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Determinism of the induction of the reproductive cycle in female Eurasian perch, *Perca fluviatilis*: Identification of environmental cues and permissive factors

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Abstract

In Eurasian perch, *Perca fluviatilis*, gametogenesis is induced by decrease of both temperature and photoperiod. However, a multiplicity of other factors can display non-permissive or modulating effects on the induction of the reproductive cycle. Consequently, a 9-week study was carried out to determine the environmental cues and permissive factors controlling the induction of the reproductive cycle in this species. A two-level fractional factorial design 2^{8-4} was used in order to identify the influent factors from 8 environmental and nutritional ones and their 28 interactions. Tested factors were: (1) amplitude of temperature decrease, (2) time, (3) kinetics and (4) amplitude of photoperiod decrease, (5) initial nutritional state, (6) handling, (7) feeding rate and (8) light spectrum. Increase of gonadosomatic index (GSIi), proportion of female in exogenous vitellogenesis (EVP), plasma 17 β-estradiol (E_2) and cortisol levels, fat consumption and food intake were evaluated.

This study showed that the amplitude of the decrease of temperature and the time of photoperiod decrease are the two main environmental cues controlling the induction of the reproductive cycle in Eurasian perch. GSIi was the highest (3.8%) when females were exposed to both low amplitude of temperature decrease and precocious decrease of photophase. It was the lowest (1.1%) when high amplitude of temperature decrease and late decrease of photophase were applied. Handling in association with temperature modulated the broodstock response. 100% of the unhandled fish held at 14 °C were at the exogenous vitellogenesis stage with mean E_2 and basal cortisol levels of 1.6 ng mL^{-1} and 9 ng mL^{-1} respectively. Handled fish and fish held at 6 °C exhibited lower vitellogenesis (40–73%) associated with lower E_2 (0.6–1.1 ng mL^{-1}) and higher basal cortisol levels (37–89 ng mL^{-1}). No other factor nor interaction displayed a cueing or non permissive effect on the induction of the reproductive cycle in female Eurasian perch. A first schematic model is proposed to explain the factorial determinism of the induction of the reproductive cycle.

Keywords: *Perca fluviatilis*; Factorial design; Reproductive cycle; Gonadal recrudescence

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1. Introduction

In temperate fish species, the induction of the reproductive cycle is mainly determined by annual photoperiod and/or temperature variations (Bromage et al., 2001). In Percids, and especially in Eurasian perch, *Perca fluviatilis*, the inductive roles of temperature and photoperiod on gametogenesis have been characterized (Migaud et al., 2002, 2003, 2004). Migaud et al. (2002) showed that a decrease of temperature was necessary to allow gametogenesis in Eurasian perch. However, these authors noticed that constant long days (16 L:8 D or continuous lighting) were inhibitive under natural temperature decrease (few or no gonadal recrudescence). Besides, during the same experiment, 100% female induction was observed with an artificial progressive decrease of photoperiod in association with the natural temperature decrease. Thus, temperature and photoperiod decreases are both required to induce gametogenesis in Eurasian perch, albeit their respective roles are still unknown. Moreover, information is scarce about which characteristics of these decreases (time, amplitude and kinetics) are actually playing a role in the induction of the reproductive cycle. In natural habitat, photophase starts decreasing approximately two months before water temperature and gametogenesis is initiated concurrently with the decrease of temperature (Sulistyo et al., 1998). Consequently, one question is whether there is an impact of the time of photophase decrease in relation to the beginning of the temperature decrease. Fontaine et al. (2006) have suggested that the threshold of amplitude of photophase decrease below which gametogenesis is induced could be less than 1 h. However, no information is available about the effects of the amplitudes of photophase and temperature decreases. It is also unknown whether kinetics of temperature and photophase decreases are important for the induction of the reproductive cycle. Finally, interactions between all of these characteristics are likely to exist, but have never been studied.

In addition to these inductive cues, it is important not to neglect the multiplicity of other factors that could modulate the broodstock response (Bromage et al., 2001). Such factors which have only permissive or modulating effects could still inhibit the onset of gametogenesis in some cases. For example, in some species, the nutritional status is of paramount importance for the fish to be able to reproduce. Indeed, it was shown that a reduction in feeding rate could cause an inhibition of gonadal maturation in several fish species, such as goldfish (*Carassius auratus*), European seabass (*Dicentrarchus labrax*) and male Atlantic salmon (*Salmo salar*), (Izquierdo et al., 2001). In other studies, food restriction led to decreases of fecundity and/or egg size as well as spawning rates in sea bass, rainbow trout and brown trout (*Salmo trutta*), (Billard and De Frémont, 1980; Bromage and Cumaranatunga, 1988; Bromage et al., 1992; Cerda et al., 1994; Carrillo et al., 1995). Percids are thought to be capital breeders (Henderson et al., 1996). This indicates that these species would store energy in the adipose tissue (i.e. mesenteric fat in Percids) before the beginning of the reproductive cycle to allocate this energy to ovarian growth during gametogenesis. Henderson et al. (1996) observed that the mesenteric fat content of female walleye (*Stizostedion vitreum*) decreased throughout a reproductive cycle while the lipid content of the ovary increased. From their results, they also hypothesized that a female with insufficient mesenteric fat content could not begin a reproductive cycle.

Another factor that strongly affects the reproductive success is breeding-stress (handling, breeding conditions…). In fish reared under stressful conditions, it has been postulated that a trade-off between energy allocation for reproduction and maintenance can occur (Schreck et al., 2001). Thus, it has been shown that repeated handling throughout a reproductive cycle could lead to smaller eggs and lower progeny survival (Campbell et al., 1992, 1994). Environmental factors such as lighting conditions (spectrum, intensity) and tank colour have been shown to modify fish sensitivity to stress (Ali et al., 1977; Bonga and Balm, 2003; Head and Malison, 2000; Volpato and Barreto, 2003). Physiologically, chronic stress depresses the circulating levels of sexual steroids via the action of cortisol (Pankhurst and Van Der Kraak, 1997). Thus, in female, reduced levels of 17 β-estradiol lead to reduced levels of vitellogenin and consequently less vitellogenesis (Schreck et al., 2001).

Little is known about the combined effects of environmental cues and permissive factors on the induction of the reproductive cycle in fish and virtually nothing is known about their interactions. It is likely that the determinism of the induction of the reproductive cycle in fish is multifactorial. Consequently, a study was carried out on the basis of a fractional factorial design to (i) identify the major environmental cues and permissive or modulating factors of the induction of the reproductive cycle in Eurasian perch and (ii) elaborate a first qualitative model of the determinism of its reproductive cycle.

2. Materials and methods

2.1. Fish

A set of 1500 fish (mean weight of 122 g, sex-ratio male/female of 1/2) were purchased from fish-farm