Diverging reproductive phenologies caused by climate warming – a conceptual approach on responses among spring and autumn spawning fish

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Summary

Climate warming have profound effects on ectotermic fish because increasing water temperatures induces altered timing of reproductive events. As climate continue to change, affected populations may increase or decrease in size depending on the impact of climate changes. This article provides a general framework to address reproductive challenges inflicted on spring and autumn spawning fish species subject to climate warming and phenological responses. Diverging pattern between the timing of ovulation and spawning is highlighted as two important within-species phenological responses to climate warming. The negative effect is explained by over-ripening of ovulated but non-spawned eggs within the body cavity of females. This phenomenon is therefore proposed as a physiological response of climate warming, capable of inflicting negative impact on offspring vitality and demographic trends. Comparisons between autumn and spring spawners are discussed, and it is postulated that spring spawners are more adaptable to climate changes than autumn spawners.

Sammendrag

Divergerende reproduktive fenologier forårsaket av et varmere klima – en konseptuell tilnærming til ulike responser hos vår- og høstgytende fiskearter. Et varmere klima har tydelige effekter på vekselvarme fiskearter fordi økende vanntemperatur medfører endringer i den tidsmessige synkroniseringen av reproduktive hendelser. Etter hvert som klimaet fortsetter å endre seg, vil de påvirkede populasjonene enten øke eller avta, avhengig av klimaendringenes effekt. Denne artikkelen gir et generelt rammeverk for å adressere reproduktive utfordringer hos høst- og vårgytende fiskearter som lever i stadig varmere klima. Divergerende mønstre mellom timingen av eggløsning og gytestart fremheves som to viktige fenologiske responser innen arten. Negative effekter forklares med overmodning av forløste egg som blir liggende inne i hunfiskene i lengre tid frem til gytingen starter. Dette fenomenet foreslås som en fysiologisk respons av et varmere klima, og som kan gi avkommet redusert overlevelse og avtakende bestandsstørrelse. Sammenligning av høst- og vårgytende fiskearter diskuteres, og det fremsettes en teori om at vårgytende arter kan tilpasse seg slike klimaendringer bedre enn høstgytende arter.

Introduction

The functionality of ecosystems and the life histories of its inhabitants around the world are increasingly modified by human activities linked to production and expenditure of commercial energy. Climate warming is largely a consequence of energy expenditure by industrial activities, and the process is driven by emissions of greenhouse gases into the atmosphere. Increasing temperatures have profound effects on organisms (Parmesan and Yohe 2003) and ectotherms in particular (Sinervo et al. 2010; Wake and Vredenburg 2008; Moore et al. 2011). Anthropogenic climate change inflicts considerable impact on biological systems around the World (Rosenzweig et al. 2008). Climate warming, regardless of its causes, impose reproductive challenges fish species in particular because increased temperature have induced altered timing of reproductive events (Wedekind & Küng 2010), trophic mismatches (Edwards and Richardson 2004) and even species extinctions (Helmuth et al. 2006; Moore et al. 2011).

Modern conservation biology needs to address climate change, habitat destructions and connectivity in an integrated way (Hannah 2011). As climate continue to change, affected populations may increase or decrease in size depending on the impact. Extirpation of some populations will be replaced by colonization of others, and major geographical shifts in distribution ranges will largely depend on the species ability to disperse (Davis & Shaw 2001). This integrated multidisciplinary concept of conservation (see Hannah 2011) illustrate the importance of conserving a network of habitats and their connectivity to allow climate driven shifts in species distribution with low risk of species extinctions.

The aim of this conceptual article is to provide a general framework to address reproductive challenges inflicted on autumn and spring spawning fish species subject to climate warming, directional phenological responses and adaptation dilemmas. The article comprises of a shortened summary of the author's Philosophiae Doctor (Ph.D) Thesis on reproductive and migratory challenges inflicted on brown trout (*Salmo trutta*) (Kraabøl 2012). The part of the Thesis covering migratory challenges is not included.

The concept on diverging reproductive phenologies and climate change

Phenological responses are commonly used as indicators for detecting impacts of climate changes. The timing of phenological phases mirror actual temperature changes in the environment experienced by fish species. The basic biological theory underlying this conceptual paper is that the timing of ovulation, and spawning onset, may in some species display diverging responses to warming environments, thus being key parameters to be investigated among fishes exposed to warming climate. The timing of completed ovulation are believed to advance whilst timing of spawning is expected to be delayed as a response to postponed occurrence of the temperature threshold that triggers spawning onset (see further evidence below).

As a consequence, a diverging pattern between these two important phenological traits may occur for autumn spawning fish (Figure 1 a). The oocytes will be kept within the female body cavity for a prolonged time due to the increasing time lag between ovulation and spawning. Over-ripening of ovulated eggs is therefore proposed as an effect of climate warming, and may inflict negative impact on offspring vitality and population abundance. Divergence between the timing of ovulation and spawning may also inflict an adaptation dilemma because fitness will be compromised by adapting to either optimize timing of ovulation or spawning. Higher mortality in early life stages caused by deleterious effects from over-ripening may in worst case scenarios contribute to negative demographic trends in the long run.

Among spring spawners, however, similar consequences of temperature increases are not expected because a parallel advancement of both ovulation and spawning is proposed to be a more likely scenario (Figure 1 b). Spring spawning fish populations are thus predicted to be more adaptable to climate warming compared to autumn spawners, and climate warming may disturb the balance between autumn and spring spawning fishes living in sympatry.

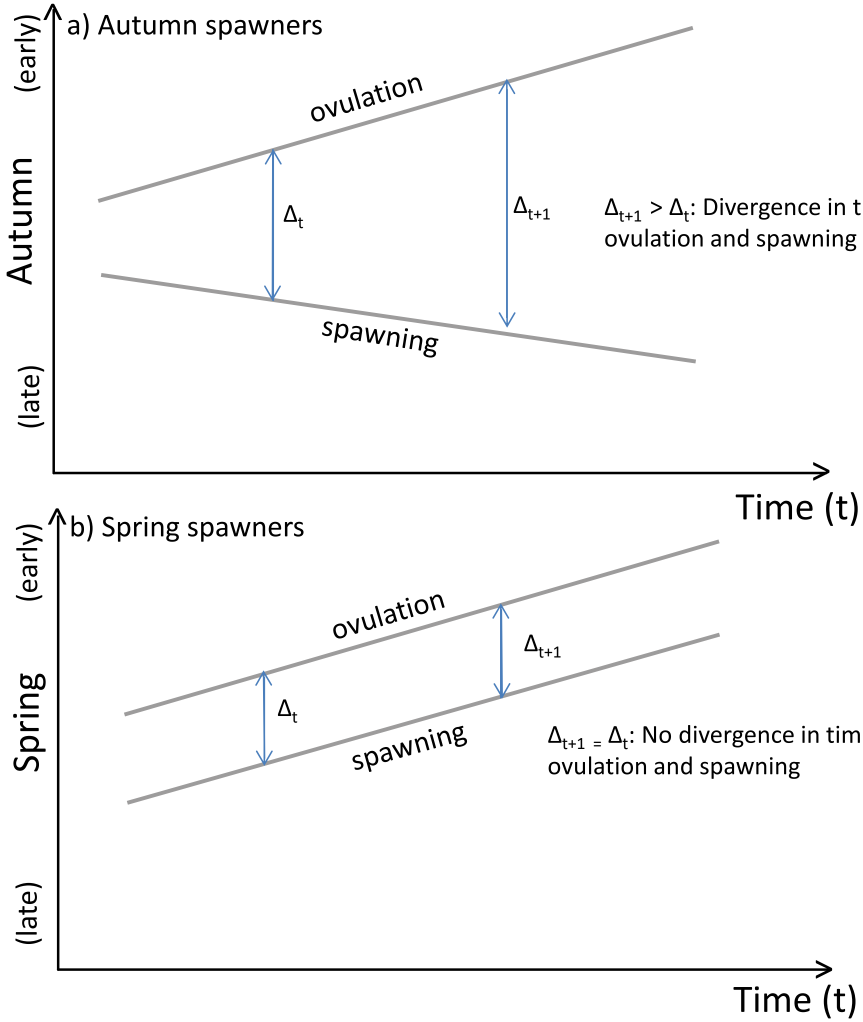

Figure 1. Conceptual sketch of directional courses of two reproductive phenologies in autumn spawning (panel a) and spring spawning (panel b) fish species exposed to warming climate over time.

What is phenology?

The words "phenology", along with "phenomenon" and "phenotype", stem from the Greek "*phainomai*", meaning, "to appear". Before calendars, humans depended on the predictability of seasonal events in nature to optimize their agricultural, gathering, hunting and fishing activities. Today this has become a biological discipline, which examines recurring plant and animal lifecycle events and their connection to the shifting weather and meteorological conditions. Phenology is therefore defined as the study of the temporality of key events in the life cycle of all species of plants and animals. However, it is most commonly applied in botany. Reproductive phenology deals with the timing of events linked to reproduction, i.e. spawning in fishes, mating in mammals, arrival and departure of migrating birds, diapause induction in insects and flowering in plants. The timing of such events strongly influence the matching between the organisms and their changing environment. Phenology is reported to constitute a major structuring element in nearly all areas of ecology and evolution and is regarded as an important component of the evolution of species-specific ecological strategies. Phenology determines the stage of development reached by an organism or population when challenged by its environment. Due to the discipline's importance for plant cultivation, much phenological research has focused on pest management, agricultural meteorology and horticulture, but a growing body of research literature address animals and their interactions with their environment. Phenological shifts have been among the most obvious and thoroughly documented biological responses to climate variations of the last 150 years (see Forrest & Miller-Rushing 2010 and Segrestin et al. 2019 for further reading).

Evidence and theoretical implications

Phenologies can be considered as adaptations to avoid environmental stress driven by abiotic and/or biotic factors, and species are under continuous selective pressure to adjust their phenologies in order to reduce fitness costs associated with poor timing of phenological traits (Pau et al. 2011) and subsequent trophic mismatches (Edwards & Richardson 2004).

Phenology in general is strongly linked to climate change, and phenological studies constitute a substantial part of the evidence that species respond to climate change (Walter et al. 2002). Climate changes have resulted in shifts in phenology for a variety of species around the World (i.e. Sparks and Carey 1995; Crick et al. 1997; Menzel and Fabian 1999; Stefanescu et al. 2003; Wedekind and Küng 2010; Moore et al. 2011). However, there is a shortage of studies covering the scenario involving two diverging reproductive phenologies within the same species as a response to climate warming.

As the timing of ovulation advances as the spawning onset is delayed, the corresponding increase in time lag between ovulation and spawning is suggested to result in oocyte ageing (over-ripening of eggs within the body cavity of female fish). This phenomenon impose a reproductive challenge inflicted by climate warming. Biotic impacts on warming ectotherms are mediated through physiology (Dillon et al. 2010), and the rate of female gonadal development (vitellogenesis) is directed by general bioenergetics like Van't Hoffs rule, stating that for every 10°C increase in temperature, the biological rates of metabolic components typically doubles (Brown & Krygier 1967; Caissie 2006). It is well documented that increasing ambient temperatures within the species-specific tolerance limits leads to acceleration of vitellogenesis and hence advanced ovulation time (e.g. Korsgaard et al. 1986; Olin and Von Der Decken 1989; Gillet 1991; MacKay and Lazier 1993; King et al. 2003; Sato et al. 2006).

Elevated water temperature speeds up the developmental rate of spawned eggs and therefore shortens the duration of post-spawning embryonic development (Elliott and Hurley 1998). Autumn spawners are able to adapt to this by delaying their spawning time (Figure 2) in order to maintain timing of the swim-up to exogenous feeding unchanged (Quinn et al. 2002; Jonsson and Jonsson 2009). Natural selection acts to prevent temporal mismatch of the offspring's transition to exogenous feeding and peak prey availability, survival and growth (Crisp 1981; Cushing 1982; Pau et al. 2011). Therefore, among autumn spawning fish species, it is hereby proposed that climate warming may cause divergence between timing of ovulation and spawning. This scenario is further suggested to inflict reproductive challenges by over-ripening of eggs, as demonstrated for Atlantic salmon (de Gaudemar and Beall 1998).

An adaptation dilemma may also be a part of the reproductive challenge because individual

Figure 2. The timing of spawning onset among autumn spawners (i.e. brown trout) is usually defined as the date of which the female starts to excavate the redd (Illustration photo: M. Kraabøl).

fish experience two phenologies diverging at the same time, and adaptation to any of these changes will inflict fitness costs as a result of poor timing of either one of the reproductive phenologies in question. Over-ripening is deleterious for a variety of reproductive features, such as fertilization and egg/embryonic developing mechanisms (Lahnsteiner 2000; Aegerter and Jalabert 2004; Cingi et al. 2010), progeny survival (de Gaudemar and Beall 1998), depletion of oocyte adenosine triphosphate (ATP) levels (Boulekbache et al. 1989) and occurrence of triploidy (Varkonyi et al. 1998; Yamazaki et al. 1989). Negative demographic trends are suggested as possible long-term outcomes from these within-species reproductive challenges.

Phenological responses among spring spawning freshwater fish, on the other hand, are in not characterised by diverging timing of ovulation and spawning. Both ovulation (Figure 3) and onset of spawning has advanced considerably among a variety of spring spawning species in Europe and USA (Gillet and Quétin 2006; Schneider et al. 2010; Wedekind and Küng 2010). It is therefore concluded that parallel advancements in the timing of ovulation and spawning are a documented scenario for spring spawners experiencing climate warming within their tolerance limits. Thus, over-ripening of eggs due to diverging reproductive phenologies is not expected. If so, spring spawners in general can adapt better to climate warming compared to autumn spawners.

It is postulated that a possible reproductive challenges posed by diverging timing of ovulation and spawning are defined by oocyte ageing within the body cavity of autumn spawning females, followed by reduced offspring viability. Spring spawners seem to display a parallel response of ovulation and spawning, which possibly make these species more adaptable to warming climate. Studies dealing with multiple within-species phenological responses to climate changes have rarely been reported, and is thereby proposed as a new approach to understand biological impacts and adaptation dilemmas rising from climate warming among spring and autumn spawning fish populations.

Figure 3. The timing of ovulation among spring spawners (i.e. grayling (Thymallus thymallus)) is defined by stripping of ovulated eggs (Illustration photo: M. Kraabøl).

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