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# Effect of size on spawning time in the lesser sandeel *Ammodytes marinus*

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Ovarian development was examined in relation to size and temperature in late pre-spawning *Ammodytes marinus* over 5 years. Oocyte diameter was positively related to length indicating that larger females spawned earlier. Age and temperature, whilst accounting for the effect of length, were not found to affect oocyte development, although the thermal range examined was only 1·3° C.

Key words: *Ammodytes marinus*; oocyte development; size effects; spawning time.

The timing of spawning in temperate species is usually strongly connected to re-occurring, cyclical conditions favouring offspring survival (Cushing, 1990). Large intra and interannual variation in offspring survival rates would be expected to select for a high number of spawnings per season and life time (Stearns, 1992) and asynchronous and protracted spawning is commonly observed within fish populations (Wright & Trippel, 2009). A few species, however, exhibit short, highly synchronized spawning seasons and this is often linked to high intra-season variation in selection on progeny birth date (Wright & Trippel, 2009). In some cases, larger, older or experienced adults have been found to spawn before young, first-time spawners (Slotte *et al.,* 2000; Wright & Gibb, 2005). This may relate to some ontogenetic predisposition to alter the onset of spawning times or just reflect the tendency for high conditioned fishes to spawn earlier (Trippel *et al.,* 1997). Although size dependent differences in spawning time have been most widely reported in multiple batch spawners, it has also been found in total spawners such as capelin *Mallotus villosus* (Müller 1776) (Carscadden *et al.,* 1997) and Atlantic herring *Clupea harengus* L. 1758 (Lambert, 1987). Such size-related differences in spawning time may lead to successive waves of spawning (Ware & Tanasichuk, 1989).

Possible maternal size effects on spawning time must be set against a backdrop of other factors affecting spawning time. Temperature can be an important influence on spawning time as a rise in temperature can lead to a faster rate of vitellogenic

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oocyte development (Kjesbu, 1994). Consequently, the combination of warming seas and changes in stock size composition has the potential to alter the onset and period of spawning.

The lesser sandeel *Ammodytes marinus* Raitt 1934 is an important forage species subject to a major fishery in the North Sea, spawning a single batch of demersal eggs between December and January (Macer, 1966). Observations on the availability of *A. marinus* to fisheries (Macer, 1966) and their occurrence in the sediment suggests that spawning aside, *A. marinus* in the North Sea rarely emerge to feed from the seabed between September and March. Although there is little information on the timing and duration of spawning, larvae hatch after a long embryonic phase over many weeks to months (Wright & Bailey, 1996). Data from *A. marinus* collected from sandeel grounds off south-west Norway, however, do suggest that spawning occurs somewhere between December and January (Bergstad *et al.,* 2001). The present study examines the effect of maternal size on spawning time using oocyte diameter as a predictor of spawning over a 5 year timescale. Oocyte diameter has been shown to be a good proxy for spawning time, successfully predicting spawning time in female Atlantic cod *Gadus morhua* L. 1758 (Kjesbu, 1994) and is likely to be particularly suited to a group synchronous total spawner like *A. marinus* as the ovary contains a relatively homogeneous single batch of vitellogenic oocytes (Boulcott & Wright, 2008). The potential role of temperature in oocyte development was also examined.

*Ammodytes marinus* specimens were collected annually between 2010 and 2014 off mainland Scotland, U.K., between 56 and 58° N using a 1·2 m scallop dredge fitted with a 6 mm mesh bag (Fig. 1). Sample dates (4–18 December) corresponded to the period immediately prior to spawning (Gauld & Hutcheon, 1990). Total length ($L_T$, ±0·1 cm), ovary mass ($M_O$, ±0·01 g) and eviscerated mass ($M_E$, ±0·01 g) were taken from a minimum of 40 mature females each year. Age was estimated from sagittae (ICES, 1995) or, in a minority (<5%) of otoliths that were found to be unreadable, by fitting multinomial logistic models to site-specific age estimates taken from yearly survey data (Gerritsen *et al.,* 2006).

Individual, mean oocyte diameter, measured according to Thorsen & Kjesbu (2001), was estimated from a minimum sample of 100 oocytes. To account for shrinkage during fixation in formalin, recorded diameters of fixed oocytes were transformed using the relationship $y = 0{\cdot}9063x + 52{\cdot}1986$ ($n = 36$, $r^2 = 0{\cdot}97$, $t_{34} = 34{\cdot}4$, $P < 0{\cdot}001$), where $y$ = fresh oocyte diameter (μm) and $x$ = fixed oocyte diameter (μm).

A weekly bottom temperature dataset (http://marine.gov.scot/context/coastal-monitoring-site-stonehaven/) within 100 km of the sample sites was used to infer temperature exposure during the vitellogenic phase. As there was no way of knowing the timing of the onset of vitellogenesis in individuals, a fixed date (17 August) was assumed based on a previous laboratory study (Boulcott & Wright, 2008). Degree days for the vitellogenic period (days) were then calculated from this start to the date of capture. As individuals were captured within an 11 day window in December throughout the 5 year study and temperature variation in the month of August was low, individual differences in start dates would have had little effect on calculated degree days. Average daily temperature ($T$, °C) experienced by *A. marinus* over the vitellogenic period ($D_V$) was estimated from a thin plate regression spline fitted to the weekly temperature data using the generalized additive modelling facilities in the R package mgcv (www.r-project.com; Wood, 2011).

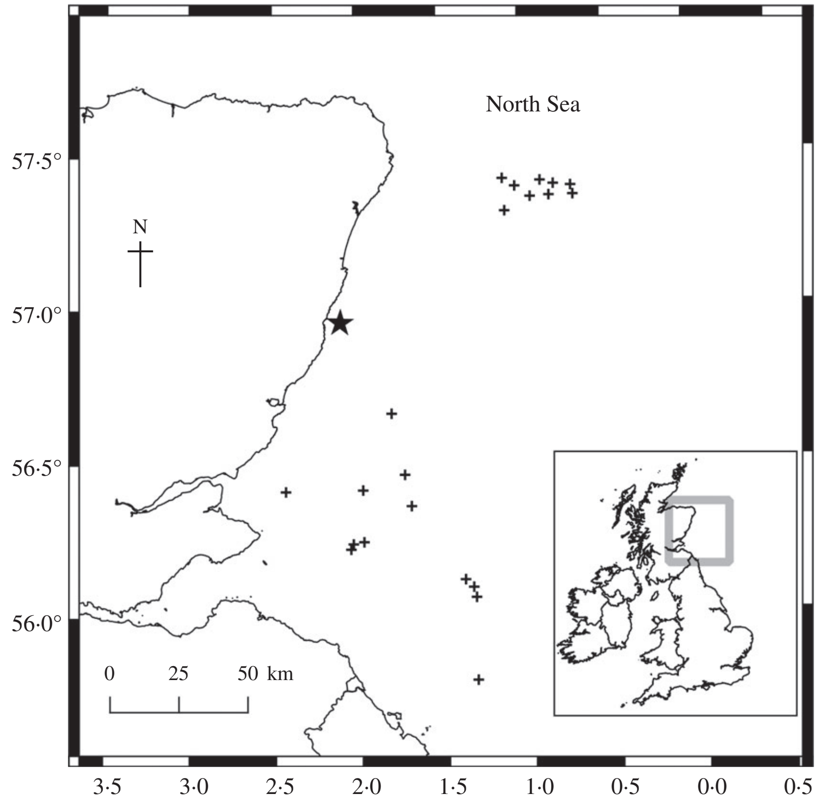

FIG. 1. Locations of fishing positions (+) in the North Sea off north-east Scotland for *Ammodytes marinus* and the Stonehaven coastal ecosystem monitoring site (★).

The effects of $L_T$, average daily temperature ($T$), vitellogenic period ($D_V$) and age ($A$) on oocyte diameter ($O_D$) were examined using a generalized linear mixed model (GLMM) within the R package, lme4 (Bates *et al.,* 2015). The full fixed effect structure was: $O_D \sim L_T + T + D_V + A$. The correlation between the explanatory variables was checked for collinearity using Spearman rank correlations and variance inflation factors (VIF). Total mass was excluded from the modelling process due to its high collinearity with $L_T$ ($r = 0·95$, $P < 0·001$). To allow for possible sub-regional variation in life-history characteristics between *A. marinus* aggregations (Boulcott *et al.,* 2007; Boulcott & Wright, 2011) and for possible random differences between years and haul, the intercept was allowed to vary randomly with each combination of sub-area (north or south of 57° N), year (2010–2014) and haul. The full model was then simplified in a backwards stepwise procedure with model selection based on Akaike's information criteria (Akaike, 1974). The relative importance of each was assessed by a likelihood ratio test and estimated $P$ values were computed from the Kenward-Roger correction using the R package pbkrtest. Residual plots were used to examine normality and homogeneity of variance.

Females (age 1–4 years) ranged in $L_T$ from 10·1 to 20·4 cm ($n = 270$, mean = 14·3 cm). Variation in oocyte diameter did not suggest that oocyte development

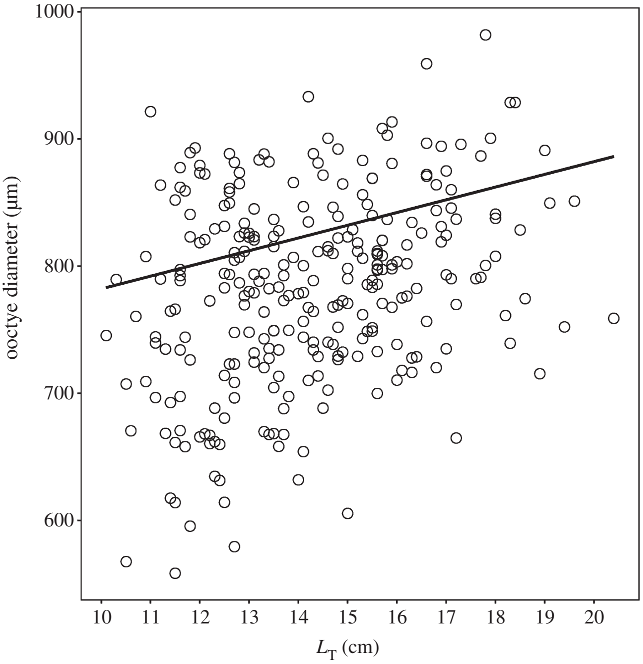

FIG. 2. The fitted relationship between the total length ($L_T$) of females (○) and mean oocyte diameters (——) in *Ammodytes marinus* ($n = 279$).

was highly synchronized within the study area as the total range was 558–982 µm and annual average diameter was from 753–859 µm. $L_T$ ($F_{1,259.7} = 21{\cdot}15$, $P < 0{\cdot}001$) was found to have a significant effect on oocyte development (Fig. 2). Oocytes in *A. marinus* enter the maturation phase by around 650–700 µm and begin the final hydration process associated with germinal vesicle breakdown around 850 µm (Wright *et al.,* 2017). Hence, large individuals sampled in this study will have been caught close to their spawning time while some of the smallest individuals were in the final stages of vitellogenesis. Average daily temperature recorded within the vitellogenic period ranged between 11·1 and 12·4° C across the 5 years of study, but was not found to influence oocyte diameter ($F_{1,39.2} = 2{\cdot}37$, $P > 0{\cdot}05$). Similarly, no effect of age ($F_{1,255.7} = 1{\cdot}82$, $P > 0{\cdot}05$) or the duration of vitellogenesis prior to capture ($F_{1,48,1} = 2{\cdot}07$, $P > 0{\cdot}05$) on oocyte development was detected.

The positive effect of $L_T$ on oocyte diameter in December indicates an earlier onset of spawning in large female *A. marinus*. A similar length effect on relative ovary size has been linked to two waves of spawning in Norwegian spring spawning *C. harengus* (Slotte *et al.,* 2000). Although little is known about the precise timing of spawning in *A. marinus*, the present study suggests that asynchrony in the onset of spawning could extend the period over which individuals spawn within a population. Such a protracted spawning period may partly explain why the hatching period of *A. marinus* extends over many weeks to months (Wright & Bailey, 1996) despite it being a total spawner. The effects of maternal size on final egg size, an effect that is common to many species (Hutchings, 1997), has not yet been investigated in *A. marinus*.

The lack of a temperature effect on oocyte development apparent in this study contrasts with evidence from a range of species including cyprinids and gadids (Bye, 1984; Kjesbu *et al.,* 2010). The relatively narrow range in temperature (1·3° C) variation among years, however, the use of a fixed onset of vitellogenesis and the large individual variation in oocyte diameter, may make it difficult to disentangle effects. Due to this uncertainty, experimental investigations into the effect of temperature and energy allocation would be beneficial.

The evidence for a length effect on spawning time is important as there is considerable variation in *A. marinus* length composition across the North Sea and significant differences have been found at spatial scales down to 5 km (Jensen *et al.,* 2011). The length effect on oocyte development probably reflects differences in energy stores as larger *A. marinus* attain a higher condition by the onset of over-wintering (Rindorf *et al.,* 2016). The early onset of spawning has also been found to be related to somatic condition in *C. harengus*, another capital breeder (Slotte *et al.,* 2000). Indeed, some of the most extensive evidence of size-dependent spawning time has been found in *C. harengus* (Ware & Tanasichuk, 1989) and it is thought that this trend in wild fish is caused by fish of different sizes experiencing different environmental conditions, such as temperature. Clearly, further work is needed to understand how the variation in adult length and local environment translate into differences in the onset and duration of spawning at the wider North Sea scale.

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