Chapter 3
Broodstock Management and Control of the Reproductive Cycle

P. Fontaine, N. Wang, and B. Hermelink

Abstract The annual reproductive cycles of percid fish have been clearly characterized for males and females in various natural habitats mainly from North-America or Eurasia, including morpho-anatomical, histological and physiological studies. From this strong basal knowledge, numerous experimental approaches were conducted to understand the environmental and hormonal controls of these reproductive cycles, and to develop artificial programmes in order to obtain delayed or out-of season spawning. It was demonstrated that photoperiod and temperature variations were the major environmental cues. Now efficient photo-thermal programmes exist and have been used by SMEs in intensive fish farming conditions (water recirculating systems).

Keywords Percids • Spawning • Reproductive cycle • Hormonal control • Maturity

3.1 Introduction

Over the last two decades, percid fish culture has progressively appeared as a real way of diversification for the freshwater inland aquaculture sector in temperate areas (Kestemont and Mélard 2000; Fontaine 2004). Consequently, domestication of percid species has been and still is progressing (Teletchea and Fontaine 2014) and the first commercial farms have been recently built in Europe, mainly based on water recirculating aquaculture system(s) (RAS) (Dalsgaard et al. 2013). To support this development focusing on human consumption markets, secured hatchery and nursery productions must be expanded in order to highly increase the availability of

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P. Fontaine (✉) • N. Wang
Unité de Recherche Animal et Fonctionnalités des Produits Animaux, Université de Lorraine,
USC INRA 340, Vandoeuvre-lès-Nancy F-54505, France
e-mail: p.fontaine@univ-lorraine.fr

B. Hermelink
Leibniz-Institute of Freshwater Ecology and Inland Fisheries,
Mueggelseedamm 310, 12587 Berlin, Germany

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juveniles for on-growing farms (particularly by obtaining several reproductions per year). To achieve this objective, a precise knowledge of the natural reproductive cycle (part 1 of this chapter) and its environmental control (part 2) is required to obtain out-of-season spawning and high quality gametes and larvae (Bromage and Roberts 1995). Strict control of the reproductive cycle is a key factor in the domestication of new species, like percid fishes, and the future implementation of breeding programmes for further improvement of cultured percid performances (growth, stress or disease resistance, etc.).

3.2 Natural Reproductive Cycle of Percid Fishes

3.2.1 Gonad Ontogenesis, Sexual Maturity and Gonad Morpho-anatomy

Percid oogenesis and spermatogenesis can start in fish of very small size, i.e. between 3 and 8 cm in length (Malison et al. 1986; Zakes and Demska-Zakes 1996; Lappalainen et al. 2003). This timing is age and size dependent and differs between males and females. In pikeperch *Sander lucioperca*, the first onset of oogenesis in females takes place at a size of approximately 8 cm total length (TL), while males seem to start spermatogenesis later at a larger body size of approximately 12 cm TL (Demska-Zakes and Zakes 1995; Zakes and Demska-Zakes 1996; Lappalainen et al. 2003). A similar pattern can be observed in walleye *Sander vitreus*, a species closely related to pikeperch. In this species, the first differentiation of oogonia occurs in fish from 7.5 cm TL upward, while first spermatogenesis does not begin before fish reach 15 cm TL (Malison et al. 1990).

The age at the onset of sexual maturity (puberty) varies greatly depending on sex and geographical origin (latitude). With respect to the effect of sex, males are mature at a younger age and at a smaller size than females (Alm 1954; Kukuradze 1974; Craig 1977; Papageorgiou 1977; Raikova-Petrova and Zivkov 1998; Henderson and Morgan 2002; Lappalainen et al. 2003). For example, male pikeperch become mature earlier than females at an age of (1) 2–3 years when they have grown up to more than 21 cm, while females do not usually mature before they have reached their third year of age and sizes of more than 28 cm (Raikova-Petrova and Zivkov 1998; Lappalainen et al. 2003). The effect of geographical origin (fish location) is linked to environmental conditions and food availability over the year. More favourable environmental and nutritional conditions allow higher growth and consequently earlier sexual maturity (Colby and Nepszy 1981; Houthuijzen et al. 1993). Maturity is reached at younger ages and smaller sizes in southern populations as compared to northern populations (Raikova-Petrova and Zivkov 1998; Lappalainen et al. 2003). In the southern Baltic Sea, pikeperch mature earlier (3–4 year old) whereas, due to lower growth rates at lower temperatures, pikeperch of the northern Baltic mature generally later (4–5 year old)

(Lehtonen et al. 1996). In percid fishes, as observed in yellow perch (Malison et al. 1986), body size is the most important factor in the control of sexual maturity. All these data result from studies of wild or pond cultured populations subjected to natural climate variations (temperature, photoperiod). Recently, it has been shown that sexual maturity is achieved much earlier when fish are reared under RAS conditions and maintained under constant photo-thermal conditions (20–22 °C, L:D 16:8) (Ben Ammar et al. 2012). Eurasian perch puberty can be achieved within 11–14 months post-hatching in both sexes.

Regarding the anatomy of the reproductive system, the ovaries of percid fishes are initially paired. However, a particularity exists in *Perca* species in which the ovaries fuse together during gonadogenesis to form a single ovarian mass, whereas two paired ovaries are conserved in *Sander* species (Figs. 3.1 and 3.2) (Craig 2000).

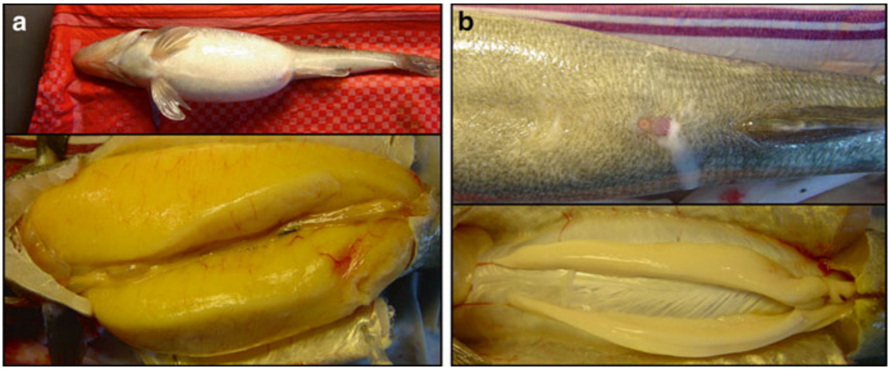

Fig. 3.1 Fully mature female pikeperch and corresponding ovaries (**a**) and fully mature male pikeperch and corresponding testicles (**b**)

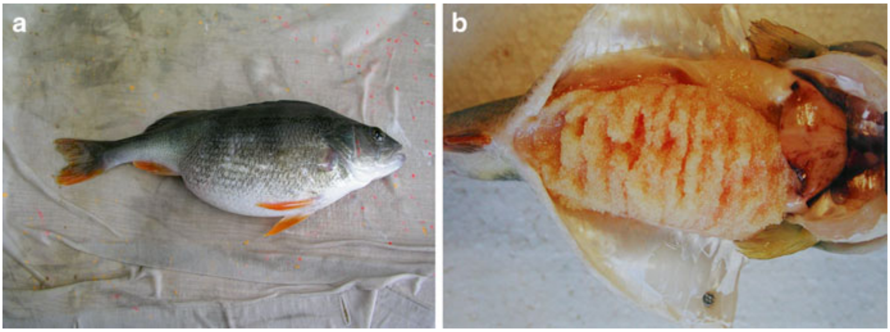

Fig. 3.2 Fully mature female Eurasian perch (**a**) and ovarian mass organized in one unique ribbon (**b**)

3.2.2 Male Reproductive Cycle

3.2.2.1 Testicle Development

In wild populations of perch, walleye and pikeperch caught in natural habitats (lakes, ponds or rivers) of northern temperate or Mediterranean areas, it is observed that males display low gonado-somatic index GSI ([gonad weight/body weight] × 100, %) during the summer period (Turner 1919; Le Cren 1951; Craig 1974; Treasurer and Holliday 1981; Tanasichuk and Mackay 1989; Hayes and Taylor 1994; Malison et al. 1994; Sulistyo et al. 2000; M'Hetli et al. 2011). During this period, male GSI is below 1 % and only spermatogonia are found in the testicles (Craig 1974; Sulistyo et al. 2000). Depending on the species and geographical location, multiplication and differentiation of spermatogonia into advanced spermatogenic cells begin over the period late August–December. Consequently, male GSI highly and rapidly increases during this period and often reaches a peak: 0.5–1 % in pikeperch (Uysal et al. 2006; M'Hetli et al. 2011), 2.5 % in walleye (Malison et al. 1994) and 6–10 % in Eurasian perch (Turner 1919; Le Cren 1951; Craig 1974; Treasurer and Holliday 1981; Hayes and Taylor 1994; Sulistyo et al. 2000). At the end of the autumnal development, spermatogenesis is actually completed. Testes are filled with spermatozoa (>95 % of germ cells) and males are often able to express fluid milt (Malison et al. 1994; Sulistyo et al. 2000). Then male GSI remains relatively stable from October to November until spawning in spring (Tanasichuk and Mackay 1989; Dabrowski et al. 1994; Dabrowki and Ciereszko 1996; Henderson et al. 1996). Sometimes, a slight decrease or increase in GSI was reported prior to the spawning season in both Eurasian and yellow perch (GSI = 4–6 %) (Craig 1974; Hayes and Taylor 1994; Sulistyo et al. 2000), or in walleye (3.2 %) (Malison et al. 1994).

3.2.2.2 Testicular Steroidogenesis

Plasma levels of steroid hormones show significant variations during male gonad maturation (Schulz et al. 2010). Androgens (Testosterone, T; 11-ketotestosterone, 11KT) were identified as major sex steroids involved in spermatogenesis and spermiation in fish (Billard et al. 1990; Borg 1994). Androgens are effective in supporting either the whole process of spermatogenesis, or at least some steps such as spermatogonia multiplication, spermatocyte formation/maturation and spermiation (Schulz et al. 2010). For instance, when water temperatures decrease to 10–12 °C in autumn, spermatogenesis in male pikeperch leads to rising plasma levels of the androgens testosterone (T) and 11-ketotestosterone (11-KT) (Hermelink et al. 2011, 2013).

Serum T levels vary according to variations in GSI, with very low levels (often undetectable) in summer (<0.5 ng mL^{-1}), followed by a high increase (first peak) in November-December (1.6 ng mL^{-1} in walleye, 12.3 ng mL^{-1} in Eurasian perch), a decrease in winter (January-February) and finally a second peak (2.8 ng mL^{-1} in walleye and 6.8 ng mL^{-1} in Eurasian perch) prior to spawning in March-April

(Malison et al. 1994; Sulistyo et al. 2000). The first increase is thought to regulate male germ cell differentiation and the pre-spawning peak may stimulate secondary sexual behaviours, increase the pituitary GTH levels or serve as a precursor for the production of other steroids like 11-KT (Crim et al. 1981; Kobayashi et al. 1989). As for 11-KT, plasma levels in males remain low during the summer period and the beginning of autumn (<10 ng mL^{-1} in walleye and <0.5 ng mL^{-1} in Eurasian perch) (Malison et al. 1994; Sulistyo et al. 2000). Then, a high increase is observed concomitantly with the T plasma level increase in yellow perch in autumn (Dabrowski et al. 1996) or later in January-March as measured in walleye (Malison et al. 1994) and Eurasian perch (Sulistyo et al. 2000). Consequently, higher 11-KT levels are measured in winter: 1.2–1.5 ng mL^{-1} in yellow perch, 4.5–5 ng mL^{-1} in Eurasian perch and 40 ng mL^{-1} in walleye. Levels of 11-KT remain high until spawning and may have a major role in maintaining spermatozoa viability during the prolonged period of sperm storage within the testes. Levels of both T and 11-KT decrease sharply at the onset of spawning. Such a rapid drop in androgens may reflect a shift in the steroidogenic pathway from C19 androgens to C21 progestogen production at the onset of spermiation to regulate the process of spermiation and control male spawning behaviour (Malison et al. 1994).

3.2.3 Female Reproductive Cycle

3.2.3.1 Ovary Development

According to many studies (Malservisi and Magnin 1968; Treasurer and Holliday 1981; Jamet and Desmolles 1994; Malison et al. 1994; Dabrowski et al. 1996; Sulistyo et al. 1998; Lappalainen et al. 2003), percid ovarian development is group synchronous meaning that at most two distinct oocyte developmental stages can be seen within the ovary during sexual resting and maturation (Wallace and Selman 1981; Nagahama 1983). One population consists of a heterogeneous group of small oocytes, and the other is made up of a group of larger oocytes developing synchronously the following spawning season (Malison and Held 1996a). As for GSI and oocyte diameter (OD) variations over an annual reproductive cycle, similar patterns are observed in all percid fishes including five main stages: (1) very low values over the post-spawning period and summer (quiescent or sexual rest period), (2) a rapid increase in autumn (vitellogenesis), (3) a slow or reduced increase in winter, (4) a second high GSI increase before spawning (oocyte hydratation) and (5) a sharp decrease after spawning. In walleye (Minnesota, USA), GSI and OD increase rapidly from October to November (up to 7.6 % and 1,000 μm, respectively) and reach a maximum just prior to spawning (15 %, 1,500 μm) (Malison et al. 1994). Higher GSIs (18–22 %) were recorded by Henderson and Nepszy (1993) in Lake Erie. In pikeperch (Poulet 2004; Uysal et al. 2006), Eurasian perch (Craig 1974; Sulistyo et al. 1998; Noaksson et al. 2004) and yellow perch (Dabrowski et al. 1994; Hayes and Taylor 1994; Dabrowki and Ciereszko 1996; Henderson et al. 2000), female

GSI increases steadily from the beginning of autumn until the spawning period. For example, in Eurasian perch, the OD increases from 200 μm in August to 750 μm in December (Treasurer and Holliday 1981; Sulistyo et al. 1998). However, the GSI increase is slower during the winter period (Sulistyo et al. 1998; Poulet 2004). Prior to spawning, maximum female GSIs are 20–31 % for Eurasian and yellow perch (Treasurer and Holliday 1981; Heidinger and Kayes 1986; Jamet and Desmolles 1994; Dabrowki and Ciereszko 1996; Sulistyo et al. 1998) and 8–10 % for pikeperch (Poulet 2004). Consequently, in percid fishes, especially in female perch, the investment in reproduction is very high and much higher than in males. Moreover, with increasing age, more and more energy is required for ovary maturation. Fecundity and gonad size correlate with somatic and gonad energy density (Henderson et al. 2000). For example, the energy invested in eggs by Eurasian perch females can be superior to 86 % of the energy stored by the soma in 1 year, while the energy invested in the testes is at most 10 % (Craig 1977).

3.2.3.2 Ovarian Steroidogenesis

In females, increases in LH and FSH activate the synthesis of 17β-estradiol (E2) and its precursor hormone T catalysed by aromatase (Hermelink et al. 2011, 2013). Oogenesis correlates with changes in serum levels of sex steroids (17β-estradiol-, E_2; testosterone, T) (Lubzens et al. 2010). E2 is secreted by the ovaries and released into the bloodstream where it is transported to the liver, bound to the sex hormone binding globulin (SHBG). In response to the increasing E2 blood concentrations, vitellogenin is synthesised in the liver. Vitellogenin in turn is also released in the bloodstream and is taken up by the oocytes by receptor-mediated endocytosis (Tao et al. 1996). In the oocytes vitellogenin is cleaved into the final egg-yolk proteins (lipovitellins and phosvitins) and deposited in the yolk granules (Wallace 1978). The process of vitellogenesis lasts until rising water temperatures induce final maturation. At the end of the vitellogenesis process, the oocytes are filled up with a few large lipid droplets and the nucleus is located centripetally. Final maturation is characterised by germinal vesicle breakdown (GVBD). GVBD is regulated by a maturation-inducing steroid (MIS). In salmonids and many other species 17,20β-P is this MIS, while 17,20β,21-trihydroxy-4-pregnen-3-one is also often found in perciforms (Young et al. 2005; Nagahama and Yamashita 2008; Lubzens et al. 2010). Pankhurst et al. (1986), Barry et al. (1995), Fontaine et al. (2003), and Migaud et al. (2003a) reported that 17,20β-P is the potential MIS in walleye and Eurasian perch. After GVBD the ripe eggs can be ovulated and fertilized.

As far as the natural female reproductive cycle is concerned, serum E_2 levels in percid females increase rapidly from basal values in early autumn (September-October, <0.1 ng mL^{-1}) to peak values in late autumn (late October-November, 3–4 ng mL^{-1}), which coincides with the period of maximum ovarian growth (Malison et al. 1994; Sulistyo et al. 1998; Noaksson et al. 2004). Subsequently, in walleye, E_2 levels decrease steadily from December through spawning (Malison et al. 1994), whereas in Eurasian perch they remain high until spawning (Sulistyo et al. 1998; Noaksson et al. 2004). In this species, a peak (4 ng mL^{-1}) is often measured in April during the peri-ovulatory period (Sulistyo et al. 1998; Migaud et al. 2003a). In yellow perch, a study dealing with in vitro production of ovarian steroids shows peaks of E_2 production in early autumn (October) and during the peri-ovulatory period (Dabrowski et al. 1996) and confirms data obtained from in vivo studies. E_2 stimulates the synthesis of vitellogenin (De Vlaming et al. 1977, 1980; Wallace and Selman 1981). In walleye, vitellogenesis is completed by early winter, whereas an active vitellogenesis is maintained until spawning in Eurasian perch. In walleye (Malison et al. 1994), serum T levels exhibit a bimodal pattern with two peaks in November (1.6 ng mL^{-1}) and April, just prior to spawning (3.3 ng mL^{-1}). This second peak could be related to final oocyte maturation and ovulation (Young et al. 1983). The simultaneous E_2 level decrease and T level increase from November to the spawning period suggest a decrease in aromatase activity. In Eurasian perch, the plasma T level remains very low until November, then increases dramatically in December (15–20 ng mL^{-1}) and stabilizes until the peri-ovulatory period (Sulistyo et al. 1998). A similar plasma T profile was observed by Noaksson et al. (2004) in a Swedish lake (Lake Djursjön). Such high plasma T values in perch females during the peri-ovulatory period have been also observed by Dabrowski et al. (1996) and Migaud et al. (2003a).

3.2.4 Reproductive Strategy

Mainly based on eco-physiological studies of wild populations from various water bodies, the previous parts of this chapter suggest that all percid fishes display similar reproductive cycles. A recent analysis of 29 reproductive traits in 65 temperate freshwater fish species (including 5 percid fishes from Eurasia and North-America) demonstrates that all percid fishes are clustered in the “early-spring spawners” group (Teletchea et al. 2009a). The (three) main phases of the percid reproductive cycle have been specified by Wang et al. (2010): (1) induction of gametogenesis by decreasing both temperature and photoperiod, (2) vitellogenesis during the autumnal chilling period and (3) synchronization of final stages (oocyte maturation, spawning) by increasing temperatures. Thus the reproductive cycle of percid fishes is controlled by annual variations in both photoperiod and temperature. Its environmental control is therefore more complex than in other species like salmonids. As photoperiod is the most accurate environmental zeitgeber in temperate areas (Migaud et al. 2010), this factor is strictly implicated into the control of the percid reproductive cycle. Numerous studies suggest that temperature changes also play their part, especially during winter and spring periods (Hokanson 1977; Schlumberger and Proteau 1996; Sandström et al. 1997; Gillet and Dubois 2007). For example, induction and intensity of pikeperch spawning are controlled by variations of water temperature (Lappalainen et al. 2003).

Despite many similarities between percid reproductive cycles, high ecological plasticity related to both their huge biogeographical distribution (Thorpe 1977) and

Table 3.1 Intraspecific variations of spawning period and temperature in Eurasian perch populations from the North hemisphere

Location and country	Spawning period	Spawning temperature (°C)	Authors
Mirgenbach reservoir, France[a]	Late February–mid April	12–14	Flesch 1994
Lake Agios Vasilios, Greece	Mid March–early April	8	Papageorgiou 1977
Slapton Ley, England	Mid March–early May	8–14	Craig 1974
Ivan'kovo reservoir, Russia	April–May	7–15	Makarova 1973
Forsmark and Oskarshamn basins, Sweden[a]	Early April–late June	7–24	Sandström et al. 1997
Loch Kinord and Davan, Scotland	Late April–mid May	9–11	Treasurer 1983
Lake Zürich, Switzerland	Late April–early June	8–15	Zeh et al. 1989
Lake Geneva, France	Late April–early June	8–16	Gillet and Dubois 1995
La Gombe, Belgium	Late April–mid June	8.5–13.5	Dalimier et al. 1982
Loch Leven, Scotland	Late April–mid June	9–11.5	Jones 1982
Windermere, England	Mid May–mid June	9–18	Guma'a 1978
Lake Saarlampi, Finland	Mid may–late May	12–14	Urho 1996

[a] Water bodies receiving cooling water discharged by nuclear power stations

habitat diversity can be noted for numerous reproductive traits for each species. For example, the broodstock characteristics at maturity for pikeperch (Lappalainen et al. 2003) or spawning time and temperature for Eurasian perch (see Table 3.1) are highly variable. In fact, over the northern hemisphere, Eurasian perch populations spawn between February and June over a 7–20 °C temperature range (Sandström et al. 1997; Gillet and Dubois 2007). Furthermore, within a same area or ecosystem, significant variations can be observed. Indeed, in the southern Baltic Sea pikeperch spawn in late April–early May and in late May–June in the northern Baltic (Baltic Proper, Gulf of Finland) due to a water temperature rise occurring later in the season (Lehtonen et al. 1996; Lappalainen et al. 2003).

In addition, ovarian development is not fully synchronous within a same population, explaining the long spawning period (Henderson et al. 2000; Migaud et al. 2003b). Similar variations are also observed for yellow perch (Scott and Crossman 1973; Hokanson 1977; Heidinger and Kayes 1986) and walleye (Malison and Held 1996b). The geographical effect is often related to marked variations in fish reproductive performance. For example, based on a study of 75 Eurasian perch populations, Heibo et al. (2005) reported a negative correlation between fecundity and latitude. Likewise, the spawning performance of percid fishes is also affected by the condition of the females, presumably reflecting the net acquisition of energy in the preceding growing season (Henderson and Nepszy 1993; Henderson et al. 1996; Henderson and Morgan 2002).

Finally, population structure or water quality could also affect the reproductive performance. In pikeperch a greater range of age classes participating to spawning increases the duration of the spawning season (Lappalainen et al. 2003). The oldest pikeperch initiate the spawning season while the youngest and smallest end it. Interestingly, freshwater pikeperch of the same latitude spawn earlier than the individuals living in brackish water. Habitat parameters within the population location also influence fecundity. Pikeperch which have spent their whole lifetime in brackish water show higher fecundity than freshwater ones (Lehtonen et al. 1996).

3.2.5 Conclusion

All percid fishes have similar reproductive cycles and belong to a homogenous group (early spring spawners). In the North hemisphere, after a short quiescent post-spawning period (May-June), gonadal recrudescence and oocyte growth in females occur over a decreasing photoperiod and water temperature period in fall. After a long wintering period, final oocyte maturation, ovulation and spawning are observed in spring (mainly over April-May) when water temperature and photoperiod increase, confirming the importance of these two environmental factors in the control of percid reproductive cycle. Finally, according to the diversity of the habitat and the geographical location, high ecological plasticity is recorded for major reproductive traits like female fecundity. It suggests that numerous factors (environment, nutrition and population) can modulate the reproductive performance.

3.3 Environmental Control of the Reproductive Cycle

3.3.1 Hormonal Regulation of the Reproductive Cycle

In fish, especially in temperate areas, photoperiod and temperature are the only two environmental signals that can provide a consistent timing message for broodstock (Craig 2000; Migaud et al. 2010). According to these authors, photoperiod variations are transduced by a photoneuroendocrine system (retina, suprachiasmatic nucleus and pineal gland) which releases the hormone melatonin exclusively at night. The duration of the melatonin secretion varies according to night length. Melatonin mediates the transduction of photoperiodic information to the hypothalamus-pituitary-gonad (HPG) axis (Amano et al. 2000). Like in other teleosts, the reproduction of male and female percid fishes is regulated by photo-thermal variations and the hypothalamus-pituitary-gonad (HPG) axis (via hormones). The hypothalamus acts as an interface between the nervous system and the endocrine system, incorporating internal (e.g. nutritional conditions) as well as external (e.g. photoperiod, temperature) triggers. Key regulators of the HPG axis are the pituitary gonadotropins, the luteinizing hormone (LH) and the follicle-stimulating hormone (FSH) and at the level of the gonads, the sex steroids (Zohar et al. 2010). The knowledge on neuroendocrine regulation of fish reproduction has increased tremendously over the past 10 years (Migaud et al. 2010). The brain-pituitary-gonad (BPG) cascade has been well described, notably the kisspeptin control of gonadotropin-releasing hormone (GnRH) synthesis. Synthesis of the sex steroids is stimulated by the gonadotrophins. This is crucially important for reproductive processes like the spermatogenesis in males or the vitellogenesis in females and the final maturation in both (Lubzens et al. 2010; Schulz et al. 2010).

Consequently, over the last two decades, some studies were conducted to control percid reproductive cycles by regulating photoperiod and temperature for to either (1) extending the natural spawning period (advanced or postponed spawning) or (2) obtaining out-of-season spawning (often in combination with hormonal injection to induce ovulation and spawning in females and sperm production in males). In the first case, broodstock was first maintained under natural conditions in ponds or floating cages (i.e. natural induction of the reproductive cycle), then subjected to artificial conditions during the final part of their reproduction cycle. In the second case, broodstock was exposed to artificial conditions during the whole reproduction cycle. In that case, broodstock is disconnected from natural cycles and their manipulation starts with fish at a sexual resting stage.

3.3.2 Environmental Control of the Reproductive Cycle

3.3.2.1 Extending the Natural Spawning Season by Advancing Spawning Time

Due to a longer duration of the vitellogenesis process in perch females, causing spawning to start earlier seems to be an effective option for pikeperch and walleye, but not a reliable one for perch. In walleye, gonadal maturation is essentially completed by mid-winter (several months before spawning) suggesting the possibility to induce walleye to spawn earlier (i.e. from January to March) using relatively simple environmental/hormonal manipulations (Malison et al. 1994). A few years later, using wild broodstock caught in lakes or reservoirs in autumn and then overwintered in ponds, Malison et al. (1998) showed that walleye can be induced to spawn up to 10 weeks (late January) prior to the normal spawning season by using relatively simple environmental (temperature increase from 2 to 10 °C over a 1-week period, 12L:12D) and hormonal treatments (human chorionic gonadotropin, hCG; des-Gly^{10} [D-Ala^{6}] LHRH-ethylamide, LHRHa). They reported that the eggs are of similar quality (% of live eggs at 6 days post fertilization) to those from walleye spawning during the normal reproductive season. In pikeperch, using a very similar method (broodstock under natural photo-thermal conditions until late December, then gradual increase in temperature and photoperiod up to 12 °C and 14L:10D, respectively, over a 1-month period and injection of human chorionic gonadotropin hCG), similar results were obtained by Zakes and Szczepkowski (2004) or Zakes (2007) with spawning advanced by 3 months (early February) compared to the natural spawning season. Similar advanced pikeperch spawning (2 months before the natural spawning season) can be achieved without hormonal injection, but only with temperature and photoperiod manipulations. In their study, Müller-Belecke and Zienert (2008) accelerated maturation and spawning of mature (adult) pikeperch at 15 °C and 16 h light after a cooling period below 10 °C combined with a photoperiod of 8 light (L):16 dark (D). However, these authors did not succeed in obtaining postponed spawning with viable larvae.

In yellow perch, Kayes and Calbert (1979) did not succeed to advance spawning in wild breeders caught in February by warming up the water temperature precociously (up to 12 °C). In their experiment, spawning occurred at the same time as in the corresponding wild population. In a similar trial, using yellow perch broodstock caught in September, an artificial photo-thermal programme (photoperiod and temperature decrease down to L:D 10:14 and 7.5 °C from September to October, followed by stable conditions and finally photoperiod and temperature increase up to L:D 15:9 and 13 °C in January) allowed advanced spawning to be obtained (1 month earlier as compared to the natural spawning occurring in April in the control group) (Dabrowski et al. 1996). However, lower maximum GSI (14 % vs 22 %) and viability of eggs (36 % vs 81 %) were recorded. These authors concluded that condensing the photo-thermal cycle, in expense of the vitellogenic phase, is not an effective method to induce advanced spawning in female yellow perch. According to them, photo-thermal manipulation during the period of active ova growth and vitellogenesis, as well as during the post vitellogenic phase of ovarian development, does not lead to accelerated and/or normal spawning in yellow perch. In males, patterns of changes in GSI, milt weight and sperm concentrations in groups with one out of the two factors shifted (temperature, photoperiod) were not significantly different from those of the control group (ambient temperature and photoperiod). It thus seems that variation of only one factor is enough to drive spermatogenesis until the spawning period. Males and females yellow perch respond differently to such photoperiod and temperature variations.

3.3.2.2 Obtaining Out-of Season Spawning

In percid fish, photoperiod and/or temperature manipulations can be used to delay the onset of the reproductive cycle and to avoid negative effects of undesirable reproductive cycles during the on-growing phase (negative interactions with growth). It was shown that the application of continuous light (L:D 24:0) or constant light based on a long day length (L:D 14:10, L:D 16:8 or L:D 17:7) inhibits the onset of puberty in Eurasian perch (Migaud et al. 2003b, 2004a; Abdulfatah et al. 2011), yellow perch (Shewmon et al. 2007) or pikeperch (Ben Ammar et al. 2015), even if water temperature is decreased. In Eurasian perch a photoperiod increase is also effective in delaying the onset of puberty (Fontaine et al. 2006). Generally, simulation of summer conditions delays gonad development and puberty (Dabrowski et al. 1996). The inhibition of the female reproductive cycle by constant photo-thermal conditions may be related to lower sex steroid levels and to an inhibition of ovarian regulation by gonadotropins, probably stopping gonadogenesis before the vitellogenesis stage (Milla et al. 2009).

Under farm conditions (RAS), out-of-season spawning based on a complete control of the reproductive cycle, from its initial induction to spawning, is currently used for Eurasian perch or pikeperch production in Europe (between 4 and 12 spawnings per year according to SMEs). Management of the reproductive cycle is based only on temperature and photoperiod manipulations, combined or not with hormonal treatments for spawning synchronization (see Chap. 4). In percid fishes, the reproductive cycle is induced by decreasing both temperature and photoperiod, then a chilling period to allow vitellogenesis and finally increasing temperature so as to synchronize the final stages of the maturational process (Wang et al. 2010). A reliable photo-thermal protocol has been finalized for Eurasian perch, which allows 100 % gravid females, spawning and spermiating males to be obtained at each out-of-season spawning period after 11 months of photo-thermal manipulations (Fig. 3.3, Abdulfatah 2010). To achieve such performance, the main critical steps that need to be followed are:

- The application of a photoperiod decrease (high amplitude, 4 or 8 h) followed by a gradual temperature decrease 1 month later (Wang et al. 2006; Abdulfatah et al. 2011, 2013),
- A long wintering period with a low temperature (6 °C) and constant short day length (L:D 8:16) (Abdulfatah 2010; Abdulfatah et al. 2013) and
- A water temperature increase up to 12–14 °C (Abdulfatah et al. 2012).

Furthermore, some recommendations should be mentioned. An initial low amplitude photoperiod decrease (1 h) is too close to the threshold of sensitivity below which females do not perceive photoperiod variations (Abdulfatah et al. 2011). Even if the water temperature remains constant at 22 °C, a photoperiod decrease from summer conditions (L:D 16:8) to winter conditions (L:D 8:16) induces the

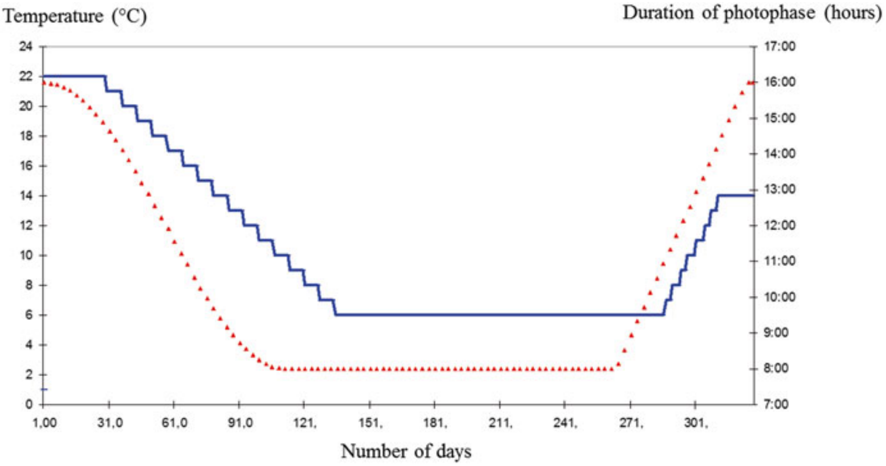

Fig. 3.3 Photo-thermal protocol applied under farm conditions to obtain out-of-season spawning in Eurasian perch (Abdulfatah 2010). *Blue line*: variations of temperature, *red line*: variations of photophase duration

reproductive cycle in females (Abdulfatah et al. 2013). Similar results were observed in yellow perch (Shewmon et al. 2007).

Recently, research has also been examining how to induce out-of-season spawning in pikeperch. Taking into account the results of Müller-Belecke and Zienert (2008) and Hermelink et al. (2011, 2013) set up an experiment about the induction of puberty in virgin pikeperch of 2 years old (mean body weight: 350 g) by different temperature regimes under a constant photoperiod (L:D 12:12). In their first study, broodstock was subjected to five different cooling regimes (from 23 °C to 6 °C, 9 °C, 12 °C, 15 °C or 23 °C over a 30-day period) and then fish were reared at these 5 temperatures for 5 months. After 4 months (including the initial cooling period), female pikeperch reared at 12 °C showed a significant increase in GSI and plasma E2 concentration and 90 % of the females were in mid-vitellogenesis. Later, significant oogenesis development was also observed at 9 and 15 °C, whereas at 6 and 23 °C in nearly all females stagnation of oogenesis was recorded. They concluded first that a moderate temperature (12 °C) is most efficient and that high (23 °C, no thermal change) and low (6 °C) temperatures prevent gonadal maturation, and second that temperature is the prime factor in the induction of puberty in pikeperch (Hermelink et al. 2011). In the framework of a second study (Hermelink et al. 2013), gametogenesis was induced by a 14-day cooling period (23 °C down to 12 °C) followed by subsequent rearing at 12 °C for 12 weeks at a fixed L:D 12:12 photoperiod, and finally breeders (250 g) were kept for 12 more weeks at 12 °C, 14 °C, 16 °C or 18 °C. It was shown that post pubertal temperatures about 14 °C promoted complete ripening in pikeperch of both sexes within 8 weeks, whereas higher temperatures constrained full gonadal maturation. Furthermore, with reference to the optimal temperature for the induction of puberty, slightly higher temperatures about 14 °C are optimal for post pubertal maturation.

All these studies indicate that the induction of out-of-season reproduction in percid fishes (based on a complete control of the reproductive cycle) requires using RAS systems equipped with cooling units allowing temperature to be accurately controlled. Pikeperch seem to be less dependent on photoperiod variations than Eurasian perch. Nevertheless, it was recently demonstrated that photoperiod conditions modify pikeperch spawning performances such as spawning timing, so that fish under L:D 24:0 spawned earlier than those of other photoperiods (Sara Poursaeid et al. 2012). As it was demonstrated in Eurasian perch that photoperiod conditions are determinant during the initial induction phase and in the control of the final gamete quality (Migaud et al. 2004b, 2006) further studies will be necessary to specify the role of photoperiod in pikeperch out-of-season spawning.

3.4 Regulation of Reproductive Performance

The regulation of fish reproductive performance is multifactorial, with many environmental, nutritional or populational (related to broodstock characteristics) factors affecting them (Bromage and Roberts 1995). In percid fishes, few studies have examined this issue. Within the environmental factors, the effect of light has already been considered. It was shown that photoperiod affects gametogenesis, spawning time, spawning rate, egg quality and broodstock mortality (Migaud et al. 2006; Abdulfatah 2010; Sara Poursaeid et al. 2012). More particularly, Migaud et al. (2006) demonstrated that daily light variations are important in the control of Eurasian perch spawning. Likewise, Wang (2006) observed that male Eurasian perch sperm quality is affected by light intensity in interaction with their initial nutritional status. Males with low initial reserves (perivisceral adipose tissue) subjected to low light intensity (100 vs 1,000 lx) develop higher GSI with sperm in larger amount and with higher spermatozoa concentrations. Obviously, temperature is another key factor to obtain normal gametogenesis and high spawning quality. The wintering temperature must be kept low, under a threshold that seems to be different for Eurasian perch and pikeperch (Abdulfatah 2010; Hermelink et al. 2011, 2013). For example, in Eurasian perch, a wintering temperature of 14 °C is associated with advanced spawning with “white eggs” (no larvae) (Abdulfatah 2010). For this species, the wintering temperature must be below 14 °C in accordance with what Hokanson (1977) suggested for yellow perch (below 10 °C). Handling also appears as an important factor regulating percid reproductive performance. In Eurasian perch (Wang et al. 2006), handling combined with temperature modulated the broodstock response. One hundred per cent of the unhandled females held at 14 °C after the initial cooling period (9 weeks) were at the vitellogenesis stage with low plasma levels of cortisol (9 ng mL^{-1}) and high levels of E2 (1.6 ng mL^{-1}). In comparison, handled fish held at 6 °C exhibited a lower rate of females at the vitellogenesis stage (40–73 %) associated with higher plasma levels of cortisol (40–90 ng mL^{-1}) and lower levels of E2 (0.6–1.1 ng mL^{-1}). When a handling stress is applied later, for example during the spawning season, it can result in a delay or lack of spawning as observed in pikeperch (Sara Poursaeid et al. 2012). Broodstock diet was also shown to be another major issue for percid reproduction. Concerning nutritional factors, the initial status of broodstock is important while the initial fat storage of male pikeperch influences the quality of sperm, in terms of spermatozoa concentration and motility, and timing of spermiation. Fish with higher initial fat storage (fat index: 1.11 % vs 0.58 %) spermiated earlier during the spawning season than broodstock with a low level of fat (Teletchea et al. 2009b). Indeed, Wang et al. (2009) reported that the dry feed they had used was not totally adequate for percid reproduction. Henrotte et al. (2010a) have proved that the optimal dietary ratio for DHA/EPA/ARA must be 3/2/2 for Eurasian perch broodstock. These authors also showed that the dietary n-3/n-6 ratio affects the lipid composition of male perch semen but not the indicators of sperm quality (Henrotte et al. 2010b and Chap. 22).

3.5 Conclusions

Valuable results obtained over the last two decades have provided a real knowledge of percid broodstock management and the control of their reproductive cycles, especially to extend the natural spawning season (advanced spawning) and to induce out-of-season spawning with a complete control of the reproductive cycle and production of viable larvae. Reliable protocols are now available. However, further research is needed to secure the reproductive performance and to reduce the cost of juvenile production. Priority should be given to (1) the identification of the upper threshold for the wintering period, and (2) a better knowledge of the multifactorial regulation of reproductive performance.

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