Journal of Sea Research 134 (2018) 34–41

Contents lists available at ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

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

Thomas Régnier*, Fiona M. Gibb, Peter J. Wright

Marine Scotland Science, 375 Victoria Road, Aberdeen AB11 9DB, Scotland, UK

ARTICLE INFO

Keywords:
Temperature
Incubation
Development rate
Hatching
Ammodytes marinus

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

---

* Corresponding author.
E-mail address: T.Regnier@marlab.ac.uk (T. Régnier).

https://doi.org/10.1016/j.seares.2018.01.003
Received 4 October 2017; Received in revised form 29 January 2018; Accepted 30 January 2018

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:

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

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 *λ1* (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:

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

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

And $a \sim N(m4, t4)$

$b \sim N(m5, t5)$

$tau2_t \sim G(r2, \lambda 2)$

In which, $OGvol_{t,h}$ is the volume of the oil globule of a larvae hatching at temperature *t*, on day *h* and is drawn from a normal distribution with mean $mu2_{t,h}$ and precision $tau2_t$. Temperature-specific parameters a_t and b_t were drawn from normal distributions with hyperparameters *m4*, *t4* and *m5*, *t5* respectively, while $tau2_t$ was drawn from a Gamma distribution with parameters *r2* and *λ2*. Hyperparameters were given uninformative uniform priors. The model was also fitted in R and JAGS as described previously.

2.3.3. Oil globule and yolk depletion rate

Depletion of the yolk sac and the oil globule after hatching at 8 °C were described using an exponential decay model with square root transformed volumes, where:

$OGvol_d\,(\text{or } YOLKvol_d) \sim N(mu3_d, tau3)$

With $mu3_d = a \times \exp(b \times d)$
And $a \sim U(0{,}100)$

$b \sim U(-1, 1)$

$tau3 \sim U(0, 1 \times 10^{10})$

In which, $OGvol_d$ is the volume of the oil globule ($YOLKvol_d$, for yolk volume) of a larvae *d* days after hatching, and is drawn from a normal distribution with mean $mu3_d$ and precision *tau3*. Parameters *a* and *b* and *tau3* were given uninformative uniform priors. The model was also fitted in R and JAGS as described previously.

3. Results

3.1. Development rate

Hatching started as early as 19 days post fertilisation at the highest incubation temperature (11 °C) and as late as 36 days post fertilisation at the lowest (6 °C; Fig. 1). 50% hatching was reached after 22 and 39 days at 11 °C and 6 °C respectively, with hatching lasting between 17 and 25 days in the range 6 to 10 °C, while at 11 °C all larvae had hatched within just 9 days. D_R was significantly and positively influenced by temperature (Fig. 2), as parameter estimates were α = 0.51 (95%CI: 0.49–0.54, significantly different from 0: *t*-value = 44.46, $p < 0.0001$) and β = 0.85 (95%CI: 0.49–0.54, significantly different from 0: *t*-value = 79.57, $p < 0.0001$). The ratio of the residual sum of square on the total sum of square further indicates that 52% of the variation in D_R was accounted by the temperature effect. Therefore the model provided a good fit as predicted (average) development time between fertilisation and hatching was 40 days at a temperature of 6.3 °C, and 24 days at a temperature of 11.7 °C for median incubation durations of 39 and 22 days observed at these temperatures respectively.

3.2. Phenotype at hatching

L_T of larvae at hatching decreased with temperature, while variations in length increased (6 °C: 6.29 ± 0.42 mm (S.D.), 7 °C: 6.23 ± 0.45 mm, 8 °C: 6.06 ± 0.53 mm, 9 °C: 5.78 ± 0.65 mm, 10 °C: 5.74 ± 0.61 mm, 11 °C: 5.31 ± 0.69 mm). The fitted Von Bertalanffy model revealed significant temperature effects on the relationship between L_T at hatching and hatching day (Table 1). In particular, temperature differences were present in the first days of hatching but disappeared by the middle of the hatching period (Fig. 3).

The volume of the oil globule decreased throughout the hatching sequence and the model revealed significant differences in temperature-specific parameters (Table 2). However, little variation among incubation temperatures were observed in the resulting estimated trajectories (Fig. 4). Larvae that hatched on or after the 15th day of the hatching period had very little endogenous stores (Fig. 4).

3.3. Oil globule and yolk depletion rate

The volume of the oil globule was strongly related to yolk-sac volume ($F_{1,62} = 465$, $r^2 = 0.88$, $p < 0.0001$), and both decreased rapidly after hatching (Fig. 5). After 10 days post hatching at 8 °C, 50% of the larvae were predicted to reach a stage of depletion where < 5% of the initial yolk or oil globule remained (where 100% is the volume at

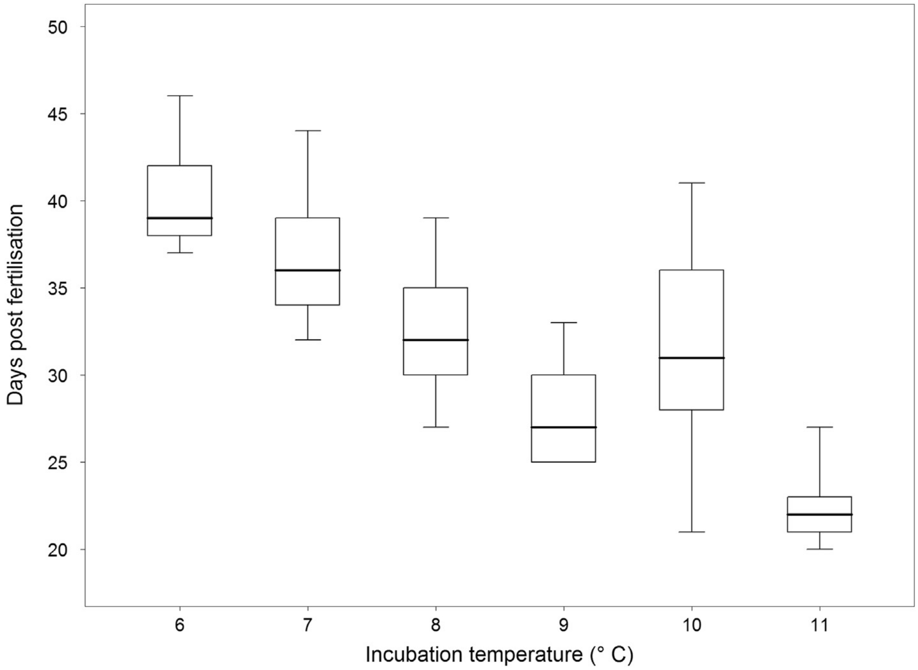

Fig. 1. Boxplots of *Ammodytes marinus* egg development to hatch (in days post fertilisation) at six incubation temperatures. The bold lines represent median hatching days, the edges of the boxes represent 25 and 75% hatching (lower and upper edges respectively) and the lower and upper whiskers represent 5 and 95% hatching respectively.

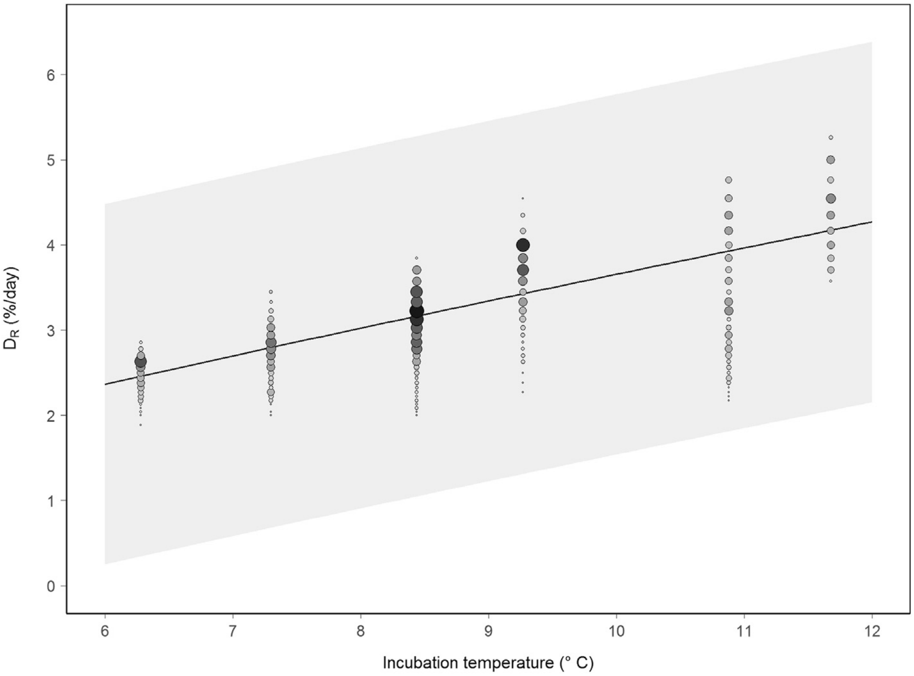

Fig. 2. Relationship between *Ammodytes marinus* egg development rate ($D_{R)}$) and Temperature (D_R = a.Temperature^b). The shaded area represents the 95% CI, both sizes and colours (shades of grey) of the points reflect the abundance of data.

Table 1
Temperature-specific parameter estimates for the Von Bertalanffy model describing *Ammodytes marinus* body size at hatching. 95% CI is indicated between brackets.

Temperature	K	Linf	t0	Variance
6	0.37 (0.19–0.65)	6.41 (6.31–6.58)	−5.66 (−12.43–2.64)	0.18 (0.15–0.21)
7	0.4 (0.2–0.71)	6.3 (6.23–6.42)	−4.49 (−11.07–1.93)	0.2 (0.17–0.23)
8	0.73 (0.57–0.91)	6.18 (6.13–6.22)	−0.66 (−1.56–0.1)	0.23 (0.2–0.25)
9	0.39 (0.29–0.49)	6.28 (6.16–6.41)	−1.07 (−2.39–0.22)	0.25 (0.22–0.29)
10	0.55 (0.41–0.74)	5.95 (5.88–6.01)	−1.49 (−2.47–0.78)	0.2 (0.17–0.24)
11	0.19 (0.12–0.3)	6.2 (5.88–6.58)	−6.15 (−10.05–3.67)	0.32 (0.25–0.4)

hatching, Fig. 5).

4. Discussion

Sandeels have a very protracted embryonic period relative to other winter hatching species (Smigielski et al., 1984; present study). In the North Sea, the hatching period of plaice (*Pleuronectes platessa*), haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) all overlap with that of *A. marinus* (Munk et al., 2009). However, in contrast to these species, the time to 50% hatching is more than twice as long as that reported for plaice (Fox et al., 2003), haddock (Martell et al., 2005) and cod (Geffen et al., 2006) and the variation in hatch times for a given temperature is considerably greater. While these other species have pelagic eggs, spring spawning herring (*Clupea harengus*) from the Clyde (Scottish west coast) that spawn demersal eggs like sandeel, have a far shorter embryonic phase (Gamble et al., 1985). Consequently, temperature dependent egg development and individual variation in *A. marinus* appears to be a comparatively important source of hatch date variation in relation to other winter hatching species.

Temperature had a positive effect on *A. marinus* egg developmental rates, as is typical of marine fish (Peck et al., 2012a). However, egg developmental times were slightly different than that reported by Winslade (1971) for *A. marinus*, as he found that 50% hatching was reached 26 days post fertilisation at 8.7 °C (the only incubation temperature tested), compared to an estimated 31 days in the present experiment. However, uncertainty remains concerning the exact date of fertilisation in Winslade (1971), as fish bred in the holding tank and eggs were discovered a few days after spawning. The influence of temperature on egg developmental rates also differed from that observed in two closely related species, *A. americanus* (Smigielski et al., 1984) and *A. personatus* (Yamashita and Aoyama, 1985). While incubation in *A. americanus* and *A. personatus* have a relatively similar response to temperature over the range considered in the present study (*A. americanus*: 48 days at 7 °C and 30 days at 10 °C, *A. personatus*: 51 days at 6.5 °C and 25 days at 10.5 °C), embryonic development in *A. marinus* appears to be much faster at the cold end of the temperature range and quite similar at the warm end of this range (39 and 36 days at 6° and 7 °C, 27 and 31 days at 9° and 10 °C). Incubation in *A. marinus* thus appears less sensitive to temperature than in *A. americanus* and *A. personatus*. In the North Sea, eggs would typically experience temperatures between 5 and 7 °C as the temperature declines from January to March (Berx and Hughes, 2009). Light intensity has been found to delay hatching in halibut (Helvik and Walther, 1993), and might have been responsible for the prolonged hatching period observed at 10 °C as the treatment tank was closest to the only light source.

Over the range of increasing temperature considered in the present study, the overall duration of incubation decreased by 16.6 days. For comparison, over the same temperature range, development time between the egg and adult stage of the sandeel's two main Calanoid copepod prey would be reduced by 24.5 days for *Calanus finmarchicus* and 37.7 days for *C. helgolandicus* (Cook et al., 2007). Therefore, a change in temperature has the potential to affect the temporal co-occurrence of sandeel and their prey and their respective growth and survival rates. During the last two decades, average February temperatures measured near the sea bed in the nearby monitoring station of Stonehaven varied between 5.59 °C and 7.08 °C (http://data.marine.gov.scot/dataset/scottish-coastal-observatory-data). According to the present results, this difference would potentially lead to a difference of around one week in median incubation times (37 and 45 days for the lowest and

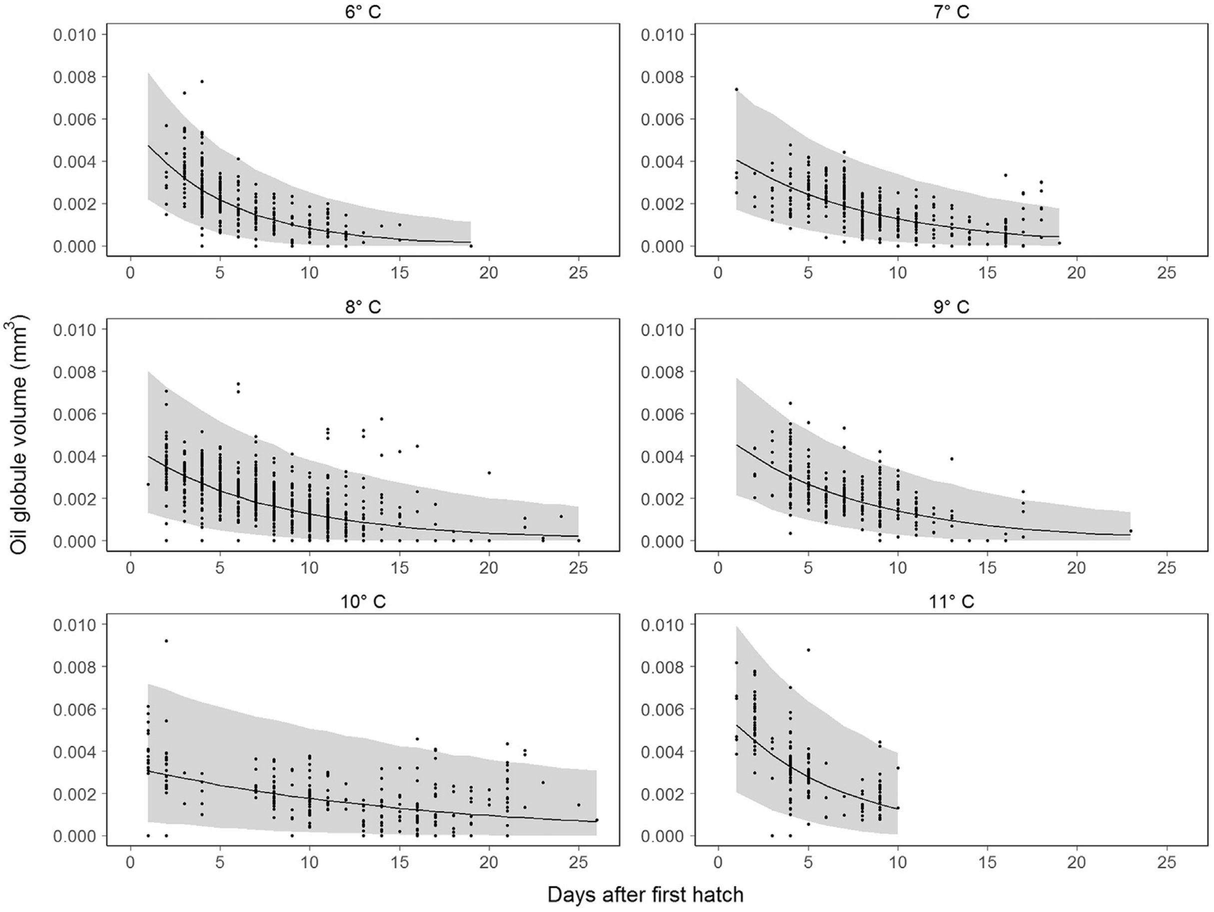

Fig. 3. *Ammodytes marinus* L_T at hatching for six incubation temperatures. Average predictions and 95% CI from the Von Bertalanffy model are presented with solid and dotted lines respectively.

Table 2
Temperature-specific parameter estimates for the model describing *Ammodytes marinus* oil globule volume at hatching. 95% CI is indicated between brackets.

Temperature	a	b	Variance
6	0.0758 (0.0708–0.0811)	−0.1 (−0.11–0.09)	0.00012 (0.0001–0.00014)
7	0.0679 (0.0633–0.0726)	−0.06 (−0.07 − −0.06)	0.00013 (0.00011–0.00015)
8	0.067 (0.0637–0.0705)	-0.06 (−0.07–0.06)	0.00018 (0.00016–0.0002)
9	0.0717 (0.0676–0.0759)	−0.07 (−0.07–0.06)	0.00011 (0.00009–0.00013)
10	0.0571 (0.0524–0.0621)	−0.03 (−0.04–0.02)	0.00022 (0.00019–0.00026)
11	0.0785 (0.0728–0.0848)	−0.08 (−0.1–0.06)	0.00018 (0.00015–0.00023)

highest temperature respectively). Inter-annual differences in female size at the time of spawning may account for some further variation in hatch dates (Boulcott et al., 2017). However, differences of up to 30 days in median population hatching dates were observed during this period (Régnier et al., 2017), indicating that other sources of inter-annual variability in spawning date might play a greater role in determining hatching date. In accordance, when the observed response of D_R to temperature and time series of median population hatching dates and sea temperatures (Régnier et al., 2017) are considered, spawning peaks are predicted to occur between mid-January and mid-February in *A. marinus*. Although temperature is likely to be the primary influence on egg development, incubation time may also be affected by other variables such as oxygen tension associated with demersal eggs being covered with sand (Winslade, 1971) or maternal phenotype (Boulcott et al., 2017). While mature females have been observed in a reproductive state as early as December, consistent with estimates from the present study, peak spawning appears to be later, in January–February (Gauld and Hutcheon, 1990; Bergstad et al., 2001; Boulcott et al., 2017). In accordance, further research is needed to understand the influence of spawning date and its dependence on temperature, as highlighted by experimental studies (Wright et al., 2017a), on the mismatch between sandeel larvae and their prey and subsequent consequences for the long term structure of the North Sea trophic chain.

Consistent with other studies (Ojanguren and Braña, 2003; Peck et al., 2012b), incubation temperature had an effect on phenotype, as the average size of newly hatched larvae decreased with increased incubation temperatures. The fitted Von Bertalanffy model revealed size differences during the early stages of larval development, as size reached a common plateau after around 5 days post-hatch. In addition, early hatching individuals had more remaining energy resources, as measured by the volume of the oil globule. This pattern has previously been observed at an early, similarly critical, stage of development in another fish species (Régnier et al., 2012), and was found to be related to individual energetic status. Energetic status is a measure of a period of time an individual can survive on its available energy (stores), knowing its daily energy expenditure (metabolic rate) (Régnier et al., 2012). Therefore, if maintaining sufficient energy stores to face food shortage for a given period of time is adaptive, then individuals with the highest energy requirements will hatch earlier (as endogenous stores are depleted faster), and with a larger amount of endogenous stores (as, relative to individuals with a lower metabolic rate, more energy is needed to survive the same period of time). However, further

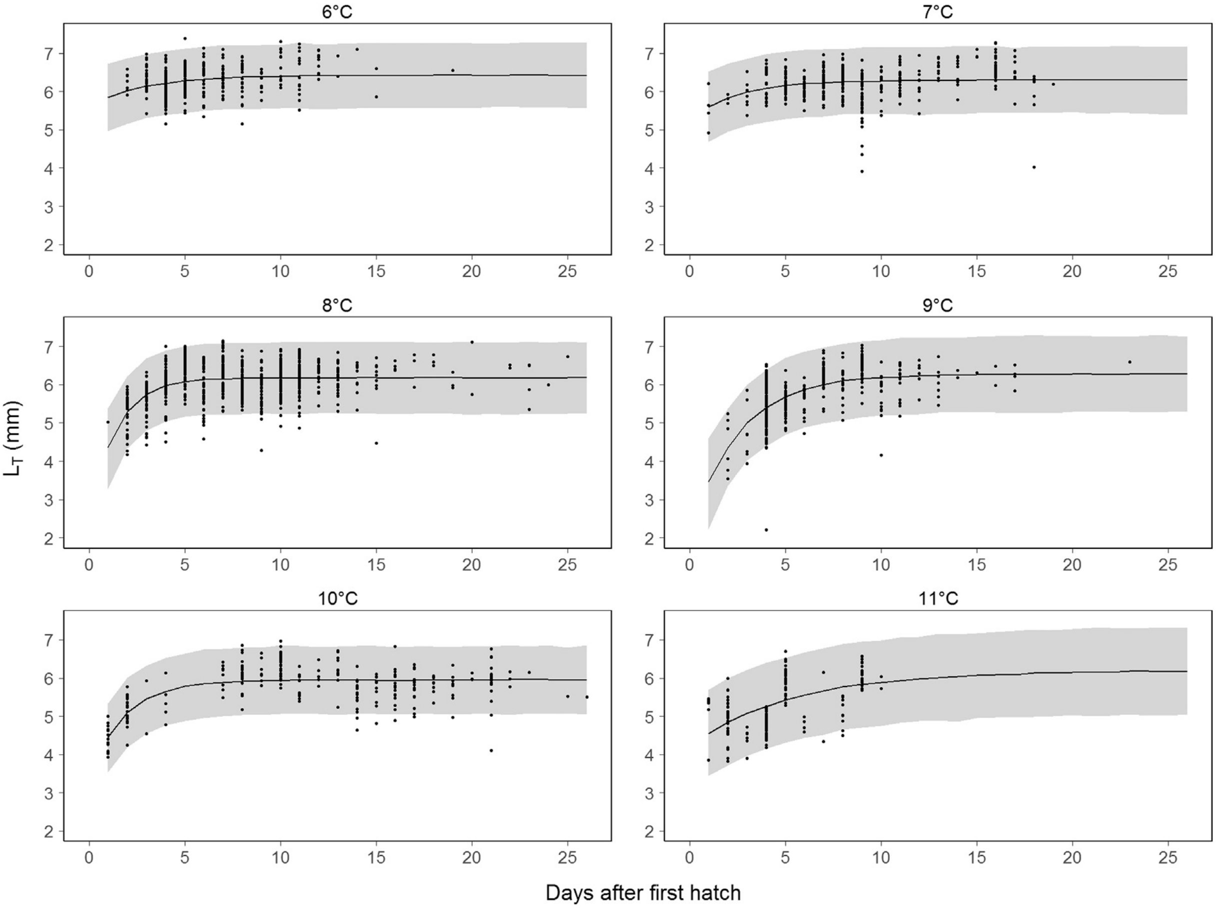

Fig. 4. *Ammodytes marinus* oil globule volume at hatching for six incubation temperatures. Model predictions and 95% CI are presented with solid lines and dotted lines respectively.

work is needed to support this hypothesis and confirm that early hatching individuals in *A. marinus* indeed have a higher metabolic rate. Alternatively, if the amount of remaining yolk at hatching is not related to a larva's energetic requirements, the present findings imply that late hatching individuals have a very narrow safety margin in terms of energy stores and need to secure access to an exogenous food source at hatching or very soon after.

The endogenous energy stores, measured as either yolk sac or oil globule volume, were depleted within a period of 10 days post-hatching for most individuals (measured at 8 °C). These results are similar to those of Winslade (1971), where complete resorption was reached after 10 and 12 days (at 10 °C and 7 °C respectively), and marked the start of a period of increasing starvation mortality. While resorption was only measured at one temperature treatment in the present study, it is known to vary positively with temperature (reviewed by Kamler, 2008) and, given the experimental temperatures are typical of the months of February and March in the North Sea, remaining yolk might provide a buffer period of up to 2 weeks (Winslade, 1971). Therefore, hatching within two weeks of the production peak of their copepod prey is important to secure access to a sufficient amount of prey of a suitable size (Wright and Bailey, 1996; Régnier et al., 2017) and survive the early larval period. Any temperature rise is likely to differentially affect predator and prey phenology as well as increase yolk depletion rate, which will dramatically increase the consequences of mismatch on larval survival rate.

The present study revealed that temperature had not only a great influence on *A. marinus* egg developmental rates, but had also an effect on phenotype at hatching. An increase of sea temperature has therefore the potential to alter the synchrony between the phenology of sandeel, their prey, but also their predators and ultimately the long-term stability of the North Sea trophic chain. While temperature significantly affects egg development rates, the contribution of this to the variation in hatch dates is probably minor relative to factors affecting spawning date such as temperature and parental condition (Wright et al., 2017a, 2017b; Boulcott et al., 2017). Therefore future studies should focus on variation in spawning date and should also consider variations among sandeel stocks, given the considerable observed variation in growth and condition across the North Sea (Rindorf et al., 2016). In particular, the study of temperature sensitivity along a latitudinal gradient might give important insights in the ability of this important forage fish to cope with climate change.

Funding

This work was supported by the Scottish Government (Project ST007).

Conflict of interest

The authors declare that they have no conflict of interest.

Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in this study were in accordance with the ethical standards of the institution at which the study was conducted and complied with Home Office regulations. The study of yolk sac depletion was performed on yolk-feeding larvae and terminated prior to the onset of external feeding and therefore did not constitute a procedure under the Animals

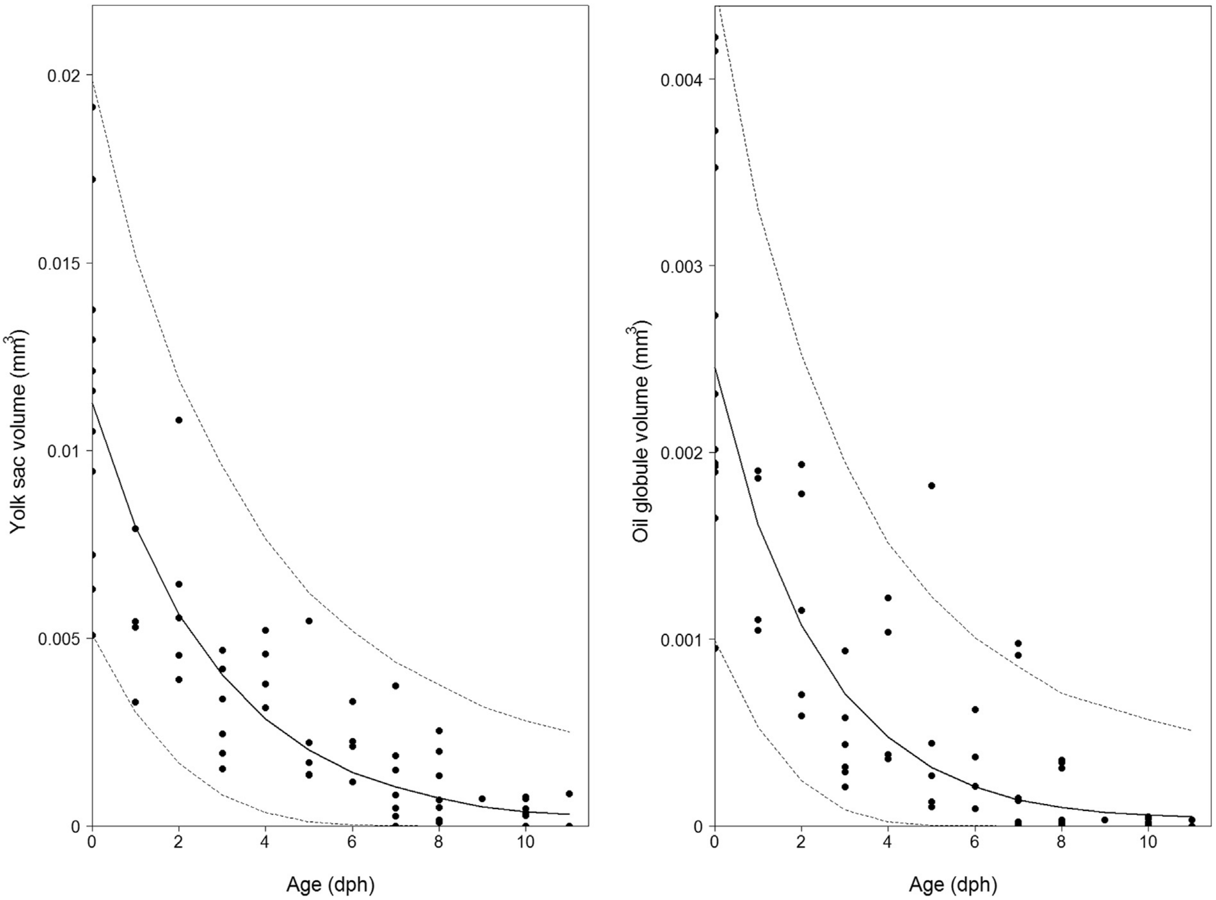

Fig. 5. *Ammodytes marinus* yolk-sac and oil globule volumes as a function of age (in days post hatching; dph). Model predictions and 95% CI are presented with solid lines and dotted lines respectively.

(Scientific Procedures) Act 1986.

Acknowledgements

We gratefully acknowledge the help provided by P. Macdonald and J. Brown for the adult fish collection and by B. Williamson and M. Patterson for the egg rearing.

References

Bergstad, O.A., Hoines, Å.S., Krüger-Johnsen, E.M., 2001. Spawning time, age and size at maturity, and fecundity of sandeel, *Ammodytes marinus*, in the north-eastern North Sea and in unfished coastal waters off Norway. Aquat. Living Resour. 14, 293–301. http://dx.doi.org/10.1016/S0990-7440(01)01134-2.

Berx, B., Hughes, S.L., 2009. Climatology of surface and near-bed temperature and salinity on the north-west European continental shelf for 1971–2000. Cont. Shelf Res. 29, 2286–2292. http://dx.doi.org/10.1016/j.csr.2009.09.006.

Boulcott, P., Wright, P.J., 2008. Critical timing for reproductive allocation in a capital breeder: evidence from sandeels. Aquat. Biol. 3, 31–40. http://dx.doi.org/10.3354/ab00063.

Boulcott, P., Wright, P.J., Gibb, F.M., Jensen, H., Gibb, I.M., 2007. Regional variation in maturation of sandeels in the North Sea. ICES J. Mar. Sci. 64, 369–376. http://dx.doi.org/10.1093/icesjms/fsl033.

Boulcott, P., Clarke, J., Wright, P.J., 2017. Effect of size on spawning time in the lesser sandeel *Ammodytes marinus*. J. Fish Biol. 91, 362–367. http://dx.doi.org/10.1111/jfb.13341.

Cook, K.B., Bunker, A., Hay, S., Hirst, A.G., Speirs, D.C., 2007. Naupliar development times and survival of the copepods *Calanus helgolandicus* and *Calanus finmarchicus* in relation to food and temperature. J. Plankton Res. 29, 757–767. http://dx.doi.org/10.1093/plankt/fbm056.

Cushing, D.H., 1969. The regularity of the spawning season of some fishes. ICES J. Mar. Sci. 33, 81–92. http://dx.doi.org/10.1093/icesjms/33.1.81.

Cushing, D.H., 1990. Plankton production and year-class strength in fish populations, an update of the match/mismatch hypothesis. Adv. Mar. Biol. 26, 249–293. http://dx.doi.org/10.1016/S0065-2881(08)60202-3.

Daan, N., 1989. Data base report of the stomach sampling project 1981. ICES Coop. Res. Rep. 164, 1–144. Available from: http://www.ices.dk/sites/pub/Publication%20Reports/Cooperative%20Research%20Report%20(CRR)/crr164/CRR164.pdf.

Edwards, M., Richardson, A.J., 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430, 881–884. http://dx.doi.org/10.1038/nature02808.

Eerkes-Medrano, D., Fryer, R.J., Cook, K.B., Wright, P.J., 2017. Are simple environmental indicators of food web dynamics reliable: exploring the kittiwake-temperature relationship. Ecol. Indic. 75, 36–47. http://dx.doi.org/10.1016/j.ecolind.2016.12.019.

Eliasen, K., Reinert, J., Gaard, E., Hansen, B., Jacobsen, J.A., Grønkjær, P., Christensen, J.T., 2011. Sandeel as a link between primary production and higher trophic levels on the Faroe shelf. Mar. Ecol. Prog. Ser. 438, 185–194.

Fox, C.J., Geffen, A.J., Blyth, R., Nash, R.D.M., 2003. Temperature-dependent development rates of plaice (*Pleuronectes platessa* L.) eggs from the Irish Sea. J. Plankton Res. 25, 1319–1329. http://dx.doi.org/10.1093/plankt/fbg099.

Gamble, J.C., Maclachlan, P., Seaton, D.D., 1985. Comparative growth and development of autumn and spring spawned Atlantic herring larvae reared in large enclosed ecosystems. Mar. Ecol. Prog. Ser. 26, 19–33. Available from: http://www.int-res.com/articles/meps/26/m026p019.pdf.

Gauld, J.A., Hutcheon, J.R., 1990. Spawning and fecundity in the lesser sandeel, *Ammodytes marinus* Raitt, in the north-western North Sea. J. Fish Biol. 36, 611–613. http://dx.doi.org/10.1111/j.1095-8649.1990.tb03561.x.

Geffen, A.J., Fox, C.J., Nash, R.D.M., 2006. Temperature-dependent development rates of cod *Gadus morhua* eggs. J. Fish Biol. 69, 1060–1080. http://dx.doi.org/10.1111/j.1095-8649.2006.01181.x.

Gurkan, Z., Christensen, A., Maar, M., Møller, E.F., Madsen, K.S., Munk, P., Mosegaard, H., 2013. Spatio-temporal dynamics of growth and survival of lesser Sandeel early life-stages in the North Sea: predictions from a coupled individual-based and hydrodynamic-biogeochemical model. Ecol. Model. 250, 294–306. http://dx.doi.org/10.1016/j.ecolmodel.2012.11.009.

Helvik, J.V., Walther, B.T., 1993. Environmental parameters affecting induction of hatching in halibut (*Hippoglossus hippoglossus*) embryos. Mar. Biol. 116, 39–45. http://dx.doi.org/10.1007/BF00350729.

ICES, 2004. Report of the working group on the assessment of the demersal stocks in the North Sea and Skagerrak. In: ICES C.M. 2004/ACFM:07.

ICES, 2016. ICES report on ocean climate 2015. In: Larsen, K.M.H., Gonzalez-Pola, C., Fratantoni, P., Beszczynska-Möller, A., Hugues, S.L. (Eds.), ICES Cooperative Research Report No. 331, 79p.

Kamler, E., 2008. Resource allocation in yolk-feeding fish. Rev. Fish Biol. Fish. 18, 143–200. http://dx.doi.org/10.1007/s11160-007-9070-x.

Langham, N.P.E., 1971. The distribution and abundance of larval Sandeels (*Ammodytidae*) in Scottish waters. J. Mar. Biol. Assoc. UK 51, 597–707. http://dx.doi.org/10.1017/S0025315400015071.

Lasker, R., 1964. An experimental study of the effect of temperature on the incubation time, development, and growth of Pacific sardine embryos and larvae. Copeia 1964, 399–405. Available from: http://www.jstor.org/stable/1441033.

Lilliendahl, K., Sólmundsson, J., 1997. An estimate of summer food consumption of six seabird species in Iceland. ICES J. Mar. Sci. 54 (4), 624–630.

Lowe, J.A., Howard, T.P., Pardaens, A., Tinker, J., Holt, J., Wakelin, S., Milne, G., Leake, J., Wolf, J., Horsburgh, K., Reeder, T., Jenkins, G., Ridley, J., Dye, S., Bradley, S., 2009. UK Climate Projections Science Report: Marine & Coastal Projections. Met Office Hadley Centre, Exeter, U.K. Available from: http://ukclimateprojections.metoffice.gov.uk/media.jsp?mediaid=87906&filetype=pdf.

Martell, D.J., Kieffer, J.D., Trippel, E.A., 2005. Effects of temperature during early life history on embryonic and larval development and growth in haddock. J. Fish Biol. 66, 1558–1575. http://dx.doi.org/10.1111/j.1095-8649.2005.00699.x.

Munk, P., Fox, C.J., Bolle, L.J., Van Damme, C.J.G., Fossum, P., Kraus, G., 2009. Spawning of North Sea fishes linked to hydrographic features. Fish. Oceanogr. 18, 458–469. http://dx.doi.org/10.1111/j.1365-2419.2009.00525.x.

Nakazawa, T., Doi, H., 2012. A perspective on match/mismatch of phenology in community contexts. Oikos 121, 489–495. http://dx.doi.org/10.1111/j.1600-0706.2011.20171.x.

Ojanguren, A.F., Braña, F., 2003. Thermal dependence of embryonic growth and development in brown trout. J. Fish Biol. 62, 580–590. http://dx.doi.org/10.1046/j.1095-8649.2003.00049.x.

Peck, M.A., Huebert, K.B., Llopiz, J.K., 2012a. Intrinsic and extrinsic factors driving match-mismatch dynamics during the early life history of marine fishes. Adv. Ecol. Res. 47, 177–302. http://dx.doi.org/10.1016/B978-0-12-398315-2.00003-X.

Peck, M.A., Kanstinger, P., Holste, L., Martin, M., 2012b. Thermal windows supporting survival of the earliest life stages of Baltic herring (*Clupea harengus*). ICES J. Mar. Sci. 69, 529–536. http://dx.doi.org/10.1093/icesjms/fss038.

Régnier, T., Labonne, J., Gaudin, P., Bolliet, V., 2012. Influence of energetic status on ontogenetic niche shifts: emergence from the redd is linked to metabolic rate in brown trout. Oecologia 168, 371–380. http://dx.doi.org/10.1007/s00442-011-2109-7.

Régnier, T., Gibb, F.M., Wright, P.J., 2017. Importance of trophic mismatch in a winter hatching species: evidence from lesser sandeel. Mar. Ecol. Prog. Ser. 567, 185–197. http://dx.doi.org/10.3354/meps12061.

Richardson, A.J., 2008. In hot water: zooplankton and climate change. ICES J. Mar. Sci. 65, 279–295. http://dx.doi.org/10.1093/icesjms/fsn028.

Rindorf, A., Wright, P.J., Jensen, H., Maar, M., 2016. Spatial differences in growth of lesser sandeel in the North Sea. J. Exp. Mar. Biol. Ecol. 479, 9–19. http://dx.doi.org/10.1016/j.jembe.2016.02.007.

Sherman, K., Belkin, I.M.I., Friedland, K.D., O'Reilly, J., Hyde, K., 2009. Accelerated warming and emergent trends in fisheries biomass yields of the world's large marine ecosystems. Ambio 38, 215–224. http://dx.doi.org/10.1579/0044-7447-38.4.215.

Smigielski, A.S., Halavik, T.A., Buckley, L.J., Drew, S.M., Laurence, G.C., 1984. Spawning, embryo development and growth of the American sand lance (*Ammodytes americanus*) in the laboratory. Mar. Ecol. Prog. Ser. 14, 287–292. http://dx.doi.org/10.3354/meps014287.

Sparholt, H., 1990. An estimate of the total biomass of fish in the North Sea. J.du Con. ICES J. Mar. Sci. 46, 200–210. http://dx.doi.org/10.1093/icesjms/46.2.200.

Wanless, S., Wright, P.J., Harris, M.P., Elston, D.A., 2004. Evidence for decrease in size of lesser sandeels *Ammodytes marinus* in a North Sea aggregation over a 30-yr period. Mar. Ecol. Prog. Ser. 279, 237–246. http://dx.doi.org/10.3354/meps279237.

Winslade, P.R., 1971. Behavioural and Embrylogical Investigations of the Lesser Sandeel, *Ammodytes marinus* Raitt. University of East Anglia, Norwich (PhD Thesis).

Wright, P.J., Bailey, M.C., 1996. Timing of hatching in *Ammodytes marinus* from Shetland waters and its significance to early growth and survivorship. Mar. Biol. 126, 143–152. http://dx.doi.org/10.1007/BF00571386.

Wright, P.J., Orpwood, J.E., Scott, B.E., 2017a. Impact of rising temperature on reproductive investment in a capital breeder: the lesser sandeel. J. Exp. Mar. Biol. Ecol. 486, 52–58. http://dx.doi.org/10.1016/j.jembe.2016.09.014.

Wright, P.J., Orpwood, J.E., Boulcott, P., 2017b. Warming delays ovarian development in a capital breeder. Mar. Biol. 164, 80. http://dx.doi.org/10.1007/s00227-017-3116-y.

Yamashita, Y., Aoyama, T., 1985. Hatching time, yolk sac absorption, onset of feeding and early growth of the Japanese sandeel *Ammodytes personatus*. Nippon Suisan Gakkaishi 51, 1777–1780. http://dx.doi.org/10.2331/suisan.51.1777.

Yamashita, Y., Aoyama, T., 1986. Starvation resistance of larvae of the Japanese sand eel *Ammodytes personatus*. Nippon Suisan Gakkaishi 52, 635–640. http://dx.doi.org/10.2331/suisan.52.635.