1998; 1999; Endal et al., 2000; Peterson and Harmon, 2005; Schulz et al., 2006). Continuous light (LL) treatment from mid winter onwards has proved to be a simple way to reduce the incidence of early puberty in salmon in sea cages (e.g. Taranger et al., 1995; Porter et al., 1999). This has been successfully applied in commercial scale cages (Taranger et al., 1995), and is routinely used on salmon farms to combat problems with early maturation (Hansen et al., 2000). Photoperiod treatment can also be applied to induce precocious maturation in salmon (King et al., 2003). Moreover, LL treatment has also been found to delay age at puberty when applied to underyearling postsmolts in sea cages (Oppedal et al., 2003) or seawater tanks (Duncan et al., 1999). However, the LL treatment was found to increase the incidence of early puberty when

applied from the time of seawater transfer in the autumn to next summer by Oppedal et al. (2003), and also when applied after the summer solstice in sea water tanks (Duncan et al., 1999a). The effect of the LL treatment on puberty also varies between studies and depends amongst others on the timing of the LL treatment in winter (Taranger et al., 1998), and most likely on other factors such as body size, adiposity and/or stage of gonadal development (Taranger et al., 1999). In some cases, the LL treatment can even give the opposite result, with an increase of the incidence of early puberty (Kråkenes et al., 1991; Endal et al., 2000).

Atlantic cod

LL treatment was found to arrest or delay pubertal development when applied to cod in indoor tanks from around mid-summer onwards (Hansen et al., 2001; Davie et al., 2003; Norberg et al., 2004; Karlsen et al., 2006a; Davie et al., 2007b). The effect on puberty depended on the timing of the exposure to the LL treatment (Hansen et al., 2001; Davie et al., 2007b; Almeida et al., 2009). LL treatment indoors appears to arrest oocyte development in the cortical alveoli stage (i.e. previtellogenesis) in female cod (Hansen et al., 2001), whereas the effects on testis development were more variable with some individuals showing full spermatogenesis but with a low testis weight compared to controls under ambient light (Almeida et al., 2009). Interestingly, when cod were transferred back from LL to natural light in mid-winter, puberty resumed and spawning occurred within a few months (Hansen et al., 2001; Almeida et al., 2009). However, LL treatment was less effective when applied in commercial sea cages (Taranger et al., 2006; Trippel et al., 2008), and appeared to depend on the intensity of the artificial light (Dahle et al., 2000; Trippel et al., 2008). The difference in effectiveness was attributed to the strong ambient light in the cages relative to the artificial LL light that was superimposed on the ambient light cycle (Taranger et al., 2006). Recent studies on cod in outdoor tank subjected to LL of different intensities in superimposed on the ambient light cycle show that that higher intensities of the LL treatment were more efficient in delaying puberty, possibly by being more effective in overruling the strong ambient light signal (Kristoffersen, Karlsen, Norberg and Taranger, unpublished results).

Atlantic halibut

Attempts to control maturation by photoperiod manipulation have yielded varying results in Atlantic halibut, and appear to depend on the timing of manipulation, as regards both to time of year and initial age of the fish (Norberg et al., 2001; Imsland and Jonassen, 2005; Imsland et al., 2006). Juvenile halibut exposed to LL displayed higher growth and lower incidence of maturation than fish held at simulated natural photoperiod or on a short day regime (Imsland and Jonassen, 2003; 2005). On the other hand, LL applied 15 or 5 months prior to maturation accelerated growth, but also advanced maturation by 3 months, while a period of LL from 15 to 5 months prior to maturation, followed by natural photoperiod reduced incidence of maturation and promoted growth (Norberg et al., 2001). Moreover, exposure to LL for two years prior to first maturation reduced the incidence of male maturation and promoted growth, while shorter LL exposure either advanced maturation, or was inefficient (Imsland et al., 2008).

European sea bass

The first detailed study on the effect of modified photoperiod cycles to delay the first maturity in sea bass (Rodríguez et al., 2001b) investigated the long-term (starting with 4 month-old sea bass and during three consecutive years) effects of a constant long photoperiod (15L:9D) on pre-pubertal male sea bass. Gonadal maturation was significantly delayed compared to fish exposed to simulated natural photoperiods. Recently (Carrillo et al., 2008a), confirmed the delaying effects of long photoperiods on the onset of puberty in out-door floating cage culture

system. The first evidence for the LL effects on gonadal maturation in sea bass was obtained by Begtashi et al. (2004). These authors reported that juvenile fish exposed to LL throughout a year showed a drastic reduction in the rates of male entering early puberty (0-3% in LL treated fish versus 22% in ambient controls). Recently it has also been shown that shorter LL treatments, lasting 4 or 6 months during pre-gametogenesis and gametogenesis , respectively (Felip et al., 2008a) resulted in similar low rates of precocity as when maintained under LL all the year round. These studies paved the way for screening the period August-November with LL windows of short duration (2 months) to find a the most sensitive period to block gametogenesis in sea bass (Carrillo et al., 2008b).

7.4. Induced sterility

7.4.1. Triploidy

Sterile fish can be an effective means to combat problems associated with early puberty, both to avoid negative effects on production performance, health and welfare, as well as to prevent any negative genetic impacts of fish farming on wild populations. Triploidy is relatively easily achieved in many fish species, either by pressure or temperature shocks on the eggs just after fertilization. Triploid fish are normally fully sterile, but the males can develop large gonads and display secondary sexual characters. By contrast, triploid females will normally only develop small gonads and avoid development of secondary sexual characters. Hence, it is commonly beneficial to combine triploid sterile fish with all-female stocks.

All-female production can be achieved in many fish species by either hormone or enzyme inhibitor treatments in early life, normally applied to the generation prior to the on-growing fish.The mechanisms of sex differentiation, impact of environmental factors on sex differentiation and effects of sex steroids and enzyme inhibitors on sex reversal and ultimately the production of monosex stocks has been reviewed several times (e.g. Piferrer 2001; Devlin and Nagahama, 2002; Gomelsky, 2003; Shelton, 2006), and is not detailed further in the current paper.

Methods for triploidy induction – success and survival

Production of triploids is still recognized as the most practical, economic, and effective method for large scale production of sterile fish. The induction of triploidy throughout chromosome set manipulation has been applied on many cultured fish species, especially freshwater, including mainly salmonids, cyprinids, cichlids, and ictalurids. Several studies have applied these manipulations also to about a dozen marine species, including sparids, moronids and flatfishes (Ihssen et al., 1990; Pandian and Koteeswaran, 1998; Benfey, 1999; Felip et al., 2001a; Hulata, 2001; Tiwary et al., 2004; Maxime, 2008).

Triploidy is induced by forcing retention of the second polar body by applying temperature (hot or cold), hydrostatic pressure, anaesthetics or chemical shocks, shortly after a normal fertilization. Of these methods, temperature and hydrostatic pressure shocks are in practical use. Temperature and hydrostatic pressure shock treatments are inexpensive to apply and can be successfully adapted for mass production by fishfarms. Cold shock in general has been most successful in warm water fishes (Felip et al., 2001a) with good examples from sea bass (Felip et al., 1997) and turbot (Piferrer et al., 2000). Heat shock has been 100% effective in producing triploids in tilapia (Varadaraj and Pandian, 1990), rainbow trout (Solar et al., 1984) and gilthead sea bream (Gorshkov et al., 1998). Hydrostatic pressure shock has been successfully used to produce triploids in several species, e.g. zebrafish (Streisinger et al., 1981), rainbow trout (Lou and Purdom, 1984), Atlantic salmon (Benfey and Sutterlin, 1984), common carp (Linhart et al., 1991), Nile tilapia (Hussain et al., 1991), yellow perch (Malison et al., 1993), coho salmon (Piferrer et al., 1994), yellowtail flounder (Manning and Crim,

2000) and Atlantic cod (Trippel et al., 2008). Generally, pressure shocks seemed to be less harmful and give higher survivalthan cold shocks (Peruzzi and Chatain, 2000) and heat shocks (Carrillo et al., 1993; Teskeredžić et al., 1993; Haffray et al., 2007).

Survival

After the initial mortality associated with the handling and shock treatments in the triploidisation protocols, the difference in survival between triploids and diploids are less pronounced. In Atlantic salmon, freshwater mortality is reported to be higher in triploids in both experimental and commercial studies (McGeachy et al., 1995; O'Flynn et al., 1998; Benfey, 2001a; Cotter et al., 2002). However, mortality rates are often within commercially acceptable levels, with the highest mortality during embryonic and larval development prior to first-feeding (Johnson et al., 2004). Higher mortality in triploids has also been found in sea bass up to 3 months of age (Peruzzi et al., 2004) and rainbow trout (Quillet et al., 1987). However, examples with no difference in survival between triploids and diploids were reported in Thai silver barb (Koedprang and Na-Nakorn, 2000), and higher survival were found in triploid turbot compared with diploid controls (Cal et al., 2006).

Growth

Quillet et al., (1988) reviewed the growth of diploids and triploids from 19 publications and Pandian and Koteeswaran (1998) added 13 papers to a total of 32 papers in a later review. The triploid/diploid (T/D) ratio for weight varied from 0.38 to 1.43 in the pre-maturation phase, but triploids grow generally slower than diploids. However, in the post-maturation phase the triploids took advantage of their sterility and in almost all species the triploids grew 10-30% faster than diploid controls. Moreover, triploids from herbivorous species (*Cyprinidae* and *Cichlidae*) appear to be less negatively affected than carnivorous species during the pre-maturation phase, and more positively affected during the post-maturation phase. There is also a general tendency that triploids grow faster when reared alone than when they are reared in commune with diploids. This is possibly because the triploids are less aggressive and have a lower ability to compete for food (Maxime, 2008).

In one of the few studies to show enhanced growth of triploid salmon under commercial conditions it was evident that there were significant family/year class differences observed between ploidies advocating the need for selection to obtain the best performers (O'Flynn et al., 1997). Numerous studies now recommend the need for selection programs for successful triploid production in salmonids, particularly since triploids often show greater variability in performance both within and between families (Bonnet et al., 1999; Friars et al., 2001; Cotter et al., 2002; Oppedal et al., 2003). Significantly enhanced growth of triploid Atlantic salmon under continuous light (LL) relative to diploids has been observed (Oppedal et al., 2003), suggesting that some environmental conditions are particularly beneficial for triploids, and that poorer growth reported in some triploid stocks may be due to unfavourable husbandry regimes.

Morphology and deformities

Several morphological differences and deformities has been reported in triploid non-salmonids like tilapia (Varadaraj and Pandian, 1990), pejerrey (Strüssmann et al., 1993), carp (Gomelsky et al., 1992), tench (Flajshans et al., 1993), bighead carp and grass carp (Tave, 1993) and catfish (Varkonyi et al., 1998).In salmonid farming the occurrence of specific morphological abnormalities in triploids has significantly hindered the adoption of this technology. The most commonly described deformity in triploid salmon is the “lower jaw deformity syndrome” (Sutterlin et al., 1987; Jungalwalla, 1991; Benfey, 2001b; Sadler et al., 2001). Other deformities include shortened gill covers, reduced numbers of primary gill

filaments and eye cataracts. Prevalence and occurrence of specific abnormalities differs between rearing environments, stocks and strains. Furthermore, deformities are not always observed, and occurrence of deformities may not neccecary be the result of triploid induction methods as such, as similar levels of deformity have been found in diploids (Sutterlin et al., 1987; Kacem et al., 2004).

Immunology and disease resistance

The reported differences between diploid and triploid immunology and disease resistance are generally small. Yamamoto and Iida (1994) found similar complement activity in triploid and diploid rainbow trout, and Langston et al. (2001) found a small delay in the complement activity and hypoferraemic response in Atlantic salmon. Budino et al. (2006) found no differences in total respiratory burst activity and phagocytosis between triploid and diploid turbot because the lower blood cell number of the triploids was compensated by a larger size and a higher activity per cell. The differential cell count, serum complement and lysozyme or bactericidal activities was similar in both types of fish, indicating that the activities of the humoral components of the innate immune system tested are similar in diploid and triploid fish. Also, Small and Benfey (1987) found a higher cellular phagocytic activity in triploid salmon, but this was balanced by a lower number of leucocytes (Yamamoto and Iida, 1994; Benfey, 1999). Also challenge tests did not uncover differences in disease resistance between diploids and triploids. Yamamoto and Iida (1995b) found no differences in susceptibility of diploid and triploid rainbow trout for Infectious Haematopoietic Necrosis (IHN) virus, furunculosis and vibriosis, and Dorson et al. (1991) found no difference in the susceptibility of diploid and triploid rainbow trout, arctic charr, brook trout and lake trout for Infectious Pancreatic Necrosis virus, Viral haemorrhagic septicemia virus type 1 and 3 and IHN virus. Moreover, Yamamoto and Iida (1995a) found a similar response to vaccination in diploid and triploid rainbow trout.

Sensitivity of triploids to sub-optimal environmental conditions

Triploid fish have been reported to be more sensitive to environmental changes than diploid fish. Triploid brook trout, rainbow trout and Atlantic salmon have been shown to have the same response to acute stress (handling and crowding) as diploid fish (Biron and Benfey, 1994; Benfey and Biron, 2000). Primary and secondary stress responses do not differ, suggesting that mortalities reported under commercial conditions cannot be attributed to differences in their physiological response to stress in relation to husbandry or management practices (Sadler et al., 2000a; Leggatt et al., 2006). It is plausible that intolerances to environmental extremes may explain the higher mortalities at times of increased physiological stress in triploid fish.

Triploid red blood cells exhibit increased mean corpuscular volume (MCV), which decreases the surface-to-volume ratio and may have marked effect on triploid physiology, as the total area available for oxygen assimilation and other diffusion processes will be reduced. In triploid fish, this may result in a reduced aerobic capacity. However, this has not been definitively demonstrated in any species (Benfey and Sutterlin, 1984; Yamamoto and Iida, 1994; Cal et al., 2005; Peruzzi et al., 2005). Ventilation rate is higher in triploid than diploid Atlantic salmon (Benfey, 1999), but not in brook trout (Stillwell and Benfey, 1996), again suggesting that triploid state is not necessarily associated with reduced aerobic capacity. It would thus appear that farm mortalities of triploids in response to stress are not due to failure in respiratory homeostasis (Sadler et al., 2000a; Sadler et al., 2000b).

Such problems may therefore relate to other sub-optimal rearing conditions which need to be clearly identified.

Increased mortality in triploid trout has been reported when the temperature is at its highest in the summer (Ojolick et al., 1995; Altimiras et al., 2002). Stillwell and Benfey, (1996) demonstrated that triploid brook trout had lower metabolic rate (i.e. oxygen requirement) than diploids, a possible compensation for a reduction in the efficiency of gas exchange. However, the metabolic rate dis not differ between ploidy in brown trout at thermal optima, but at higher temperatures the metabolic scope was reduced, thus lowering the energy available for the animal to grow, digest food, support locomotion etc, and may be a factor explaining the increase in mortality often seen in triploid trout at higher temperatures. In triploid brown trout evidence was lacking to support reduced maximal heart capacity between ploidies, although maximal performance may be limited at higher temperatures potentially contributing to an increased mortality (Mercier et al., 2002).

Triploidy in European sea bass

In European sea bass induced triploidy disrupts gametogenesis resulting in functional sterility with more pronounced effects in females than in males. Specifically it was found that triploidy blocked the initial phases of meiosis in females and the late phases of meiosis in males, resulting in the absence of, or a reduction in gonadal development, respectively. Specifically, in females, triploidy blocked meiosis during the zygotene stage, preventing the pairing of homologous chromosomes. In contrast, in males, triploidy blocked meiosis during the transformation of secondary spermatocytes into spermatids, thus preventing spermiogenesis (Felip et al., 2001b).The induction of triploidy in sea bass conferred functional sterility in both males and females, thus proving a good model to describe the effects of triploidy on the gonadal development in the two sexes.

The reviews of Zanuy et al. (2001) and Felip et al. (2001a) summarize the methodologies used to obtain triploid sea bass and the yields obtained after its application. Among those cold shock has proven to be the most reliable and simple procedure ready to be used in large-scale production of triploid sea bass. Felip et al. (1997) found the optimal conditions for induction of triploidy in sea bass to be 10 minutes of 0ºC cold shock administered 5 minutes after fertilization. The resulting yield of triploids of this procedure was around 80%.. Later on Peruzzi and Chatain (2000) induced 100% triploidy in sea bass using very similar conditions. During their 3–4 first years of life, triploid sea bass grew in a similar fashion to diploids in fork length but slower than diploids in body weight, even when the diploids reached full sexual maturity. On the other hand, older triploids (from 5 to 7 year old fish) showed gender related dimorphic growth with triploid females attaining the largest body size (Felip, Zanuy, Carrillo, unpublished results).

The presence of jaw, operculum and vertebral column deformities was also observed in triploid sea bass, but have been attributed to handling during artificial fertilization, inbreeding or chromosomal aberrations (Felip et al., 2001a). This suggests that development and the external morphology of triploid fish is essentially similar to that of diploids. However, more studies are needed to more fully ascertain the usefulness of triploid sea bass under intensive culture conditions.

7.4.2. Other methods for sterility

Recently, functional studies have identified genes involved in regulating the migratory behaviour of primordial germ cells (PGCs) during embryogenesis in fish (Doitsidou et al., 2002; Slanchev et al., 2005). When suppressing the function of these genes that encode a cytokine attracting PGCs to the genital ridge or the receptor for this cytokine on the migrating PGCs, the migratory direction of PGCs becomes random, so that most PGCs “miss” the genital ridge and become apoptotic.

An even more effective manner of generating animals with germ cell-free gonads is to interfere with the expression of the dead end (*dnd*) gene, since PGC migration is blocked at very early stages (within 12 hrs after fertilisation) of embryogenesis, leading to the loss of all PGCs by apoptosis (Weidinger et al., 2003). The approach to interfere with the expression of the *dnd* gene has been transferred successfully to other fish species (Saito et al., 2008). Moreover, techniques have been developed allowing the transient (i.e. non-transgenic) labelling of PGCs with fluorescent proteins that is applicable to different species (Yoshizaki et al., 2005) and that is an excellent tool to control the efficiency of *dnd* knock-down. Clearly, however, these approaches are not suitable for generating a large number of individuals. The mutagenesis-induced loss of function of the ziwi gene (Houwing et al., 2007) leads to a similar phenotype of the gonads, which stay small due to the complete loss of all germ cells up until day 12-14 after fertilization. Interestingly, as in the case of *dnd* knock down, all zebrafish without germ cells develop as phenotypic males, so that the default state of sex differentiation for the somatic compartment of the gonad in the absence of germ cells seems to be male. These animals apparently go through normal puberty and show typical male reproductive behaviour, so that the production of sex steroids does not seem to be affected. Despite the experimental state of these techniques, it can be anticipated that technical developments may allow the use of this knowledge for applied purposes in the future in a manner compatible with regulations and consumer interests.

8. Gaps in knowledge and research directions

Early puberty represents a major problem in farming of many fish species due to negative effects on growth, feed utilization, health and welfare, and potential genetic effects on wild stocks after escape or release of fertilized eggs into natural ecosystems. In some species, late puberty leads to increased cost with broodstock management, while in other species a complete block of puberty under farming conditions prevents reproduction and closure of the life cycle.

There is still limited knowledge on the neuroendocrine mechanisms that control onset and/or completion of puberty in fishes and other vertebrates. These mechanisms are sensitive to external factors, such as environmental and husbandry conditions. For example, there is a strong link between feeding level/somatic growth and early puberty, but the underlying physiological mechanisms are still to be elucidated. More knowledge is needed on both fundamental and applied aspects for a full and targeted control of puberty. This will also allow developing cost-effective methods for delaying or advancing/inducing puberty that are acceptable in terms of fish welfare, environmental impact, and consumer interests.

Selective breeding has a large potential for delaying age and size at puberty in fishes, but genotype-environment interactions need further investigations to improve breeding programs operating under changing environmental and husbandry conditions. Moreover, breeding programs could benefit from the identification of genetic markers for age at puberty to assist selection, and by a deeper understanding of the interplay between genetic and environmental factors in controlling puberty.

Photoperiod control has been successfully applied to both delay and advance puberty in farmed fish. However, such protocols do not always work when applied in commercial rearing systems. Moreover, photoperiod effects can depend on interactions with other factors such as genetic background, growth and adiposity. Although photoperiod effects have been extensively investigated in fishes, the mechanistic basis for photoperiod-mediated changes in the activity of the neuroendocrine systems regulating puberty still awaits elucidation, the interactions with other factors are poorly studied; this also applies to the secure application with a more predictable outcome of these techniques under commercial rearing conditions.

Induced sterility, e.g. by triploidy, can eliminate the risk of a genetic impact of farmed fish on wild stocks, and can also mitigate or prevent many or all of the negative impacts of early puberty on farmed fish. Triploidy induction is possible in several species and there is information on the performance of triploid fish in fish farming. However, despite clear benefits, this technique is not yet applied commercially in many species, due to production and welfare related problems under certain environmental conditions. Hence, more knowledge is needed on the physiology, health and welfare of triploid fish, in the light of environmental conditions required to secure optimal production performance and welfare. Such knowledge will also allow the design of breeding programs in order to select for more robust triploid fish.

Triploidy is often combined with all-female production to get the beneficial effects of sterilization on production performance and health of the fish; after all, despite sterility (i.e. no production of fertile sperm), the maturation of the somatic component of the testis does occur, including the increased sex steroid levels and their pleiotropic effects. However, the techniques to produce all-female populations are not yet available in all farmed fish species, and more knowledge is needed on sex determination and sex differentiation to provide more secure methods for mono sex production.

Finally, efforts should be directed towards the development of new sterility models, including techniques to induce germ cell free gonads (e.g. *dead-end* knock down approach) that could result in both a robust and sterile fish, and would avoid the complications associated with the use of mono-sex techniques.

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Figure legends

Figure 1. Concept of relation between somatic growth and age and size at puberty in fishes. Arrows represent different growth trajectories and shaded columns represent potential spawning seasons. The optimal time of spawning within a year for a given species and strain at moderate and high latitudes is often limited by environmental conditions and food availability for the offspring. Slower growth will normally result in delayed puberty to maintain fitness, and because of the strong seasonality of optimal spawning time, puberty completion is delayed with one or more years. The effects of slower growth on size at puberty can vary, possibly due to complex trade-offs between growth, survival to reproduction and offspring survival. The higher growth rates typically seen in fish farming normally results in puberty occurring both at an earlier age and at a smaller body size, compared to wild populations.

Figure 2. Concept of photoperiodic effects on the timing of puberty in salmonids. The dotted curve represents a yearly ambient photoperiod cycle at high latitudes, and arrows represent artificial changes in photoperiod that can affect timing of puberty. Long photoperiods or continuous light early in the season are believed to phase advance circannual rhythms that control the seasonal timing of onset and completion of puberty, whereas short photoperiods early in the season delay such rhythms (Bromage et al. 2001). Long photoperiods or continuous light from midsummer onwards also delay such rhythms, whereas short photoperiods from around spring/early summer advances such rhythms. Advancing photoperiod signals can either accelerate the seasonal timing of gonadal growth and spawning or – alternatively - result in puberty being delayed to the next spawning season. The outcome of the advancing signals on puberty, i.e. either advancing the seasonal timing of puberty completion - or a complete delay until the next year - can depend on the exact timing of the long photoperiod signal in the season as well as the physiological readiness of the individual to proceed to pubertal completion. This physiological readiness, in turn, can depend on factors such as body size, growth rate, adiposity and stage of development of the brain-pituitary-gonad axis. Delaying photoperiod signals will normally have the opposite effect; the timing of spawning in the season is delayed and more individuals can reach the physiological thresholds to complete puberty in a given year. Hence, advancing photoperiod tends to reduce the proportion of fish reaching puberty in a given year whereas delaying photoperiods increase this proportion. These principles appears also to apply to other fish species at moderate to high latitudes such as European sea bass, Gilthead sea bream, Atlantic cod and Atlantic halibut. However, in some species like Atlantic cod, continuous light or long photoperiod from mid-summer and onwards can inhibit the onset of puberty by one or more years.

Figure 3. Schematic representation of selected, regulatory pathways in the brain-pituitary-gonad axis during puberty in teleost fish. It is hypothesised that peripheral signals related to somatic growth and/or energy storage are integrated in the brain with external (biotic and abiotic) signals, as well as with endocrine feedback from the gonads to activate Gnrh neurons. Gnrh, in turn, triggers production and/or release of gonadotropins (Fsh and Lh) in the pituitary via activation of Gnrhrs). Other pituitary hormones such as growth hormone (Gh) can also modulate gonadal development and activity during puberty onset and completion. Fsh and Lh stimulate germ cell development via activation of the Fshr and Lhr, in part by stimulating the production of sex steroids in gonadal somatic cells and by releasing gonadal paracrine growth factors that control germ cell growth, development and survival. Gonadal sex steroids and growth factors exert positive and negative feedback effects on the brain and/or pituitary level to modulate Fsh and Lh production and secretion. Leptin, ghrelin and Igf1 are candidate factors that may be involved in mediating information on somatic growth and energy storage

to the brain, but these endocrine factors may also have direct effects on the gonads. The Kiss/Gpr54 system may have a role in the brain in mediating such growth/energy related signals, gonadal feedback and external cues into regulatory input for the activation of the Gnrh neurons, thereby activating the pituitary gonadotropes during puberty.

Fig. 1

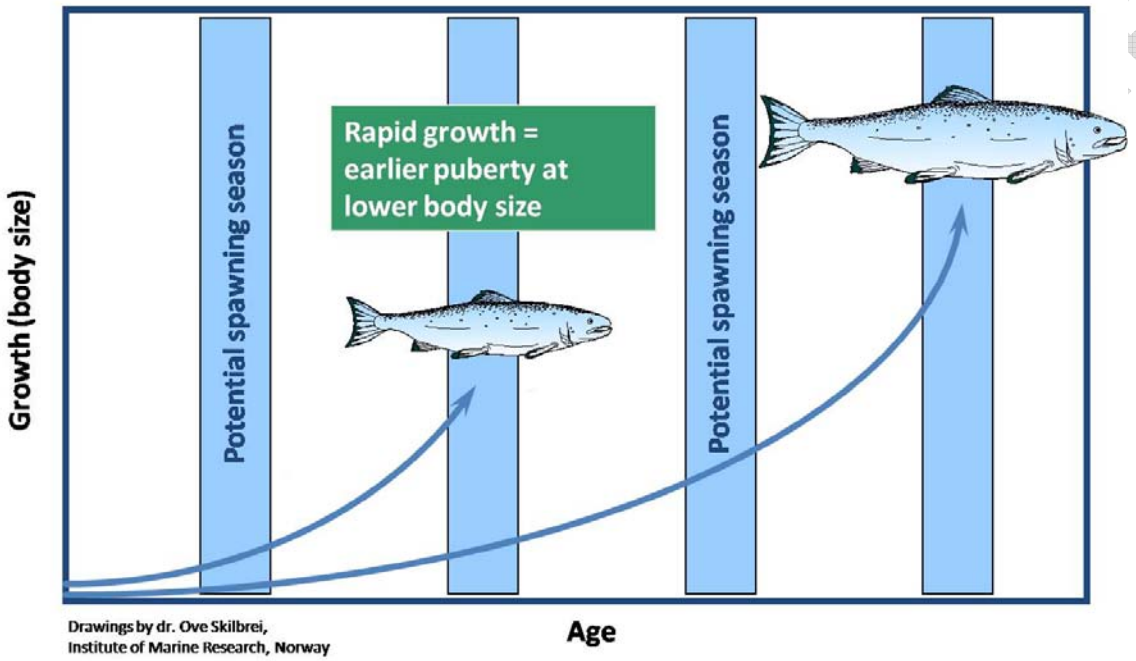

Fig. 2

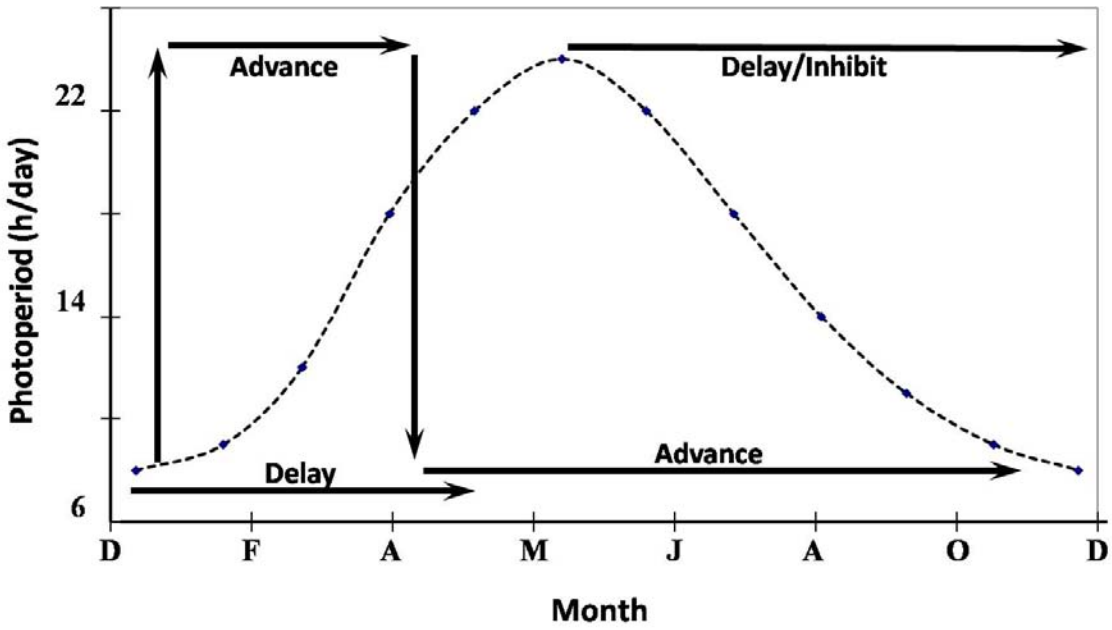

Fig. 3