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Temperature effects on egg development and larval condition in the lesser sandeel, *Ammodytes marinus*

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ABSTRACT

Understanding the influence of temperature on egg development and larval condition in planktonic fish is a prerequisite to understanding the phenological impacts of climate change on marine food-webs. The lesser sandeel, *Ammodytes marinus* (Raitt 1934), is a key trophic link between zooplankton and many piscivorous fish, sea birds and mammals in the northeast Atlantic. Temperature-egg development relationships were determined for batches of lesser sandeel eggs. Hatching began as early as 19 days post fertilisation at 11 °C and as late as 36 days post fertilisation at 6 °C, which is faster than egg development rates reported for closely related species at the lower end of the tested temperature range. The average size of newly hatched larvae decreased with increasing incubation temperatures in early hatching larvae, but this effect was lost by the middle of the hatching period. While the study revealed important temperature effects on egg development rate, predicted variability based on the range of temperatures eggs experience in the field, suggests it is only a minor contributor to the observed inter-annual variation in hatch date.

1. Introduction

Marine ecosystems in Northern Europe, particularly within the North Sea, are predicted to be significantly impacted by climate change, as attested by the 1.3 °C rise observed over the last 25 years (Sherman et al., 2009) with recent years showing the warmest winters in a 40 year time-series (ICES, 2016). Being ectotherms, fish are sensitive to such warming as critical phenological traits such as incubation duration and the date of first feeding are influenced by water temperature. As the sensitivity of phenology to temperature varies between species (Edwards and Richardson, 2004; Peck et al., 2012a), trophic chain and whole ecosystem structure might be modified by climate change through temporal alterations of species interactions such as the mismatch between predators and prey (Nakazawa and Doi, 2012). In marine fish, the match-mismatch hypothesis (Cushing, 1969, 1990), which proposes that the synchrony between hatching and seasonal prey production determines growth and survival, has been repeatedly advanced as a cause of fluctuations in fish recruitment (Richardson, 2008). Differences in the temperature sensitivity of predators and prey phenology have the potential to directly affect fish recruitment, by impacting the temporal overlap between fish hatching and prey production. In addition, temperature has a direct influence on larval condition at hatching, with respect to the amount of endogenous resources remaining in the yolk sac (Kamler, 2008). Yolk is the sole resource fuelling early larval development and provides a buffer allowing larvae to survive for a short period in the absence of prey (Yamashita and Aoyama, 1986). Therefore, acquiring empirical evidence on the influence of temperature on egg development and larval condition of key marine species is a prerequisite to understanding the phenological impacts of climate change on important trophic interactions (Peck et al., 2012a).

Both empirical and modelling studies indicate that the match between larval hatch times and the spring zooplankton bloom is key to the early survival of the lesser sandeel, *Ammodytes marinus* (Raitt 1934) (Wright and Bailey, 1996; Gurkan et al., 2013; Régnier et al., 2017). Sandeel are abundant in the North Sea, representing up to 15% of the total biomass (Sparholt, 1990), 90% of which are estimated to be *A. marinus* (ICES, 2004). As this species is a key trophic link between secondary production and many piscivorous fish, sea birds and mammals in the northeast Atlantic (Daan, 1989; Wanless et al., 2004; Lilliendahl and Sólmundsson, 1997; Eliasen et al., 2011), an understanding of the phenological variation in *A. marinus* is important in predicting the effect of climate change on marine food webs (Eerkes-Medrano et al., 2017). Larvae hatch over an extended period from February to April in the North Sea (Langham, 1971; Wright and Bailey, 1996; Régnier et al., 2017). The timing of hatching is linked to environmental and demographic influences on both gonad development and embryonic development. Spawning in *A. marinus* can occur from

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December – February based on the incidence of their demersal eggs and observations of gonadal development (Gauld and Hutcheon, 1990; Bergstad et al., 2001; Boulcott et al., 2017). Although *A. marinus* only spawns a single batch of eggs (Boulcott and Wright, 2008), considerable variation in female gonad maturation has been found, with an earlier onset of spawning in larger females (Boulcott et al., 2017).

Temperature is known to affect sandeel reproduction, with inhibited gonad investment observed at higher temperatures (Wright et al., 2017a), which may in turn affect spawning date. This is because exogenous vitellogenesis is entirely dependent on the allocation of stored energy, as *A. marinus* bury in sand during this reproductive phase (Boulcott and Wright, 2008; Wright et al., 2017b). Whilst temperature dependent egg development has been examined in two species of *Ammodytes* (Smigielski et al., 1984; Yamashita and Aoyama, 1985), none have focussed on *A. marinus* and little is known about the effect of this factor on larval condition at hatching.

In the present study, the effect of temperature on *A. marinus* egg developmental rate and larval condition at hatching was investigated in the laboratory. Eggs from a single North Sea parental stock were incubated over a range of temperatures that eggs experience in the wild (6–9 °C; Berx and Hughes, 2009) and the expected rise up to 11 °C by the end of the century (Lowe et al., 2009).

2. Materials and methods

2.1. Gamete collection

Sandeel (*Ammodytes marinus*) > 9 cm total length (L_T), corresponding to the size range of mature fish in the region (Boulcott et al., 2007), were caught off Stonehaven Bay (57°57′N; 2°06′W) in August 2016 by demersal trawl by the RV *Temora*, and transferred into an outdoor 3 m tank at Marine Scotland Science aquarium facilities (Aberdeen). Conditions within the tank mimicked the wild habitat as much as possible; sand covering the bottom (10 cm layer), natural photoperiod with a continuously filtered inflow of ambient water temperature (positively correlated to the temperature recorded in the nearby monitoring station of Stonehaven: r = 0.96, p < 0.0001). Fish were fed on a diet consisting of a mixture of krill and *Artemia* until the start of the winter spawning season, when cessation of feeding naturally occurs in the wild. A sub-sample of fish was sampled on a fortnightly basis from late December to screen for signs of sexual maturation. When it was determined that spawning was imminent (January 26, 2017), females (N = 3) and males (N = 15) were manually stripped of their gametes. After fertilisation, eggs were divided equally between the 6 groups corresponding to the temperature treatments.

2.2. Egg incubation

The fertilised eggs were introduced to six 1 m tanks within half an hour of fertilisation, with water temperature in each tank controlled by SeaChill TR-30 Aquarium Chiller units (Sterner AquaTech, U.K.), equipped with a large air stone and a temperature logger which was corroborated manually by a thermometer each day. A fine mesh bag covered each tank's water inflow (100 L·hour^{-1}) to prevent fouling. A large tray with drainage holes on the bottom was suspended within each tank, into which three small fine mesh-bottomed incubators (diameter 7.5 cm) were inserted. The fertilised eggs from each of the three females were divided equally among incubators in each of the six tanks (i.e. 18 incubators in total). Each incubator cell housed an average 400 eggs from each female. Four tanks were immediately set to their experimental temperature (8°, 9°, 10° and 11 °C) as they were within 1–2 °C of the parental tank. The other two tanks were set initially at 8 °C before being set at experimental levels (6° and 7 °C) the next day to avoid shocking the eggs. The set temperatures remained fairly constant throughout the experimental run, with means of 6.28 °C (S.D. = 0.26), 7.3 °C (S.D. = 0.15), 8.44 °C (S.D. = 0.13), 9.27 °C (S.D. = 0.25), 10.88 °C (S.D. = 0.21) and 11.68 °C (S.D. = 0.29) for temperatures in the 6°, 7°, 8°, 9°, 10° and 11 °C tanks respectively. The room was held under red light conditions and disturbance was kept to a minimum. Egg incubators were checked daily, by close inspection through the top of the open incubators, and all visible larvae were removed on the day of hatch. Larvae were euthanized with an overdose of anaesthetic (MS-222) and immediately photographed with a QCAM camera under a Leica MZ9.5 microscope at ×12–16 magnification (larvae presenting obvious signs of shrinkage were discarded). Precise measurements of L_T and yolk sac oil globule volume (to give an indication of remaining energy resources) were obtained from the calibrated digital images (to the nearest 0.01 mm/mm^2 respectively) using image analysis (Image Pro Insight, Media Cybernetics, Coventry, UK). Yolk and oil globule volume were calculated as $V = 4/3\pi.a.b^2$, where a is the larger radius and b the smaller radius. A sample of newly hatched larvae from the 8 °C treatment (N = 64) were isolated in two separate incubators on the 26th and 27th of February, and on each day from the 28th of February, and up to the eleventh day post hatching, 4–5 individuals were euthanized and photographed as described previously. L_T, oil globule and yolk-sac volumes were measured on these individuals to assess the rate at which energy stores were depleted.

2.3. Statistical analyses

2.3.1. Development rate

The influence of incubation temperature on egg development rate (D_R) was modelled as a power function (Lasker, 1964; Peck et al., 2012a):

$$D_R = \alpha \times T^{\beta}$$

where D_R is expressed as a percentage per day, where 100% corresponds to the total duration of incubation. T is incubation temperature, α and β are the parameters to estimate. The model was fitted using a weighted non-linear least square method with weights set to 1/variance at each temperature.

2.3.2. Phenotype at hatching

In order to describe variations in larval size at hatching between treatments, a hierarchically structured Von Bertalanffy model was used, where:

$$L_{T_{i,h}} \sim N(mu_{t,h}, tau_t)$$

With $mu_{t,\,h} = Linf_t \times (1 - \exp(-K_t \times (h - t0_t)))$

And $Linf_t \sim N(m1, t1)$

$$K_t \sim N(m2, t2)$$

$$t0_t \sim N(m3, t3)$$

$$tau_t \sim G(r1, \lambda 1)$$

In which, $L_{T\,t,h}$ is the length of a larvae hatching at temperature t, on day h and is drawn from a normal distribution with mean $mu_{t,h}$ and precision tau_t. Temperature-specific parameters $Linf_t$, K_t and $t0_t$ were drawn from normal distributions with hyperparameters *m1*, *t1* (Mean and precision), *m2*, *t2* and *m3*, *t3* respectively, while tau_t was drawn from a Gamma distribution with parameters *r1* (shape) and λ*1* (inverse scale). Hyperparameters were given uninformative uniform priors. The Bayesian model was fitted in R and JAGS using the "rjags" package, an initial burn-in of 10,000 iterations preceded the 100,000 iterations used to produce the parameters estimates.

Variations in the volume of the oil globule at hatching were also described using a hierarchically structured model with square root transformed volumes, where:

$$OGvol_{t,h} \sim N(mu2_{t,h}, tau2_t)$$

With $mu2_{t,\,h} = a_t \times \exp(b_t \times h)$