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Light impacts embryonic and early larval development of the European eel, *Anguilla anguilla*

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ABSTRACT

Little is known about the natural ecology of European eel during early life history. We extend our understandings on the ecology of this species by studying how early life stages perform under various light regimes. We assessed the effects of intensity, photoperiod (12:12 and 24:0 h light/dark) and spectral composition on embryonic survival, hatch success, larval morphology and survival at 5 days post-hatch. Treatments consisted of low intensity white (full spectrum, 2.2 μmol m^{-2} s^{-1}), blue (~470 nm, 0.7 μmol m^{-2} s^{-1}), green (~530 nm, 0.4 μmol m^{-2} s^{-1}), red (~690 nm, 0.2 μmol m^{-2} s^{-1}) and high intensity white (full spectrum, 10.5 μmol m^{-2} s^{-1}), blue (~470 nm, 3.9 μmol m^{-2} s^{-1}), green (~530 nm, 1.5 μmol m^{-2} s^{-1}), and red light (~690 nm, 1.1 μmol m^{-2} s^{-1}). Additionally, offspring were reared in continuous darkness (0:24 h light/dark). Results showed that light critically influenced early life stages. In particular, for the 12:12 h photoperiod, embryonic survival, until 26 h post-fertilization was significantly higher when reared under low (62 ± 13%) than those reared under high intensity light (42 ± 13%). Furthermore, embryos reared in low light had a higher hatch success (16 ± 7%) than those in high intensity light (12 ± 7%). Larval yolk-sac area was significantly affected by photoperiod and body area was significantly affected by the interaction between intensity × photoperiod. The highest incidence of deformities (75%) occurred when embryos were reared in high intensity white light under a 24:0 h light/dark photoperiod. Larval survival was significantly affected by light regime, such that larvae reared in low light intensity had higher survival (20 ± 8%) than those reared in high intensity (11 ± 8%), larvae reared in the 12:12 h photoperiod had higher survival (19 ± 8%) than those reared in the 24:0 h light/dark photoperiod (13 ± 8%), and larvae reared in red light (22 ± 8%) had higher survival than those reared in green (14 ± 8%) or white light (11 ± 8%). Under continuous darkness, development and survival of offspring was as high as the best intensity-photoperiod-spectral composition regime. For all early life history traits, a strong maternal effect was evident, such that offspring of 'poorer' quality showed lower adaptability to extrinsic factors than offspring of higher quality. Together, these findings suggest a preference for no or low light during embryogenesis and no or 12:12 h low red light during the pre-leptocephalus stage.

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1. Introduction

Light influences the development of living organisms from early life (Downing and Litvak, 2002) to adult reproductive stages (Mangor-Jensen and Waiwood, 1995). Most animals possess well-developed photoreceptors and neuronal networks to organize, identify, and interpret sensory information through the perception of light in order to react to environmental changes and adapt accordingly (Meissl et al., 1986). In the aquatic environment, the quantity and quality of incident light varies (Jerlov, 1968) as water acts as a chromatic filter, absorbing wavelengths below violet (λ < 390 nm) and beyond red (λ > 600 nm) quicker, while blue wavelengths (λ ~ 450 nm) penetrate deeper in the aquatic environment (Villamizar et al., 2011). Light intensity attenuates rapidly with depth, i.e. from 10,000 lux at the surface to 0.5 lux at 200 m in the clearest ocean (Helvik and Walther, 1992). Thus, oceanic organisms may be exposed to highly variable light conditions within their natural range of vertical distribution.

It has been shown that fish embryos can respond to external stimuli by altering density in order to avoid unwanted conditions, such as suboptimal light exposure (Mangor-Jensen and Waiwood, 1995; Olla and Davis, 1993). Photoperiodic alterations have been shown to inhibit hatching, or influence time periods until hatching or the length of the hatching window in several species (Brännäs, 1987; Downing and Litvak, 2002; Helvik and Walther, 1992; Nissling et al., 1998), while in other species, embryogenesis does not seem to be affected by light variations (Iglesias et al., 1995). For instance, in the zebrafish, *Danio rerio* embryos, the circadian clock becomes functional on the first day of development (Dekens and Whitmore, 2008), and before their visual system is functional, cerebral lateralization was shown to be affected by early light stimulation (Andrew et al., 2009). Light stimulation just

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before hatch affected cerebral lateralization and can lead to anatomical and functional asymmetries of the offspring in chicks and pigeons (Chiandetti et al., 2013). Mammalian embryos are also affected by light/dark conditions, where mouse and hamster zygotes most optimally developed to fetuses in the absence of light (Takenaka et al., 2007).

Before hatch, the retinae of most teleost larvae consist of only cone photoreceptors and development is not completed until metamorphosis (Blaxter and Staines, 1970). Primarily under the control of rods, scotopic vision seems impaired in early life stages (Powers and Raymond, 1990), but early-developed pineal photoreceptors are well suited for detecting luminance changes (Kusmic et al., 1992; Meissl and Ekström, 1988), though responses to altering light conditions among and within species vary.

Larvae of some species survive better when reared under certain photoperiod regimes like senegal sole, *Solea senegalensis* (Cañavate et al., 2006) and meagre, *Argyrosomus regius* (Vallés and Estévez, 2013). Other species develop better in complete darkness like the Atlantic halibut, *Hippoglossus hippoglossus* (Bolla and Holmefjord, 1988) and gilthead sea bream, *Sparus aurata* (Sahin et al., 2001), or in contrary, under constant lighting conditions like haddock, *Melanogrammus aeglefinus* (Downing and Litvak, 1999) and Atlantic cod, *Gadus morhua* (Puvanendran and Brown, 2002). Interestingly, a reduction in light intensity during the late larval cod stages was found to enhance foraging efficiency and growth performances (Monk et al., 2006), indicating different preferences for extrinsic factors at different developmental stages. Furthermore, enhanced larval survival rates due to microalgae (Salvesen et al., 1999) and their potential antibacterial effects, both under light and dark conditions (Kokou et al., 2012), have been previously observed.

Timing and development of larval color sensitivity is not clearly understood. Influences of light spectral composition on growth of Atlantic salmon, *Salmo salar* were investigated during smolting, but no effect was observed (Stefansson and Hansen, 1989). Additionally, spectral composition had no influence on growth (Downing, 2002), but significantly influenced feeding success of larval haddock (Downing and Litvak, 2001). Furthermore, European seabass, *Dicentrarchus labrax* larvae develop better under 12:12 h light/dark blue light conditions (Villamizar et al., 2009). Thus, development of visual systems of larvae seems to be species-specific and should be predisposed to increase larval performance under spectral conditions most frequently encountered in their particular ecological niche. In a world where organisms are evolutionary forced to adapt and specialize in order to survive in a specific ecological niche, and by taking previous studies into consideration, research should not only focus on a species by species investigation but also consider the different life history stages within a species.

The life cycle of catadromous eels is distinct. The oceanic pre-leptocephalus larvae of European eel, *Anguilla anguilla* develop into a migratory leaf-shaped stage, i.e. leptocephalus larvae that transform into glass eels, reaching the European continent (Tesch, 2003). Juvenile elvers and yellow eels inhabit coastal waters, lakes, and rivers before they undergo the intricate silvering process, preceding maturation (Dufour et al., 2003; Vidal et al., 2004). Even though, eel's natural reproduction remains an enigma, their oceanic spawning area in the Sargasso Sea, whereto they migrate after the onset of silvering, was documented through the occurrence of early larval stages (Schmidt, 1922; Schoth and Tesch, 1982). Yet, no spawner was caught and current knowledge on European eel reproduction is mainly based on experimental studies.

Breeding eels in captivity is a complex procedure. However, recent advances in assisted reproduction, adopting methodologies developed for the Japanese eel, *Anguilla japonica* (Kagawa et al., 2005), and established egg and larval culturing methods now allow mass production of high-quality gametes, embryos, and pre-leptocephali larvae of European eel (Tomkiewicz et al., 2012). This enables experimental research on larvae and major leaps in our understandings of the species' biology and eco-physiology by studying captive-bred offspring. Little is known about the habitat of the earliest life stages of the European eel larvae in the Sargasso Sea and embryos have never been encountered in nature. Pre-leptocephali have been sporadically captured at depths between 50 and 350 m (Castonguay and McCleave, 1987; Schoth and Tesch, 1984). Leptocephali are assumed to be present in the upper 100 m layer at night and migrate to greater depths with lower light intensity during daytime (Castonguay and McCleave, 1987; Schoth and Tesch, 1984). Deeper distributions of later developmental stages (60-85 mm) of European eel leptocephali have also been reported, i.e. at depths of 300-650 m during day (Tesch, 1980). Early life stages of European eel remain oceanic for such a long period that prevailing light conditions may have a major influence on larval development success and survival of this species.

Therefore, the objective of the present study was to assess the effects of light intensity, photoperiod, and spectral composition on embryonic and early larval development and survival of European eel. Understanding the photo-regulated responses, limits and possible adaptabilities of the most fragile early life history stage of eel, will provide insights into the species response to ecological regimes encountered in nature, and furthermore enhance cultivation techniques in captivity.

2. Materials and Methods

2.1. Broodstock management and offspring production

Female broodstock eels were obtained from Lake Vandet, a freshwater lake in Jutland (Denmark), while male eels were obtained from a Danish commercial eel farm (Stensgård Eel Farm A/S). Eels were transported to an experimental facility of the Technical University of Denmark (55.407444 N: 9.403414E) and transferred to 300 L tanks equipped with a re-circulation system (Tomkiewicz, 2012). Eels were maintained under low light (~20 lux), salinity of ~36 ppt, and temperature of ~19 to 21 °C. Acclimatization took place over 14 days. Prior to experimentation, eels were anaesthetized (ethyl p-aminobenzoate, 20 mg L^{-1}; Sigma–Aldrich Chemie, Steinheim, Germany) and tagged with a passive integrated transponder (PIT tag).

Females used for experiments (n = 4; hereafter *f1-f4*) had a mean (±SEM) standard length and body weight of 70.75 ± 6.47 cm and 830.25 ± 240.88 g, respectively. To induce vitellogenesis females received weekly injections of salmon pituitary extract (Argent Chemical Laboratories, Washington, USA) at 18.75 mg kg^{-1} body weight (Kagawa et al., 2005; Tomkiewicz, 2012). To stimulate follicular maturation and induce ovulation, females received 17α,20ß-dihydroxy-4-pregnen-3-one (Sigma-Aldrich, St. Louis, MO, USA) at 2 mg per kg^{-1} body weight (Ohta et al., 1996). Within 12-14 h, females were stripped, using the same anaesthesia as above to tranquilise specimens.

Male eels used in the experiment (n = 16) had a mean (±SEM) standard length and body weight of 38.1 ± 0.3 cm and 110.0 ± 2.0 g, respectively. Males received weekly injections of recombinant human chorionic gonadotropin (Ovitrelle, Madrid, Spain) at 1.5 IU g^{-1} fish (Gallego et al., 2012). Prior to fertilisation, an additional injection was given and milt was collected ~12 h after administration of hormone. Milt samples were pipetted into an immobilizing medium, P1 (for formulation, see Peñaranda et al., 2010) and used for fertilization within 4 h of collection (Butts et al., 2014).

In 2013, the experiment was repeated 4 times, within the same spawning season. Here, eggs from a female were "crossed" with a sperm pool from four males on June 14, June 20, June 24, and June 29 (thus, 4 females × 16 males in total). Eggs from each female were stripped into dry 36 × 30 × 7 cm plastic containers and fertilized separately. Gametes were swirled together and then 39.9 ppt, 0.2 μm filitered UV sterilized seawater was added; seawater was obtained from the North Sea and salinity was adjusted using Red Sea Salt (Red Sea Europe, Verneuil-sur-Avre, France). After a 5 min gamete contact time, eggs were transferred into 20 L plastic containers containing 36 ppt, 0.2 μm filtered UV sterilized seawater (Butts et al., 2014).

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