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The time-keeping hormone melatonin: a possible key cue for puberty in freshwater eels (*Anguilla* spp.)

Erik Burgerhout · P. Mark Lokman · Guido E. E. J. M. van den Thillart · Ron P. Dirks

Abstract Worldwide, there is a dramatic decline in freshwater eel populations (*Anguilla* spp.), resulting in an urgent need to improve eel management and artificial reproduction protocols. Unfortunately, eels in captivity do not reproduce spontaneously as they remain in a (pre)-pubertal state resulting from a strong neural blockage. Eel propagation is possible to some extent by applying extensive, expensive, unnatural hormonal treatments. However, the success rates are still far too low to support a sustainable farming industry, due to low gamete quality and low survival rates of larvae. Artificial reproduction of eels has been pursued for almost 80 years, and maturation protocols have changed little. In order to improve current protocols it is clear that a different approach towards stimulating sexual maturation is required. In many fish species, changes in external environmental cues, such as photoperiod and temperature, are crucial to induce gonadal recrudescence and development. Still, the natural triggers involved in the gametogenesis of eels are poorly understood. The time-keeping hormone melatonin is a well-known transmitter of external cues, and influences various physiological processes, including reproduction. In eels, we hypothesize that melatonin is an important key player in the regulation of sexual maturation. Thus far, its mode of action is still an area which needs to be explored. In this review, we provide an overview of the current knowledge of studied natural cues possibly affecting reproductive function and the plausible role of melatonin in the regulation of puberty in eels.

Keywords Artificial reproduction · Daily rhythms · Environmental factors · Melatonin system · Photothermal period · Puberty

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Introduction

The enigmatic freshwater eels (*Anguilla* spp.) are distributed over a large part of the world. After spending most of their life in continental waters, they migrate for hundreds to thousands of kilometers to their spawning area in oceanic waters (Fig. 1, Schmidt 1923; Tesch 2003; Tsukamoto et al. 2003, 2011; van Ginneken and Maes 2005; Aoyama 2009; Tsukamoto 2009). Worldwide, populations of the ecologically and
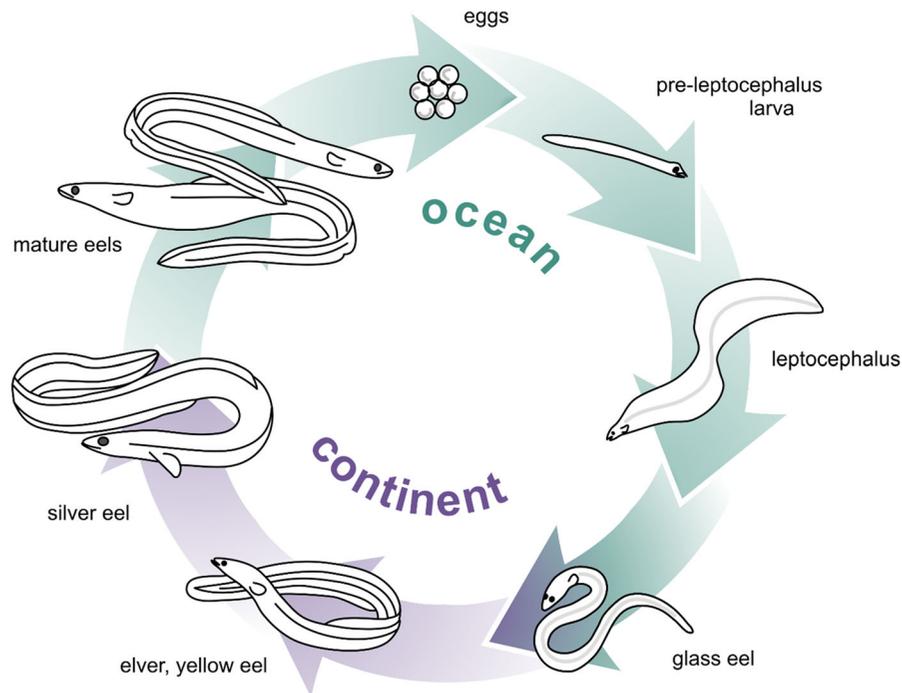
Fig. 1 The life cycle of the European eel. After hatching, presumably in the Sargasso Sea, cylindrical larvae develop into leaf-shaped leptocephalus larvae, which after drifting on the Gulf Stream for approximately 1 year metamorphose into glass eels close to the European coast. The glass eels may stay at the coast or migrate upriver, where they stay as juveniles (elvers and yellow eels) for many years (depending on the region: males 4–6 years, females 8–12 years). Finally, they develop into migrating silver eels; the cause and timing of silvering is not well understood. They mature during or after migration to the spawning grounds. Reproduced and with permission from Henkel et al. (2012a)

economically valuable anguillids have shown a dramatic decline since the 1980s (Richkus and Whalen 2000; Dekker 2003; Dekker et al. 2003; Stone 2003; Hanel et al. 2014). Several *Anguilla* species were added to the IUCN Red list as endangered or critically endangered (Jacoby and Gollock 2014; Jacoby et al. 2015), and all species are now considered for inclusion on that list (Dekker and Casselman 2014). Therefore, to restore wild populations and reduce pressure from fisheries, there is an urgent need to improve the management of natural eel stocks (c.f., ICES 2012) and to close their life cycle in captivity. However, eels in captivity do not mature spontaneously and when prevented from their reproductive migration, remain in a (pre)-pubertal state (Dufour et al. 2003; Rousseau et al. 2009).

Eels can be propagated artificially by applying extensive hormonal treatments, but the success rates remain far too low for uptake of this technology to create a sustainable eel aquaculture industry (see below). In order to improve the currently applied

protocols for artificial maturation of eels with respect to gamete quality and welfare, but also with respect to expenses, the hormonal treatments need to be replaced by manipulation of external cues, which are generally used to affect reproduction of many other fish species. This can be achieved by further extending our knowledge and understanding of the reproductive physiology of eels. In this review, we present a holistic overview of the current knowledge about the principal environmental cues that affect the reproductive system of freshwater eels and discuss the possible role of one of the key regulators of onset of puberty, the so-called 'time-keeping hormone' melatonin.

Artificial control of reproduction

In captivity, gonadal development in eels does not spontaneously progress beyond the peri-pubertal stage due to dopaminergic inhibition and a deficient secretion of key hormones of the reproductive axis, i.e.

gonadotropin-releasing hormone (Gnrh), follicle-stimulating hormone (Fsh) and luteinizing hormone (Lh) (Fig. 2; Dufour et al. 1988, 1993; Vidal et al. 2004; Weltzien et al. 2006, 2009; Rousseau et al. 2013). To some extent, full sexual maturity can be induced artificially by circumventing this strong neural blockage using expensive hormonal treatments, i.e. administering salmon or carp pituitary extracts (SPE or CPE) to females and human chorionic gonadotropin (hCG) to males (e.g. Fontaine 1936; Fontaine et al. 1964; Yamamoto and Yamauchi 1974; Boëtius and Boëtius 1980; Ohta et al. 1996, 1997; Lokman and Young 2000; Tanaka et al. 2001, 2003; Pedersen 2003, 2004; Palstra et al. 2005; Oliveira and Hable 2010; Burgerhout et al. 2011a; Butts et al. 2014, 2016; Okamura et al. 2014; Sørensen et al.

2016). In general, achieving full sexual maturity appears to be easier in male eels than in female eels. A single hCG injection can result in acquisition of sperm (e.g. Miura et al. 1991; Peñaranda et al. 2010), whereas up to 29 weekly injections with pituitary extracts are required to obtain fully mature female eels (e.g. Lokman and Young 2000; Pedersen 2004). Over the last decades, steady progress has been achieved with regard to the reproduction of eels (reviewed by Ijiri et al. 2011; Okamura et al. 2014), but the method of maturing eels using hormonal treatment has changed little, except perhaps with regard to the use of slow-release osmotic pumps to provide constant plasma hormone levels instead of weekly injections in some studies (Kagawa et al. 2009, 2013). The most notable advance during the last decade, however, has
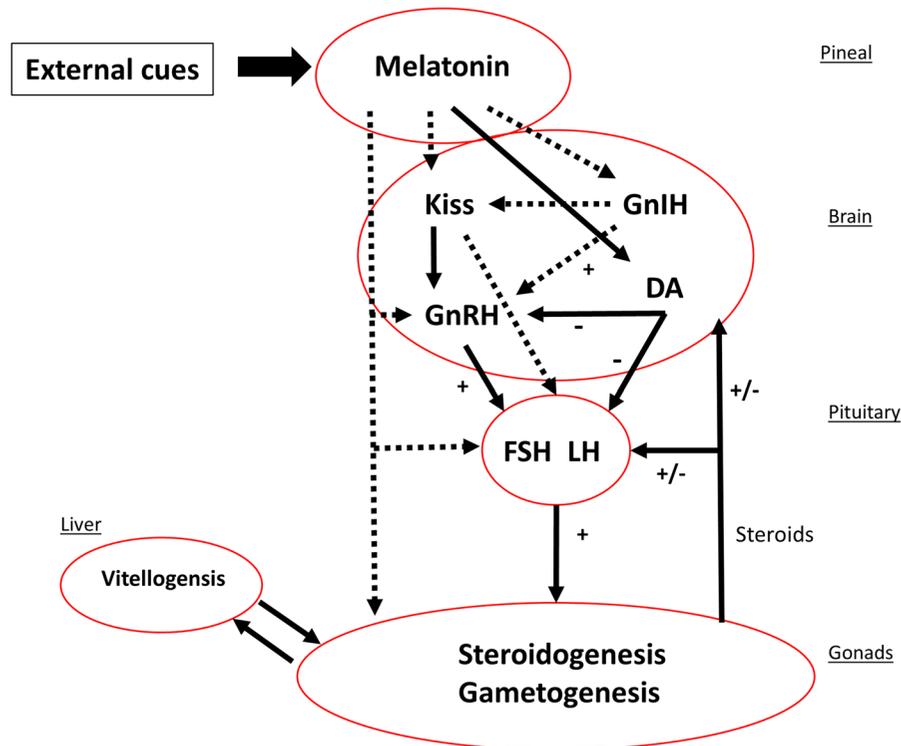
Fig. 2 Schematic representation of the proposed neurohormonal control of puberty in eels. External cues, such as photoperiod, temperature and salinity, regulate the daily synthesis and release of melatonin (MEL), which transmits the external cues on all levels of the brain–pituitary–gonad (BPG) axis. Subsequently, MEL stimulates dopamine (DA) synthesis (Sébert et al. 2008). DA inhibits gonadotropin releasing hormone (GnRH) and synthesis and release of gonadotropins follicle-stimulating hormone (FSH) and luteinizing hormone (LH), which regulate gonadal activity (steroidogenesis and

gametogenesis) (Dufour et al. 1988, 1993; Vidal et al. 2004; Weltzien et al. 2006, 2009; Rousseau et al. 2013). Sex steroids (e.g. 17β-estradiol, 11-ketotestosterone, testosterone) exert positive and negative feedbacks on different levels in the BPG axis and liver. It is expected that MEL affects the KiSS/GPR54 system (KiSS) and/or GnRH, directly or indirectly via gonadotropin inhibiting hormone (GnIH), and thereby inducing puberty (Dufour et al. 2010; Migaud et al. 2010; Falcón and Zohar 2018). Decreasing melatonin is expected to result in an inhibition of DA and thereby stimulate sexual maturation

arguably been the optimization of spontaneous spawning by artificially matured brood stock—as opposed to strip-spawning approaches—highlighting that mimicking of "natural" cues may well prove effective to artificially propagate the eel in the future.

Although the life cycle of the Japanese eel (*A. japonica*) was recently closed (Masuda et al. 2012), numbers of offspring that reach the glass eel stage have remained extremely low, mainly due to low egg quality and fertilization rates, and high mortality of the larvae (Adachi et al. 2003; Ijiri et al. 2011; Okamura et al. 2014; Izumi et al. 2016). These major problems are most likely caused by the unnatural stimulation of gametogenesis, resulting in, amongst others, handling stress, physiological stress associated with greatly fluctuating hormone levels (Sato et al. 2000, 2003) and possibly, asynchronous oocyte development (Palstra et al. 2005). Additionally, the gonadotropins Fsh and Lh differentially regulate full sexual maturity in eels and are under positive and negative feedback control by sex steroids (Quérat et al. 1991; Suetake et al. 2002, 2003; Schmitz et al. 2005; Jeng et al. 2007; Kazeto et al. 2008). The Lh receptor can only be activated by Lh, while the Fsh receptor was found to be activated by both Fsh and Lh (Kazeto et al. 2008; Minegishi et al. 2012). Besides, Fsh is likely to be the principal gonadotropin during early stages of vitellogenesis in eels, at least in wild-caught midvitellogenic *A. dieffenbachii* (Saito et al. 2003). As pituitary extracts often contain both Fsh and Lh (e.g. Suetake et al. 2002; Aroua et al. 2005; Schmitz et al. 2005), they may therefore compromise gametogenesis and potentially contribute to the observed low gamete quality. Aside from these concerns about gonadotropin signaling, pituitary extracts also contain many other bioactive compounds (e.g., prolactin, growth hormone, adrenocorticotropin) that conceivably exert their effects during gametogenesis. Moreover, it has already been shown earlier that exposure of teleost fish to stressors negatively affects the rates of reproductive success (e.g. Barton and Iwama 1991; Schreck 2010).

Pre-treatment of oogenesis

There is a wide range in responsiveness to hormonal treatments (Lokman and Young 2000; Pedersen 2003, 2004; Palstra et al. 2005) and often > 50% of female broodstock do not reach full maturity (Palstra

and van den Thillart 2009; Burgerhout et al. unpublished data). The differential response to hormonal treatments is at least in part due to differences in the initial stage of oogenesis (Ijiri et al. 1995, 1998; Durif et al. 2006; Okamura et al. 2008; Dirks et al. 2014; Burgerhout et al. 2016). For example, it was shown that wild Japanese eels in the yellow stage do not respond to hormonal treatments, while silver stage 1 and stage 2 eels respond with approximately 80% and 100% efficacy, respectively (Okamura et al. 2008). The response to hormone treatment in farmed eels is, in general, slower and egg quality is lower compared to wild female eels (Ijiri et al. 1995, 1998), also indicating a difference in initial body and/or ovarian composition (e.g. Adachi et al. 2003). Recently, it was found that the response to the hormonal treatment in wild female European eels may be dependent on the transcriptional dynamics of ribosomal genes, with the 5S/18S ratio of non-responding fish corresponding to that of previtellogenic stage fish (Rojo-Bartelomé et al. 2017).

Over the last decade, studies on the effects of broodstock diet on egg and larval quality received increased attention (Furuita et al. 2007, 2009; Heinsbroek et al. 2013; da Silva et al. 2016; Støttrup et al. 2016). Moreover, feminization of eels by administering 17β-estradiol (E2) with the diet during the early growth phase resulted in a better response to the hormone treatments, albeit still below the response shown by wild female anguillids, as shown for Japanese eels (Ijiri et al. 1998; Chai et al. 2010). In addition, pre-treatment with androgens (17-methyltestosterone and 11-ketotestosterone (11-KT)) also has been shown to affect the response to hormonal treatment in wild New Zealand short-finned eels (*A. australis*), as it resulted in a reduced number of CPE injections needed to reach the pre-ovulatory stage (Lokman et al. 2015). Similarly, androgen co-treatment in European eel females also resulted in a reduction of time to spawning, and further, in increased fertilization, hatching and survival rates (di Biase et al. 2017; Mordenti et al. 2018). It is, therefore, of great importance to elucidate the hormonal mechanisms and the cues initiating silvering in farmed eels.

Natural conditions

Although the artificial control of reproduction of freshwater eels has been pursued for approximately 80 years, it is surprising that the natural cues that may induce vitellogenesis, final oocyte maturation and ovulation in eels are still insufficiently studied. This may be due to the fact that their oceanic life phase is still largely unknown, and information about the environmental conditions encountered during the reproductive migration is scarce.

Full sexual maturity needs to occur during or after the spawning migration (Dufour et al. 2003). Recently, it has been proposed that vitellogenesis and final maturation may take place at or near the spawning grounds as swimming exercise suppressed hepatic vitellogenesis in European eels (*A. anguilla*) (Palstra et al. 2010). It was suggested that this suppression may be a strategy to avoid drag associated with increased abdominal girth and precocious muscle atrophy during long-distance swimming (Palstra et al. 2010). However, several other *Anguilla* spp., such as the New Zealand long-finned eel *A. dieffenbachii* and *A. celebesensis*, show developmental stages up to mid-vitellogenesis (gonadosomatic index (GSI) up to around 10%) prior to the onset of their migration (e.g. Lokman et al. 1998; Hagihara et al. 2012). An advanced stage of gonadal development at the onset of the spawning migration appears to be negatively correlated with the migration distance (Todd 1981a; Dufour et al. 2003). Indeed, vitellogenesis in temperate fish species is a slow process that can comprise several months (Patiño et al. 2001; Wang et al. 2010), which appears to correlate with the average period necessary to artificially mature females by hormone treatments (ca. 2–6 months, e.g. Ohta et al. 1996; Lokman and Young 2000; Tanaka et al. 2001; Palstra et al. 2005; Oliveira and Hable 2010). Additionally, by applying hormonal treatments, mid-vitellogenic stages (even GSI > 10%) can be obtained without an increase in maximum body girth in European eel (Burgerhout, Brittijn, Dirks, van den Thillart, unpublished data), suggesting that up to this stage an increase in drag is most likely not an issue. On the other hand, some silver *A. dieffenbachii* (GSI unknown, but likely to be in the 5–10% range) clearly show an increased body girth (Fig. 3), which may suggest the difference between the natural situation and the laboratory or may indicate species-specific differences.

Currently, reproduction of many fish species can be controlled by manipulation of environmental conditions, especially photoperiod and temperature (Taranger et al. 2010; Wang et al. 2010). Major barriers at several phases of the reproductive cycle, such as the induction of puberty (e.g. gonadal growth, vitellogenesis), can be expected to be overcome using natural cues.

The melatonin system and reproduction

Melatonin, the time-keeping hormone, is produced by the pineal gland and the retina (Ekström and Meissl 1997). Pineal melatonin shows an increased synthesis and release during the night and corresponding decreases during the day, as well as season-dependent fluctuations, thus providing information about time of day and year (Zachmann et al. 1992a; Falcón et al. 1992, 2007, 2010a, b; Gern et al. 1991; Reiter 1993; Ekström and Meissl 1997; Migaud et al. 2010; Falcón and Zohar 2018; Saha et al. 2018). Melatonin is produced from serotonin via tryptophan and regulated by the rate-limiting enzyme aralkylamine *N*-acetyltransferase (AANAT, Fig. 4) (Falcón et al. 2010a,b; Falcón and Zohar 2018). In teleost fish there are two AANATs present; the retinal AANAT1 and pineal AANAT2 (Falcón et al. 1996, 2003). Pineal AANAT2 responds to temperature, and therefore is the amplitude of the pineal melatonin production temperature-dependent (Zachmann et al. 1992b; Falcón et al. 2010a,b; Falcón and Zohar 2018; Saha et al. 2018). Melatonin produced by the retina, on the other hand, is not per se dependent on the night; it is catabolized in situ and used for autocrine/paracrine purposes (Falcón and Zohar 2018).

Melatonin has a key role in transmitting external cues (Fig. 2), thereby synchronizing behavioural and physiological processes, such as gonadal development, in all classes of vertebrates (Underwood 1989; Falcón et al. 1992, 2010a, b; Zachmann et al. 1992a; Mayer et al. 1997; Pandi-Perumal et al. 2006; Li and Zhou 2015; Falcón and Zohar 2018; Saha et al. 2018). Recently, Falcón and Zohar (2018) reviewed in great detail the complex actions of melatonin on all levels within the reproductive system in fish (see particularly Fig. 2 of that review).

Fig. 3 Female New Zealand long-finned eel, *Anguilla dieffenbachii,* at the onset of the oceanic migration showing an increased body girth (GSI estimated 5–10%). Scale bar: 10 cm. *Photo credit*: Ms Pauline Jéhannet
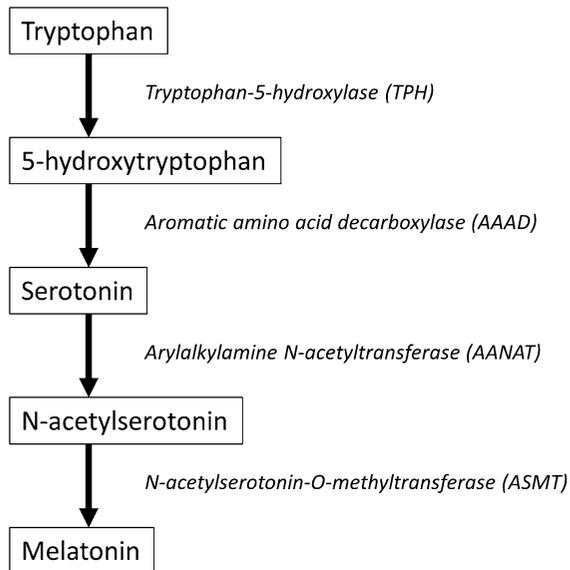
Fig. 4 Biosynthetic pathway of melatonin, which is synthesized from tryptophan via four enzymatic steps (Falcón et al. 2010a, b; Falcón and Zohar 2018)

Substantial evidence from numerous studies on vertebrates shows that the daily changes in melatonin levels are crucial for the onset of puberty and final oocyte maturation (Malpaux et al. 2001). Melatonin can further affect the secretion of Gnrh and Lh, as well as the synthesis of testosterone (Fig. 2, Falcón et al. 2007, 2010a, b; Migaud et al. 2010; Li and Zhou 2015; Falcón and Zohar 2018). Depending on the timing of the onset of gonadal recruitment (autumn–winter or spring–summer) either an increase or a decrease in melatonin is necessary to activate the reproductive axis (Malpaux et al. 2002; Anand et al. 2007). Moreover, melatonin is hypothesized to stimulate the KiSS/GPR54 system (Migaud et al. 2010), which was shown to be involved in the reproductive cycle acting upstream of GnRH and subsequently on gonadotropins. Kisspeptin is considered an important gatekeeper for puberty in mammals, as well as in fish (Elizur

2009; Zohar et al. 2010; Tena-Sempere et al. 2012), although based on gene knockout studies it was shown that in zebrafish this system is not essential for the development of the reproductive system (Tang et al. 2014). Intriguingly, studies in medaka (*Oryzias latipes*) showed an important role for kisspeptin during embryonic development, as severe effects on morphology and survival resulted from gene knockdown (Hodne et al. 2013).

Recently, it was shown in zebrafish (*Danio rerio*) and male European sea bass (*Dicentrarchus labrax*) that melatonin affects the *kiss* expression levels (Carnevali et al. 2011; Alvarado et al. 2015). Kisspeptin selectively inhibited *lhb* expression in primary cultures of eel pituitary cells, while no effect was found regarding *fshb* and *tshb* expression. It was suggested that the inhibitory effect of kisspeptin on *lhb* expression may be part of the species specific prepubertal blockage found in eels (Pasquier et al. 2011). However, kisspeptin may have a different effect in vivo due to possible feedback mechanisms, which to date still needs to be elucidated. Gonadotropin inhibiting hormone (Gnih), a neuropeptide that affects the expression of Gnrh, appears also regulated by melatonin (Falcón and Zohar 2018). Currently, there is no data available regarding the function of Gnih and its interaction with melatonin in the reproduction of freshwater eels. Understanding its role within the reproduction of eels will be of great interest for future research.

The melatonin mechanism of action in eels is thus far an unexplored field with only one publication in the context of reproduction by Sébert et al. (2008). In that study, the effect of melatonin on puberty in female European eels was examined. Administration of melatonin resulted in a stimulation of the dopaminergic system, thereby inhibiting the reproductive function as shown by a significant decrease in expression of *fshb* and *lhb* in the pituitary and a reduction in levels of sex steroids in plasma. However, administration of

melatonin to zebrafish resulted in a positive effect on the reproductive axis, as shown by an increase in GSI, and increases in mRNA levels of, for example, *kiss1*, *kiss2*, *gnrh3* and *lhb* (Carnevali et al. 2011). Positive effects of melatonin administration on the reproductive axis were also found in other fish, including masu salmon (*Oncorhynchus masou*) (Amano et al. 2000), Indian major carp (*Labeo rohita/Catla catla*) (Chattoraj et al. 2005; Maitra et al. 2005), and mummichog (*Fundulus heteroclitus*) (Lombardo et al. 2012, 2014). In male European sea bass, on the other hand, a catadromous species like the eel, administration of melatonin resulted in a decrease of expression levels of *gnrh1*, *gnrh3* and *gnrh* receptors (Servili et al. 2013). Moreover, melatonin administration resulted in suppression of gonadogenesis, and a decrease in serum levels of steroids and gonadotropin (Alvarado et al. 2015). Also, in whole brain of the sapphire devil (*Chrysiptera cyanea*) the dopaminergic activity was increased after treatment with melatonin (Badruzzaman et al. 2013). The same study showed a decrease in GSI and in the number of vitellogenic oocytes after dietary melatonin administration.

Clearly, the melatonin mechanism with respect to reproduction appears to be species-specific, which may reflect the differences in life cycles and timing of spawning of the species. We therefore hypothesized that in freshwater eels a decrease of melatonin levels may result in the release of the dopaminergic inhibition and thereby stimulate the reproductive axis. Preliminary research based on the recently published draft genome sequences of the European and Japanese eels (Henkel et al. 2012a, b; Jansen et al. 2017) revealed the nucleotide sequences of seven melatonin receptors (Table 1, unpublished data). In addition, sequences of the putative genes within the

biosynthetic pathway of melatonin, which is synthesized from tryptophan via four enzymatic steps (Fig. 4), are now available (Table 2, unpublished data).

Environmental factors affecting the melatonin system

Annual cycles of reproduction are often linked to changes in photoperiod and temperature regimes. For many fish species, such as salmonids, percids and cyprinids, the effects of photothermal exposure on the induction of vitellogenesis or final maturation have been extensively studied and used to manipulate the reproductive cycle (Taranger et al. 2010; Wang et al. 2010). In general, photoperiod is assumed to be the principal and temperature the secondary determinant to entrain and synchronize reproductive development in temperate fish (Bromage et al. 2001; Pankhurst and Porter 2003; Migaud et al. 2010).

The onset of silvering and the eel's reproductive migration in autumn appear to coincide with a decrease in photoperiod and in water temperature, and with an increase of the river's water discharge, and is found dependent on wind speed and lunar phase (for examples, see Deelder 1954; Todd 1981b; Vøllestad et al. 1994; Haro 2003; Durif et al. 2005; van Ginneken et al. 2007a; Bruijs and Durif 2009; Sandlund et al. 2017; Sudo et al. 2017). European eels mostly migrate between a temperature range of 6 °C to 15 °C, and migration proceeds more quickly when daylight decreases. Japanese eels migrate between temperatures of 10 °C and 20 °C (Sudo et al. 2017). It has further been proposed that decreasing photoperiod and/or a decrease in temperature accelerates the last

Table 1 Putative melatonin receptor genes of the European eel, *Anguilla anguilla* (unpublished)

A. anguilla Scaffold Nr.	Nr. exons	Protein size (aa)	Assigned gene name	Receptor type	Best BLASTP hit (Acc. Nr.; species)
1557	2	350	MT1a	7TM GPCR	XP_012690673.1; *Clupea harengus*
28	2	318	MT1b	7TM GPCR	XP_018588973.1; *Scleropages formosus*
14	2	354	MT2a	7TM GPCR	XP_018604071.1; *Scleropages formosus*
87, 57	2	346	MT2b	7TM GPCR	XP_018604071.1; *Scleropages formosus*
409	2	355	Mel1Ca	7TM GPCR	XP_018602080.1; *Scleropages formosus*
73	2	355	Mel1Cb	7TM GPCR	XP_018602080.1; *Scleropages formosus*

Table 2 Putative enzymes involved in the melatonin biosynthetic pathway of the European eel, *Anguilla anguilla* (unpublished)

| Predicted cDNA Contig nr.	Validated Contig nr	*A. anguilla* Scaffold Nr.	Nr. exons	Protein size (aa)	Assigned gene name	Best BLASTP hit (Acc. Nr.; species)
17636	25676	3906, 74508, contig3559887	11	469	Tryptophan 5- hydroxylase 1 (TPH1)	XP_005728010.1; *Pundamilia nyererei*
21538	22897	6622	10	451	Tryptophan 5- hydroxylase (TPH1-like)	XP_018619488.1; *Scleropages formosus*
N/A	N/A	12667, 8710 (partial)	> 6	> 119	Tryptophan 5- hydroxylase 2 (TPH-2)	ADK46901.1; *Clarias gariepinus*
3396	20143	210	13	487	Aromatic amino acid decarboxylase (DDC)	XP_021412916.1; *Oncorhynchus mykiss*
N/A	56960	6643 (partial)	> 2	195	Arylalkylamine *N*-acetyltransferase 1 (AANAT1)	AAY78956.1; *Acipencer sturio*
N/A	N/A	639	> 2	> 172	Arylalkylamine *N*-acetyltransferase 2 (AANAT2)	AKT76090.1; *Dicentrarchus labrax*
12683	15867	1865 (partial)	> 14	605	*N*-acetylserotonin *O*-methyltransferase (ASMLT)	XP_007227926.2; *Astyanax mexicanus*

N/A not available

stages of the silvering process (Vøllestad et al. 1994; Durif et al. 2005; Bruijs and Durif 2009).

During their oceanic migration, eels show notable diel vertical migrations (DVMs) (Jellyman and Tsukamoto 2002, 2005, 2010; Aarestrup et al. 2009; Manabe et al. 2011; Schabetsberger et al. 2013, 2015; Béguer-Pon et al. 2015; Chow et al. 2015; Wysujack et al. 2015; Amilhat et al. 2016), a behaviour also found in other fish species (see e.g. Beamish 1966; Neilson and Perry 1990; Watanabe et al. 1999). Based on the information derived from these field studies it can be deduced that eels clearly exhibit a daily rhythm, and thereby encounter daily fluctuations in temperature, as well as hydrostatic pressure and presumably, photoperiod, oxygen content and salinity.

Photoperiod

During the transition from yellow to silver eel, the eye diameter increases and by switching from freshwater to seawater, opsin the retinal pigment becomes more sensitive to blue wavelengths (Beatty 1975; Pankhurst 1982; Pankhurst and Lythgoe 1983; Archer et al. 1995; Zhang et al. 2000; Durif et al. 2005; Thomson-Laing

et al. 2018). Anadromous salmonids also show plasticity of the photoreceptors (Cheng and Flamarique 2004), reflected in a switch in the composition of visual pigments towards red during their reproductive migration from seawater to freshwater (e.g. Beatty 1966; Flamarique 2005). In eels, the switch indicates that they pre-adapt to the photic environments of mesopelagic oceanic waters, which is also reflected in the clear DVM behaviour associated with sunrise and sunset (Jellyman and Tsukamoto 2002, 2005, 2010; Aarestrup et al. 2009; Manabe et al. 2011; Schabetsberger et al. 2013, 2015; Béguer-Pon et al. 2015; Chow et al. 2015; Wysujack et al. 2015; Amilhat et al. 2016). Interestingly, a recent telemetry study showed that there was also a direct impact of the lunar cycle on swimming depths of *A. marmorata* (Fig. 5); during full moon eels were found at greater depths (ca. 230 m) than during new moon (ca. 170 m) (Schabetsberger et al. 2013). It was shown for other fish species that moonlight can also alter melatonin production and expression of melatonin receptors (e.g. Takemura et al. 2010a; Park et al. 2014). In addition, it was reported that blue wavelengths decrease plasma melatonin levels in European sea bass (Bayarri et al. 2002) and zebrafish (Ziv et al. 2007). Although
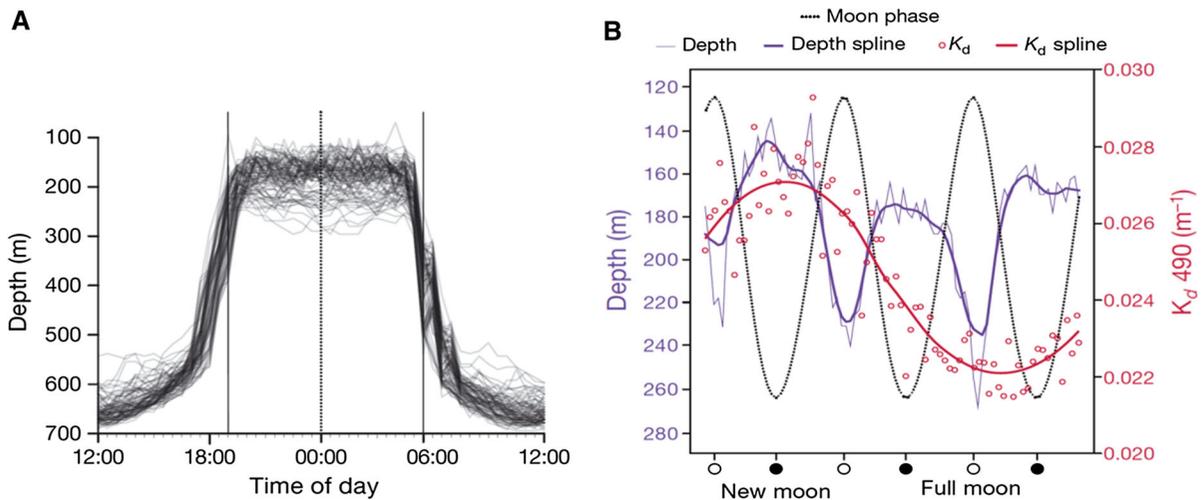
Fig. 5 Diel vertical migration (a) and night-time upper migration depths (b) (daily median: thin blue; spline curve: bold blue) of *Anguilla marmorata* followed over 3 months using pop-up satellite tags. The daily and monthly/seasonal rhythms (new and full moon) are clearly visible, indicating an effect of photoperiod and or light intensity on the migratory behaviour of eels. In **a**, solid vertical lines correspond to sunset and sunrise; the dotted line indicates midnight. In **b**, moon phase (dotted black line), and spectral irradiance at 490 nm (daily K_d estimates: red dots; spline curve: bold red) along a straight line between release and pop-up location (Schabetsberger et al. 2013. With permission)

predator avoidance is supposed to be the primary driver for the DVM (reviewed by Righton et al. 2012), this behaviour may well also be involved in enhancing gonadal development instead of delaying it as suggested by Boëtius and Boëtius (1967).

Through these DVMs, the photoperiod and light intensity eels encounter may change, coinciding with a possible reduction in daily melatonin production, both with respect to peak levels and duration. In Atlantic salmon, for example, additional illumination during night time resulted in a decrease of melatonin levels during the dark phase, resulting in a significantly lower number of fish that matured (Porter et al. 1998). Also, constant illumination or relatively long photoperiods can delay sexual development and ovulation in the likes of Atlantic salmon (Taranger et al. 1998), Atlantic cod (Hansen et al. 2001; Davie et al. 2003, 2007) and European sea bass (Bayarri et al. 2004). It is hypothesized that the inhibition of maturation in Atlantic salmon was mediated through a reduction in the plasma melatonin amplitude below a certain threshold level during the dark phase (Porter et al. 1998). In eels, the opposite to that seen in salmonids may occur, i.e. the onset of vitellogenesis is induced when the amplitude of melatonin plasma levels gets below a certain threshold. An argument for this hypothesis is

that salmonids are typically autumn and winter spawners (Pankhurst and King 2010), while eels are considered spring and summer spawners (Schmidt 1923; McCleave 2003; Tsukamoto et al. 2003; Tsukamoto 2009).

The effect of photoperiod on gonadal recruitment in wild female European eels was investigated in combination with hormonal stimuli (Mordenti et al. 2012; Parmeggiani et al. 2015). Briefly, eels were subjected either to 'light' 14:10 L:D (400 lx at the bottom of the tank without water) or to continuous 'dark' (40 lx at the bottom of the tank without water). For comparison, the light intensity of a full moon on a clear night is < 0.20 lx (e.g. Fraser and Metcalfe 1997), which eels can sense at over 200 m depth (Schabetsberger et al. 2013). It was found that under 'dark' conditions, females showed a significantly higher GSI after 16 hormone injections and an increase in the number of eggs released (Mordenti et al. 2012). Parmeggiani and co-workers (2015) showed that eels from the 'dark' group displayed higher blood plasma E2 and testosterone levels, and a higher GSI compared to the 'light' group. However, based on histology, no differences were found on the stage of gonadal development between the two groups. It is clear that the effects of photoperiod or light intensity, among the best-known

cues regulating the reproductive axis in fish, should be investigated in more depth.

Temperature

To entrain and synchronize full sexual maturity, temperature is considered the secondary determinant (Bromage et al. 2001; Pankhurst and Porter 2003; Migaud et al. 2010), and it has been shown that temperature affects melatonin profiles in fish (e.g. Zachmann et al. 1992b; Iigo and Aida 1995; Porter et al. 2001; Vera et al. 2007). The amplitude of the nocturnal surge of melatonin is controlled by temperature through the rate-limiting enzyme in the biosynthetic pathway, aralkylamine *N*-acetyltransferase (AANAT, Fig. 4) (Falcón et al. 2010a, b; Falcón and Zohar 2018; Saha et al. 2018).

During their oceanic migration, eels encounter daily fluctuations in water temperatures (Aarestrup et al. 2009; Jellyman and Tsukamoto 2002, 2005, 2010; Manabe et al. 2011; Schabetsberger et al. 2013, 2015; Tesch 2003; Chow et al. 2015; Wysujack et al. 2015; Amilhat et al. 2016). For example, during the first $\sim$ 1300 km of their migration, European eels showed a temperature range between 8 and 13 °C, with a daily average of 10.1 °C (Aarestrup et al. 2009). Interestingly, during the migration in the Mediterranean Sea, the temperature did not change despite the DVMs (13.2–13.4 °C; Amilhat et al. 2016). A much wider temperature range was found for the Japanese eel (*A. japonica*), namely between 4 and 10 °C during the day and 15–24 °C during the night (Manabe et al. 2011). Also, *A. marmorata* shows a range similar to that of the Japanese eel (Schabetsberger et al. 2013). These species-specific differences should probably be taken into account with respect to the artificial control of reproduction. It was hypothesized that the relatively low temperatures encountered during parts of the oceanic journey may delay gonadal development (Boëtius and Boëtius 1967). However, a so-called cold or chilling period—a period maintaining a temperature below a certain threshold, above which gametogenesis would be impaired—is necessary or suggested to advance vitellogenesis in several fish species, such as striped bass, European sea bass and Atlantic cod (Wang et al. 2010), and was recently also proposed for pike perch (Hermelink et al. 2011, 2013). In eels a similar mechanism may be involved, and as in

other fish species, it appears that temperature affects melatonin levels. Sébert et al. (2008) reported that low temperature down-regulates the secretion of melatonin in European eels.

Several studies have addressed the effects of temperature on artificial induction of full sexual maturity in male (Gallego et al. 2012; Baeza et al. 2014) and female eels (Sato et al. 2006; Dou et al. 2008; Pérez et al. 2011; Mazzeo et al. 2014) or they evaluated whether temperature advanced early oogenesis (Zadmajid et al. 2015). It needs to be noted that temperature manipulations were performed in combination with hormonal treatments, which stimulate gonadogenesis unnaturally by circumventing the endogenous regulatory processes. Still, Sato et al. (2006) concluded that in Japanese eels: "… water temperature is an important factor for the artificial induction of ovarian maturation, and an effective temperature for the induction of ovarian development is 20 °C". As compared to 20 °C, ovarian development was slow at 10 °C, and final maturation and ovulation could not be induced within 13 weeks. However, in the study of Pérez et al. (2011), using female European eels, a temperature regime from 10 to 20 °C accelerated oocyte development until week 8 (Fig. 6). In addition, higher levels of *fshb*, *lhb* and estrogen receptor 1 (*esr1*) mRNA, and of plasma E2 were observed. In male European eels, the best results concerning various sperm parameters, such as volume, density and motility, were obtained at 20 °C, compared to 10 °C or 15 °C. Hence, it was suggested that the optimum temperature to induce maturation in male eels via weekly injections with hCG is around 20 °C (Gallego et al. 2012).

Simulating change of water temperatures encountered during migration may be of notable importance to stimulate the reproductive axis. By changing temperatures between 5 and 15 °C, one female Japanese eel showed an increase in gonad development (GSI = 8.5%) without hormonal treatment (Mikawa et al. 2008). After repeating this experiment in combination with swimming exercise, no apparent change was found (K. Tsukamoto, pers. comm.). The effects of temperature decrease on the onset of vitellogenesis of farmed female Japanese eels were studied in order to simulate the downstream migration (Sudo et al. 2011a). It was shown that oocyte diameter increased and that they had accumulated oil droplets when the temperature was decreased over a 50-day

Fig. 6 Effect of temperature on vitellogenesis during hormonal treatment in the European eel. A. Water temperature treatments during treatment with carp pituitary extract (CPE) in female silver eels. Arrows indicate the sampling times at weeks 0th, 4th, 8th and 12th. Line indicates the period when ovulations were obtained in T10 group. B. Percentage of the different stages of ovarian development at 0th, 4th, 8th and 12th weeks of CPE treatment (n = 10/week) in each temperature treatment. PV, previtellogenic stage; EV, early vitellogenic stage; MV, mid-vitellogenic stage; LV, late vitellogenic stage (Pérez et al. 2011. With permission)
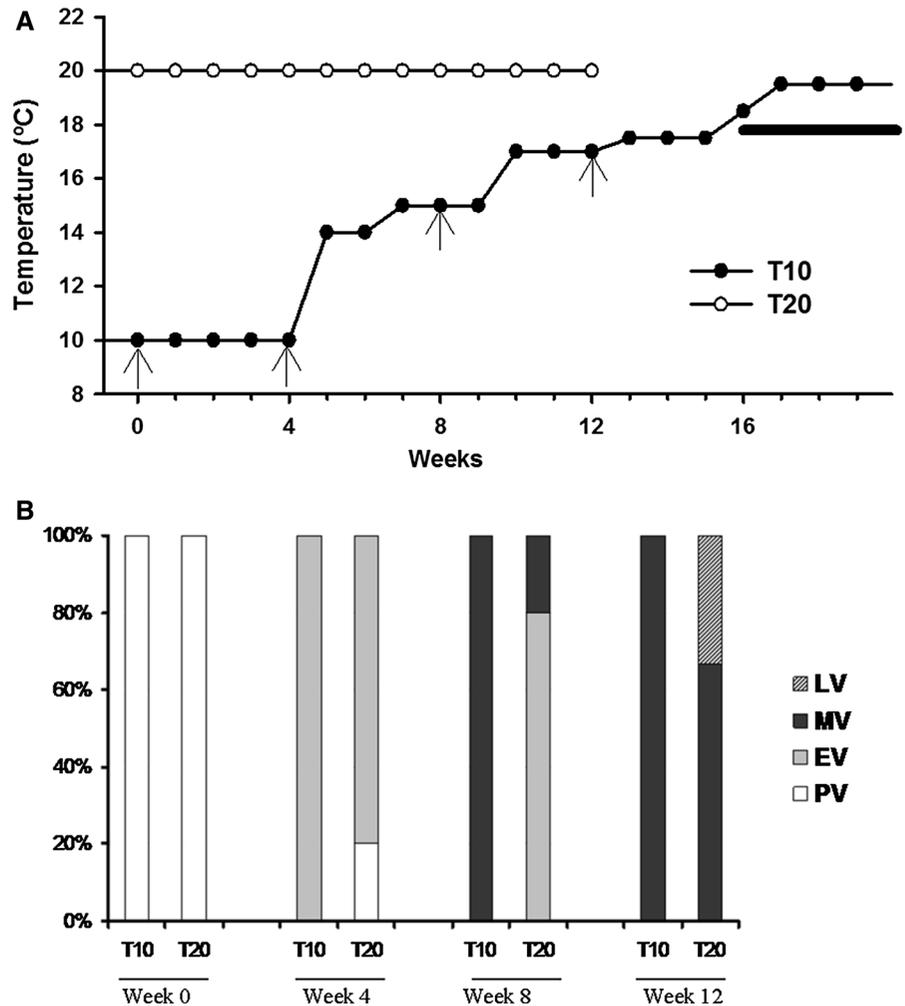
period from 25 to 15 °C. Although *fshb* and *lhb* expression in the pituitary were reduced, blood levels of 11-KT increased. 11-KT can induce previtellogenic oocyte growth and is considered an important factor to stimulate early gonadal development (Lokman et al. 1998, 2007; Rohr et al. 2001; Matsubara et al. 2003; Sudo et al. 2011b). Further, advancement of oogenesis (i.e. vitellogenesis) was not observed. Therefore, it was suggested that other environmental cues participating in the process, such as photoperiod or salinity, are required (Sudo et al. 2011a). However, in temperate fish species, vitellogenesis takes up to several months (Patiño et al. 2001; Wang et al. 2010), suggesting that during a prolonged chilling period the growth of oocytes may have occurred. In addition, there may be a temperature threshold above which

gametogenesis is impaired and a threshold below which it is stimulated (Wang et al. 2010).

Environmental factors potentially affecting the melatonin system

In teleost fish, photoperiod and temperature are proposed as the major environmental cues affecting the melatonin system (Zachmann et al. 1992a; Falcón et al. 1992, 2007, 2010a, b; Gern et al. 1991; Reiter 1993; Migaud et al. 2010; Falcón and Zohar 2018). Eels pre-adapt to mesopelagic oceanic life during silvering (van Ginneken and Maes 2005; Tsukamoto 2009). Changes in salinity and hydrostatic pressure could, therefore, also have an effect on the melatonin

system and may contribute to stimulating sexual maturation in eels.

Salinity

The effect of changing salinity on gonadogenesis has hardly been studied, most studies instead having been conducted on eels in seawater. One study assessed the effect of salinity on induced maturation in female eels (Kagawa et al. 1998; Kagawa 2003). Briefly, farmed female Japanese eels were subjected to seawater for 1 week or for 1 or 3 months. After 3 months GSI, oocyte diameter and oocyte stage (early vitellogenesis) had increased compared to groups exposed to seawater for 1 week or 1 month. When subjected to hormonal treatment, females held in seawater for 3 months needed a significantly smaller number of weekly injections to complete vitellogenesis than those held in seawater for only 1 week or 1 month. These results indicated that rearing in seawater advanced gonadal development and increased responsiveness to treatment with pituitary extracts in farmed female Japanese eels. In female European eels, plasma E2 concentrations had significantly increased 2 months after seawater transfer (Quérat et al. 1987) and seawater acclimation resulted in an increase in *fshb* mRNA levels in the pituitary (albeit not significantly) in female Japanese eels (Suetake et al. 2002, 2003).

Interestingly, salinity was seen to affect the production of melatonin and its receptors in European sea bass. Increasing salinity resulted in a significant reduction in melatonin plasma levels during the night. In addition, melatonin receptor densities significantly decreased in the optic tectum and retina (López-Olmeda et al. 2009). In eels, acclimation to seawater triggered early vitellogenesis (Kagawa et al. 1998; Kagawa 2003), which may have been mediated by a reduction in plasma melatonin levels. Clearly, additional studies are needed to clarify the effects of salinity on gonadal development in eels.

Hydrostatic pressure

Eels show DVMs over several hundreds of meters, resulting in strong daily fluctuations in hydrostatic pressures (HP) (Aarestrup et al. 2009; Jellyman and Tsukamoto 2002, 2005, 2010; Manabe et al. 2011; Schabetsberger et al. 2013, 2015; Tesch 2003; Chow

et al. 2015; Wysujack et al. 2015). Within approximately an hour, eels are able to descent or ascent between 200 and 500 m (Chow et al. 2015). Similar DVM behaviour within the same depth range has also been observed in, for example, bigeye tunas (*Thunnus obesus*) (Dagorn et al. 2000). It has been shown that eels are able to withstand HP up to 100 ATA, which is equivalent to the pressure at 1000 m depth (Sébert et al. 1987, 1990; Simon et al. 1992). The effect of HP on vitellogenesis in eels, has to date only been explored in two studies (Fontaine et al. 1985; Sébert et al. 2007). In the first study, caged female European eels were sunk to a depth of 450 m in the Mediterranean Sea for 3 months, which resulted in increased GSI and pituitary LH content (Fontaine et al. 1985). In the second study, females and males were subjected to 101 ATA for respectively 3 and 7 weeks. Females of the HP group showed significantly greater oocyte diameters and higher E2, 11-KT and vitellogenin levels in plasma as compared to the control group. In addition, the *lhb/fshb* ratio in females of the HP group was significantly higher; *fshb* expression was lower than in the control group, but not significantly so. Males subjected to HP showed a higher plasma 11-KT level, accompanied by higher pituitary *lhb* and lower *fshb* expression; however, these changes were not statistically significant. Based on these results, it was concluded that HP plays a positive role in the onset of gonadogenesis of eels, but other factors are needed for completing sexual maturation (Sébert et al. 2007). Interestingly, in the three-spot wrasse (*Halichoeres trimaculatus*), it was found that dopaminergic activity was decreased when fish were kept at a depth of 3 m compared to 0 m. Although this wrasse is a tropical species that spawns daily, it shows that HP due to daily tidal changes affects the reproductive axis (Takemura et al. 2010a, b, 2012). Also, in flounder (*Platichthys flesus*) subjected to daily fluctuating HP, a decrease in dopamine levels was found (Damasceno-Oliveira et al. 2007). Moreover, it was reported that daily fluctuating HP in female flounder resulted in an increase in pituitary FSH protein, correlated with vitellogenic oocyte development (Damasceno-Oliveira et al. 2014). However, a decrease in levels of metabolites of the maturation-inducing hormone 17α,20β-dihydroxy-4-pregnen-3-one (DHP) was also observed. Therefore, it was suggested that HP stimulates

ovarian development, but may delay final oocyte maturation (Damasceno-Oliveira et al. 2012). Strong rhythmic, daily changes in HP also occur during the migration of eels, and evaluation of the daily effects of HP on the melatonin system and the reproductive axis would be of great interest.

Combination of environmental factors

Puberty of eels is most likely induced and facilitated by a combination of the previously discussed environmental factors. Thus far, the effects of manipulation of multiple environmental factors on gonadogenesis in eels has received little attention (e.g. Boëtius and Boëtius 1967; Nilsson et al. 1981). Recently, attempts were made to simulate the freshwater downstream migration over 2 weeks and the oceanic migration over 9 weeks (total distance swam of 3792 km) in order to study the combined effects of photothermal regime, salinity and swimming exercise on farmed male and female European eels (Mes et al. 2016). No major changes occurred during this period with regard to gonadogenesis. While photothermal regime and salinity are expected to be involved in inducing gonadogenesis, the effect of swimming exercise remains unclear. When subjected to swimming exercise, a suppression of vitellogenesis was found in wild female European eels (Palstra et al. 2008a, 2010) and no changes in reproduction-related end points, such as GSI and plasma levels of testosterone and Lh, were found in farmed male European eels (Burgerhout et al. 2013a). Only a relatively small study (n = 6 per group) yielded increased GSI and *lhb* mRNA levels in wild male silver European eels subjected to swimming exercise for 3 months at relatively low speed of ca. 0.12 m s^{-1} compared to resting eels (Palstra et al. 2008a). The difference in response found between the study of Palstra et al. (2008a) and Burgerhout et al. (2013a) is possibly due to differences in the initial maturity status of the eels at the start of the trials, as reflected in a GSI ≤ 0.3 in the former (Palstra et al. unpublished data) and a GSI ≤ 0.09 in the latter study (Burgerhout et al. 2013a). This once again reinforces the hypothesis that the initial maturation status appears to be of great importance (Durif et al. 2006; Okamura et al. 2008; Dirks et al. 2014; Burgerhout et al. 2016; Rojo-Bartolomé et al. 2017).

In addition, it is expected that migrating eels are actively swimming during their migration and experiments involving swimming exercise are commonly performed against a current. However, the downstream migration of silver eels is found to increase with increased river discharge, indicating the use of water currents (Deelder 1954; Durif et al. 2003; Tesch 2003; see also Bruijs and Durif 2009). Moreover, swimming speeds found for eels equipped with pop-up satellite tags during their oceanic migration (*A. anguilla*: up to 0.29 m s^{-1} (Aarestrup et al. 2009), *A. dieffenbachii*: up to 0.36 m s^{-1} (Jellyman and Tsukamoto 2002); *A. japonica*, up to 0.17 m s^{-1} (Manabe et al. 2011) were lower than the optimal swimming speeds (i.e., the speed with the minimal cost of transport) found under laboratory conditions (*A. anguilla*: up to 0.68 m s^{-1} (Palstra et al. 2008b; Burgerhout et al. 2011b, 2013b; Tudorache et al. 2014, 2015); *A. australis*: up to 0.51 m s^{-1} (Tudorache et al. 2015)). The differences in swimming speeds observed between eels in the field and in the laboratory could very well be due to the increased drag resulting from the tag (Burgerhout et al. 2011b; Methling et al. 2011; Tudorache et al. 2014). However, it seems equally plausible that eels use oceanic currents during their journey, as suggested by Fricke and Kaese (1995). Although it has been shown that eels are highly efficient swimmers (van Ginneken and van den Thillart 2000; van Ginneken et al. 2005, 2007b; Palstra et al. 2008b; Burgerhout et al. 2013a, b), any reduction in energy use during migration is likely to benefit reproductive success at the spawning grounds.

Summary and future recommendations

In order to improve current protocols of artificial control of propagation of freshwater eels, we suggest that the hormonal treatments need to be replaced by use of simulated environmental conditions. However, the environmental cues inducing full sexual maturity have still been insufficiently studied, which probably reflects the limited knowledge of the natural conditions encountered during the oceanic spawning migration. Moreover, the majority of studies involving the examination of environmental factors are, unfortunately, combined with the hormonal treatments (Pérez

et al. 2011; Gallego et al. 2012; Baeza et al. 2014; Mordenti et al. 2012; Parmeggiani et al. 2015).

The major crux for inducing or advancing gonadogenesis in eels is overcoming the inhibition by dopamine, which is rather extreme as compared to other fish species (Vidal et al. 2004; Dufour et al. 2005, 2010). Knowledge of the (neuro)-endocrine pathways that control spontaneous gonadal development is of crucial importance to understand how dopaminergic inhibition may be exerted, and consequently, to override this inhibition. Information on entry into vitellogenesis may be obtained by studying closely related eel species that are far more advanced at the onset of their oceanic migration, such as New Zealand longfinned eels, *A. dieffenbachii* (Lokman et al. 1998) or the Indonesian *A. celebesensis* (Hagihara et al. 2012).

Some insights into the dopaminergic inhibition of the eel BPG axis are provided by administration of melatonin to female eels, which resulted in stimulation of the inhibitory tone (Sébert et al. 2008). It is therefore suggested that a decrease of melatonin levels, below a certain threshold, may result in the release of the dopaminergic inhibition and thereby stimulate maturation. Artificially decreasing melatonin levels using an antagonist would be an experiment we would like to recommend to conduct. Further, melatonin levels can most likely be decreased by changes in environmental factors, such as salinity (López-Olmeda et al. 2009), temperature (Zachmann et al. 1992a, b; Porter et al. 2001; Sébert et al. 2008), photoperiod (Taranger et al. 1998; Porter et al. 1998; Hansen et al. 2001; Bayarri et al. 2004), blue light (Bayarri et al. 2002; Ziv et al. 2007) or a combination of multiple parameters. Melatonin is known to be mainly regulated by photoperiod and temperature, and therefore it is highly recommended for future studies to investigate the effects of those two environmental factors on the induction of full sexual maturity of freshwater eels.

Thus far, melatonin and its interaction with the reproductive axis in eels is still a little-explored field. Understanding the effects of melatonin and the daily rhythms of the involved natural factors on puberty will have great potential for creating important new insights into the eel reproduction problem and may prove to be essential for eel aquaculture.

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