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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