Mar Biol (2017) 164:80
DOI 10.1007/s00227-017-3116-y

ORIGINAL PAPER

Warming delays ovarian development in a capital breeder

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Received: 22 September 2016 / Accepted: 22 February 2017 / Published online: 17 March 2017

Abstract The consequences of rising temperature to reproductive development in the lesser sandeel, *Ammodytes marinus*, were studied in captive fish held at three temperatures to reflect the present day and future predicted winter temperature of North Sea habitat. Our results showed that an increase in temperature of 5 °C led to more than a 2 month delay in the timing of oocyte maturation. The inverse relationship between the stage of ovarian development and temperature in *A. marinus* is in contrast with that seen in many early year spawners. A close relationship between relative ovary size and ovarian development, as well as an overlap in oocyte diameter among treatments suggested that this temperature effect is mediated via an energetic constraint on reproductive investment. Temperature had no effect on the potential fecundity—length relationship in December, and while the intensity of preovulatory atresia did not reflect condition, it was found to increase with temperature and decrease with oocyte diameter. The magnitude of potential temperature-related changes in spawning phenology could have important implications to the future match between hatching times of *A. marinus* and prey availability, although this may be partially mitigated by the positive temperature dependence of embryonic development.

Responsible Editor: G. H. Engelhard.

Reviewed by P. R. Witthames and E. Johnsen.

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Introduction

Variation in spawning time can be critical to reproductive success, because it affects the early environmental conditions experienced by progeny, and the period they have to complete phases of development (Cushing 1990; Sinclair and Tremblay 1984; Pope et al. 1994; Wright and Trippel 2009). Although spawning time is in part a heritable trait (Leder et al. 2006; Otterå et al. 2012), reproductive cycles are often influenced by environmental conditions. Temperature can be a key factor affecting reproductive development, acting both as a cue to entrain spawning time and directly on the expression and activity of regulatory proteins that influence the rate of oocyte growth and development (Pankhurst and Porter 2003).

As climate change affects the relative timing of food requirement and availability for various organisms, it is important to consider whether warming effects on reproductive timing will shift in accordance with changes in the phenology of their prey species or lead to a mismatch between predator and prey (Durant et al. 2007). Given the importance of synchrony between the hatching of fish larvae and the availability of their planktonic prey (Cushing 1990), a warming-induced mismatch in phenology could have major implications to reproductive success. Most field studies have indicated a positive influence of temperature on the onset of spawning and migrations to spawning grounds (Ware and Tanasichuk 1989; Carscadden et al. 1997; Jansen and Gislason 2011; Fincham et al. 2013). However, in flounder, *Platichthys flesus*, spawner migration to open-sea spawning grounds was found to begin earlier when the estuarine overwintering habitats were colder which may have been related to the need to maintain gonad development prior to spawning (Sims et al. 2004). As temperature is only one of a number of factors influencing the

time and duration of spawning (Wright and Trippel 2009), approaches other than just field observations are needed to understand the potential effects of warming on reproductive timing.

Experimental studies have often proved useful in elucidating the direct effects of temperature on reproductive development. For example, Kjesbu et al. (2010) found that an experimentally determined relationship between oocyte maturation and temperature for Atlantic cod (*Gadus morhua*) could explain stock related differences in the timing of spawning. Other studies suggest that fish have an optimum temperature for the production of gonad steroids (Van der Kraak and Pankhurst 1997; Miranda et al. 2013), and in many early year spawners, such as Atlantic cod, a rise in temperature during the pre-spawning period can cause an increase in the level of the steroid E2 leading to an advance in the onset of spawning (Miranda et al. 2013). However, in some species, ovulation can be delayed in response to unfavourably high temperatures (Tveiten and Johnsen 1999) and unseasonal temperature elevations have been linked to high levels of pre-ovulatory atresia (Davies and Hanyu 1986; Miranda et al. 2013).

Species showing a high degree of site fidelity are most likely to be impacted by changing thermal regimes (Heath et al. 2012). The family Ammodytidae (sandeels) includes several species that show high fidelity to sandy habitats following settlement (Gauld 1990; Haynes and Robinson 2011). *Ammodytes marinus*, Raitt 1934, is the most economically and ecologically important sandeel in the North Sea supporting a large industrial fishery and is a key trophic link between zooplankton and many piscivorous fish and top predators (Daan et al. 1990; Wanless et al. 2004). Overwintering buried *A. marinus* remain in the sand from around September until March–April, except when they emerge to spawn in December–January (Macer 1966; Reay 1970; Gauld and Hutcheon 1990). Gonad development in sandeels during this period is entirely dependent on stored energy (Robards et al. 1999a; Boulcott and Wright 2008). The duration of embryonic development is inversely related to temperature in sandeels (Smigielski et al. 1983) and lasts for many weeks to months in *A. marinus* (Winslade 1971), resulting in larvae hatching between February and April (Langham 1971; Wright and Bailey 1996). Empirical and modelling studies indicate that the match with the spring bloom in zooplankton is key to the early survival of *A. marinus* (Wright and Bailey 1996; Gurkan et al. 2013). This is important as year-class strength may be established as early as the larval phase (Lynam et al. 2013).

During their period of overwintering, *A. marinus* can experience monthly temperatures ranging between 5 and 15 °C (Berx and Hughes 2009; van Deurs et al. 2011). Average winter temperatures are expected to increase by 2–3.5 °C in some parts of the species range by the end of the century (Lowe et al. 2009). If oocyte development responds positively to these autumn/winter temperature changes, then warming may lead to early spawning. Such a response could lead to a mismatch between hatching and larval prey (Cushing 1990), especially when combined with a shorter embryonic phase due to the higher temperature (Winslade 1971; Smigielski et al. 1983). Conversely, if spawning time is determined by daylength, the higher respiration costs associated with higher temperature would reduce energy available for reproductive investment and might lead to a greater atretic down regulation of the number of developing oocytes, affecting size specific fecundity.

The consequences of autumn/winter warming to reproductive development was studied in captive groups of *A. marinus* held at three temperatures to reflect the present day (Berx and Hughes 2009) and future predicted (Lowe et al. 2009) average temperature of North Sea sandeel habitat. By comparing the state of ovarian development and fecundity in December with temperature exposure, size, and age, the effect of temperature on ovarian development rate and fecundity of *A. marinus* was examined. By this means, the study tested the following hypotheses:

1. Warm temperature promotes oocyte development and early spawning.
2. Oocyte development is related to the level of reproductive investment.
3. Temperature affects the rate of pre-ovulatory atresia.
4. Temperature affects potential fecundity in addition to length and age.

Methods

Experiment

A sample of *A. marinus* was collected from off the east coast of Scotland (56°58′ N, 2°12′ W) using a bottom trawl in April 2007. Fish were acclimated for 4 weeks in cylindrical tanks (2 m diameter × 1.2 m depth), with a thin layer of sand to allow them to bury and maintained at 10 ± 0.2 °C until the experimental trial in September. During this period, fish were fed a mixture of frozen *Calanus* and mysid shrimps to excess during daylight hours and uneaten food was removed each day. Photoperiod was adjusted to ambient using artificial lighting to mimic the natural photoperiod cycle for the latitude of capture. In September, between 60 and 68, fish were assigned to each of six, replicate 1 m cylindrical tanks that maintained at 7.5, 10.5, or 12.5 ± 0.2 °C, and feeding stopped, while fish over-wintered in sand. Mortality during experiment was low with only 1 fish dying in each of the 7.5 and 12.5 °C treatments and 2 from the 10 °C treatment. Although the

study examined female gonad development, these tanks contained both sexes as sandeels are sexually monomorphic. Between 5 and 10 December 2007, 300 sandeels were killed by over anaesthesia using MS222 for the purposes of examination as this time corresponds to the period immediately prior to spawning in the wild (Gauld and Hutcheon 1990). However, from an initial assessment of gonad state in December, an additional sample of 40 fish per treatment was maintained in the 10.5 and 12.5 °C tanks until sacrifice on 29 February 2008. Table 1 gives the numbers per treatment and sample date.

Measurements

Total length (L; ± 0.1 cm), eviscerated mass (M; ± 0.01 g), and ovary mass (Mo; ± 0.01 g) in mature females were recorded. Specimens were then dried to constant mass in a convection oven at 60 °C and reweighed to determine water content of the somatic tissue, which is inversely related to lipid and energy content (Hislop et al. 1991). Relative condition factor (Kn) was calculated according to Le Cren (1951):

$$\mathrm{Kn} = 100 \times \frac{M_\mathrm{i}}{\hat{M}}$$

where M_i is the individual wet eviscerated mass (g), and $\hat{M}$ is the predicted eviscerated mass for a given length based on a mass–length relationship calculated from all experimental fish according to

$$M = 0.0011 \times L^{3.2771}$$

An index of relative gonad mass (I_g) was calculated as: ovary mass/eviscerated mass. To normalise the data, I_g and proportion water content was logit transformed.

Ovaries were removed and stored in 4% borax-buffered formaldehyde for oocyte measurements and a subset of 12 per treatment were fixed in a buffered solution composed of 2.5% gluteraldehyde, 2% paraformaldehyde in a 0.06 M cacodylate, 2.7% sucrose buffer¸ and pH 7.4 at 4 °C for histology. Age was estimated from counts of annual increments in the sagittal otoliths, according to the protocol of ICES (1995).

Ovary tissue for histology was dehydrated, infiltrated, and embedded in resin using a HistoResin embedding kit (Leica Microsystems GmbH., Germany; http://www.leica-microsystems.com). Serial sections (2 µm) were cut using a rotary microtome (RM2155, Leica Instruments GmbH., Germany) and one from each specimen stained with each of the following stains: haematoxylin and eosin, Periodic Acid Schiff and alcian blue, and a 0.5% toluidine blue stain. Oocyte development was classified according to Brown-Peterson et al. (2011) to identify fish in a spawning capable and active spawning phase.

Oocyte diameter (D_o) measurements and estimates of potential fecundity (F_p) were obtained following the auto-diametric method described by Thorsen and Kjesbu (2001), with the necessary species parameters being derived from a previous gravimetric study of 300 *A. marinus* (Boulcott and Wright 2008). For each individual, mean oocyte diameter (±9 microns per pixel) was estimated from a sample of 200–300 oocytes taken from the mid-section of the ovary. Measurements were made using images taken on a stereomicroscope (Leica MZ9.5) with the automatic selection of particles controlled within an image analysis program (Image Pro Insight 9, Mediacybernetics) with area and roundness factor thresholds set at >0.05 mm^2 and >1.10, respectively, to omit residual connective tissue and damaged or clumped oocytes. **S**hrinkage during formalin fixation was accounted for using a pre-determined relationship for this species (Boulcott et al. in review).

Predicted potential fecundity was expressed according to

$$F_\mathrm{p} = M_0 \times 2605.6 \times D_0^{(-2.7689)} (250 \le D_0 \le 1000)$$

where D_0 is the mean oocyte diameter in fresh ovary (µm) and M_0 is ovary mass.

Prevalence and intensity of pre-ovulatory atresia, the degeneration and reabsorption of oocytes, were estimated from counts of α-stage atretic oocytes distinguishable by their irregular shape and uneven transparency, using the method of Óskarsson et al. (2002; see also Boulcott and Wright 2011). Counts from whole mounts were also compared with the intensity of atresia estimated from the histological preparations for the same fish. Histological sections were separated by a distance that was at least equal to the diameter of the leading cohort of oocytes from that ovary, so that the same oocytes were not counted twice. At least 100 oocytes were counted, and the intensity of atresia was calculated as the percentage of atretic oocytes of all oocytes counted, i.e., atretic × 100/(normal + atretic).

Table 1 Summary of number of mature females by temperature, treatment, and tank replicate, sampled for total length, eviscerated and gonad mass, oocyte diameter, and whole mount atresia estimate

Temperature (°C)	Tank replicate	Sample month	
		December	February
7.5	1	27	
7.5	2	24	
10.5	1	21	10
10.5	2	29	10
12.5	1	30	8
12.5	2	27	9

Statistical analyses

Generalized linear models (GLM) implemented within the mgcv package in R (Wood 2011) were used to examine the effect of treatments and fish state on ovarian development and potential fecundity. A gaussian distribution was used in the model of D_0, according to

$$D_0 \sim f\left(\frac{T}{t}\right) \times f(A) \times L_T$$

where temperature treatment (T), tank replicate (t), and age (A) are factors. To normalise the data, oocyte diameter measurements were ln transformed.

The relationship between logit I_g, the relative index of gonad mass, and ln oocyte diameter in December was examined to consider whether ovary mass reflected ovarian development according to

$$D_0 \sim I_g \times f(A)$$

The relationship between potential fecundity (Fp) and L was examined using a gamma response distribution coupled with a log-link function to account for the increased predictor variance with increasing response variable. Mass was not used as the metric of size, because it declines during the winter fast and length has been found to be a better predictor of potential fecundity (Boulcott and Wright 2011). The additions of age and temperature terms were used to test whether these factors had a significant additional effect according to

$$F_p = L + f(T) + f(A)$$

The relationship between atresia, oocyte diameter, relative condition, and temperature was also examined within a GLM framework using a gaussian distribution. Due to downregulation from pre-ovulatory atresia, there is often a significant negative effect of oocyte diameter on the fecundity–size relationship of group synchronous spawners (Kurita et al. 2003) and so this variable was also considered. Intensity of atresia (A_i) was related to temperature treatment and a measure of condition (where C is either Kn or logit water content) according to

$$A_i = f(T)/f(t) + C$$

Final explanatory variables and interactions for the minimum adequate models were obtained through a process of stepwise deletion with model selection based on Akaike's Information Criteria (Akaike 1974). The residuals from all GLMs were tested for normality using an Anderson–Darling test and plots of residuals against fits were plotted to confirm that the data tested complied with homogeneity of variance (Sokal and Rolf 1995). Where these assumptions were not met, the Spearman rank correlation was used.

Results

In December, 3 months after the onset of the temperature treatments that started in September, 158 mature females were obtained from the experiment ranging from 10.5 to 16.8 cm TL and ages 1 ($n = 81$) to 2 ($n = 74$). Sample sizes were 51, 50, and 57 for the 7.5, 10.5, and 12.5 °C temperature treatments, respectively. D_o differed significantly among temperature treatments (GLM, $F_{2,152} = 79.74$; $P < 0.0001$; Fig. 1), being significantly larger in the 7.5 °C than in the 10.5 °C treatment (Bonferroni post hoc test $P < 0.0001$) and in the 10.5 °C compared to 12.5 °C treatments (Bonferroni post hoc test $P < 0.0001$). There was no significant difference between replicates within treatments (GLM, $P = 0.65$). Neither age (GLM, $P = 0.17$) nor length ($P = 0.41$) had a significant additional effect on D_o. There was a positive relationship between I_g and ln oocyte diameter in December (GLM, $r^2 = 0.69$; $F_{1,155} = 396.4$; $P < 0.0001$; Fig. 2). There was no significant age effect on I_g in addition to oocyte diameter (GLM, $F_{1,152} = 0.36$; $P = 0.55$).

By December, all mature females were in the spawning capable phase in all three temperature treatments as characterised by tertiary vitellogenic (Fig. 3a) or early stage maturing oocyte stages (OM; Fig. 3b). However, while 29% of the oocytes in females from the 7.5 °C treatment had reached the OM stage, only 4% of the 10.5 °C treatment had transitioned and none from the 12.5 °C treatment. Consistent with a group–synchronous total spawning mode, where only one batch of eggs are released per breeding season, the only other oocytes present in ovaries were in the primary phase (Fig. 3a). A further 20 and

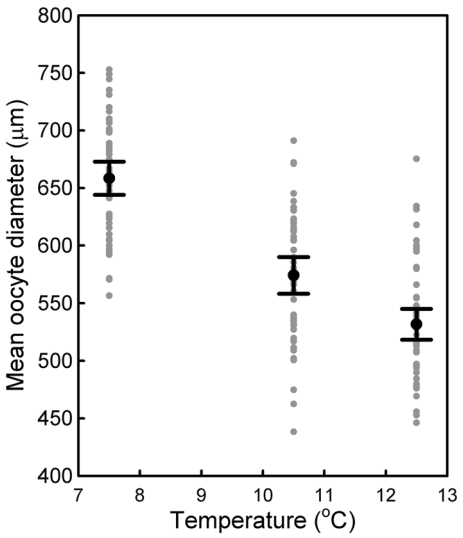

Fig. 1 Difference in mean (±95 CI) oocyte diameter (*black*) among three temperature treatments together with data points (*grey*)

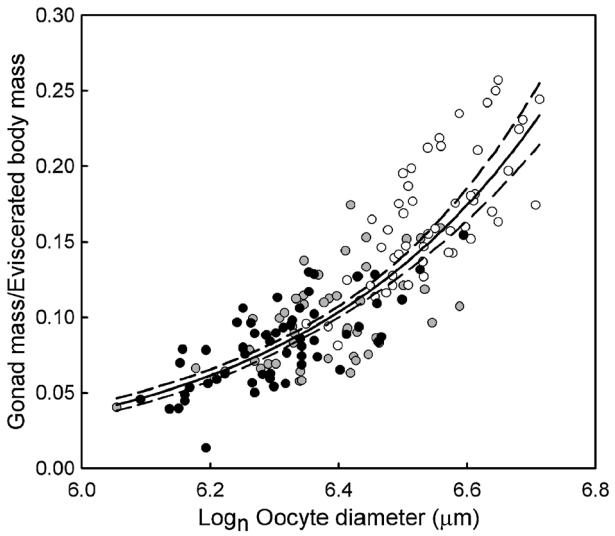

Fig. 2 Relationship between mean oocyte diameter and relative gonad mass (I_g gonad mass as a proportion of total eviscerated mass). *Open, grey* and *black circles* refer to 7.5, 10.5, and 12.5 °C treatments, respectively. Fitted linear regression (*solid line*) and 95% confidence interval (*dashed line*) are shown

17 mature females were obtained in the February sample from the 10.5 and 12.5 °C treatments, respectively. Of these, 27% of females from the 10.5 °C were in the final stage of OM while none were ready to spawn in the 12.5 °C treatment.

Potential fecundity (*F*p) in December was found to vary from 2375 to 12896 for fish ranging in length from 10.5 to 15. 1 cm and increased significantly with length ($F_{1,\ 105}$ = 180.21, $P<0.001$; Fig. 4). Given that oocyte diameter was influenced by temperature, the addition of these two terms to the potential fecundity (*F*p)–length relationship was considered separately. However, neither temperature treatment (GLM, $F_{2,152} = 1.9767$; $P=0.14$) nor oocyte diameter (GLM, $F_{1,153} = 0.495$; $P=0.483$) significantly influenced *F*p in addition to length. There was also no significant additional effect of age (GLM, $F_{1,150} = 1.585$; $P=0.21$).

There was no significant difference in the estimates of pre-ovulatory atresia between the two methods based on pairwise comparisons of counts from whole mounts and histological material (paired *t* test; $t_{2,33} = -0.39$; $P=0.70$). Pre-ovulatory atresia (Fig. 5) was found in 91% of samples, although prevalence differed with temperature: 100, 93, and 78% in the 12.5, 10.5, and 7.5 °C treatments, respectively. The mean intensity of pre-ovulatory atresia was 2.7%, and there was a significant increase with temperature (GLM, $F_{2,134} = 24.932$; $P<0.0001$). However, neither relative condition ($P=0.121$) nor logit proportion water content ($P=0.07$) had a significant additional effect on mean intensity of pre-ovulatory atresia. As temperature influenced oocyte diameter (see Fig. 1), the intensity of atresia

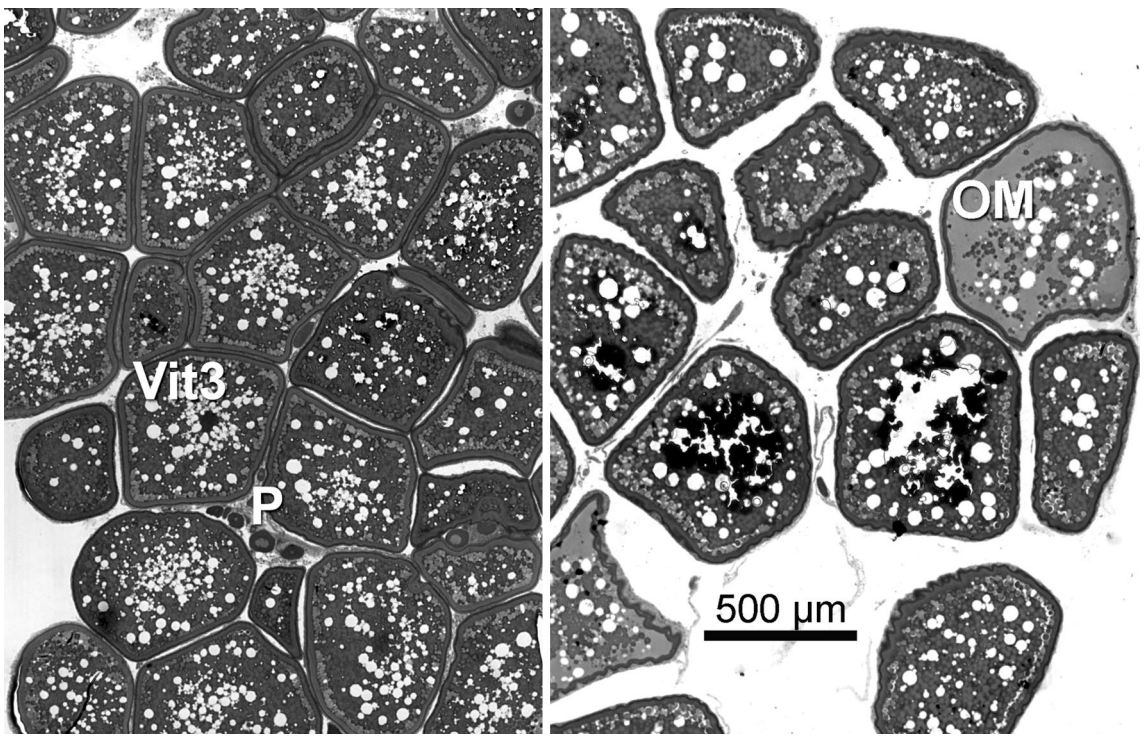

Fig. 3 Images showing **a** tertiary phase vitellogenic (*Vit3*) and primary (*P*) oocytes and early mature (*OM*) oocytes. *Scale bar* 500 μm

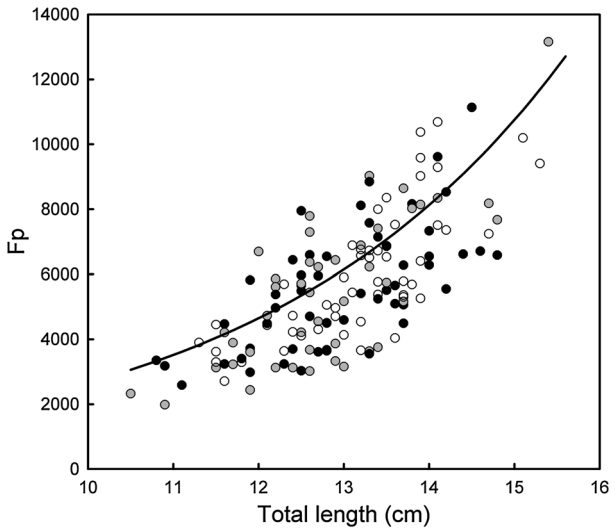

Fig. 4 Potential fecundity (*F*p) – length relationship for experimental fish. Regression line for fitted generalized linear model is shown (*solid line*). *Open, grey*, and *black circles* refer to 7.5, 10.5, and 12.5 °C treatments, respectively

also declined with oocyte diameter (Spearman Rank $r_s = -0.22$; $P = 0.05$; $n = 137$).

Discussion

Warm temperature did not promote oocyte development and early spawning. Rather higher temperature reduced ovarian development in *A. marinus* in this experimental study, and based on the presence of maturing oocytes, females may have begun spawning soon after the December sampling in the 7.5 °C treatment. In contrast, spawning had not even begun by the end of February in the 12.5 °C treatment. Hence, the difference in spawning onset given this 5 °C difference would have been greater than 2 months. The magnitude of difference in ovarian development among the temperature treatments from this experimental study suggests that future warming could lead to a considerable delay in spawning in this capital breeder.

Inhibition of vitellogenesis by rising temperature seen in *A. marinus* contrasts with that seen in many other early year temperate spawners including cyprinids and gadids (Bye 1984; Kjesbu et al. 1994; Tobin and Wright 2011). In such species, warming increases the level of the steroid E2, leading to a more rapid oocyte development rate (Miranda et al. 2013). Nevertheless, there appear to be species and population specific temperature optima for the production of gonad steroids (Van der Kraak and Pankhurst 1997; Tveiten and Johnsen 1999) and so it could be postulated

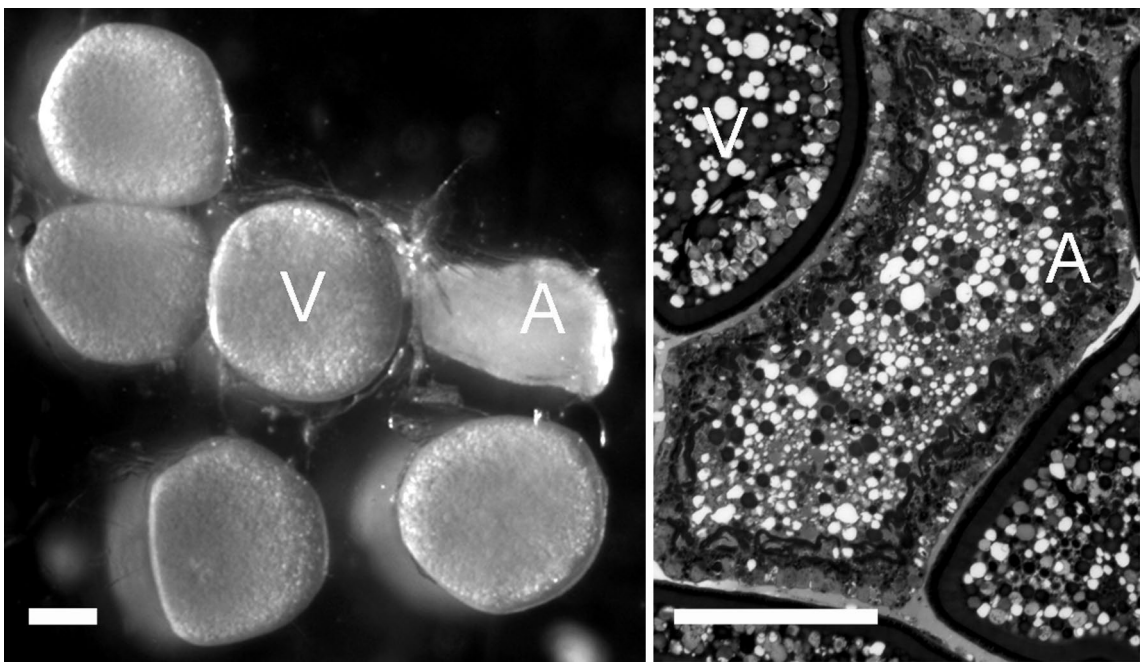

Fig. 5 Images comparing the appearance of an α-stage pre-ovulatory atretic oocyte (*A*) stained with toluidene blue in a 2 µm histological section with that seen in a whole mount along with vitellogenic oocytes (*V*). *Scale bars* 200 µm

that the high temperatures in the present study were super-optimal for ovary development in *A. marinus*. However, super-optimal temperatures tend to inhibit E2 synthesis leading to mass pre-ovulatory atresia and ovarian regression (Miranda et al. 2013). As there was no evidence of mass atresia even in the warmest treatment, it appears unlikely that the two higher temperatures were super-optimal for ovary development.

Oocyte development was related to the level of reproductive investment, as indicated by the relation between oocyte diameter and relative gonad mass. This suggests that changes in energy allocation to reproduction can explain the observed temperature-related differences in oocyte development. As *A. marinus* is entirely dependent on stored energy reserves for survival and gonad development during autumn and winter (Boulcott and Wright 2008), warming imposes a substantial energetic cost due to its affect on the standard metabolic rate (van Deurs et al. 2011). Mature *A. marinus* reduce energy investment in gonads rather than compromise the energetic stores needed to maintain the standard metabolic rate during the period they remain buried and so high autumn/winter temperatures lead to low relative gonad mass (Wright et al. 2017). Hence, the close relationship between oocyte diameter and relative gonad mass found in the present study indicates that ovarian development rate simply reflects energy allocation to reproduction. Variation in individual energy state and allocation may similarly explain why the range in oocyte diameters overlapped among the temperature treatments. Although the endocrine links between energy reserves and reproductive investment are not fully understood, hormones, such as IgF-1, are expected to influence the hypothalamic–pituitary–gonadal axis, modulating gonadotropin release which affects the production of follicle stimulating hormone in the pituitary and hence E2 secretion that promotes oocyte development (Migaud et al. 2010; Taranger et al. 2010). The apparent importance of energetic limitation on oocyte development in *A. marinus* contrasts with that seen in herring, where ration experiments conducted before and during vitellogenesis, had no effect on final oocyte diameter (Ma et al. 1998). Such differences in how the environment influences ovarian development among early season capital breeders highlights that reproductive responses to a warming climate cannot be generalized among fishes.

As atretic down regulation declined with oocyte size in *A. marinus* and oocyte development was more advanced in the coldest treatment, the higher prevalence and intensity of pre-ovulatory atresia with increasing temperature may simply reflect the earlier phase of oocyte development. Neither condition nor water content, which is inversely related to lipid reserves (Hislop et al. 1991; Robards et al. 1999b; Anthony et al. 2000), explained any further variation in the intensity of atresia. Consequently, although relative energy investment appears important to the level of pre-ovulatory atresia seen in *A. marinus*, there was not the typical inverse relationship between pre-ovulatory atresia and condition reported in other group synchronous breeders (Kurita et al. 2003; Kennedy et al. 2008, 2009).

Potential fecundity in *A. marinus* was strongly influenced by length in this experiment as found in the field (Boulcott and Wright 2011). This is to be expected given that the energy for ovarian development is solely acquired during summer feeding (Boulcott and Wright 2008; Wright et al. 2017) and the energy content of this species is closely correlated to length at the end of summer (Hislop et al. 1991). As the onset of vitellogenesis corresponds to the beginning of the treatment, the initial size of the oocyte batch recruited will not have been influenced by temperature, as all fish experienced the same conditions. However, differences in energy allocation would be expected to affect the degree of atretic down regulation, leading to differences in fecundity at length among temperature treatments, as has been demonstrated in a range of group synchronous early year spawners (Kurita et al. 2003; Kennedy et al. 2008, 2009). There was indirect evidence for greater downregulation in the warmer and, therefore, more energetically costly treatments. Despite no difference in the potential fecundity–length relationships among temperature treatments in December, realised fecundity at length would be expected to be lower in the higher temperature treatments because of the higher intensity of atresia and longer period of ovarian development. Nevertheless, the temperature effect on realised fecundity is unlikely to be substantial given the generally low intensity and reduction in atresia with oocyte development. Moreover, the intensity of atresia in experiments was comparable to observations on pre-spawning individuals in the field (Boulcott and Wright 2011).

While the potential for a climate induced phenological mismatch between the offspring of early year spawners and their prey has been widely considered, most attention has focussed on variation in zooplankton phenology (Cushing 1990; Durant et al. 2007). However, spawning and hatching times are typically variable among years, even in some total spawning species (Ware and Tanasichuk 1989; Wright and Trippel 2009) and the present study indicates that the potential magnitude of temperature-related changes in *A. marinus* spawning time is important to consider. Given that there are extensive empirical and model evidence that a temporal match between hatching and the production of their zooplankton prey is important to year-class strength in *A. marinus* (Wright and Bailey 1996; Gurkan et al. 2013; Régnier et al. 2017), the potential delay in *A. marinus* spawning time if average autumn/winter temperatures do increase by 2–3.5 °C by the end of the century as predicted (Lowe et al. 2009) could be considerable. Moreover, increased temperature during any period of energy intake

and allocation could affect an individual's mass prior to overwintering and subsequently the surplus energy available to allocate to reproductive development. Although there could be a substantial impact on spawning time, the effect of warming on subsequent hatching of larvae may be partially mitigated by the positive temperature dependence of embryonic development (Winslade 1971; Smigielski et al. 1983). For example, according to the embryonic development rate reported for *Ammodytes americanus* (Smigielski et al. 1983), an increase from 7.5 to 10.5 °C or 10.5 to 12.5 °C would shorten the embryonic phase by 19 and 13 days, respectively. The different effect of temperature on oocyte and embryonic development could be seen as an adaptation to reduce the potential for temperature-related variation in hatch times. Other factors are also known to affect embryonic development, such as oxygen concentration (Winslade 1971). However, how these factors combine to determine hatch date is unclear given the large observed intra-annual variation in hatch date (Wright and Bailey 1996; Régnier et al., 2017). Clearly, further work is needed to elucidate the mechanisms affecting larval hatching time, but this study highlights that the warming trend has the potential to lead to a significant mismatch arising from thermally mediated changes in spawning time.

Acknowledgements Ben Williamson, Clive Norris, Rory Long, and Brian Gall for providing technical support for the experimental work, Iain Gibb for age reading, Francis Neat, Declan Tobin, and Martha O'Sullivan for assisting with tagging and measuring the fish and Marlene Quintal for assistance with oocyte analysis. Georg Engelhard and two reviewers provided helpful comments on an earlier version of this manuscript. This work was funded by the Scottish Government (ROAME MF0765 and ST007), and all experimental work was carried out under a United Kingdom Home Office licence.

Compliance with ethical standards

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All work was carried out in accordance with the U.K. Animals Scientific Procedures Act 1986.

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