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Variation in fecundity in the lesser sandeel: implications for regional management

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The number of eggs produced by a parental stock is central to fisheries advice on recruitment potential. However, stock based estimates of egg production may give a misleading index of recruitment potential in stocks containing several reproductively isolated populations. This paper examines the ability of length, condition and oocyte developmental stage to predict levels of potential fecundity in the sandeel, Ammodytes marinus, *in three important fished areas in the North Sea. Our results indicate that regional variation in this relationship exists, with fecundity in central areas of the North Sea being higher than those found just off the north-east UK. Oocyte diameter was also found to have a significant effect on potential fecundity, suggesting a down-regulation of oocyte numbers arising from pre-ovulatory atresia, however, this effect was not apparent in every model tested. Our findings have relevance to the local sustainability of spawning components and thus the regional management of the North Sea sandeel stock.*

Keywords: sandeel, *Ammodytes marinus*, fecundity, stock reproductive potential, atresia, stock assessment

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INTRODUCTION

Whilst current fishery management is most commonly based on a single stock assumption, it has long been recognized that the stocks of many marine fish comprise several spawning components with a variable degree of geographical and even reproductive segregation (McQuinn, 1997; Smedbol & Stephenson, 2001). Such stocks are considered to be population rich. The lesser sandeel, *Ammodytes marinus*, appears to be one such population rich species where, within the North Sea, there are several geographically distinct spawning aggregations with limited movement between them (Proctor *et al.*, 1998; Pedersen *et al.*, 1999; Munk *et al.*, 2002; Christensen *et al.*, 2008). Failure to account for population richness in fisheries management may lead to the depletion of stock components with unknown ecological consequences (Stephenson, 1999; Frank & Brickman, 2000) and could critically affect the long-term stability and sustainability of the entire stock (Hilborn *et al.*, 2003). Short-term, localized stock failures, although perhaps small in number relative to the entire stock, can have a significant impact on the breeding success of marine top predators such as seabirds (Monaghan, 1992; Wright, 1996; Frederiksen *et al.*, 2005). Indeed, the localized nature of the sandeel stock has lead to the precautionary closure of the fishery off the north-east UK coast since 2000.

Despite such concerns, stock productivity in the sandeel, in terms of the recruitment potential of a stock, is currently based on spawning biomass and estimated using a mean weight and age-at-maturity schedule calculated for the whole stock. Here, spawning stock biomass is as a proxy for total egg production and this may be problematic because fecundity per unit mass can vary with age and condition (Marshall *et al.*, 1998). For example, significant population level departures from these stock parameters may make a component population more or less vulnerable to depletion. A recent comparison of sandeel maturity–size relationships demonstrated significant differences in size- and age-at-maturity among the main fished regions in the North Sea (Boulcott *et al.*, 2007). Similar variability has also been reported outside the main North Sea assessed region (Gauld & Hutcheon, 1990; Bergstad *et al.*, 2001). Given these differences in size-at-age, age specific fecundity may also be expected to vary between spawning aggregations unless fish from slower growing regions exhibit higher fecundity per unit size. The available information on the fecundity–size relationships for this species does not suggest regional differences in fecundity at size (Macer, 1966; Gauld & Hutcheon, 1990; Bergstad *et al.*, 2001), although these studies do not consider many of the important fished areas. Regional differences in size and condition may also be reflected in the rate of atresia. Atresia has been related to low condition in other species (Ma *et al.*, 1998) and so sandeels from areas of low growth may be expected to exhibit a higher incidence of atresia.

Spawning stock biomass (SSB) models of recruitment potential implicitly assume an isometric proportionality between total egg production and SSB (Serebryakov, 1990); however, whether such assumptions are biologically relevant to the North Sea sandeel stock is questionable. Studies of gadoid species have shown that egg production for a given SSB can vary because female size, age and condition can all lead to deviations in the fecundity–mass relationship (Hodder, 1965; Hislop, 1988; Kjesbu *et al.*, 1991). Indeed, given recently documented demographic variation in the age-at-maturity in sandeels (Boulcott *et al.*, 2007), it is imperative that future models of recruitment potential consider how the size composition of the spawning stock affects the total number of eggs produced per SSB. This position is further

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underlined when one considers that recruits to spawning aggregations off the Firth of Forth, Scotland, and occurring in the east and west central North Sea are likely to originate locally (Proctor *et al.*, 1998; Munk *et al.*, 2002), and that differences in local egg production could affect the vulnerability of these stock components to mortality by predators and the fishery.

Until recently, *Ammodytes marinus* supported the largest fishery in the North Sea (ICES, 2005) and still forms an important component of the food webs in the North Atlantic (Sherman *et al.*, 1981; Daan, 1990). The aim of our study was to determine the relationship between potential fecundity, size, and age in phenotypically distinct populations. The key populations that were the subject of our study were chosen on the basis of current fishing activity and previously recorded regional differences in life history characteristics (Boulcott *et al.*, 2007).

MATERIALS AND METHODS

Sample collection

Collections of sandeel were made during several North Sea surveys conducted by the Danish Institute for Fisheries Research (now DFU-Aqua) and MSS in 1999, 2003 and 2004. In all instances sampling took place between late October and early December; a time which coincided with *A. marinus*' period of over-wintering in the sand, shortly after the summer growing season and prior to winter spawning. Collections for all three regions in 2004 took place within a 16 day window between November and December. The samples were collected from the sediment using a modified scallop dredge with a 15 cm tooth-bar. Surveys were undertaken at three key fishing areas for which considerable variation in length-at-age has been found to exist (Boulcott *et al.*, 2007): North-West Rough, Elbow Spit and the Firth of Forth (Figure 1). Surveys conducted in a fourth sample area, Fisher Bank, during 1999 and 2004 were unable to yield sufficient numbers for the purposes of meaningful comparison and were not included in subsequent analyses. Previous work has revealed that sandeels from Fisher Bank mature earlier and at a larger size than the other areas tested in this study (Boulcott *et al.*, 2007), and its omission due to poor recruitment, although unavoidable, is regrettable. Upon capture, all fish were frozen before their transferral to the laboratory. Age was estimated from sagittal otoliths by an experienced reader using the method given in ICES (1995).

Atresia

A sub-sample comprising all age-1 females (N = 110) caught in the three regions during 2004 was used to determine the prevalence and relative intensity of atresia. Here, intensity was calculated as the proportion of α-atretic oocytes to vitellogenic oocytes found to occur in a sample of approximately 250 oocytes taken from the mid-section of the ovary. Óskarsson *et al.* (2002) demonstrated that it was possible to examine the level of pre-ovulatory atresia in whole-mount preparations of herring ovary. To test whether this technique was valid in the sandeel, 20 ovary samples were examined for atresia both histologically and under the binocular microscope. Around 100 vitellogenic oocytes were examined for evidence of α-stage atresia in both histological and whole mounts. As in herring, whole-mount atretic oocytes tended to be irregular in shape, relatively smaller than the normal ones and with an uneven transparency (Figure 2a, b). Intensity of atresia estimated under the binocular microscope and the corresponding histological sections were compared using a paired *t*-test. There was no significant difference in intensity between the two methods ($t_{2,18} = -1.16$; $P = 0.22$) although the mean incidence of atresia was low, i.e. 1.7 and 1.8% for histological and whole mount, respectively.

In addition to atresia rates, condition, and eviscerated weight were also recorded for each individual. Relative condition factor (*Kn*) was calculated in the following manner: $Kn = 100\cdot(W/\hat{W})$ (Le Cren, 1951); where W is the individual wet weight (g), and $\hat{W}$ is the predicted weight for a given length based on a weight–length relationship (where $W = aL^b$) calculated from a representative sample of over 6000 North Sea sandeels. When comparing atresia rates across regions, only those data collected during the same 16 day window in 2004 were used (N = 110).

Fecundity estimation

In total, 253 mature, age-1 and 2 females were sampled from the three regions. Since *A. marinus* is a group, synchronous determinate total spawner, producing a single batch of oocytes that are spawned over a short spawning period (Gauld & Hutcheon, 1990), potential fecundity could be defined as the number of vitellogenic oocytes found in the ovary immediately prior to spawning (Kjesbu *et al.*, 1998). The fact that no fish in our study displayed evidence of

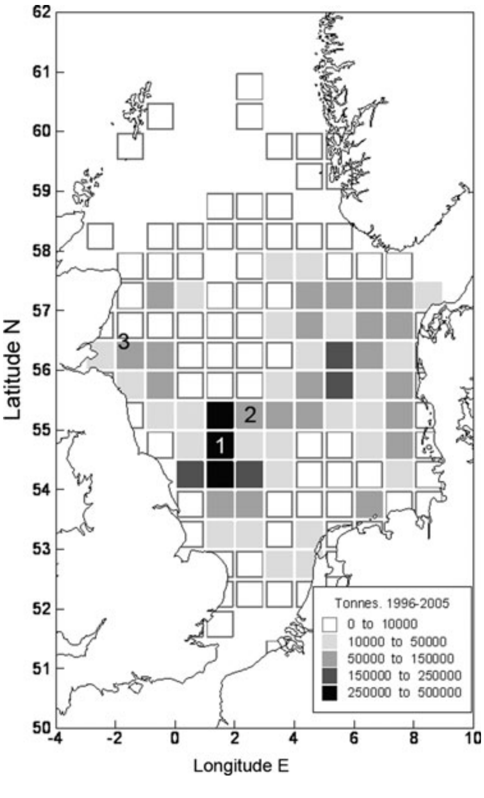

Fig. 1. The distribution of Danish sandeel landings between 1996 and 2005 (DIFRES). The three sample regions used in our study are: (1) North-West Rough; (2) Elbow Spit; and (3) the Firth of Forth.

having already spawned (i.e. no hydrated oocytes were present) permitted us to produce a reliable estimate of potential fecundity. In addition to estimates of fecundity, total length (± 1mm), whole body weight (± 0.001g), eviscerated weight (± 0.001g) and ovary weight (± 0.001g) were also measured. Using eviscerated weight (W), relative fecundity was derived in the following manner:

$$RF = PF/W$$

Estimates of potential fecundity were produced using the auto-diametric fecundity method (Thorsen & Kjesbu, 2001), with the necessary species parameters being derived from a previous gravimetric study of 300 *A. marinus* sandeels (Boulcott & Wright, 2008). The successful application of the auto-diametric method also requires that the size distribution of oocytes in the ovary is homogeneous, a fact which has been confirmed by previous studies of *A. marinus* (Gauld & Hutcheon, 1990; Bergstad *et al.*, 2001; Boulcott & Wright, 2008). Under the auto-diametric method, predicted potential fecundity was expressed as follows: $PF = M_O \times 2605.6 \times D_O^{-2.7689}$ ($250 \leq D_O \leq 1000$), where M_O is the ovarian weight (g) and D_O is the mean oocyte diameter in fresh ovary (μm). For each individual, mean oocyte diameter was estimated from a sample of 100–200 oocytes.

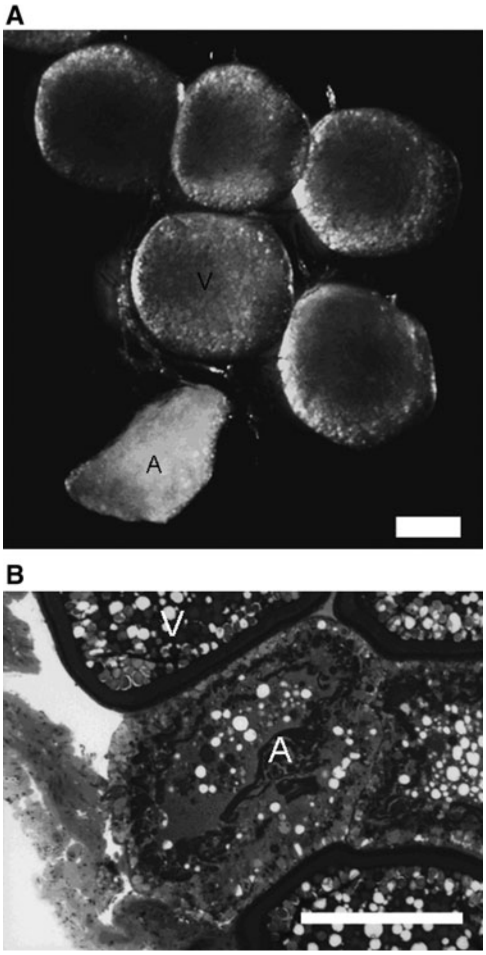

Fig. 2. Images of formalin-fixed late α- atretic (A) and vitellogenic oocytes (V) under (A) binocular microscope and (B) historesin section stained with toluidine blue from a 1 year old *Ammodytes marinus*. Scale bar = 200 μm.

It is important to correct any estimate of potential fecundity collected over different dates for pre-ovulatory atresia because of down-regulation in the period between the end of follicle proliferation and spawning (Kennedy *et al.*, 2007). As our sampling regime extended over 39 calendar days, ovaries collected from different sample years proved to be at different developmental stages, with those samples collected later in the calendar year presumably exposed to greater losses from atresia (Ma *et al.*, 1998; Kurita *et al.*, 2003). To correct PF for the number of oocytes resorbed through atresia (N_{res}), the likely down-regulation of potential fecundity due to atresia was incorporated in each statistical model by including oocyte diameter as a standardizing factor (see Thorsen *et al.*, 2006). Potential fecundity data were not adjusted by applying an estimate of turnover rate as the lack of information on atretic degeneration times for the study species would add a high level of uncertainty.

Statistical analyses

All data were tested for normality, using a Shapiro–Wilk test, and for homogeneity of variance (Sokal & Rohlf, 1995). Fecundity–length relationships across regions were fitted using a general linear model (GLM). Models initially included all explanatory variables. Non-significant terms were then removed from the model sequentially by a process of stepwise deletion. A measure of model fit was based on a pseudo-coefficient of determination (Swartzman *et al.*, 1995), which was taken to be the fraction of the total variation explained by the model: $r^2 = 1 -$ (residual variance/null variance). When examined together, the regions North-West Rough, Elbow Spit and the Firth of Forth were initially expressed within the model as a three level factor. Where stated, significance levels represent the minimal model. Atresia versus body condition relationships were also analysed using a GLM. To comply with the requirements of normality, atresia estimates were square-root transformed prior to analysis.

It was our intention in both the analysis of potential fecundity and atresia to adopt a fully balanced design which included all regions, years and ages sampled. In practice, due to exceptionally poor recruitment in certain year-classes and areas, only sufficient samples were obtained from the Firth of Forth for such an analysis. Therefore, GLMs were only applied to those datasets, according to year, age and region, which yielded sufficient numbers.

RESULTS

Atresia

A 99% prevalence rate of atresia was recorded for fish from all three regions collected within the 16 day collection period in 2004. Taking age-1 individuals collected in 2004, the only age group for which we had sufficient sample numbers in each region, the average intensity of atresia recorded from these fish was 6.4% (minimum = 0.9%, maximum = 15%). Oocyte diameter ranged from approximately 200 to 1000 μm. No effects of condition (GLM; $F_{1,\ 105} = 0.97$; $P = 0.33$), length ($F_{1,\ 105} = 0.94$; $P = 0.33$), region ($F_{2,\ 105} = 0.82$; $P = 0.44$) or oocyte diameter ($F_{1,\ 105} = 0.23$; $P = 0.63$) were found to have a bearing on atresia rates.

Table 1. Fish sample numbers collected in 1999, 2003 and 2004 split according to age and region. Mean total lengths and mean gutted weights (in parentheses) of surveyed fish are stated below sample numbers. Quoted error terms represent one standard deviation from the mean.

Year	Age	Region		
		North-West Rough	Elbow Spit	Firth of Forth
1999	1			N = 30 12.0 ± 0.9 (4.3 ± 1.3)
	2			N = 34 13.1 ± 1.4 (5.8 ± 2.0)
2003	1	N = 44 14.1 ± 0.6 (7.1 ± 0.7)		
2004	1	N = 32 12.2 ± 1.6 (4.5 ± 1.9)	N = 30 13.7 ± 1.2 (5.1 ± 1.7)	N = 48 13.6 ± 1.2 (6.1 ± 1.6)
	2			N = 35 12.7 ± 1.1 (5.1 ±1.4)

Potential fecundity

Taking the data from all three sampling years (N = 253), potential fecundity was found to vary from 913 to 10,527 for fish ranging in size from 9.9 to 16.3 cm total length. Relative fecundity was found to range from 226 to 1524 oocytes.g^{-1} of eviscerated weight. Potential fecundity was found to increase significantly with length and the relationship best described as a power function: ($PF = 0.3829 \times L^{3.59}$, $r^2 = 0.67$). Similarly, the relationship between potential fecundity and weight was best described as a power function: $PF = 632.31 \times W^{1.06}$, $r^2 = 0.64$. Sample numbers, mean total lengths and mean gutted weights for age-1 and 2 fish split according to region and year of collection are given in Table 1.

To assess the possible influence of region on potential fecundity, data for age-1 individuals caught in the three regions within a 16 day period in 2004 were analysed. An initial analysis, where each region was modelled individually by a three level factor, did not reveal a significant regional effect ($t_{2,\ 105} = -1.55$; $P = 0.12$). Combining the data from the two neighbouring sites within the Dogger Bank area, North-West Rough and Elbow Spit, allowed us to compare these similar sites with the Firth of Forth. The results from this model indicated a significant effect of region, length, mean oocyte diameter and condition on potential fecundity (Table 2). Length accounted for 85% of the variation in potential fecundity with region, mean diameter and condition accounting for 1%, 0.4% and 0.3%, respectively. Derived parameters for the fecundity–length relationship in *A. marinus* obtained from this study and from others are given in Table 3. The relationship between potential fecundity and length was highest for the combined Dogger Bank sites; indicating that fish collected from the Firth of Forth produce relatively fewer eggs per unit size than elsewhere, with this disparity increasing with body size (Figure 3). Estimating potential fecundity between these regions for a standard fish length of 12 cm yields an expected oocyte number of 3558 (North-West Rough + Elbow Spit combined), and 2735 (Firth of Forth).

Comparing data collected for age-1 and age-2 individuals from the Firth of Forth during 2004 (Table 2) revealed a significant effect of length, mean oocyte diameter and condition, but not age. Length accounted for 69% of the variation in potential fecundity, with condition contributing to 5% of the variation. When comparing data collected in 2003 and 2004 in North-West Rough for age-1 individuals, a significant effect of length, but not year or condition was found. Length was found to account for 85% of the variation in potential fecundity. Comparing data collected for age-1 and age-2 individuals from the Firth of Forth in 2004 with data collected during the 1999 survey for the same demographic group revealed a significant effect of length and condition, but not age or year. Length was again found to be the main predictor

Table 2. The output of four general linear models (GLM) fitted to each dataset containing estimates of potential fecundity. Models initially included all explanatory variables prior to the removal of all non-significant terms by a process of stepwise deletion (significant differences in bold).

Dataset	Explanatory variable	Potential fecundity			
		df	*t*	*P*	R^2
Age-1 individuals in 2004 with location split Firth of Forth versus North-West Rough + Elbow Spit (combined)	Length	1,105	4.07	**<0.001**	85%
	Region	2,105	−2.24	**0.03**	1%
	Mean oocyte diameter	1,105	−2.51	**0.01**	<1%
	Condition (K)	1,105	2.51	**0.01**	<1%
Age-1 and 2 individuals from the Firth of Forth in 2004	Length	1,79	12.9	**<0.001**	69%
	Age	2,78	0.80	0.42	–
	Mean oocyte diameter	1,79	−2.53	**0.01**	<1%
	Condition (K)	1,79	3.70	**<0.001**	5%
Age-1 individuals from North-West Rough in 2003 and 2004	Length	1,73	16.1	**<0.001**	85%
	Year	2,72	−0.87	0.39	–
	Mean oocyte diameter	1,73	−1.72	0.08	–
	Condition (K)	1,71	0.21	0.83	–
Age-1 and 2 individuals from the Firth of Forth in 1999 and 2004	Length	1,143	19.6	**< 0.001**	72%
	Age	2,142	1.62	0.11	–
	Year	2,141	0.85	0.40	–
	Mean oocyte diameter	1,143	−3.03	**<0.01**	<1%
	Condition (K)	1,143	4.77	**<0.001**	4%

Table 3. Estimated parameters of the fecundity–length relationship in *Ammodytes marinus* where: log *Fecundity* = log *a* + *b* log *Length*. Egg production numbers are fitted estimates of production at stated fish length.

Area	Year	Age-class	N	Log *a*	*b*	R^2	No. of eggs per fish			Source
							120 mm	150 mm	180 mm	
Firth of Forth	2004	1	48	−0.72	3.47	0.73	2735	5973	–	
Firth of Forth	2004	2	35	−0.69	3.47	0.56	2807	6092	–	
North-West Rough + Elbow Spit	2004	1	62	−0.14	3.35	0.91	3558	7508	–	
North-West Rough	2004	1	32	−0.06	3.32	0.90	3581	7505	–	
North-West Rough	2003	1	44	−4.13	4.79	0.61	2358	6862	–	
Firth of Forth	1999	1	30	−2.83	4.22	0.59	2114	5420	–	
Firth of Forth	1999	2	34	−1.60	3.76	0.77	2307	5339	–	
Shetland	1985	–	156	−3.75	3.51	0.85	3531	7728	14656	Gauld & Hutcheon, 1990
Moray Firth	1986	–	17	−4.54	3.87	0.96	3209	7612	15414	Gauld & Hutcheon, 1990
Fair Isle	1987	–	50	−5.03	4.07	0.73	2706	6710	14092	Gauld & Hutcheon, 1990
Southern North Sea/Faroe	1966	–	35	0.31	3.05	–	4053	8140	13988	Macer, 1966

of potential fecundity, accounting for some 72% of variation, with condition accounting for 4% of the variation.

DISCUSSION

Potential fecundity

The derived relationships for potential fecundity indicate that there are marked differences in egg production between regional spawning aggregations in the North Sea. Such disparities in egg production are further amplified by differences in population growth rates and maturation profiles across these aggregations. Most notably, lower fecundity-at-length of sandeels collected from the Firth of Forth, coupled with a reduced level of maturity-at-age in this region (Boulcott *et al.*, 2007), will result in a lower number of eggs per biomass for a given age-class compared to other regions. A previous study of the Firth of Forth (Boulcott *et al.*, 2007) indicates that sandeels from this region are slower growing than the other North Sea regions. Such a disparity may reflect differences in local productivity since the sandeel's zooplankton prey tends to only have one short spring bloom in the vicinity of the Firth of Forth compared to more protracted spring and autumn peaks in other North Sea regions (Franz *et al.*, 1991).

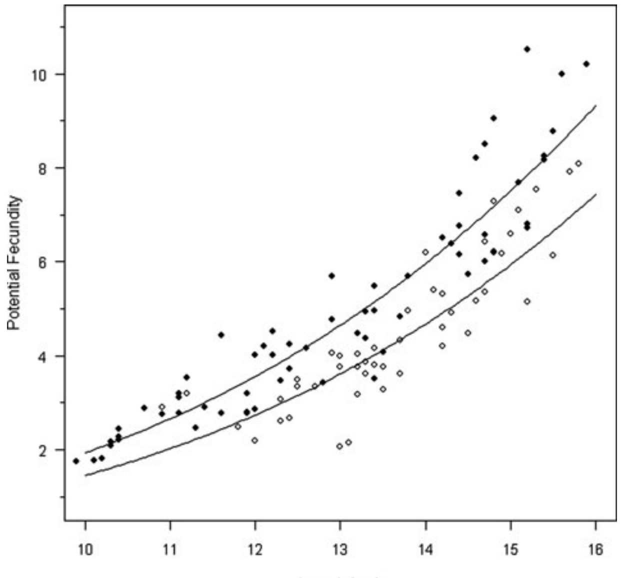

Fig. 3. The relationship between potential fecundity and length for age-1 individuals collected in 2004 from the Firth of Forth (open circles) and the combined Dogger Bank sites, North-West Rough and Elbow Spit (black circles).

As is typical, fecundity in *Ammodytes marinus* is strongly influenced by size (Lambert *et al.*, 2003). One possible explanation for this strong influence is that *A. marinus* is a capital breeder, solely reliant on stored energy reserves whilst over-wintering in the sand prior to its emergence to spawn. Although weight is often a better predictor of fecundity than length (Koops *et al.*, 2004), this was not found to be the case in this study. Sandeels decline in weight during the period of vitellogenesis so length may be a more reliable predictor of fecundity (Boulcott & Wright, 2008). Predicted by life history theory (Stearns & Crandall, 1984; Trippel, 1998) to affect potential fecundity, age was not, however, found to be a significant factor affecting fecundity in our study. Nonetheless, parameters which attempt to describe potential fecundity presuppose the occurrence of maturation, and it is the probability of maturation that is affected by age during the first three years of development (Boulcott *et al.*, 2007). Similarly, our study did not detect a significant effect of year when comparing collections over the 5 year study period. This finding was unexpected as plasticity in life history characteristics caused by both environmental perturbation and density dependent competition (Stearns, 1992) would be likely to play some part in determining fecundity. For example, the density dependent nature of fecundity has been found in herring; another single, demersal spawner found in the North Sea (Messieh *et al.*, 1985; Bailey & Altamar, 1989).

Fecundity is believed to be constrained by genes and modulated by somatic growth and/or nutrition (Wootton, 1979; Tyler & Sumpter, 1996). Hence, ovarian development occurring during a period of partial or complete fasting tends to lead to stronger relationships between condition, energy reserves, and potential fecundity than one for a period of feeding (Lambert *et al.*, 2003). Since the energy for oocyte development in the sandeel is derived from stored energy acquired during summer feeding (Boulcott & Wright, 2008), a relationship between fecundity and condition may also be expected in *A. marinus*. For example, fecundity is related to condition in a species with a similar ovarian cycle to sandeels, the Atlantic herring, *Clupea harengus* (Ma *et al.*, 1998;

Kurita *et al.*, 2003). That condition was found to be a poor predictor of potential fecundity in the models tested could relate to the fact that fish were sampled long after the decision to commit to egg production had taken place (Boulcott & Wright, 2008).

Atresia

Bromley *et al.* (2000) suggest that atresia in species with determinate fecundity could be a mechanism to fine-tune batch sizes in response to food shortage. The small effect of oocyte diameter on potential fecundity seen in this study could be explained as down-regulation of oocyte numbers arising from pre-ovulatory atresia. However, it should be noted that oocyte diameter was not found to be a significant, explanatory variable in all the models tested. Whilst down-regulation through atresia probably has only a small effect on fecundity over the sampling period, over the entire period of vitellogenesis (September–December; Boulcott & Wright, 2008) such intensity may have a considerable effect. Our estimates of the intensity of atresia are comparable with those found in herring (Kurita *et al.*, 2003). Although herring experience a similar restive over-wintering period to sandeels in some cases (Kurita *et al.*, 2003), the similarity in down-regulation between the two species is unexpected given that herring also undergo energetically demanding migration events. Here, higher rates of down-regulation might act as a buffer against unpredictable and potentially large energetic demands. Nevertheless, few studies of atresia and condition based on data collected from the field exist (Lambert *et al.*, 2003), and where they do the results are often conflicting, suggesting that the predicted relationship may be not applicable to all stages of development (Kurita *et al.*, 2003) or all species.

Whatever the cause, the low intensity of atresia in sandeels suggests that once committed, egg production does not reduce differentially in response to other energetic constraints such as somatic maintenance or unfavourable temperatures during the first reproductive season. Our study also indicates that regional egg production is not affected by regional differences in the prevalence and intensity of atresia.

Relevance to management

The results of our study, when taken in combination with the disparities in maturity–size relationships found in these regions (Boulcott *et al.*, 2007), are relevant to attempts to replace spawning stock biomass with measures of stock reproductive potential (SRP) (Trippel, 1999), that more closely reflect a stock's ability to produce viable eggs. In order to provide estimates of stock egg production, relative egg production estimates need to be combined with accurate information on the biomass-at-age for each region. Attempts have also been made to consider the contribution of regional sandeel stock components to produce spatially explicit models of models of sandeel abundance (Christensen *et al.*, 2008), however, further data, such as the information provided in this study, are required before such models can accurately model regional variation across the North Sea stock. The value of such approaches is highlighted in the Firth of Forth in circumstances where age-1 fish dominate the stock. Here, only a proportion of the dominant age-class will mature with each being relatively less productive than other sandeel aggregations in the North Sea. Given such regional differences in productivity, sandeels in the Firth of Forth region may be more susceptible to growth over-fishing than other regions. Whilst the North Sea is currently managed as a single stock, concern over the local fishing impact off the north-east UK coast on sandeel availability for seabirds, together with evidence for reproductive isolation (Proctor *et al.*, 1998; Munk *et al.*, 2001), led to the precautionary closure of this region. Our Firth of Forth data lend weight to the argument for a regional management plan that protects sufficient sandeel resources for local predator populations, such as seabirds (Monaghan, 1992; Wright, 1996; Fredriksen *et al.*, 2005). In the context of stock reproductive potential, our conclusions support the call for the adoption of more realistic proxies of egg production than current stock-level spawning stock biomass estimates that often use knife-edge maturity relationships (Trippel, 1999).

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REFERENCES

Bailey R.S. and Altamar S.M. (1989) Variation in fecundity and egg weight of herring (*Clupea harengus* L.). Part 2. Implications for hypotheses on the stability of marine populations. *ICES Journal of Marine Science* 45, 125–130.

Bergstad O.A., Høines Å.S. and 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 un-fished coastal waters off Norway. *Aquatic Living Resources* 14, 293–301.

Boulcott P., Wright P.J., Gibb F.M., Jensen H. and Gibb I.M. (2007) Regional variation in maturation of sandeels in the North Sea. *ICES Journal of Marine Science* 64, 369–376.

Boulcott P. and Wright P.J. (2008) Critical timing for reproductive allocation in a capital breeder: evidence from sandeels. *Aquatic Biology* 3, 31–40.

Bromley P.J., Ravier C. and Witthames P.R. (2000) The influence of feeding regime on sexual maturation, fecundity and atresia in first-time spawning turbot. *Journal of Fish Biology* 56, 264–278.

Christensen A., Mosegaard H. and Jensen H. (2008) Spatially resolved fish population analysis for designing MPAs: influence on inside and neighbouring habitats. *ICES Journal of Marine Science* 66, 56–63.

Daan N. (1990) *Data base report of the stomach sampling project 1981*. International Council for the Exploration of the Sea (Co-operative Research Report No. 164).

Frank K.T. and Brickman D. (2000) Allele effects and compensatory population dynamics within a stock complex. *Canadian Journal of Fisheries and Aquatic Sciences* 57, 513–517.

Franz H.G., Colebrook J.M., Gamble J.C. and Krause M. (1991) The zooplankton of the North Sea. *Netherlands Journal of Sea Research* 28, 1–52.

Frederiksen M., Wright P.J., Harris M.P., Mavor R.A., Heubeck M. and Wanless S. (2005) Regional patterns of kittiwake *Rissa tridactyla* breeding success are related to variability in sandeel recruitment. *Marine Ecology Progress Series* 300, 201–211.

Gauld J.A. and Hutcheon J.R. (1990) Spawning and fecundity in the lesser sandeel (*Ammodytes marinus*, Raitt) tagged in the north-western North Sea. *Journal of Fish Biology* 36, 611–613.

Hilborn R., Quinn T.P., Schindler D.E. and Rogers D.E. (2003) Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences of the United States of America—Biological Sciences* 100, 6564–6568.

Hislop J.R.G. (1988) The influence of maternal length and age on the size and weight of eggs and the relative fecundity of haddock, *Melanogrammus aeglefinus* in British waters. *Journal of Fish Biology* 32, 923–930.

Hodder V.M. (1965) The possible effects of temperature on the fecundity of Grand Bank haddock. *International Commission on Northwest Atlantic Fisheries, Special Publication* 6, 515–522.

ICES (2005) *Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak*. International Council for the Exploration of the Sea (CM Papers and Reports) CM 2006/ACFM:09. 981 pp.

Kennedy J., Witthames P.R. and Nash R.D.M. (2007) The concept of fecundity regulation in plaice (*Pleuronectes platessa*) tested on three Irish Sea spawning populations. *Canadian Journal of Fisheries and Aquatic Sciences* 64, 587–601.

Kjesbu O.S., Klungsoyr J., Kryvi H., Witthames P.R. and Greer-Walker M. (1991) Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. *Canadian Journal of Fisheries and Aquatic Sciences* 48, 2333–2343.

Kjesbu O.S., Witthames P.R., Solemdal P. and Walker M.G. (1998) Temporal variations in the fecundity of Arcto-Norwegian cod (*Gadus morhua*) in response to natural changes in food and temperature. *Journal of Sea Research* 40, 303–321.

Koops M.A., Hutchings J.A. and McIntyre T.M. (2004) Testing hypotheses about fecundity, body size and maternal condition in fishes. *Fish and Fisheries* 5, 120–130.

Kurita Y., Meier S. and Kjesbu O.S. (2003) Oocyte growth and fecundity regulation by atresia of Atlantic herring (*Clupea harengus*) in relation to body condition throughout maturation cycle. *Journal of Sea Research* 49, 203–219.

Lambert Y., Yaragina N.A., Kraus G., Marteinsdottir G. and Wright P.J. (2003) Correlation between reproductive characteristics and environmental and biological indices as alternative methods of estimating egg and larval production. *Journal of Northwest Atlantic Fishery Science* 33, 115–159.

Le Cren E.D. (1951) The length–weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca flaviatilis*). *Journal of Animal Ecology* 20, 201–219.

McQuinn I.H. (1997) Metapopulations and the Atlantic herring. *Reviews in Fish Biology and Fisheries* 7, 297–329.

Ma Y., Kjesbu O.S. and Jørgensen T. (1998) Effects of ration on the maturation and fecundity in captive Atlantic herring (*Clupea harengus*). *Canadian Journal of Fisheries and Aquatic Sciences* 55, 900–908.

Macer C.T. (1966) Sand eels (Ammodytidae) in the south-western North Sea; their biology and fishery. *Fisheries Investigations, London* Series 2, 24, 1–55.

Marshall C.T., Kjesbu O.S., Yaragina N.A., Solemdal P. and Ulltang Ø. (1998) Is spawner biomass a sensitive measure of the reproductive and recruitment potential of Northeast Arctic cod? *Canadian Journal of Fisheries and Aquatic Sciences* 55, 1766–1783.

Messieh S., Pottle R., MacPherson P. and Hurlbut T. (1985) Spawning and exploitation of Atlantic herring (*Clupea harengus*) at Escuminac in the southwestern Gulf of St Lawrence. *Journal of Northwest Atlantic Fishery Science* 6, 125–133.

Monaghan P. (1992) Seabirds and sandeels: the conflict between exploitation and conservation in the northern North Sea. *Biodiversity and Conservation* 1, 98–111.

Munk P., Wright P.J. and Pihl N.J. (2002) Distribution of the early larval stages of cod, plaice and lesser sandeel across haline fronts in the North Sea. *Estuarine, Coastal and Shelf Science* 55, 139–149.

Óskarsson G.J., Kjesbu O.S. and Slotte A. (2002) Predictions of realized fecundity and spawning time in Norwegian spring-spawning herring (*Clupea harengus*). *Journal of Sea Research* 48, 59–79.

Pedersen S.A., Lewy P. and Wright P.J. (1999) Assessments of the lesser sandeel (*Ammodytes marinus*) in the North Sea based on revised stock divisions. *Fisheries Research* 41, 221–241.

Proctor R., Wright P.J. and Everitt A. (1998) Modelling the transport of larval sandeels on the north-west European shelf. *Fisheries Oceanography* 7, 347–354.

Serebryakov V.P. (1990) Population fecundity and reproductive capacity of some food fishes in relation to year class strength fluctuations. *ICES Journal of Marine Science* 47, 267–272.

Sherman K., Jones C., Sullivan L., Smith W., Berrien P. and Ejsymont L. (1981) Congruent shifts in sand eel abundance in western and eastern North-Atlantic ecosystems. *Nature* 291, 486–489.

Smedbol R.K. and Stephenson R. (2001) The importance of managing within-species diversity in cod and herring fisheriesof the north-western Atlantic. *Journal of Fish Biology* 59 (Supplement A), 109–128.

Sokal R.R. and Rohlf F.J. (1995) *Biometry*. New York: Freeman.

Stearns S.C. (1992) *The evolution of life histories*. Oxford: Oxford University Press, pp. 123–179.

Stearns S.C. and Crandall R.E. (1984) Plasticity for age and size at sexual maturity: a life-history response to unavoidable stress. In Potts G. and Wootton R.J. (eds) *Fish reproduction*. London: Academic Press, pp. 13–33.

Stephenson R.L. (1999) Stock complexity in fisheries management: a perspective of emerging issues related to populations subunits. *Fisheries Research* 43, 247–249.

Swartzman G., Silverman E. and Williamson N. (1995) Relating trends in walleye pollock (*Theragra chalcogramma*) abundance in the Bering Sea to environmental factors. *Canadian Journal of Fisheries and Aquatic Sciences* 52, 369–380.

Thorsen A. and Kjesbu O.S. (2001) A rapid method for estimation of oocyte size and potential fecundity in Atlantic cod using a computer-aided particle analysis system. *Journal of Sea Research* 46, 295–308.

Thorsen A., Marshall C.T. and Kjesbu O.S. (2006) Comparison of various potential fecundity models for north-east arctic cod *Gadus morhua*, L. Using oocyte diameter as a standardizing factor. *Journal of Fish Biology* 69, 1709–1730.

Trippel E.A. (1998) Egg size and viability and seasonal offspring production of young Atlantic cod. *Transactions of the American Fisheries Society* 127, 339–359.

Trippel E.A. (1999) Estimation of stock reproductive potential: history and challenges for Canadian Atlantic gadoid stock assessments. *Journal of Northwest Atlantic Fishery Science* 25, 61–81.

Tyler C.R. and Sumpter J.P. (1996) Oocyte growth and development in teleosts. *Reviews in Fish Biology and Fisheries* 6, 287–318.

Wootton R.J. (1979) Energy costs of egg production and environmental determinants of fecundity in teleost fishes. *Symposium of the Zoological Society of London* 44, 133–159.

and

Wright P.J. (1996) Is there a conflict between sandeel fisheries and seabirds? A case study at Shetland. In Greenstreet S.P.R. and Tasker M.L. (eds) *Aquatic predators and their prey*. Oxford: Fishing News Books and Blackwell Science, pp. 154–165.

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