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Review

Effects of global warming on fish reproductive endocrine axis, with special emphasis in pejerrey *Odontesthes bonariensis*

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ABSTRACT

The ongoing of global warming trend has led to an increase in temperature of several water bodies. Reproduction in fish, compared with other physiological processes, only occurs in a bounded temperature range; therefore, small changes in water temperature could significantly affect this process. This review provides evidence that fish reproduction may be directly affected by further global warming and that abnormal high water temperature impairs the expression of important genes throughout the brain–pituitary–gonad axis. In all fishes studied, gonads seem to be the organ more readily damaged by heat treatments through the inhibition of the gene expression and subsequent synthesis of different gonadal steroidogenic enzymes. In view of the feedback role of sex steroids upon the synthesis and release of GnRH and GtHs in fish, it is possible that the inhibition observed at brain and pituitary levels in treated fish is consequence of the sharp decrease in plasma steroids levels. Results of *in vitro* studies on the inhibition of pejerrey gonad aromatase expression by high temperature corroborate that ovary functions are directly disrupted by high temperature independently of the brain–pituitary axis.

For the reproductive responses obtained in laboratory fish studies, it is plausible to predict changes in the timing and magnitude of reproductive activity or even the total failure of spawning season may occur in warm years, reducing annual reproductive output and affecting future populations.

1. Introduction

Temperature is one of the most important physicochemical variables that determine the overall functioning of aquatic communities (Ficke et al., 2007; Jeppesen et al., 2010; Mooij et al., 2009; Pörtner and Farrell, 2008). All physiological processes within an organism occur within a limited temperature range, which may differ depending on the molecular and cellular mechanisms associated with each particular process (Pörtner and Farrell, 2008). In this sense, species are adapted to a certain range of temperature variation, depending largely on the geographic area where they have evolved.

Fish, as well as other ecothermic organisms, have a body temperature "virtually" equal to that of its environment, so any variation in this variable will affect them directly (Ficke et al., 2007). Thus, the temperature in aquatic ecosystems is a key variable in the geographical distribution of different fish species (Cussac et al., 2009; Perry et al., 2005), and any temporary change in its normal patterns could generate consequences such as changes in abundance, spatial distribution and even extinction (Ficke et al., 2007).

The reproduction in fish, compared with other physiological processes, only occurs in a bounded temperature range (Pörtner and Farrell, 2008) therefore, small changes in water temperature could significantly affect this process (Van der Kraak and Pankhurst, 1997; Zięba et al., 2010; Zucchetta et al., 2012). In temperate climates, the thermal conditions that allow reproduction in most fish usually occur seasonally and, together with day length (Migaud et al., 2010) determine the reproductive seasonality of different fish species (Fig. 1). This, in an evolutionary frame is interpreted as a mechanism associated with the selection of environmental conditions that increase the likelihood of survival and development of the offspring (Bromage et al., 2001; Pörtner and Farrell, 2008). In this context, abnormal water temperature conditions could generate a mismatch between reproduction and optimal environmental conditions for progeny development (Durant et al., 2007). Besides, shortening or even complete loss of the breeding season could also happen (Elisio et al., 2012a). It is important to note that any of these possible scenarios could generate a loss in the reproductive output of a given population, change its structure and may jeopardize its sustainability (Durant et al., 2007; Strüssmann et al., 2010).

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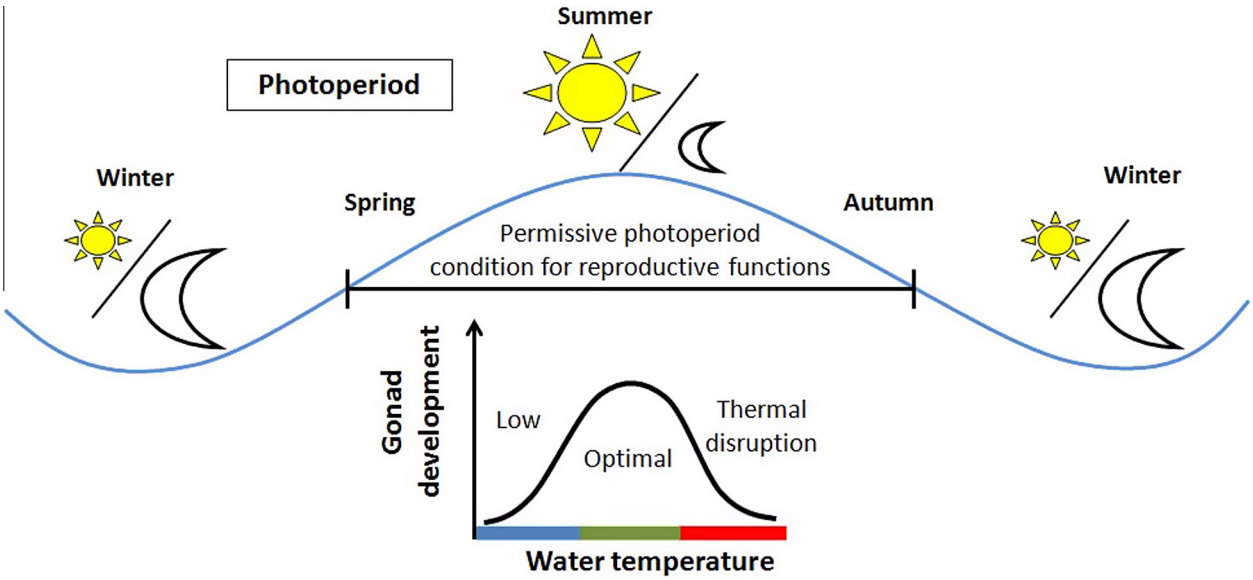

Fig. 1. Schematic representation of environmental cues that regulate reproductive cycle in temperate fish species. Photoperiod shown in the upper half of the figure by blue line and sun/moon size. Long photoperiod conditions (from beginning of spring to end of autumn) are permissive for gonad development. The influence of water temperature (*X* axis) on the gonad developmental rate (*Y* axis) when photoperiod is permissive for reproduction is shown in the lower half of the figure. Different colors of the *X* axis indicate different effects of thermal conditions on gonad development: low (blue), optimal (green) and thermal disruption (red).

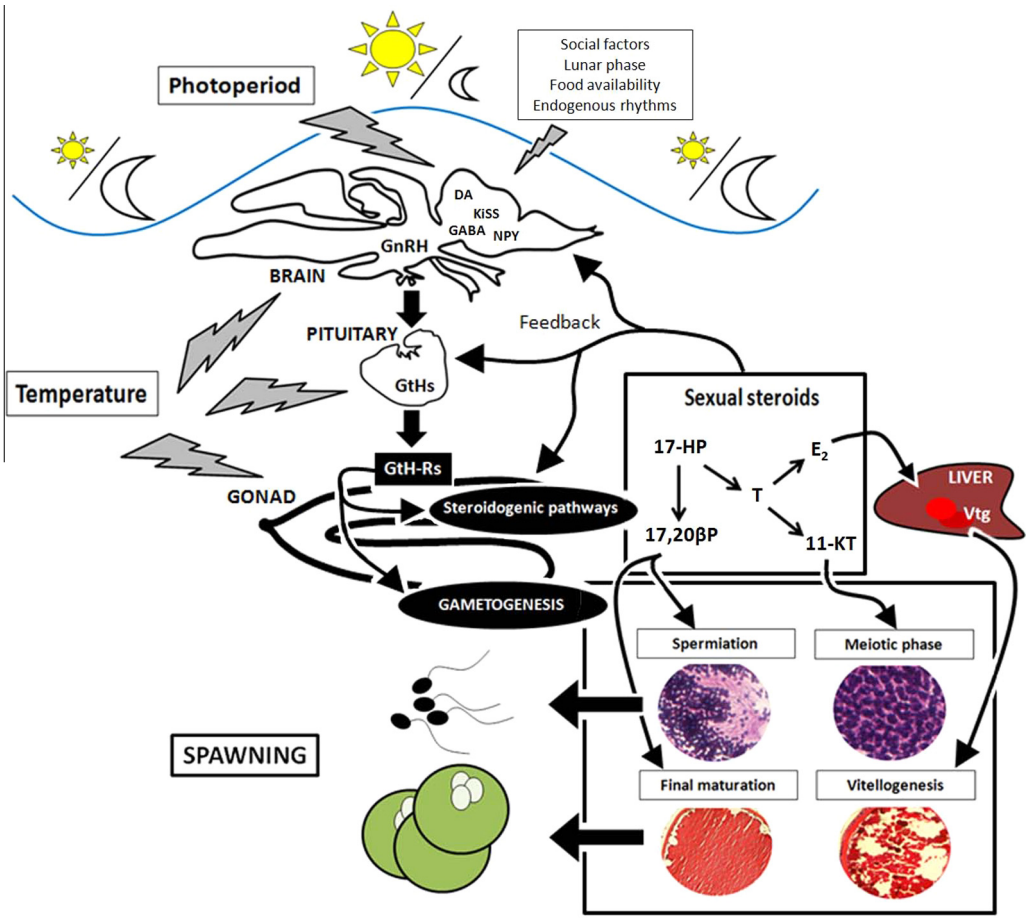

Fig. 2. Schematic representation of the environmental influences on the regulation of fish brain–pituitary–gonad axis. **Photoperiod** information is decoded by different hormonal pathways at brain level and together with other external factors (social interactions, lunar phase, food availability) and endogenous rhythms affect the reproductive functions. **Temperature**, can act directly or indirectly, enabling, inhibiting, or regulating velocity of the different metabolic pathways at all levels of the reproductive axis. **GnRH**, gonadotropin releasing hormone; **DO**, dopamine; **KiSS**, kisspepeptin; **GABA**, aminobutyric acid; **NPY**, neuropeptide Y; **GtHs**, gonadotropins; **E_2**, Estradiol; **17-HP**, 17α-hydroxyprogesterone; **T**, testosterone; **11-KT**, 11-ketotestosterone; **17,20βP**, 17,20β-dihy-droxy-4-pregnen-3-one; **Vtg**, vitellogenin. The graphic representation of brain, pituitary and gonad are based on pejerrey observations and are not represented in scale.

Among extant fishes, Atheriniformes seem to be most sensitive to temperature-induced gonadal dysfunctions and have many attributes that render them as suitable "early warning biological indicators" of the effects of global warming and climate change on fish resources and their aquatic ecosystems. For instance, many Atheriniforms have been shown to have temperature-dependent sex determination, whereby the gonadal sex of an individual is determined by water temperature during a short and critical time early in life. For example, the pejerrey (*Odontesthes bonariensis*) can be feminized or masculinized if water temperature during breeding season is too low or too high respectively (Strüssmann et al., 1997). This species also shows heat-induced gonadal degeneration and germ cell loss, whereby prolonged exposure to high water temperatures caused reduction in the number of germ cells leading to partial or even complete sterility (Strüssmann et al., 2010). Moreover, it has been recently demonstrated that pulses of warm water similar to those occasionally recorded in natural environment during pejerrey spawning season can disrupt all levels of the reproductive axis, impairing reproduction (Elisio et al., 2012a).

The knowledge of the interaction between different environmental variables that regulate the reproductive axis in fish is of great importance for the understanding and prediction of ecological phenomena related to fish populations and for possible uses in the control of fish captive breeding. In this regard, it has been recently observed that abnormal conditions of high water temperatures alter the functioning of the reproductive axis impairing fish spawning (Elisio et al., 2012a; Pankhurst and Munday, 2011). Knowledge of the physiological mechanisms by which high water temperature disrupts fish reproduction could contribute to understanding and predicting possible shifts in fish population under a changing climate scenario. In this context, the purpose of this paper is to review the current knowledge of the effects of global warming on fish reproductive endocrine axis, with special emphasis in pejerrey *O. bonariensis*.

2. Endocrine regulation of fish reproduction

At the endocrine level, fish reproduction is regulated by different hormones that control the functioning of the reproductive brain–pituitary–gonad axis (Fig. 2). The regulation of this axis is very complex, and there are certain mechanisms in fish that are not fully understood. It is known that the central nervous system plays a key role in the integration of various external (environmental) and internal (hormonal) signals regulating reproduction. Among several brain areas identified in the control of reproductive processes and behaviors, the hypothalamus seems to be the most important (Kah et al., 1993; Zohar et al., 2010). In vertebrates, brain regulates reproduction through the neuroendocrine control exerted on the pituitary. Unlike tetrapods, teleosts lack a hypothalamic-pituitary portal system, and instead the hypophysis is directly innervated by neuronal axons from the hypothalamus (Zohar et al., 2010). Several factors involved in the hypothalamic control of reproduction have been identified: gonadotropin releasing hormone (GnRH), dopamine, neuropeptide Y (NPY), gamma-aminobutyric (GABA) and more recently kisspeptin (KiSS; Zohar et al., 2010). Among these factors, the first relating to the pituitary control during reproduction was GnRH (Breton et al., 1971). This neurohormone is a decapeptide that has a master role in the control of reproduction, so much so that it is now widely used for induction of spawning in several species kept in captivity (Mylonas et al., 2010).

In fish, it has been reported the existence of up to three brain GnRH variants, which according to their anatomical location and its molecular identity can be classified as GnRH-I, GnRH-II or GnRH-III. The hypophysiotropic GnRH-I variant is expressed in the preoptic-hypothalamic area, GnRH-II is expressed in the midbrain and GnRH-III is expressed in the terminal nerve ganglion and the anterior telencephalon (Fernald and White, 1999).

The main function of GnRH-I in reproduction is to induce the synthesis and release of pituitary gonadotropins (GtHs; Levavi-Sivan et al., 2010). The GtHs, follicle stimulating hormone (FSH) and luteinizing hormone (LH), are heterodimeric glycoproteins composed of a common α subunit (α glycoprotein hormone, GPH-α) and a specific β subunit (FSH-β and LH-β). These hormones are critical in the endocrine control of reproduction, promoting the synthesis of sex steroids through the stimulation of specific enzymes (Kumar et al., 2000; Lubzens et al., 2010; Nagahama, 1994) and regulating gametogenesis (Levavi-Sivan et al., 2010). Among the steroids involved in stimulating fish gonadal development it is possible to distinguish androgens, estrogens and progestins. In general, androgens, such as testosterone (T) and the 11-Ketotestosterone (11-KT), are related with the development of spermatogenesis (Schulz et al., 2010), whereas estrogens, being estradiol (E_2) the most important, are involved in oogenesis stimulation (Lubzens et al., 2010). In addition, progestins regulate final maturation and spawning in both sexes (Nagahama, 1997; Scott et al., 2010).

3. Effects of high water temperature on the endocrine reproductive axis

High water temperature can impair gonadal development and block spawning altering different components of the endocrine reproductive axis (Pankhurst and Munday, 2011; Gillet et al., 2011; Strüssmann et al., 2010). Examples of such effects are available for both marine fish (*Pagrus major* (Okuzawa et al., 2003); *Morone saxatilis* (Clark et al., 2005); *Gadus morhua* (Tveiten and Johnsen, 2001); *Salmo salar* (Pankhurst and King, 2010) and freshwater fish (*Oncorhynchus mykiss* (Pankhurst and Thomas, 1998); *Anarhichus lupus* (Tveiten and Johnsen, 1999); *O. bonariensis* (Soria

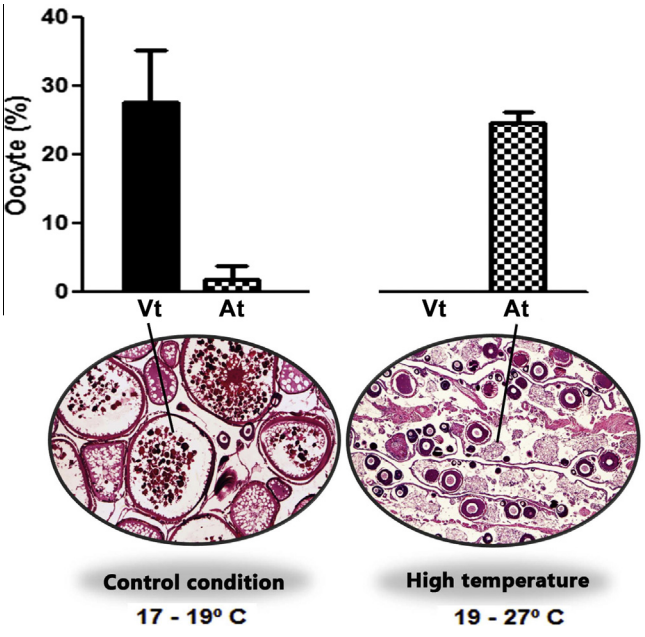

Fig. 3. Effects of high water temperature conditions (8 days of daily water temperature fluctuations from 19 °C to 27 °C) on pejerrey ovaries during spawning season. On the upper half of the figure, plots represent the proportion of vitellogenic (**Vt**, black bar) and atretic (**At**, grid bar) oocytes of control (left plot) and treated (right plot). Representative histological sections from ovaries from each condition is shown on the lower half of the figure. More details in Elisio et al. (2012a).

et al., 2008; Elisio et al., 2012a); *Coregonus lavaretus* (Wahl and Löffler, 2009); *Sander lucioperca* (Hermelink et al., 2011); *Salvelinus alpinus* (Gillet and Breton, 2009; Gillet et al., 2011); *Trichogaster trichopterus* (Levy et al., 2011)).

In the gonads, high temperature provoked a complete regression in *O. bonariensis* (Fig. 3; Elisio et al., 2012a; Soria et al., 2008), *P. major* (Okuzawa et al., 2003), *M. saxatilis* (Clark et al., 2005), *Acipenser transmontanus* (Webb et al., 1999), *Perca fluviatilis*, *Rutilus rutilus*, *Esox lucius* (Lukšienė et al., 2000) and *S. salar* (Pankhurst et al., 2011). In the case of pejerrey this condition could be reverted eleven weeks after the heat treatment (Elisio et al., 2012a).

Gonadal regression and spawning impairment in fish by high water temperature is associated with the inhibition of the expression of specific genes at different levels of brain–pituitary–gonad axis. In the brain only the hypophysiotropic GnRH variant was reported to be affected in both sexes of *T. trichopterus* (David and Degani, 2011; Levy et al., 2011) and *O. bonariensis* (Elisio et al., 2012a) and in females of *P. major* (Okuzawa et al., 2003). At pituitary level, an inhibition of *Fsh-β* expression was found in females of *T. trichopterus* (Levy et al., 2011) and pejerrey (Elisio et al., 2012a). However previous studies found a diminution only in *Lh-β* expression of females of *P. major* (Okuzawa et al., 2003) and pejerrey (Soria et al., 2008). High temperatures also reduced LH secretion in *S. alpinus* females (Gillet and Breton, 2009). On the other hand, circulating levels of FSH in *S. salar* were significantly elevated in females maintained at 22 °C compared to 14 °C during vitellogenesis, but plasma LH levels were mostly unaffected (Anderson et al., 2012).

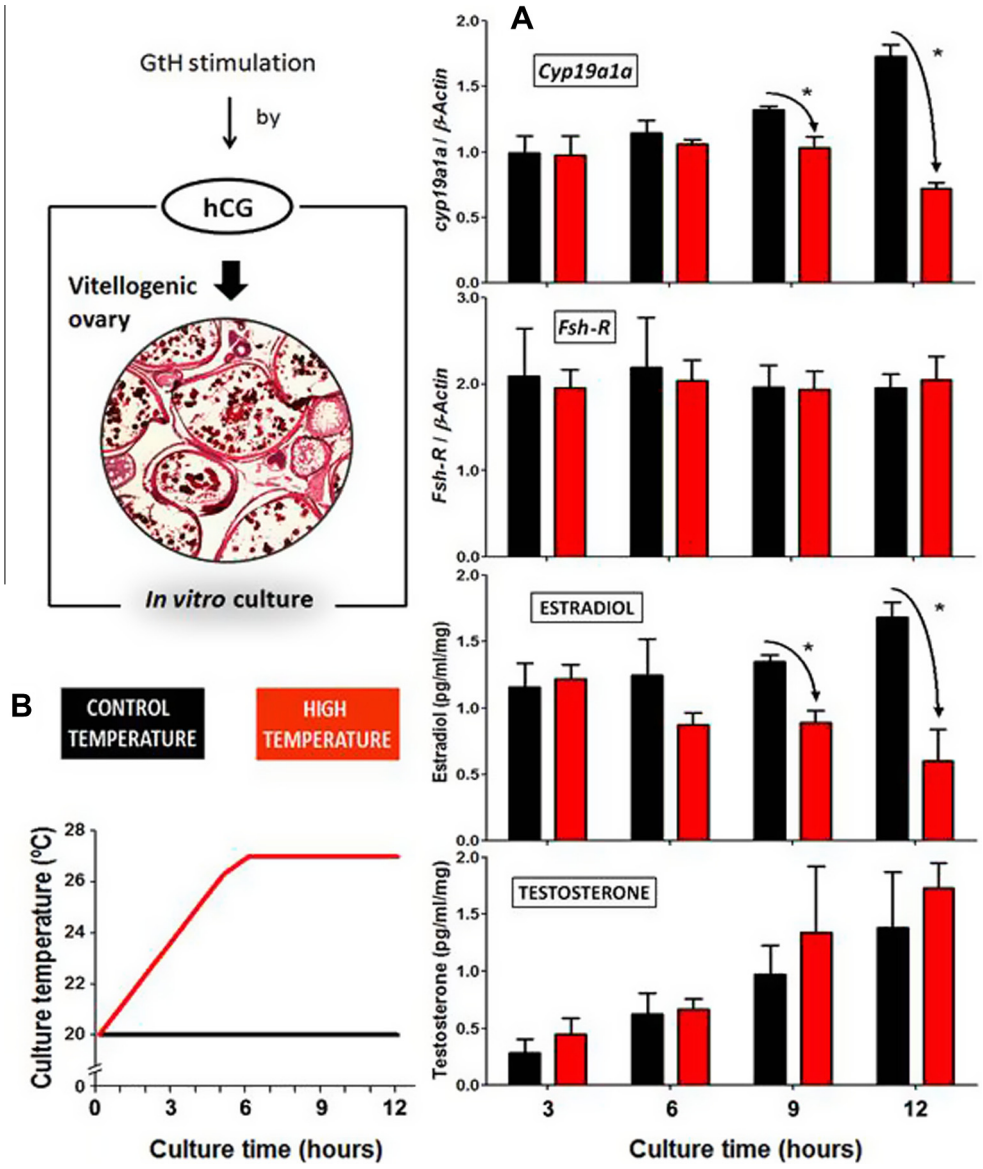

Fig. 4. (A) Effects of high water temperature on testosterone (T) and estradiol (E_2) synthesis, follicle stimulating hormone receptor (*Fsh-R*) and gonadal aromatase (*Cyp19a1a*) gene expression in pejerrey vitellogenic ovaries *in vitro*. Fragments of vitellogenic ovaries with approximately 200 mg were incubated with 10 UI of HCG (doses previously demonstrated to be effective in stimulating T and E_2 synthesis) at 20° (control temperature, in black) or 27 °C (high temperature, in red). After 3, 6, 9 and 12 h, culture media were taken for testosterone (T) and estradiol (E_2) measurement by enzyme-linked immunosorbent assay (ELISA) and, ovarian fragments were used to measure the expression levels of *Fsh-R* and *Cyp19a1a* by real-time RT-PCR. Gene expression data were normalized using *β-actin* mRNA levels. Each column represents the average and standard deviation from 3 different vitellogenic ovaries. Actual temperature during culture time is shown in B. The differences between temperature groups were analyzed using two-way (time and thermal treatment) repeated measures (in time) analysis of variance (ANOVA), followed by Bonferroni's multiple comparison test. Asterisks represent statistically significant differences between temperature groups at each culture time ($p < 0.05$). Statistical analyses were performed using SPSS 17.0 and GraphPad Prism 5.0 software.

These differences may be due to different species, gonad stage, heat treatment, and/or methods of gene expression quantification. In males, both GtH–β subunits diminished after heat treatment in *T. trichopterus* (David and Degani, 2011) and pejerrey (Elisio et al., 2012a) revealing a different mechanism of regulation from that of females. In fish testes, FSH and LH receptors expression did not change after heat exposure (Elisio et al., 2012a) but decreases observed in plasma T and 11-KT levels (Clark et al., 2005; Elisio et al., 2012a; Soria et al., 2008) suggested that steroidogenic activity was affected. Moreover, it was demonstrated in *P. major* that high water temperature depressed the expression of 11β-hydroxylase (which mediates the conversion of T to 11-KT) in juveniles (Lim et al., 2003). It is known that 11-KT is involved in proliferation of spermatogonia (Schulz et al., 2010), so the findings of Lim et al. (2003) could explain the reduction in spermatogonia and spermatocytes in males exposed to high temperatures (David and Degani, 2011; Elisio et al., 2012a).

A sharp decrease in plasma E_2 appears to be a common response to elevated temperatures in females of all fish species studied so far (Pankhurst and King, 2010; Pankhurst and Munday, 2011) but few studies have examined the mechanisms by which this suppression is mediated. An important factor affecting estrogen production is the expression and activity of the gonadal aromatase (P450arom), which converts androgens to estrogens. The thermal sensitivity of P450arom has been well studied in the context of sexual determination/differentiation of several fish species (Guiguen et al., 2010; Piferrer and Guiguen, 2008) including pejerrey (Fernandino et al., 2008). It was also demonstrated that high water temperatures suppressed the expression of P450arom gene (*cyp19a1a*) and inhibited oocyte development in the hermaphroditic

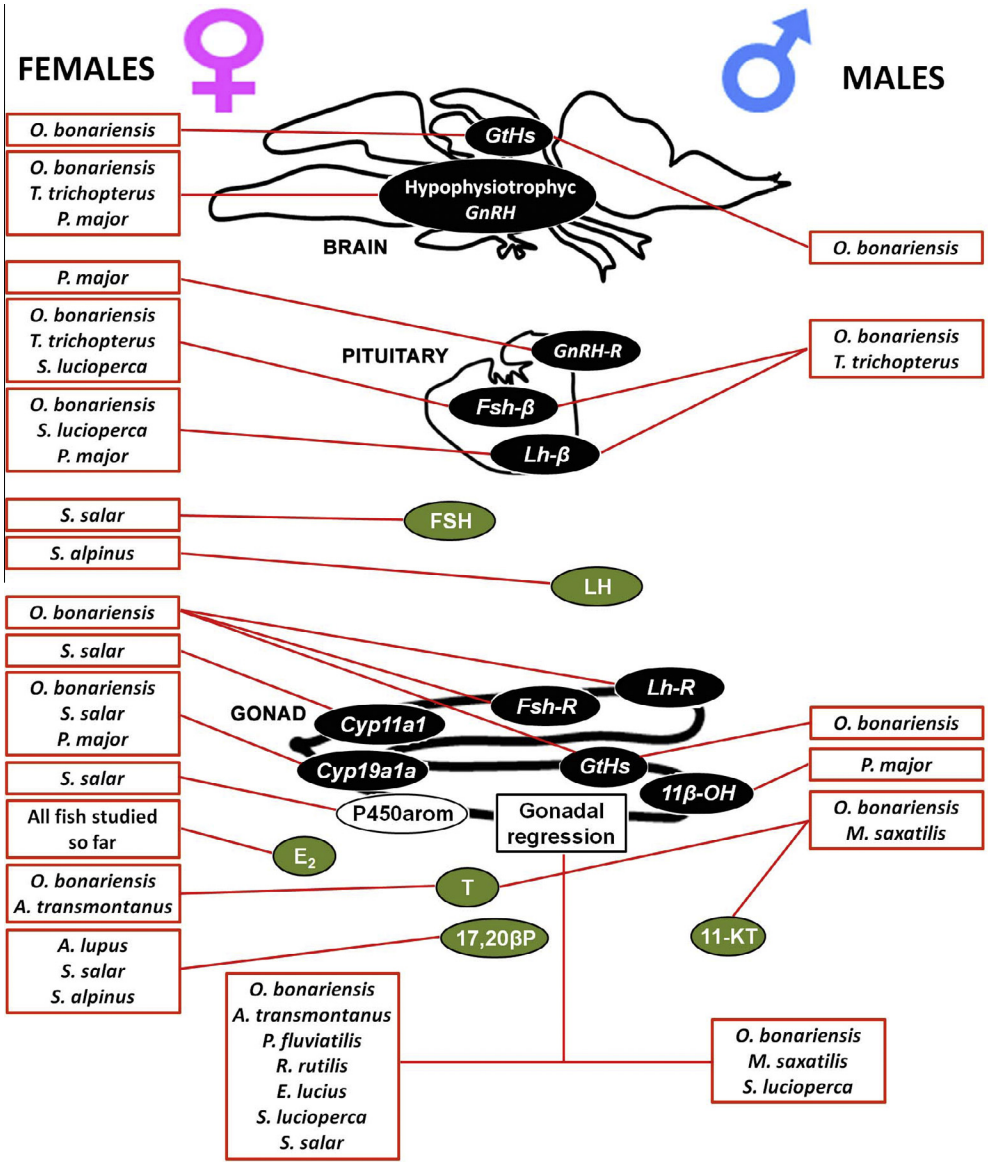

Fig. 5. Scheme summarizing the disruption by high water temperatures of the reproductive endocrine axis in fish. Results are shown separately for females and males. The red lines indicate the species studied and which component of the brain–pituitary–gonad axis was affected. Black ellipses represent thermal disruption at gene expression level, green ellipses at plasma level, and white ellipses at enzyme activity level. ***GnRH***, gonadotropin releasing hormone mRNA; ***GtHs***, gonadotropin subuinits mRNAs; ***GnRH-R***, gonadotropin releasing hormone receptor mRNA; ***Fsh-β***, follicle stimulating hormone β subunit mRNA; ***Lh-β***, luteinizing hormone β subunit mRNA; **FSH**, follicle stimulating hormone; **LH**, luteinizing hormone; ***Fsh-R***, follicle stimulating hormone receptor mRNA; ***Lh-R***, luteinizing hormone receptor mRNA; ***Cyp11a1***, cholesterol side chain cleavage protein mRNA; ***Cyp19a1a***, gonadal aromatase mRNA; **P450arom**, gonadal aromatase; ***11β-OH***, 11β-hydroxylase mRNA; **E_2**, estradiol; **T**, testosterone; **11-KT**, 11-ketotestosterone; **17,20βP**, 17,20β-dihy-droxy-4-pregnen-3-one. The schemes of brain, pituitary and gonad are based on pejerrey observations and are not drown in scale.

gonads of red seabream (Lim et al., 2003). In *S. salar*, the inhibition of P450arom activity has been shown in isolated ovarian follicles under high temperature conditions (Watts et al., 2004). Recently, it was also demonstrated a strong reduction in the expression of *cyp19a1a* in females of the same species (Anderson et al., 2012) and in pejerrey females kept in warm water (Elisio et al., 2012a). These last results suggest that the low activity of P450arom may be due to a problem in the synthesis of the enzyme rather than a possible post-translational modification. Parallel to the inhibition of E_2 synthesis in *S. salar*, an increase of T levels was observed (King et al., 2003, 2007; Pankhurst and King, 2010). However in other species, T levels were low, indicating that high temperatures also affected Androgen synthesis in females as it was also demonstrated in males (Elisio et al., 2012a; Tveiten and Johnsen, 2001).

Given the known roles of GtH and their receptors in the stimulation of oocyte development and steroidogenesis (Levavi-Sivan et al., 2010), a decrease in the expression of both receptors observed in heat treated pejerrey females (Elisio et al., 2012a; Soria et al., 2008) would seem to signal the disruption of the GtHs/GtHRs system which in turn could lead to inhibition of aromatase expression and consequently a fall in E_2 levels and oocyte atresia. However, *in vitro* assays using pejerrey vitellogenic ovaries stimulated with hCG, showed that E_2 levels and *cyp19a1a* expression significantly decreased after 9 h of culture at 27 °C compared with 20 °C, meanwhile T levels and *Fsh-R* expression remained unchanged (Fig. 4). These findings demonstrated that ovarian function is directly disrupted by high temperature independently of the brain–pituitary axis, being the inhibition of aromatase expression and consequently E_2 synthesis a primary cause behind female reproductive impairment. At final maturation stages several studies have shown that females exposed to elevated temperatures inhibit the synthesis of the maturational steroid 17,20β-dihy-droxy-4-pregnen-3-one (17,20βP) and subsequent progression of oocytes through final oocyte maturation (Gillet et al., 2011; Pankhurst and King, 2010; Tveiten et al., 2000).

Moreover, the recent discovery of extrapituitary GtHs in fish (Pandolfi et al., 2009; Parhar et al., 2003; Wong and Zohar, 2004) further complicates the study of environmental effects on reproductive endocrine regulation. In pejerrey, it was possible to identify GtH subunits in the brain and gonad of both sexes, and it was demonstrated that their expression was inhibited under temperatures that impaired reproduction (Elisio et al., 2012c). In the case of gonadal GtH subunits, they were identified in germ cells at different gametic developmental stages. Interestingly, the decrease in the expression of GtHs observed under high temperatures coincided with the partial or total disappearance of several gametic type cells (mainly vitellogenic oocytes; (Elisio et al., 2012a,c). In this sense, it would be interesting to evaluate whether the decreased expression of gonad GtH would be cause or consequence of the disappearance of such gametic stages.

A summary of the findings of various studies dealing with high temperature caused endocrine disruption of the different component of the reproductive axis in fish of both sexes is presented in Fig. 5.

4. Effects on spawning phenology, fertility and quality of gametes

One of the principal responses of wild species to the Global Warming is the change of the breeding time and its phenological phase (Parmesan and Yohe, 2003; Root et al., 2003). It has been reported that the majority of vertebrate species studied, (especially amphibians, reptiles and birds) presented the same direction of responses showing an advancement of the breeding season, being these responses stronger at higher latitudes (Parmesan, 2007). Nevertheless, in fish the impact of an increase of temperature on the phenology timing depends on when in the annual thermal cycle the spawning normally occurs (Table 1). In this sense, it is possible to differentiate two kinds of reproductive strategy in fish: (1) "*fall spawner*", the vitellogenesis period occurs during spring-sum-

Table 1
Effects of elevated water temperature during pre-spawning period in fall and spring spawner fish.

Species	Treatment	Result	Biology	References
Pejerrey (*Odontesthes bonariensis*)	Captivity	Advancement of E_2 peak and spawning, low fertility.	Estuarine-freshwater, spring spawner	This review
Atlantic cod (*Gadus morhua*)	Wild and captivity	Advancement of E_2 peak and spawning, low fertility.	Marine, spring spawner	Hutchings and Myers (1994), Tveiten (2008)
European grayling (*Thymalus thymallus*)	Wild and captivity	Spawning advance, low egg survival eye stage.	Freshwater, spring spawner	Lahnsteiner and Kletzl (2012)
Gras goby (*Zosterisessor ophiocephalus*)	Wild	Advancement of spawning.	Estuarine, spring spawner	Zucchetta et al. (2012)
Mackerel (*Scomber scombrus*)	Wild	Advancement of spawning.	Marine, spring spawner	Jansen and Gislason (2011)
Murray cod (*Maccullochella peelii peelii*)	Captivity	Advancement of reduced E_2 peak and spawning.	Freshwater, spring spawner	Newman et al. (2010)
Pumpkinseed (*Lepomis gibbosus*)	Captivity	Advancement of spawning.	Freshwater, spring spawner	Zięba et al. (2010)
Roach (*Rutilus rutilus*)	Wild	Advancement of spawning.	Freshwater, spring spawner	Gillet et al. (1983)
Sole (*Solea solea*)	Wild	Advancement of spawning.	Marine, spring spawner	Fincham et al. (2013)
Arctic charr (*Salvelinus alpinus*)	Captivity	Delayed spawning and inhibited ovulation.	Freshwater, fall spawner	Gillet (1991), Jobling et al. (1995), Gillet et al. (2011)
Atlantic halibut (*Hippoglossus hippoglossus*)	Captivity	Delayed spawning. Reduced quantity and quality of eggs.	Marine, spring spawner (spawn in depth cold water)	Brown et al. (2006)
Atlantic salmon (*Salmo salar*)	Captivity	Delayed spawning. Reduced E_2. Low fertility, egg size and embryo survival.	Marine, fall spawner.	King et al. (2003), King et al. (2007)
Common wolffish (*Anarhichas lupus*)	Captivity	Delayed spawning. Low embryo survival.	Marine fish, fall spawner.	Tveiten and Johnsen (1999)
Rainbow trout (*Oncorhynchus mykiss*)	Captivity	Delayed spawning. GtH, T and E_2 unchanged. Delay steroidogenic shift. Low egg production and embryo survival.	Freshwater, fall spawner	Pankhurst et al. (1996), Pankhurst and Thomas (1998)

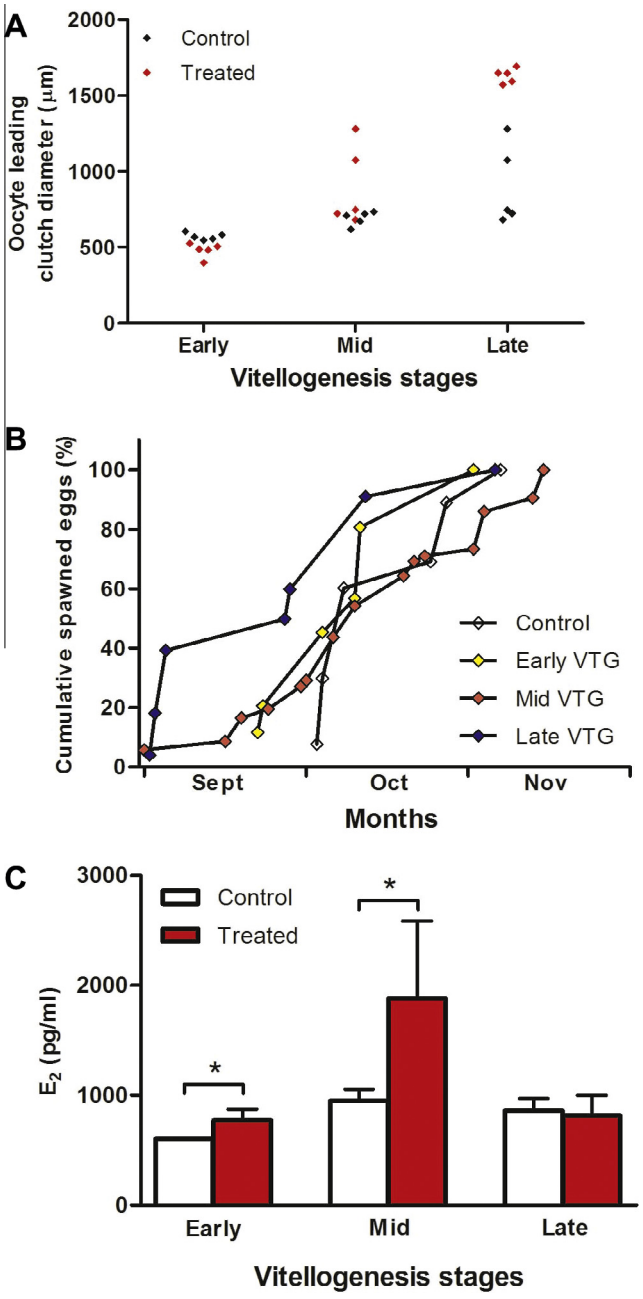

Fig. 6. Effects of pulses of warm water on pejerrey oocyte growth in *O. bonariensis* broodstocks. Four groups of fish (5 years old) were kept in captivity under natural photoperiod and temperature. Three groups were exposed to warm water pulses peak up to 20 °C during 4 days during winter. One group was exposed on the last week of June (early vitellogenesis), the second on the last week of July (mid vitellogenesis) and the third on the last week of August (late vitellogenesis). The characterization of vitellogenesis stages were done following (Strüssmann, 1989) and Elisio et al. (2012b). (A) Oocyte leading clutch diameter (μm). Red dot shows the oocyte leading clutch mean diameter of each female ($n = 5$) measured immediately after each temperature treatment compare with a control group (black dots). For each female, 200 oocytes collected by ovarian biopsy were photographed and measured using Image-Pro plus 4.5 software. In order to determine the oocyte leading clutch diameter "solver tool" application of Microsoft EXCEL was used. (B) Cumulative percentage of spawned eggs, showing the advancement of spawning. (C) Plasma E_2 levels of pejerrey females were measured immediately after heat treatment by an enzyme-linked immunosorbent assay (ELISA) using commercial kits, following the manufacturer's protocols (DRG Instruments GmBH, Frauenbergstr, Germany). Serum samples were previously extracted with diethyl-ether and resuspended in their initial volume with ELISA buffer. Values are expressed as mean ± SEM ($n = 5$). Asterisks show statistical differences between treated and control group (ANOVAs followed by Dunnett's multiple comparison test; $p < 0.05$).

mer and the spawning takes place in autumn and (2) "*spring spawner*", the vitellogenesis period occurs during autumn–winter and the spawning takes place mainly during spring (Shuter et al., 2012). For fishes that spawn during spring the effects of high water temperature during vitellogenesis can be summarized as an advance of reproductive activity, while a delay of the onset of the breeding season was observed in fall spawners (Table 1). Then, a consequence of global warming could be a shortening of the spawning season depending on the breeding strategy. Moreover, it is important to mention that in most cases the advance or delay of the breeding season also produced changes in the quality of gametes. In the case of pejerrey (spring spawner), a clear advancement of the onset of the spawning activity was observed when broodstocks were exposed to elevated temperature during early (June), mid (July) or late (August) vitellogenesis stages (Fig 6a). This advancement was higher when heat treatment was performed at the end of vitellogenesis (30 days before control group, Fig. 6b). Similar results were observed in other freshwater spring spawner such as Murray cod (*Maccullochella peelii peelii*) and the European grayling (*Thymalus thymallus*), with lower quality of gametes after warm water exposition (Lahnsteiner and Kletzl, 2012; Newman et al., 2010). On the other hand in fall spawners, it has been reported that elevated temperature during vitellogenesis period delay the spawning activity, inhibiting the final oocyte maturation and ovulation in *O. mykiss* (Pankhurst et al., 1996; Taranger and Hansen, 1993); *S. salar* (King et al., 2007); *S. alpinus* (Gillet et al., 2011), and *A. lupus* (Tveiten and Johnsen, 1999).

As it was mentioned, the quality of eggs is negatively affected when females spawned out of time due to elevated temperature. For example in *A. lupus*, low embryos survival was obtained from broodstocks reared at 12 °C compared to 4 °C and 8 °C groups (Tveiten and Johnsen, 1999). Similar finding was reported in *S. salar* with a low fertilization rate (King et al., 2007). In pejerrey, also the quality of eggs obtained from females heat treated during mid and late vitellogenesis was lower than the control group (reared under natural conditions). The mean fertilization rate was reduced 1.86 and 4.47 times compare with the control group, while no difference was observed with the group treated at the beginning of vitellogenesis. These findings clearly showed that in pejerrey females the effect of elevated temperature during vitellogenesis is more adverse at the end of this reproductive phase.

It may be possible that the effect of elevated temperature over the reproductive function in fish females is exerted principally through the inhibition of gonad E_2 production as it was demonstrated during the vitellogenesis and spawning period (Pankhurst and Munday, 2011, this review). In salmonid, it was observed that the delay in ovulation, the reduction of egg size, fertilization rate and embryos survival observed after heat treatment were at least partly a result of impaired E_2 secretion, and a subsequent diminution of hepatic vitellogenin synthesis and sequestration during critical stages of vitellogenesis (Pankhurst and King, 2010). In pejerrey females, E_2 plasma levels measured immediately after the heat treatments mentioned above increased in early and mid vitellogenic groups, may be the cause of the advancement of the date of the spawning. However, no difference between control and late vitellogenic treated group was found (Fig 6c). The low E_2 levels found in this last group can be explained in relation with the natural decrease in this steroid reported at the beginning of final maturation by a shift in the steroidogenic pathway from E_2 to 17,20βP in ovarian follicles (Nagahama and Yamashita, 2008).

There are few studies on the effects of high temperature on male reproductive physiology during pre-spawning period. Experimental data suggested that in many fish the effect of high water temperature over females is higher than over males (Lahnsteiner and Kletzl, 2012; Newman et al., 2010). Furthermore, studies on

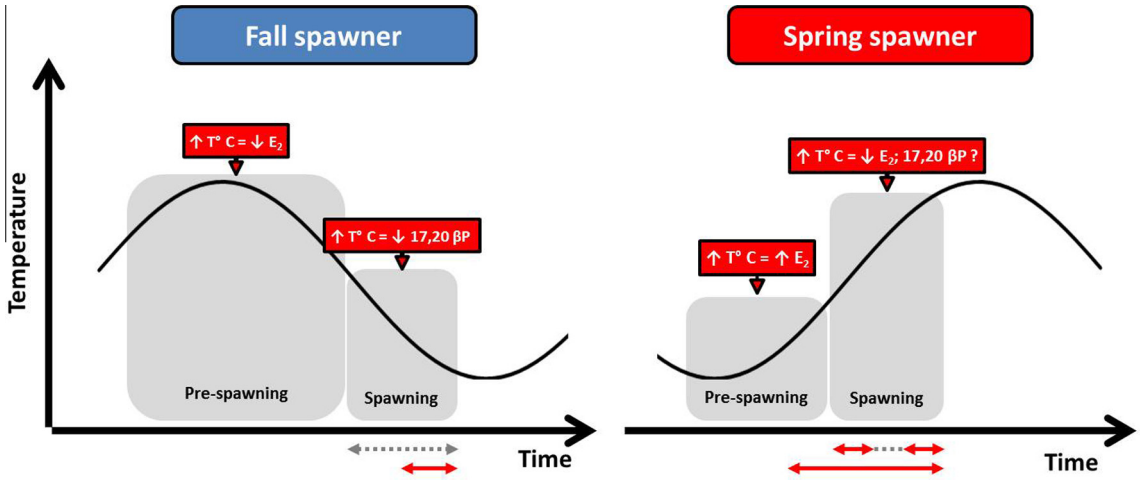

Fig. 7. Overview of the effects of high water temperature on fish spawning phenology. In fall spawners, the elevation of water temperature during pre-spawning period provoked a delayed ovulation due to low estradiol (E_2) levels while in the spawning period, the effects are a delay or a complete inhibition of ovulation by an impairment of 17,20β-dihy-droxy-4-pregnen-3-one (17,20βP) synthesis. In spring spawners, during pre-spawning period a rise in temperature causes an increase in E_2 levels advancing the spawning period. During spawning in all species studied high temperature provoked a sharp decrease in E_2 levels, but there are no data about the effect on 17,20βP. Red arrows show the length of ovulation period as consequence of different temperature treatments and grey dotted arrow represents inhibition of ovulation and spawning.

O. mykiss showed that high temperature may have a negative effect on spermatogenesis, decreasing the gonadal steroids testosterone and 11-KT (Manning and Kime, 1985). In pejerrey experiment, we found that sperm amount did not differ from control to heated fish. This result was accompanied by similar 11-KT levels at all groups, without differences between fish treated and controls. In this way the high temperature during the pre-spawning period may not be an impediment for normal gametogenesis in males.

5. Conclusions and future perspectives

Over the past 100 years, the global average temperature as well as the frequency of extreme asymmetric climatic events increased and it has been projected to rise at a rapid rate (Brander, 2010; IPCC and Climate Change, 2007). This phenomenon known as Global Warming has become a reality (Graham and Harrod, 2009) and leads to an increase in the temperature of several water bodies and affects the quality of aquatic environment and biodiversity (Ficke et al., 2007). The compelling evidence summarized in this review demonstrated that fish reproduction may be directly impaired by further global warming and that abnormal high water temperature affects the different components of fish brain–pituitary–gonad axis. At present, the component of the endocrine reproductive axis first affected by high water temperature remains unclear. In all fish studied gonads seem to be the more damaged by heat treatments through the inhibition of the expression and further synthesis of different enzymes related with gonad steroidogenesis. In view of the feedback role of sex steroids upon the synthesis and releasing of GnRH and GtHs in the brain and pituitary reported in fish (Levavi-Sivan et al., 2010; Popesku et al., 2008; Zohar et al., 2010), it is possible that the inhibition of these hormones observed in treated fish is the result of the sharp decrease in plasma steroids levels. In this sense, it is important the result presented in this review about the inhibition of pejerrey gonad aromatase expression by high temperature *in vivo* (Elisio et al., 2012a) and especially *in vitro* demonstrating that ovary functions are directly disrupted by high temperature independently of the brain–pituitary axis.

More work is needed to understand the effects of elevated temperatures on other hormones that facilitate reproductive development. In this context, thyroid hormones (THs) plasma concentrations undergo seasonal changes influenced by temperature and photoperiod (Comeau et al., 2000; Norberg et al., 2004; Swapna and Senthilkumaran, 2007). Recently it has been reported in goldfish that THs were present at the highest levels during summer after spawning corresponding with a period of minimal gonadotropic function and maximum somatotropic activities, suggesting that THs could impair reproduction by inhibiting pituitary LH and gonadal aromatase expression (Habibi et al., 2012).

As an overview of the effects of high water temperature on fish ovulation timing, it is possible to suggest that in fall spawners, the delayed ovulation is due to low E_2 levels while in the spawning period, the delay or the complete inhibition of ovulation is provoked by an impairment of 17,20βP synthesis. In spring spawners, during pre-spawning period a rise in temperature causes an increase in E_2 levels advancing the spawning period. The differences of ovulation timing between fall and spring spawners could be because the elevated temperatures tested in this period are the permissive for the onset of spawning in these fish and there are not higher enough to provoke an inhibition. During spawning period in all species studied high temperature provoked a sharp decrease in E_2 levels, but there are no data about the effect on 17,20βP in spring spawners (Fig. 7).

According to the deteriorating reproductive responses of the fish to climate warming, it is plausible that changes or total loss of the spawning season may occur in warm years, reducing annual reproductive outputs and affecting future populations of fish.

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References

Anderson, K., Swanson, P., Pankhurst, N., King, H., Elizur, A., 2012. Effect of thermal challenge on plasma gonadotropin levels and ovarian steroidogenesis in female maiden and repeat spawning Tasmanian Atlantic salmon (*Salmo salar*). Aquaculture 334–337, 205–212.

Brander, K., 2010. Impacts of climate change on fisheries. J. Marine Syst. 79, 389–402.

Breton, B., Jalabert, B., Billard, R., Weil, C., 1971. In vitro stimulation of the release of pituitary gonadotropic hormone by a hypothalamic factor in the carp Cyprinus carpio L.. In: C R Acad. Sci. Hebd Seances Acad. Sci. D 273, 2591–2594.

Bromage, N., Porter, M., Randall, C., 2001. The environmental regulation of maturation in farmed finfish with special references to the role of photoperiod and melatonin. Aquaculture 197, 63–69.

Brown, N.P., Shields, R.J., Bromage, N.R., 2006. The influence of water temperature on spawning patterns and egg quality in the Atlantic halibut (*Hippoglossus hippoglossus* L.). Aquaculture 261, 993–1002.

Clark, R.W., Henderson-Arzapalob, A., Sullivan, C.V., 2005. Disparate effects of constant and annually-cycling daylength and water temperature on reproductive maturation of striped bass (*Morone saxatilis*). Aquaculture 249, 497–513.

Comeau, L.A., Campana, S.E., Hanson, J.M., Chouinard, G.A., 2000. Seasonal changes of thyroid hormones in field-collected Atlantic cod in relation to condition indices, water temperature and photoperiod. J. Fish Biol. 57, 571–588.

Cussac, V.E., Fernández, D.A., Gómez, S.E., López, H.L., 2009. Fishes of southern South America: a story driven by temperature. Fish Physiol. Biochem. 35, 29–42.

David, D., Degani, G., 2011. Temperature affects brain and pituitary gene expression related to reproduction and growth in the male blue gouramis, *Trichogaster trichopterus*. J. Exp. Zool. 315, 203–214.

Durant, J.M., Hjermann, D.Ø., Ottersen, G., Stenseth, N.C., 2007. Climate and the match or mismatch between predator requirements and resource availability. Clim. Res. 33, 271–283.

Elisio, M., Chalde, T., Miranda, L.A., 2012a. Effects of short periods of warm water fluctuations on reproductive endocrine axis of the pejerrey (*Odontesthes bonariensis*) spawning. Comp. Biochem. Physiol. A 163, 47–55.

Elisio, M., Chalde, T., Miranda, L.A., 2012. Endocrine regulation of pejerrey (*Odontesthes bonariensis*) ovarian maturation throughout natural reproductive cycle, In: 7th International Symposium on Fish Endocrinology, Buenos Aires, Argentina, p. 75.

Elisio, M., Soria, F.N., Fernandino, J.I., Strüssmann, C.A., Somoza, G.M., Miranda, L.A., 2012c. Extrahypophyseal expression of gonadotropin subunits in pejerrey *Odontesthes bonariensis* and effects of high water temperatures on their expression. Gen. Comp. Endocrinol. 175, 329–336.

Fernald, R.D., White, R.B., 1999. Gonadotropin-releasing hormone genes: phylogeny, structure, and functions. Front. Neuroendocrinol. 20, 224–240.

Fernandino, J.I., Hattori, R.S., Shinoda, T., Kimura, H., Strobl-Mazzulla, P.H., Strüssmann, C.A., Somoza, G.M., 2008. Dimorphic expression of dmrt1 and cyp19a1 (ovarian aromatase) during early gonadal development in pejerrey, *Odontesthes bonariensis*. Sex. Dev. 2, 316–324.

Ficke, A., Myrick, C., Hansen, L., 2007. Potential impacts of global climate change on freshwater fisheries. Rev. Fish Biol. Fish. 71, 1–32.

Fincham, J.I., Rijnsdorp, A.D., Engelhard, G.H., 2013. Shifts in the timing of spawning in sole linked to warming sea temperatures. J. Sea Res. 75, 69–76.

Gillet, C., 1991. Egg production in an Arctic charr (*Salvelinus alpinus*, L) brood stock: effects of temperature on the timing of spawning and the quality of eggs. Aquat. Living Resour. 4, 109–116.

Gillet, C., Quétin, P., 1983. Effect of temperature changes on the reproductive cycle of roach in Lake Geneva from 1983 to 2001. J. Fish Biol. 69, 518–534.

Gillet, C., Breton, B., 2009. LH secretion and ovulation following exposure of Arctic charr to different temperature and photoperiod regimes: responsiveness of females to a gonadotropin-releasing hormone analogue and a dopamine antagonist. Gen. Comp. Endocrinol. 162, 210–221.

Gillet, C., Breton, B., Mikolajczyk, T., Bodinier, P., Fostier, A., 2011. Disruption of the secretion and action of 17,20β-dihydroxy-4-pregnen-3-one in response to a rise in temperature in the Arctic charr, *Salvelinus alpinus*. Consequences on oocyte maturation and ovulation. Gen. Comp. Endocrinol. 172, 392–399.

Graham, C.T., Harrod, C., 2009. Implications of climate change for fishes of the British Isles. J Fish Biol. 74, 1143–1205.

Guiguen, Y., Fostier, A., Piferrer, F., Chang, C., 2010. Ovarian aromatase and estrogens: a pivotal role for gonadal sex differentiation and sex change in fish. Gen. Comp. Endocrinol. 165, 352–366.

Habibi, H.R., Nelson, E.R., Allan, E.R.O., 2012. New insights into thyroid hormone function and modulation of reproduction in goldfish. Gen. Comp. Endocrinol. 175, 19–26.

Hermelink, B., Wuertz, S., Trubiroha, A., Rennert, B., Kloas, W., Schulz, C., 2011. Influence of temperature on puberty and maturation of pikeperch, *Sander lucioperca*. Gen. Comp. Endocrinol 172, 282–292.

Hutchings, J.A., Myers, R.A., 1994. Timing of cod reproduction: interannual variability and the influence of temperature. Mar. Ecol. Prog. Ser. 108, 21–31.

IPCC, Climate Change, 2007. The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

Jansen, T., Gislason, H., 2011. Temperature affects the timing of spawning and migration of North Sea mackerel. Cont. Shelf Res. 31, 64–72.

Jeppesen, E., Meerhoff, M., Holmgren, K., González-Bergonzoni, I., Teixeira-de Mello, F., Declerck, S.A.J., De Meester, L., Søndergaard, M., Lauridsen, T.L., Bjerring, R., Conde-Porcuna, J.M., Mazzeo, N., Iglesias, C., Reizenstein, M., Malmquist, H.J., Liu, Z., Balayla, D., Lazzaro, X., 2010. Impacts of climate warming on lake fish community structure and potential effects on ecosystem function. Hydrobiologia 646, 73–90.

Jobling, M., Johnsen, H.K., Pettersen, G.W., Henderson, R.J., 1995. Effect of temperature on reproductive development in Arctic charr, *Salvelinus Alpinus* (L.). J. Therm. Biol. 20, 157–165.

Kah, O., Anglade, I., Leprétre, E., Dubourg, P., de Monbrison, D., 1993. The reproductive brain in fish. Fish Physiol. Biochem. 11, 85–98.

King, H.R., Pankhurst, N.W., Watts, M., Pankhurst, P.M., 2003. Effect of elevated summer temperatures on gonadal steroid production, vitellogenesis and egg quality in female Atlantic salmon. J. Fish Biol. 63, 153–167.

King, H.R., Pankhurst, N.W., Watts, M., 2007. Reproductive sensitivity to elevated water temperatures in female Atlantic salmon is heightened at certain stages of vitellogenesis. J. Fish Biol. 70, 190–205.

Kumar, R.S., Ijiri, S., Trant, J.M., 2000. Changes in the expression of genes encoding steroidogenic enzymes in the Channel catfish (*Ictalurus punctatus*) ovary throughout a reproductive cycle. Biol. Rep. 63, 1676–1682.

Lahnsteiner, F., Kletzl, M., 2012. The effect of water temperature on gamete maturation and gamete quality in the European grayling (*Thymalus thymallus*) based on experimental data and on data from wild populations. Fish Physiol. Biochem. 38, 455–467.

Levavi-Sivan, B., Bogerd, J., Mañanós, E.L., Gómez, A., Lareyre, J.J., 2010. Perspectives on fish gonadotropins and their receptors. Gen. Comp. Endocrinol. 165, 412–437.

Levy, G., David, D., Degani, G., 2011. Effect of environmental temperature on growth-and reproduction-related hormones gene expression in the female blue gourami (*Trichogaster trichopterus*). Comp. Biochem. Physiol. A 160, 381–389.

Lim, B.S., Kagawa, H., Gen, K., Okuzawa, K., 2003. Effects of water temperature on the gonadal development and expression of steroidogenic enzymes in the gonad of juvenile red seabream, *Pagrus major*. Fish Physiol. Biochem. 28, 161–162.

Lubzens, E., Young, G., Bobe, J., Cerdà, J., 2010. Oogenesis in teleosts: how fish eggs are formed. Gen. Comp. Endocrinol. 165, 367–389.

Lukšienė, D., Sandström, O., Lounasheimo, L., Andersson, J., 2000. The effects of thermal effluent exposure on the gametogenesis of female fish. J. Fish Biol. 56, 37–50.

Manning, N.J., Kime, D.E., 1985. The effect of temperature on testicular steroid production in the rainbow trout, *Salmo gardneri*, in vivo and in vitro. Gen. Comp. Endocrinol. 57, 377–382.

Migaud, H., Davie, A., Taylor, J.F., 2010. Current knowledge on the photoneuroendocrine regulation of reproduction in temperate fish species. J. Fish Biol. 76, 27–68.

Mooij, W.M., De Senerpont Domis, L.N., Janse, J.H., 2009. Linking species- and ecosystem-level impacts of climate change in lakes with a complex and a minimal model. Ecol. Model. 220, 3011–3020.

Mylonas, C.C., Fostier, A., Silvia, S., 2010. Broodstock management and hormonal manipulations of fish reproduction. Gen. Comp. Endocrinol. 165, 516–534.

Nagahama, Y., 1994. Endocrine regulation of gametogenesis in fish. Int. J. Dev. Biol. 38, 217–229.

Nagahama, Y., 1997. 17α,20β-Dihydroxy-4-pregnen-3-one, a maturation-inducing hormone in fish oocytes: mechanisms of synthesis and action. Steroids 62, 190–196.

Nagahama, Y., Yamashita, M., 2008. Regulation of oocyte maturation in fish. Develop. Growth Differ. 50, 195–219.

Newman, D.M., Jones, P.L., Ingram, B.A., 2010. Advanced ovarian development of Murray cod *Maccullochella peelii peelii* via phase-shifted photoperiod and two temperature regimes. Aquaculture 310, 206–212.

Norberg, B., Brown, C.L., Halldorsson, O., Stensland, K., Björnsson, B.T., 2004. Photoperiod regulates the timing of sexual maturation, spawning, sex steroid and thyroid hormone profiles in the Atlantic cod (Gadus morhua). Aquaculture 229, 451–467.

Okuzawa, K., Kumakura, N., Gen, K., Yamaguchi, S., Lim, B., Kagawa, H., 2003. Effect of high water temperature on brain–pituitary–gonad axis of the red seabream during its spawning season. Fish Physiol. Biochem. 28, 439–440.

Pandolfi, M., Pozzi, A.G., Cánepa, M., Vissio, P.G., Shimizu, A., Maggese, M.C., Lobo, G., 2009. Presence of β-follicle-stimulating hormone and β-luteinizing hormone transcripts in the brain of *Cichlasoma dimerus* (Perciformes: Cichlidae), effect of brain-derived gonadotropins on pituitary hormone release. Neuroendocrinology 89, 27–37.

Pankhurst, N.W., Purser, G.J., Van Der Kraak, G., Thomas, P.M., Forteath, G.N.R., 1996. Effect of holding temperature on ovulation, egg fertility, plasma levels of reproductive hormones and in vitro ovarian steroidogenesis in the rainbow trout *Oncorhynchus mykiss*. Aquaculture 146, 277–290.

Pankhurst, N.W., Thomas, P.M., 1998. Maintenance at elevated temperature delays the steroidogenic and ovulatory responsiveness of rainbow trout *Oncorhynchus mykiss* to luteinizing hormone releasing hormone analogue. Aquaculture 166, 163–177.

Pankhurst, N.W., King, H.R., 2010. Temperature and salmonid reproduction: implications for aquaculture. J. Fish Biol. 76, 69–85.

Pankhurst, N.W., King, H.R., Anderson, K., Elizur, A., Pankhurst, P.M., Ruff, N., 2011. Thermal impairment of reproduction is differentially expressed in maiden and repeat spawning Atlantic salmon. Aquaculture 316, 77–87.

Pankhurst, N.W., Munday, P.L., 2011. Effects of climate change on fish reproduction and early life history stages. Mar. Fresh. Res. 62, 1015–1026.

Parhar, I.S., Soga, T., Ogawa, S., Sakuma, Y., 2003. FSH and LH-β subunits in the preoptic nucleus: ontogenic expression in teleost. Gen. Comp. Endocrinol. 132, 369–378.

Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42.

Parmesan, C., 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Global Change Biol. 13, 1860–1872.

Perry, A.L., Low, P.J., Ellis, J.R., Reynolds, J.D., 2005. Climate change and distribution shifts in marine fishes. Science 308, 1912–1915.
Piferrer, F., Guiguen, Y., 2008. Fish gonadogenesis. Part II: molecular biology and genomics of sex differentiation. Rev. Fish. Sci. 16, 35–55.
Popesku, J.T., Martyniuk, C.J., Mennigen, J., Xiong, H., Zhang, D., Xia, X., Cossins, A.R., Trudeau, V.L., 2008. The goldfish (*Carassius auratus*) as a model for neuroendocrine signaling. Mol. Cell. Endocr. 293, 43–56.
Pörtner, H.O., Farrell, A.P., 2008. Physiology and climate change. Science 322, 690–692.
Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., Pounds, J.A., 2003. Fingerprints of global warming on wild animals and plants. Nature 421, 57–60.
Schulz, R.W., França, L.R., Lareyre, J.J., Le Gac, F., Chiarini-Garcia, H., Nóbrega, R.H., Miura, T., 2010. Spermatogenesis in fish. Gen. Comp. Endocrinol. 165, 390–411.
Scott, A.P., Sumpter, J.P., Stacey, N., 2010. The role of the maturation-inducing steroid, 17,20β-dihydroxypregn-4-en-3-one, in male fishes: a review. J. Fish. Biol. 76, 183–224.
Shuter, B.J., Finstad, A.G., Helland, I.P., Zweimüller, I., Hölker, F., 2012. The role of winter phenology in shaping the ecology of freshwater fish and their sensitivities to climate change. Aquat. Sci. 74, 637–657.
Soria, F.N., Strüssmann, C.A., Miranda, L.A., 2008. High water temperatures impair the reproductive ability of the pejerrey fish *Odontesthes bonariensis*: effects on the hyophyseal–gonadal axis. Physiol. Biochem. Zool. 81, 898–905.
Strüssmann, A., 1989. Basic studies on seed reproduction of pejerrey *Odontesthes bonariensis*. Doctoral thesis, Tokyo University of Fisheries, Japan. p. 351.
Strüssmann, C.A., Saito, T., Usui, M., Yamada, H., Takashima, F., 1997. Thermal thresholds and critical period of thermolabile sex determination in two atherinid fishes, *Odontesthes bonariensis* and *Patagonina hatcheri*. J. Exp. Zool. 278, 167–177.
Strüssmann, C.A., Conover, D.O., Somoza, G.M., Miranda, L.A., 2010. Implications of climate change for the reproductive capacity and survival of atherinopsid fish species. J. Fish Biol. 77, 1818–1834.
Swapna, I., Senthilkumaran, B., 2007. Thyroid hormones modulate the hypothalamo–hypophyseal–gonadal axis in teleosts: molecular insights. Fish Physiol. Biochem. 33, 335–345.
Taranger, G.L., Hansen, T., 1993. Ovulation and egg survival following exposure of Atlantic salmon, *Salmo salar* L., broodstock to different water temperatures. Aquacult. Fish. Manage. 24, 151–156.
Tveiten, H., Johnsen, H.K., 1999. Temperature experienced during vitellogenesis influences ovarian maturation and the timing of ovulation in common wolfish. J. Fish Biol. 55, 809–819.
Tveiten, H., Scott, A.P., Johnsen, H.K., 2000. Plasma-sulfated C21-steroids increase during the periovulatory period in female common Wolffish and are influenced by temperature during vitellogenesis. Gen. Comp. Endocrinol. 117, 464–473.
Tveiten, H., Johnsen, H.K., 2001. Thermal influences on temporal changes in plasma testosterone and oestradiol-17β concentrations during gonadal recrudescence in female common wolffish. J. Fish Biol. 59, 175–178.
Tveiten, H., 2008. Temperature influence on reproductive development and gamete quality in Atlantic cod (*Gadus morhua*). Cybium 32, 195.
Van der Kraak, G., Pankhurst, N.W., 1997. Temperature effects on the reproductive performance of fish. In: Wood, C.M., Mc Donald, D.G. (Eds.), Global Warming: Implications for Freshwater and Marine Fish. Cambridge University Press, Cambridge, pp. 159–176.
Wahl, B., Löffler, H., 2009. Influences on the natural reproduction of whitefish (*Coregonus lavaretus*) in Lake Constance. Can. J. Fish Aquat. Sci. 66, 547–556.
Watts, M., Pankhurst, N.W., King, H.R., 2004. Maintenance of Atlantic salmon (*Salmo salar*) at elevated temperature inhibits cytochrome P450 aromatase activity in isolated ovarian follicles. Gen. Comp. Endocrinol. 135, 381–390.
Webb, M.A.H., Van Eenennaam, J.P., Doroshov, S.I., Moberg, G.P., 1999. Preliminary observations on the effects of holding temperature on reproductive performance of female white sturgeon, *Acipenser transmontanus* Richardson. Aquaculture 176, 315–329.
Wong, T.T., Zohar, Y., 2004. Novel expression of gonadotropin subunit genes in oocytes of the gilthead seabream (*Sparus aurata*). Endocrinology 145, 5210–5220.
Zięba, G., Fox, M.G., Copp, G.H., 2010. The effect of elevated temperature on spawning of introduced pumpkin seed *Lepomis gibbosus* in Europe. J. Fish Biol. 77, 1850–1855.
Zohar, Y., Muñoz-Cueto, J.A., Elizur, A., Kah, O., 2010. Neuroendocrinology of reproduction in teleost fish. Gen. Comp. Endocrinol. 165, 438–455.
Zucchetta, M., Cipolato, G., Pranovi, F., Antonetti, P., Torricelli, P., Franzoi, P., Malavasi, S., 2012. The relationships between temperature changes and reproductive investment in a Mediterranean goby: Insights for the assessment of climate change effects. Estuar. Coast. Shelf Sci. 101, 15–23.