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Impact of rising temperature on reproductive investment in a capital breeder: The lesser sandeel

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ABSTRACT

Capital breeding, whereby adult's build-up energy reserves at times when food is abundant in order to invest in reproduction during a time of low prey availability, is common in seasonal environments. A dependence on stored energy for reproductive investment may make capital breeders sensitive to rising temperatures during winter when activity and energy demands are typically low. The lesser sandeel, *Ammodytes marinus* (Raitt, 1934), is an extreme capital breeder, as gonad development is entirely dependent on stored energy whilst the fish remains buried in sand overwinter. In this laboratory study, the energetic consequences of high and low overwintering temperatures on energy allocation to reproduction in *A. marinus* were examined. The laboratory conditions led to growth and mass changes that were consistent with previously published field observations. Loss in wet mass was greater in the high temperature treatment, consistent with the higher metabolic cost predicted. Despite this, somatic energy loss did not differ between the two temperatures, the difference in mass being related to the lower relative gonad size in the high temperature treatment. The negative effect of temperature on reproductive investment in *A. marinus* highlights that although temperature can have a permissive effect on reproductive development it is limited by available energy reserves. Based on these findings it seems likely that warming will lead to a change in reproductive investment in *A. marinus* that mature but will not impact their overwinter survival.

1. Introduction

Energy allocation for reproduction may come from current feeding activity, termed income breeding, or stored reserves laid down during a period of abundant food supply, termed capital breeding or a combination of both (Jönsson, 1997). Capital breeding is common in strongly seasonal environments where the suitability of conditions for offspring survival peaks around the onset of plankton production, requiring adults to allocate energy to reproduction during periods of food shortage. In iteroparous capital breeders, reproductive allocation to one spawning event may affect future reproductive output if it increases the risk of mortality or has a long-lasting impact on the animal's condition. Life history theory predicts a trade-off between the energy needed for current spawning and the ability to recover energy deficits to survive and spawn in consecutive years (Stearns, 1992; Henderson et al., 1996). Depending on this residual reproductive value, elevated standard metabolic rate (SMR) during a warm period of food shortage may be expected to result in a reduction in reproductive investment, especially in long lived iteroparous species. Indeed, life history models predict that spawning should be skipped if the expected future gain in reproductive output, discounted by survival, more than balances the expected reproductive success in the current year (Jørgensen et al., 2006). Conversely, for short-lived species there can be selection for increasing reproductive investment at a cost to survival (Poizat et al., 1999).

Neuroendocrine mechanisms involved in energy partitioning generally favour processes that ensure the survival of the individual over those that promote reproduction (Schneider, 2004). Reproductive processes are regulated through the hypothalamo–pituitary–gonadal (HPG) axis and several nutritionally regulated endocrine factors exert an influence on this axis (Pankhurst et al., 2008; Migaud et al., 2010). This may explain why gonad development is sensitive to lipid stores (Henderson et al., 1996) and skip spawning is common in low conditioned adult capital breeders (Rideout et al., 2005; Jørgensen et al., 2006). Nevertheless, reproductive investment may sometimes be maintained at a severe cost to somatic condition, as in the case of northern Gulf of St. Lawrence Atlantic cod, *Gadus morhua*, (Lambert and Dutil, 2000). Therefore, it is unclear how a temperature rise will affect reproductive investment in a capital breeder.

The family *Ammodytidae* (sandeels) includes several species that are extreme capital breeders, as gonad development is entirely dependent on stored energy (Robards et al., 1999a; Bergstad et al., 2001; Tomiyama and Yanagibashi, 2004). This makes them well

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suited to exploring the relationship between somatic maintenance and energy allocation to reproduction. Sandeels spend a considerable part of the year buried in sand, a life history tactic that acts both for predator avoidance and energy conservation (Bailey et al., 1991; van Deurs et al., 2010). Due to this habit they are energetically vulnerable to changing local conditions (Heath et al., 2012). The most economically and ecologically important sandeel is *Ammodytes marinus* (Raitt, 1934). Based on the appearance of this species in the water column the overwintering period can extend from August to April, although later burying or earlier emergence is also seen (Macer, 1966; Wright et al., 2000; Rindorf et al., 2016). This overwintering period is sustained by intense feeding activity between April and June during which the condition and somatic lipid content increases rapidly and then remains largely stable until August before the overwintering phase (Hislop et al., 1991; Bergstad et al., 2002; Rindorf et al., 2016).

The sandeel, *Ammodytes marinus* has a group-synchronous total spawning mode of ovarian development (Boulcott and Wright, 2008). In the North Sea, this species emerges from the sand to spawn between December and January (Macer, 1966; Gauld and Hutcheon, 1990). As a consequence of winter spawning, the most energetically costly phase of reproduction, secondary gametogenesis, begins at the onset of the overwintering phase when *A. marinus* are buried in sand (Boulcott and Wright, 2008). Although this species is capable of maturing in their first year, most mature from ages 1–3, dependent on growth rate and population differences (Bergstad et al., 2002; Boulcott et al., 2007). Most *A. marinus* from unexploited aggregations are <8 years old whilst few exploited aggregations contain fish over 4 years old (Bergstad et al., 2002; Rindorf et al., 2016). Consequently, although an iteroparous species, most individuals are unlikely to reproduce many times in their life time.

Due to their extensive latitudinal range of 49–73°N (Reay, 1970), *A. marinus* may experience monthly winter temperatures ranging between 5 and 15 °C (Berx and Hughes, 2009; van Deurs et al., 2011). Some climate change scenarios predict a further 2–3.5 °C rise in some parts of the species range by the end of the century (Lowe et al., 2009). This increase in winter bottom temperature would be expected to increase substantially the sandeel's SMR (Behrens et al., 2007) at a time when they are overwintering and so energy reserves are likely to be depleted at a much faster rate (van Deurs et al., 2011). Sandeels exhibit a degree of metabolic depression when buried, with respiration rates reduced whilst overwintering (Quinn and Schneider, 1991; Behrens et al., 2007). Based on estimates of respiration costs, van Deurs et al. (2011) predicted that there should be a size constraint on the size at maturation that would decrease in response to higher temperature. Given future warming scenarios and the comparatively short life span of the species (Bergstad et al., 2002; Boulcott et al., 2007), any delay in reproduction could have severe consequences to population viability.

In this study the energetic consequences of two overwintering temperatures on energy allocation to gonad development in *A. marinus* were examined. The temperatures were chosen to reflect present day low winter temperature (7.4 °C) and a future warm winter temperature (12.5 °C; Lowe et al., 2009). As sandeels store lipids in somatic tissue, similar to clupeoids, replacing it with water as they are used (Hislop et al., 1991), both changes in whole wet mass and changes in water content of the soma were considered. This required experiments using a combination of both longitudinal and cross–sectional sampling. Energy changes were inferred from the water content–energy relationship developed by Hislop et al. (1991). Information on SMR was derived from direct and published information on the relation between oxygen consumption and temperature in sandeels (Quinn and Schneider, 1991; van Deurs et al., 2011). By this means it was possible to test whether individuals risked mortality by maintaining a similar level of reproductive investment regardless of temperature or reduced investment and thereby maintained residual reproductive value.

2. Methods

2.1. Sample collection

Sandeels (*A. marinus*) were collected from the wild using a bottom trawl from a site off the east coast of Scotland (56°58′ N, 2°12′ W) on 19 April 2007 and were acclimated for four weeks in cylindrical tanks (2 m diameter × 1.2 m depth) with a thin layer of sand to allow them to bury. A sub-sample ($n = 15$) taken at the time of capture revealed that all individuals were immature and either age 1 or 2, although most of these would be expected to spawn the following winter (Boulcott et al., 2007). As the fish were of unknown age, sex and eventual maturity state it was not possible to ensure a fully balanced sample design that could account for these variables. Following acclimation, all fish ($n = 266$) were tagged by subcutaneous insertion of a Visual Implant Alpha IV tags (Northwest Marine Technologies, Inc.) above the pectoral fin behind the left eye, at the beginning of the trials.

2.2. Trials

Trials were conducted between 24 May and 10 December 2007; split into a summer (May–September) and an overwinter (September–December) period. Photoperiod was adjusted to ambient, using artificial lighting to mimic the natural photoperiod cycle for the latitude of capture and time of year. For the summer trial sandeels were kept in the cylindrical tanks, fed a mixture of frozen *Calanus* and mysid shrimps and maintained at 10 °C (±0.2). Immediately following the September measurements, 62–73 fish were assigned to each of four temperature-controlled 1 m cylindrical treatment tanks. The treatment tanks were maintained at either 7.4 (±0.1) or 12.5 ± 0.1 °C by separate temperature control units. All work was carried out in accordance with the U.K. Animals Scientific Procedures Act 1986.

The longitudinal sampling provided data on length (±0.1 cm) and total wet mass (M, ±0.01 g) at approximately monthly intervals (calendar days; 149, 176, 213, 247, 277, 305 and 342) from the start of the trial (24 May; see Table 1). The final sampling in December (day 342) corresponds to the time just prior to spawning in the wild (Gauld and Hutcheon, 1990). Age, maturity state, gutted mass (M_{gut}), gonad mass (M_{gon}) and dry mass (M_{dry}) were available from the final sampling in December (day 342). During the summer trial measurements, fish were deprived of food for 24–48 h to ensure evacuation of the gut. For the overwinter trial a sub-sample of 10 sandeels per treatment were also killed in September and October in order to derive time-specific estimates of whole, gutted and gonad wet mass. Gutted specimens were dried to constant mass in a convection oven at 60 °C and reweighed to determine water content of the somatic tissue. Age was estimated from counts of annual increments in the sagittal otoliths, according to the protocol of ICES (1995). All estimates were made by an experienced reader, and a subset of annual increment counts were verified from counts of daily increments (Wright, 1993). Maturity state was assessed according to the macroscopic staging described by Boulcott and Wright

Table 1
Summary of temperature and samples taken by calendar day for the repeated measures longitudinal study of changes in wet mass and the numbers for the cross-sectional samples for whole, gutted, gonad and dry mass. Note all fish were sacrificed by day 342.

Calendar day	Temperature (°C)	Number repeated measures	Cross section number sampled
149	10	204	
176	10	204	
213	10	204	
247	7.4 or 12.5	204	20
277	7.4 or 12.5	204	20
305	7.4 or 12.5	204	
342	7.4 or 12.5	Sacrifice	20

(2008). Gonado-somatic index (GSI) was used to compare relative gonad mass among treatments according to:

$$GSI = M_{gon}/M_{gut} \times 100 \quad (1)$$

2.2.1. Statistical analyses

Analysis was restricted to age-classes and maturity states found in all treatment tanks which meant that only mature age 1 or 2 sandeels were considered in this study. The ratio of males:females was 1.05:0.95 in the two temperature treatments. Trends in total wet mass before and during the temperature treatments were examined using a linear mixed effects model (LMM) using a Gaussian response and identity function implemented in GenStat 15 (VSN Ltd., U.K.), so as to account for repeated measures on the same fish over the measurement times. Due to the large variation in mass at age, trends in mass gain and loss were compared among individuals using standardised mass according to;

$$Ms = (m_{i..n} - \mu)/sy \quad (2)$$

where μ is the individual mean for the whole monitoring period (from day 149 in May), m_i is the mass on the ith monitoring day and sy is the individual standard deviation. The transformed values of Ms are therefore centred on zero, have unit variance and are unit-less. Individual fish was fitted as a random effect, the 'full' fixed effects model had the main effects and interactions of Ms, calendar day (Day), age, tank and temperature (Temp), all treated as factors, according to:

$$Ms \sim f(Temp)/f(tank) \times f(Day) + f(age) \quad (3)$$

The model was then simplified in a backwards-stepwise procedure by removing terms non-significant at the 5% level using Wald tests (expressed as the equivalent F tests on the appropriate degrees of freedom). Following preliminary analysis, the fish random effect was assumed to vary with time according to an antedependence structure order 1 (Hand and Crowder, 1996).

Generalized linear models (GLM) with a Gaussian distribution were implemented using the mgcv package in R environment (version 2.15.2). Whilst age 1 numbers were similar between temperature treatments ($n = 61$ and 57 for 7.4 and 12.5 °C, respectively) this was not the case for age 2 ($n = 27$ and 48 for 7.4 and 12.5 °C, respectively). Consequently, separate analyses were conducted on the two age-classes. Mass measurements were log transformed and proportion water content was logit transformed to normalise the data. The proportion daily overwinter mass loss of mature sandeels [ΔM_{Winter} (g)] was calculated as the loss in wet mass between the maximum and final size such that $\Delta M_{Winter} = 1 - ((M_{final} - M_{maximum}) / M_{final})$. This proportion was used to model the effects of temperature (7.4 °C vs 12.5 °C), tank replicate number (replicate 1 vs. replicate 2 at each temperature), sex (male vs. female) and wet mass in October ($M_{maximum}$, g) on ΔM_{final} (g) for each age according to:

$$\Delta M_{Winter} \sim M_{maximum} \times f(T\,^{\circ}C)/f(tank) \times f(sex) \quad (4)$$

Tank replicate number was nested within temperature and $M_{maximum}$ was treated as the covariate, with temperature treatment, tank and sex treated as factors. Final explanatory variables and interactions for the minimum adequate model were obtained through a process of step-wise deletion with model selection based on Akaike's Information Criteria (Akaike, 1974).

Cross-sectional samples collected during the overwinter period were used to derive relationships between gonad and gutted mass and proportion water content (WC) and gutted mass according to:

$$Log\ (M_{gon}) \sim Log(M_{gut}) \times f(Day) \quad (5)$$

$$Logit\ WC \sim M_{gut} \times f(Day) \quad (6)$$

where sample time was treated as a factor. Normality of residuals from all GLMs were tested for normality using an Anderson-Darling test and plots of residuals against fits was plotted to confirm that the data tested complied with homogeneity of variance.

Calorific value (CV; $kJ \cdot g^{-1}$ wet) was inferred from estimates of water content using the relationship from Hislop et al. (1991) for this species:

$$CV\ (kJ \cdot g^{-1} \cdot wet) = -0.418WC + 37.785 \quad (7)$$

where WC is proportion water content. This allowed consideration of both potential energy reserves at the onset of overwintering and the subsequent daily energetic cost in the two temperature treatments.

Surplus energy available for reproduction was inferred by first estimating the energy needed for SMR for a given M. The linear relationship between SMR ($mg \cdot O_2 \cdot kg^{-1}\ h^{-1}$) and temperature developed by van Deurs et al. (2011) for *A. tobianus* multiplied by an oxycaloric coefficient of 14 J mg^{-1} O_2 (Brett, 1973) was used to estimate the energy needed for SMR for a given size in the two temperature treatments. In addition, new measurements of oxygen consumption at 10 and 12.5 °C for *A. marinus* from the study sample location were obtained using a recirculating respirometer (see Supplementary 1). The potential energy reserves, energy needed for SMR and surplus energy available for reproduction during the experimental period were calculated by length-class, as length does not change during the overwinter phase. To estimate energy by length, predicted M for a given length in September was derived from $M = cL^b$ and corresponding WC was derived from Eq. (4) substituting M for M_{gut}.

3. Results

3.1. Mass change

Prior to treatment, fish standardised mass increased from May to September (Fig. 1) and no individual experienced a loss in wet mass for more than a single month over this period. This trend did not vary significantly between ages 1 and 2 (LMM; $F_{1,800} = 0.19$; $p = 0.67$). Following the start of the treatment there was a significant interaction between time and temperature as the rate of standardised wet mass loss was greater at 12.5 °C than at 7.4 °C ($p < 0.001$; Table 2). There were significant differences in standardised wet mass loss between tanks within the two treatments ($p < 0.001$) but these differences were small relative to temperature related changes (Fig. 1). Wet mass loss for the 3 month period of no feeding at 12.5 °C was similar to mass gain in the month preceding the treatment.

3.2. Proportional winter loss in mass

Age 1 individuals lost a significantly higher proportion of their wet mass in the high temperature treatment than in the low temperature treatment (GLM Age 1: $F_{1,93} = 51.34$; $p < 0.001$; Table 3a) with predicted proportion daily loss in mass of 0.0012 and 0.0017 at 7.4 and 12.5 °C, respectively. Initial mass at the start of overwintering had no significant effect on proportion mass loss (GLM age 1: $F_{1,92} = 2.41$; $p = 0.12$ and age 2; $F_{1,63} = 2.08$; $p = 0.15$) and neither did sex (age 1 $F_{1,92} = 1.33$; $p = 0.23$). The results for age 2 sandeels were similar although there was also a significant difference in mass loss between replicates ($F_{2,62} = 11.99$; $p < 0.001$; Table 3b) possibly reflecting the low and uneven sample sizes among treatment tanks. Predicted age 2 proportional daily loss in mass was 0.0009 or 0.0013 at 7.4 °C and 0.0015 or 0.0018 at 12.5 °C, for replicate tank measurements.

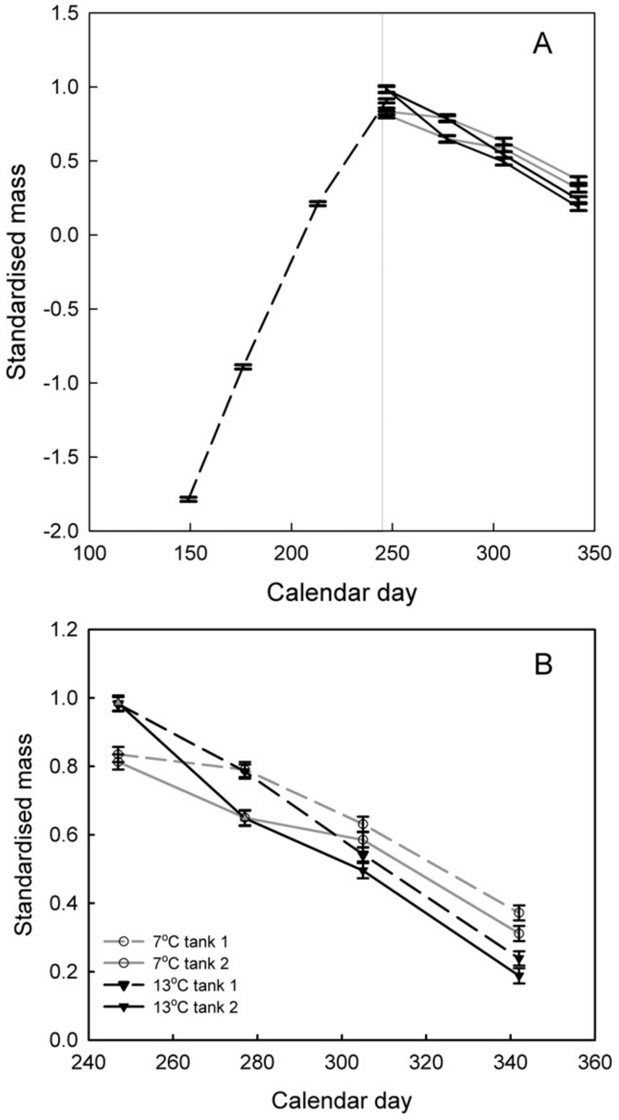

Fig. 1. Fitted standardised mass changes in sandeels ($n = 204$) during pre-treatment (May–August; shaded) and overwintering treatment (September–December) for (A) total period and (B) overwinter phase enlarged from right limb of panel A. Bars refer to 1 standard error.

3.3. Changes in gonad size

The mean length of mature sandeel was 12.4 (range: 9.7–15.1) and 13.2 (range: 11–15) cm for age 1 and 2 males and 12.7 (range: 10.1–15.5) and 13.1 (range: 10.5–15) cm for age 1 and 2 for females, respectively. Gonad mass was significantly related to log gutted wet mass and sampling time (GLM; $p < 0.001$; Fig. 2), with a major increase in GSI between October and December. By December a clear effect of temperature on the gonad-gutted mass relationship had developed, with sandeels held in the high temperature treatment having significantly smaller gonads relative to their gutted mass ($F_{1,201} = 247.3$; $p < 0.001$) and this difference was most apparent in females ($F_{1,200} = 209.3$; $p < 0.001$; Fig. 3a). Males had larger gonads for a given mass and temperature than females (Fig. 3b). Average female GSI in December was 16.4 and 8.5% at 7.4 and 12.5 °C whilst male GSI was 23.3 and 16.8% at 7 and 12.5 °C, respectively. Residual loss in wet mass after accounting for the change in gonad mass, was similar between the two temperature treatments (Age 1: $F_{1,119} = 0.19$; $p = 0.66$; Age 2: $F_{1,81} = 0.53$; $p = 0.47$). Hence, temperature effects on winter mass loss reflected differences in gonad investment, rather than loss in somatic mass.

Table 2
Linear mixed model analysis of changes in standardised mass during the overwintering phase with the fixed effects: time (day), temperature (7.4 vs 12.5 °C) and replicate tank as factors.

Fixed term	Wald statistic	n.d.f.	F statistic	d.d.f.	F pr
Day	1797.62	3	599.21	800	<0.001
f(Temp)	1.62	1	1.62	800	0.204
Day·f(Temp)	102.16	3	34.05	800	<0.001
f(Temp)·f(replicate)	32.95	2	16.48	800	<0.001
Day·f(Temp) f(replicate)	19.06	6	3.18	800	0.004

Table 3
Generalized linear model (GLM) results relating logit proportion overwinter mass loss with sample day, temperature and tank replicate. Coefficients, significance levels, degrees of freedom and deviance are given. Deviance refers to null and residual deviance (analogous to sums of squares).

Explanatory variable	df	Coefficients Estimate	 Std. error	 p	Deviance
Age 1					
Intercept	94	−6.694	0.032	<0.001	6.365
f(Temp)12.5	93	0.310	0.043	<0.001	4.101
Age 2					
Intercept	65	−6.643	0.073	<0.001	6.589
f(Temp)12.5	64	0.321	0.087	<0.001	4.146
f(Temp)7.4·f(replicate)	62	−0.392	0.101	<0.001	2.990
f(Temp)12.5·f(replicate)		−0.192	0.064	<0.001	

3.4. Changes in water content of soma

Proportion water content ranged from 0.64 to 0.81 and was inversely related to gutted wet mass. The slope of this relationship changed significantly over time (Fig. 4) leading to a reduction in the relative difference in water content with gutted mass by December. As a consequence the difference in proportion water content of soma between a 2 and 6 g sandeel decreased from 0.05 in September to 0.01 in December. The soma of females had a small but significantly lower water content than males for a given gutted mass in the final December sampling ($F_{1,201} = 24.42$; $p < 0.001$; Table 4).

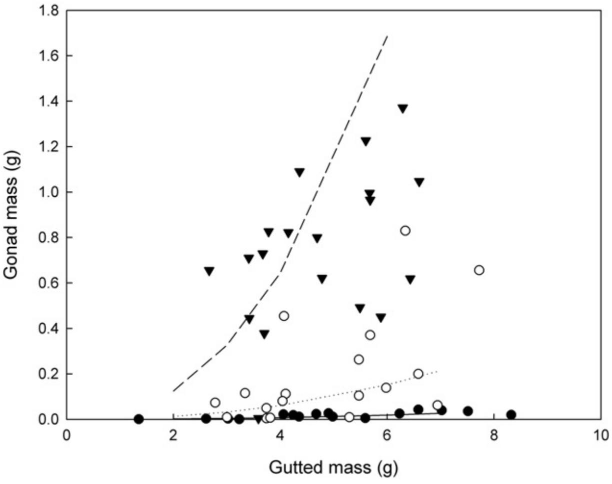

Fig. 2. Relationship between gonad and gutted mass in September (-), October (···) and December (—) cross sectional samples based on fitted generalized linear model. GLM fitted lines have been back-transformed from a log scale to aid interpretation. Symbols refer to observed data for September (●), October (○) and December (▼).

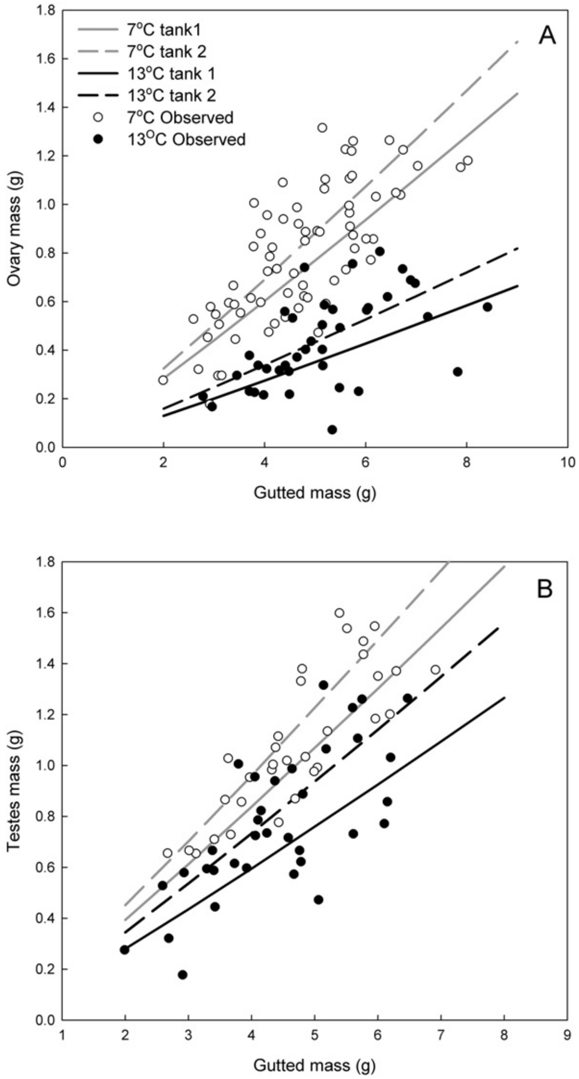

Fig. 3. Relationship between gonad and gutted mass in final December sample for (A) females and (B) males at two temperatures and replicates based on fitted generalized linear model. Symbols refer to observed data for 7.4 (○) and 12.5 °C (●).

3.5. Predicted changes in soma energy content

Estimates of potential energy reserves at the onset of overwintering, energy required for SMR and surplus energy available for reproduction in females are given in Table 5. Estimates of reserve energy were comparable between temperature treatments due to the lack of a difference in residual loss in mass. Fish lost around a third of their soma energy content between September and December. This would equate to a daily proportion energy loss of 3.39–3.56 × 10^{-3}. Had this rate of energy loss continued for the full 7 month overwintering period, it would equate to a 71–77% reduction in reserve energy content. Estimates for energy required for SMR differed depending on the relationship between oxygen consumption and temperature used. Virtually no surplus energy would have been available for sandeels <12 cm in the high temperature treatment based on the van Deurs et al. (2011) relationship for *A. tobianus* whilst considerably more surplus energy would have been available based on the oxygen consumption estimates for *A. marinus* indicated by the present study. The relationship between the energy of ovaries and this surplus energy for *A. marinus* (Fig. 5) suggests that the resulting gonads reflect around 50% of the predicted surplus energy.

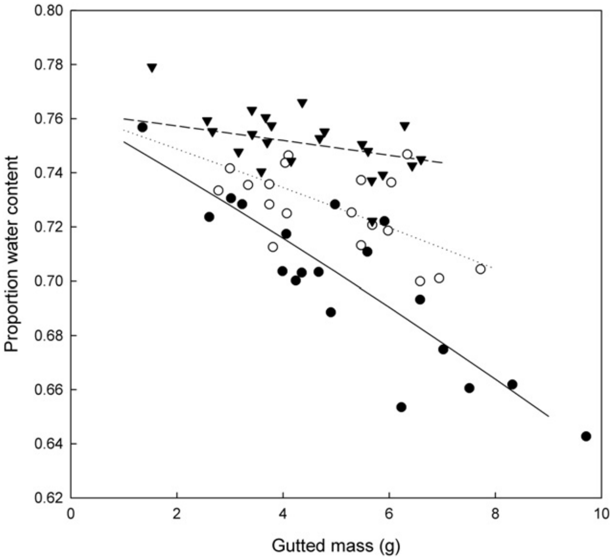

Fig. 4. Relationship between logit proportion water content and gutted mass in September (-), October (⋯) and December (—) cross sectional samples based on fitted generalized linear model. Symbols refer to observed data for September (●), October (○) and December (▼).

4. Discussion

Loss in wet mass was greater at the high temperature than at the low temperature, consistent with the higher metabolic cost. More than a twofold difference in SMR would have been expected between the 12.5 and 7.4 °C temperature (Quinn and Schneider, 1991; van Deurs et al., 2011; Supplementary 1), leading to a substantially lower surplus energy available for reproductive investment. Estimates for oxygen consumption at 10 and 12.5 °C in *A. marinus* from this study (Supplementary 1) were lower than estimates for overwintering *A. hexapterus* (Quinn and Schneider, 1991) and buried *A. tobianus* (Behrens et al., 2007; van Deurs et al., 2011), although the estimated Q_{10} fell within the range of these other studies. The oxygen consumption estimates from the present study better explained gonad size than van Deurs et al. (2011) relationship for *A. tobianus*, as the latter predicted that there would have been no energy for reproductive investment in *A. marinus* <12 cm held at 12.5 °C, despite this clearly being the case.

The lower reproductive allocation at high temperature demonstrates that *A. marinus* tries to minimise the energetic cost of increased respiration to somatic energy stores. This species typically returns to the sand for up to three months after spawning and then emerges as zooplankton production begins in the spring (Winslade, 1971; van Deurs et al., 2010). Consequently, if reproductive investment had been maintained at the high temperature it is likely that survival would have been affected. So despite being a comparative short – lived species, *A. marinus* appears to respond to energetic constraints as expected of an iteroparous species, thereby maintaining residual reproductive value. It may be relevant that the vast majority of fish in this experiment are

Table 4
Generalized linear model (GLM) results relating logit proportion water content with M_{gut} and sex in the final December sampling. Coefficients, significance levels, degrees of freedom and deviance are given. Deviance refers to null and residual deviance (analogous to sums of squares).

Explanatory variable	df	Coefficients			Deviance
		Estimate	Std. error	p	
Intercept	203	1.246	0.020	<0.001	1.289
Gutted mass	202	−0.020	0.004	<0.001	1.107
Females	201	−0.050	0.010	<0.001	0.987

Table 5
Estimated somatic energy (KJ·ind^{-1}) prior to overwinter and that lost during experimental trial for a given length-class. Predicted energy used for SMR is based on oxycalorific coefficient and temperature oxygen consumption relationships for *A. marinus* and *A. tobianus* (in parentheses) as given in supplementary information. Surplus energy is based on observed energy loss – predicted SMR energy.

			Predicted SMR energy		Surplus energy	
Length-class (cm)	September soma energy	Observed energy loss	7 °C	12.5 °C	7 °C	12.5 °C
11	18.78	6.48	1.42 (2.83)	2.94(6.14)	5.06 (3.65)	3.54 (0.34)
12	26.86	9.08	1.91 (3.81)	3.96 (8.27)	7.17 (5.27)	5.12 (0.81)
13	37.12	12.37	2.51 (5.01)	5.21 (10.88)	9.86 (7.36)	7.16 (1.49)
14	49.92	16.48	3.24(6.28)	6.72 (14.02)	13.24 (10.02)	9.76 (2.46)
15	65.62	21.53	4.1 (8.18)	8.51 (17.76)	17.43 (13.35)	13.02 (3.77)

likely to have been first time spawners, as most were under the age and length of 50% maturity (Boulcott et al., 2007). Reproductive effort does appear to increase with size in *A. marinus* as evident from the high exponent of the fecundity–length relationship (Boulcott and Wright, 2011) and so it is possible that reproductive allocation might have been greater if repeat spawners had been examined.

Contrary to the stimulatory effect of temperature on gametogenesis seen in cyprinid and gadoid fishes (Bye, 1984; Kjesbu, 1994; Tobin and Wright, 2011), high temperature inhibited gonad investment in *A. marinus*. This negative effect of temperature on reproductive investment highlights the diversity of reproductive responses to a warming climate (Van Der Kraak and Pankhurst, 1997; Pankhurst and Munday, 2011) and suggests that whilst temperature can have a permissive effect on reproductive development, this must be dependent on energy available for reproductive investment. Poor condition and low temperatures have been linked to skip spawning in many teleosts, where either oocytes remain in a pre-vitellogenic phase or females halt the development of vitellogenic oocytes and reabsorb them via follicular atresia (Rideout et al., 2005). Skipped spawning may be linked to energetically sensitive seasonal switches as for example, in walleye, *Stizostedion vitreum*, where females can respond to reduced lipid reserves in winter following an earlier commitment to mature (Henderson et al., 1996). There was no indication of a halt in reproductive investment in *A. marinus* as gonad mass was proportional to gutted mass at both temperatures tested in the present study. This implies that *A. marinus* can tightly regulate reproductive investment over short time-scales. Whilst the physiological mechanism has yet to be elucidated, such metabolic challenges can have an inhibitory effect on the HPG axis suppressing the production of follicle stimulating hormone (FSH) in the pituitary and hence reducing steroid secretion in the gonads (Migaud et al., 2010; Taranger et al., 2010). Higher temperatures alone may also have inhibitory effects due to conformational changes in proteins (e.g. FSH and their receptors, steroid-synthesising enzymes), and also the increasing tendency for steroid hormones to form water-soluble conjugates at high temperatures (Van Der Kraak and Pankhurst, 1997).

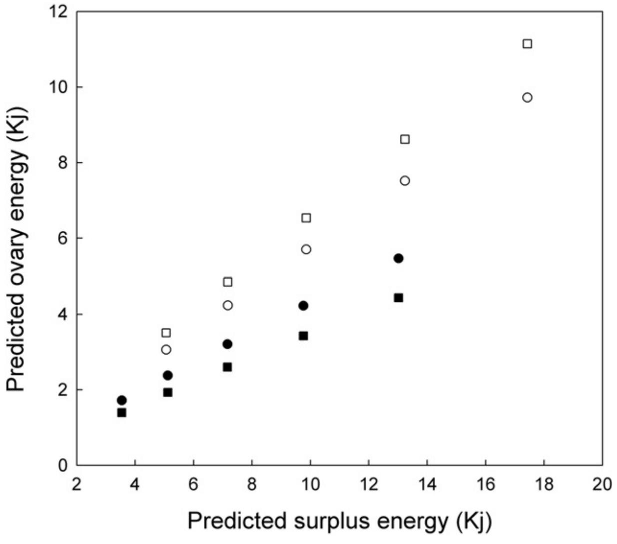

Fig. 5. Relationship between predicted gonad energy and predicted surplus energy (see Table 4) for *A. marinus*. Ovary energy was predicted from Fig. 3 relationship for 7 (open) and 12.5 °C (black) treatments and replicate tanks 1 (circle) and 2 (square). Energy density for ovary was based on 5.71 kJ·g^{-1} M$_{gon}$ (Anthony et al., 2000).

The laboratory conditions in the present study did lead to growth and mass loss changes that were consistent with previously published field observations. The rapid mass gains from May to September seen in the experimental trials were similar to estimates of growth reported in the field (Bergstad et al., 2001; Rindorf et al., 2016). Changes in gutted mass and GSI from September to December were consistent with that observed by Bergstad et al. (2001, 2002) for sandeels in the North Sea. Field estimates of the seasonal variation in energy content of sandeels suggest that by the end of overwintering around 47% of peak energy is lost in *A. marinus* (Hislop et al., 1991) and 37.5% in *A. hexapterus* (Robards et al., 1999b). The decrease in estimated energy content in this study appears high being 33% of the peak by December, i.e. halfway through the overwinter period. Given that spawning is typically in late December to January (Gauld and Hutcheon, 1990) when the experiment ended, energetic costs for the remainder of the overwintering phase should have been much reduced as energy would only be needed to cover SMR. Stored lipids can be utilised to supply the energy demands of reproduction (Henderson et al., 1996) and Pinto (1984) observed a significant loss of lipid prior to spawning in captive *A. hexapterus*. In the present study the changes in water content observed indicate a reduction in somatic lipid reserves of around 34% based on the lipid-water relationship of Hislop et al. (1991), which is similar to that seen in *A. hexapterus* (Robards et al., 1999b). Lipid loss was higher in larger individuals as a 3 g *A. marinus* would have lost 27% lipid by December compared to 42% for a 6 g individual. Sex related differences in gonad investment reflected the relative energetic costs of developing testes and ovarian tissue. Female sandeels expend more reproductive energy than males due to egg production, which requires a greater accumulation of reserves (Love, 1980; Robards et al., 1999b). Energy density of ovaries is higher than that of testes for a given reproductive stage (Anthony et al., 2000). Higher GSI in male sandeels may also reflect earlier and more rapid secondary gametogenesis as Bergstad et al. (2001) and Robards et al. (1999a) found that male GSI in species of *Ammodytes* was initially higher in the first two months of secondary gametogenesis and testes development peaked earlier than females.

In summary, the present study indicates that warming seas would lead to a change in reproductive investment in *A. marinus* but would not necessarily impact loss in somatic mass and hence overwinter survival. A female can reduce reproductive investment by either producing fewer oocytes, or by investing less in each oocyte. It is not clear whether the reduced reproductive investment observed in this study was linked to reduced size specific fecundity, less energy per oocyte, or an effect on the rate of gametogenesis. If fecundity was affected there could be an impairment of reproductive potential, although as stock-recruitment relationships are weak in this species (van Deurs et al., 2009; ICES, 2015) the consequences may be slow to detect. If gonad investment reduced eventual egg size this might impact larval viability as the protracted embryonic phase and large yolk reserves of larvae appear important to surviving to the onset of secondary production (Smigielski et al., 1983). Conversely if gametogenesis is delayed then spawning time could be delayed leading to a potential phenological mismatch.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jembe.2016.09.014.

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