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Spawning time, age and size at maturity, and fecundity of sandeel, *Ammodytes marinus*, in the north-eastern North Sea and in unfished coastal waters off Norway

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Abstract − We studied the reproductive biology of the lesser sandeel, *Ammodytes marinus*, on the fishing grounds of the east central North Sea and on an unfished ground off the coast of southwest Norway. As in other parts of the North Sea, gonad growth appeared to start in September and spawning occurred in December-January. Based on data from the spawning period, maturity ogives by length and age were derived. The length and age at 50 % maturity was 14 cm and 3.2 years respectively in both study areas. The age estimate is 1 year higher than that found previously in the southern North Sea and adopted for the ICES-assessments of the North Sea spawning stock. Estimates of fecundity appeared higher in the North Sea than in coastal waters, at least for large fish. The coastal water estimates also seemed low compared with fecundity at length relationships previously published from Shetland, Fair Isle, and Dogger bank. The sex ratio seldom deviated substantially from the 1:1 ratio, but in summer there appeared to be a surplus of females. Due to spatial differences in age-structure, the proportion of adults was generally much lower on the fishing grounds of the North Sea proper than on the unfished coastal ground. In the middle of the spawning period, however, aggregations of adults occurred on the North Sea grounds. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

exploitation effects / gonosomatic index / maturity ogive / sex ratio / spawning period / Ammodytidae

Résumé − Période de ponte, âge, taille à maturité sexuelle et fécondité du lançon, *Ammodytes marinus*, du nord-est de la mer du Nord et d'une zone non exploitée des côtes norvégiennes. Nous étudions la biologie de la reproduction du lançon, *Ammodytes marinus*, d'une zone de pêche de l'est de la mer du Nord et d'une autre zone non-exploitée au sud-ouest des côtes norvégiennes. Comme dans les autres parties de la mer du Nord, la croissance des gonades commence en septembre et la ponte se déroule de décembre à janvier. Basés sur des données recueillies lors de la période de ponte, la maturité est estimée en fonction de la taille et de l'âge. La taille et l'âge respectif de 50 % des poissons sont 14 cm et 3,2 ans pour les deux zones étudiées. L'estimation de l'âge est supérieure d'un an à celle trouvée précédemment dans le sud de la mer du Nord, et adoptée par le CIEM pour les estimations de stocks de ponte en mer du Nord. Les estimations de la fécondité semblent plus élevées en mer du Nord que dans les eaux côtières pour les poissons les plus gros mais semblent faibles comparées avec les fécondités précédemment calculées en fonction de la taille pour les îles Shetland, Fair, et Dogger bank. Le sexe-ratio dévie rarement de 1:1, mais un surplus de femelles semble apparaître en été. En raison des différences spatiales dans les répartitions en âge, les proportions d'adultes sont généralement beaucoup plus faibles sur les zones de pêche de mer du Nord que dans les zones côtières non exploitées. Cependant, au milieu de la période de ponte, des agrégations d'adultes sont notées sur les zones de pêche de mer du Nord. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

effets de la pêche / index gonosomatique / maturité sexuelle / sexe-ratio / période de ponte / Ammodytidae

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1. INTRODUCTION

Since 1953 (Macer, 1966; Lahn-Johannessen, 1970; Popp Madsen, 1994), directed bottom trawl fisheries for North Sea sandeel (Ammodytidae) have expanded in range and volume to the present level where annual landings vary in the range 0.6–1.1 million tonnes. In recent decades, almost a third of the total fish landings from the North Sea has been sandeel, of which 95 % or more is the lesser sandeel, *Ammodytes marinus* Raitt, 1934, the dominant sandeel species in offshore waters.

The sandeel stock in the North Sea is assessed annually and abundance estimates suggest that current exploitation levels may be sustainable (ICES 1999, 2000). The mortality due to natural causes apparently remains as high or higher than the mortality caused by fishing (ICES, 2000). However, the enhanced adult mortality due to fishing may affect structure and life history traits in the more heavily exploited areas. In a previous paper (Bergstad and Høines, 2001), we analysed age and size structure of *Ammodytes marinus* in several traditional sandeel grounds in the North Sea and compared them with synoptic data from an unfished coastal ground off south-western Norway. Differences that would be expected between exploited and unexploited populations were found, i.e. comparatively narrow age and size distributions in the fished vs. unfished areas, suggesting that the fishery has a structuring influence.

In this paper, based on sub-sets of the data used in the analyses of population structure, we analyse information on age and size at maturity and fecundity from sandeel areas of the North Sea. These life history traits might also be expected to be affected by changes in adult mortality rate due to fishing (e.g. Rochet, 1998; Chen and Mello, 1999). However, given the relatively short age and size range of the sandeel, the scope for change would seem limited.

Our overall null-hypothesis was that the age and size at maturity and fecundity of the lesser sandeel was the same in unexploited and exploited areas. Macer (1966) showed that *Ammodytes marinus* in the southern North Sea in 1960–1962 spawned in mid-winter, and that most spawned for the first time in the winter that they became 2-group (i.e. after two growth seasons). In a sample from the Dogger bank, in January, he found that 5 % of the 1-group, 80.5 % of the 2-group, and 98.9 % of the older fish were mature. This is similar to sandeels in the Irish Sea (Cameron, 1958) and at Shetland and in the Moray Firth of Scotland (Gauld and Hutcheon, 1990), but evidently 1 year early compared with sandeel near Novaya Zemlya in the Barents Sea (Kirillov (1936) cited by Reay, 1970).

2. MATERIALS AND METHODS

We utilised data from commercial landings and from fishery-independent samples collected by research vessels. The most substantial fishery-independent sampling was carried out on the traditional sandeel grounds in the south-western corner of the Norwegian EEZ, i.e. English Klondyke, East bank, Inner and Outer Shoal etc, hereafter referred to as the 'East Central Grounds' (ECG) (*figure 1*). For comparison, we also collected data from unfished sandeel grounds, and since truly unexploited areas are small and difficult to locate in the North Sea proper, we sampled sandeel on a coastal bank off south-western Norway where we were certain that no trawling occurred. The ground selected has a depth range (40–70 m), sediments and environmental characteristics similar to those found in adjacent parts of the North Sea, and the fish community is also similar (Høines et al. 1993, 1998).

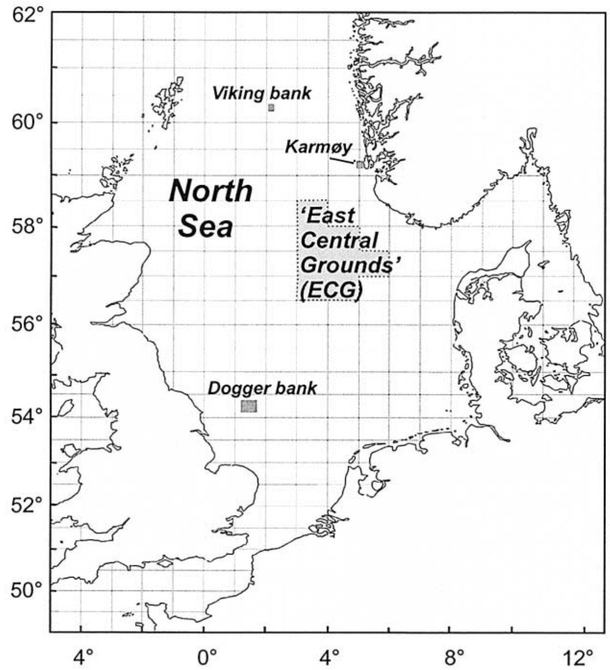

Figure 1. Areas of the North Sea where the sandeel studies were conducted. The grid of rectangles represents the system of rectangles used by ICES.

2.1. Sampling by research vessels

In the period July 1997–April 1999, samples were collected in the sandeel grounds of the North Sea and the coastal ground off SW Norway (Bergstad and Høines, 2001). In this analysis, only data from the ECG and the coastal ground off Karmøy in SW Norway was used (*figure 1*). Limited datasets from the Viking bank from October 1998 and March 1999 were also included.

In all sampling areas, sandeels were captured by bottom trawl, a modified scallop dredge, and a 0.2-m^2 vanVeen grab. Details on gears and sampling protocol are given elsewhere (Bergstad and Høines, 2001).

Benthic samplers were used when sandeel were buried in the sand, i.e. at night and/or at most times in winter, and this was particularly important when collecting maturing sandeel for the studies of maturity, spawning and fecundity.

Ammodytes marinus always dominated in catches, and random samples of this species were frozen immediately and brought to the laboratory for further study. In the laboratory, the random sample, or a subsample of around 100 specimens, was measured (nearest millimeter below) and a length frequency distribution constructed. During measuring, the sample was split into 5-cm length strata. From each length stratum, all or at least twenty specimens were selected for recording individual data: wet weight (ungutted and gutted, nearest 0.01 g), sex, wet weight of gonad (mg), and weight of liver (mg). Using the 6-point scale suggested by Macer (1966), the stage of maturity was determined by visual inspection of the gonads. Otoliths were extracted, cleaned in water, dried, and mounted in clear plastic resin on black grooved plates. Age was determined according to Macer (1966) and Anon. (1995), assuming 1 January as a common birth date. The age-structure in the two sampling areas was analysed in greater detail in Bergstad and Høines (2001). Age-length keys used in that paper were compared with those derived from Danish and Norwegian age readings and used in the ICES assessments (ICES, 2000), and there was good correspondence. The 1996 year class was exceptionally abundant in this period and this year class was prominent in both the ICES data and in our samples from the North Sea. This suggested that our age determination was in line with that adopted by others.

2.2. Sampling the commercial catches

The Norwegian Directorate of Fisheries inspectors in the landing ports collected landings samples, i.e. both length distributions and biological samples. Randomly selected vessels are sampled during the actual landing process at the factory. Samples from the ECG were available from most of the months fishing was conducted (March–October) in the years 1997–1999. The biological samples from the landings consisted of about 200 frozen specimens from each landing. These samples were processed as described for the research vessel samples. Norwegian sandeel trawlers use bottom trawls.

2.3. Analyses

As also noted by Macer (1966), it proved difficult to obtain consistently reliable data on maturity based on visual examination of the gonads, especially during the recovery and resting period of the reproductive cycle when the gonads are small and even determination of sex may be difficult in small specimens. All analyses of maturity at age and size were therefore based on data from the autumn and winter, i.e. the months November–January. Preliminary analyses showed that in the summer (May–August), the gonosomatic index (GSI), expressed as the gonad weight as percentage of the gutted weight of the specimen, was very low in all age-groups and both sampling areas. This was also the case in March-April. In the period March–August, only four individuals out of the 1 315 examined had a GSI > 2.5 %. To determine whether an individual sandeel was mature in November–January, we used either the GSI or Macer's (1966) 6-point scale. Specimens that then had GSI > 2.5 were considered to be mature or maturing, also specimens in stages 2–5 for which a GSI was not recorded, and finally fish in stage 5 (spent) with GSI < 2.5. The reason for using the combination of these two methods was that not all gonads from the smaller size-classes were weighed because the precision was considered too low, and also that fish in stage 5 would have a very low GSI. An underlying assumption was that all the stage 1 specimens recorded in November–January were juveniles, and i.e. that no 'resting' adults occurred during that period. Fish in stages 2–5 were assumed to mature in the current season. No stage 5 specimens were recorded before January, and distinguishing between stages 1 and 5 was not problematic.

2.4. Fecundity determination

Subsamples to be used for determination of fecundity were collected on the ECG and the coastal ground in December 1998. The samples of ungutted specimens were preserved in 3.6 % phosphate-buffered formaldehyde. The ovaries of all females were extracted and weighed to the nearest milligram after excess moisture had been removed with absorbent paper.

To study whether there was variation in number of developing oocytes in different sections of the ovary, two parallel subsamples from three locations on the ovary of five females were taken (anterior and posterior parts of the right ovary lobe and middle part of the left lobe). In addition, four parallel subsamples were taken from the middle part of the right lobe. Previous studies (e.g. Kjesbu et al., 1998; Ma et al., 1998) have used this location for fecundity determination. A subsample weight of approximately 100 and 150 mg for vitellogenic and ovulated oocytes respectively was found appropriate. Each subsample was counted on a partitioned Petri dish under a binocular microscope, and oocyte diameters measured by computerised image analyses (fifty oocytes per subsample). Results showed no major variation between counts from the four locations on the ovary and between parallel subsamples for each fish (coefficient of variation < 5 %). The size distribution of the oocytes was unimodal. In the final study of fecundity, two subsamples from the middle part of the right ovary lobe were used.

Potential fecundity (F_p), i.e. the number of vitellogenic oocytes in prespawning fish, was calculated by the gravimetric method (Bagenal, 1978):

$$F_p = (W_o / W_s) \times N_s$$

where W_o denotes the weight of the preserved ovary, W_s is the weight of the fixed subsample used for counting, and N_s the number of vitellogenic oocytes in the subsample.

3. RESULTS

3.1. Reproductive cycle and spawning time

The seasonal development patterns of the gonosomatic index (GSI) for the different age-groups of sandeel from the east central grounds (ECG, *figure 1*) and the coastal sampling area are shown in *figure 2*. In the age-groups where a development occurred, the gonad growth appeared to start in September-October. Closer inspection of the October samples showed that no specimens in stages 3-4 were recorded, and that those with elevated GSI were still in stage 2. High GSIs were frequent in late November and December. No spent specimens were recorded in November and December, but in early January some rather old fish had low GSI, and these specimens were spent adults (stage 5). These data suggested that in both sampling areas spawning occurred in mid-winter, probably primarily in December and January.

3.2. Maturity at length and age

In order to study maturity by age and length, we restricted the analysis to samples from the period immediately prior to and during spawning, i.e. late November–early January. Scatter plots of the fractions mature by length and age for the two areas are shown in *figures 3* and *4*. Also shown are maturity ogives fitted by logistic regression. Among the youngest mature fish, i.e. those being 2-group in January, the ratio of females to males was about 1:4. This indicated that males tended to mature slightly earlier than females. However, the difference was considered so small that in subsequent analyses both sexes were pooled. In the maturity at age plot, juveniles with uncertain sex determination were also included.

The smallest mature sandeel were 11.5–12.0 cm TL in both areas, and all fish bigger than about 17 cm were mature. The length at 50 % maturity estimated from the logistic model fitted to the data was 14.3 cm in the North Sea and 13.6 cm in the coastal ground. Although statistically significant ($P < 0.01$), this difference may not be biologically significant. The curve and estimate from the coastal ground may be biased downwards due to a couple of points that appeared as outliers.

The sandeel appeared to spawn for the first time as 2–5 group (taking into account the conventional change in age on 1 January), and there were no differences between areas. No mature 1-group fish were observed in any of the areas. In the coastal area, only a single mature 2-group fish was observed out of the eighteen specimens examined. The estimate of the age at 50 % maturity from the logistic model fitted was, however, 3.2 years in both areas.

Data from several year-classes were pooled, and since we had data for two spawning seasons only, we were unable to construct complete maturity ogives for individual year-classes (*figure 4*). For the 1996 and 1997 year-classes on the ECG, however, we could estimate the fraction that matured as 2-group in the winters of 1998 and 1999, respectively. This fraction was 0.32 ($n = 135$) for the 1996 year-class, and 0.07 ($n = 333$) for the 1997 year-class.

Size frequency distributions from the spawning period (November–January) of the juvenile and adult 2-group fish of the 1996 and 1997 year-classes are shown in *figure 5* (also incorporating fish that were 1-group in November-December and became 2-group the following January). Only the samples from the ECG were included in these distributions. The adults in this plot represent 2-year-old first-time spawners, and these appeared to be among the bigger fish of the year-classes in both spawning seasons. There appeared however to be little difference between the length distributions of the 2-year-old adults of the two consecutive year-classes.

3.3. Sex ratio

Observations of age-specific proportions of females in different months of the year were analysed. Data for 0- and 1-groups were excluded because the determination of sex was often uncertain for small juveniles. In the coastal area, where the age-range was best represented, no significant deviations from 1:1 ratio of females to males were observed in any time period except in March when there appeared to be somewhat more females than males in all age-groups (Wilcoxon signed ranks test, $P = 0.04$). Some extreme values may be attributed to small sample sizes, however. In the North Sea proper, the age-range was very limited, hence age-groups 4–6 were pooled. There were no strong deviations from a 1:1 ratio, but the May–August (essentially May-June) values seemed somewhat higher than those from the remainder of the year.

To analyse geographical variation, samples from individual ICES-square, i.e. a specific limited geographical area, were compared. Only samples representing more than twenty specimens were included and all age-groups were pooled. When the data from all time periods were compared (24 observed pairs of male-female numbers), there was no significant deviation from a 1:1 ratio (Wilcoxon signed ranks, $P = 0.07$). The observed proportion of females ranged from 0.40 to 0.67, and the mean proportion was 0.54. However, when only the ten pairs from April–June were considered, there was a significant deviation from equality ($P = 0.006$), and consistently elevated

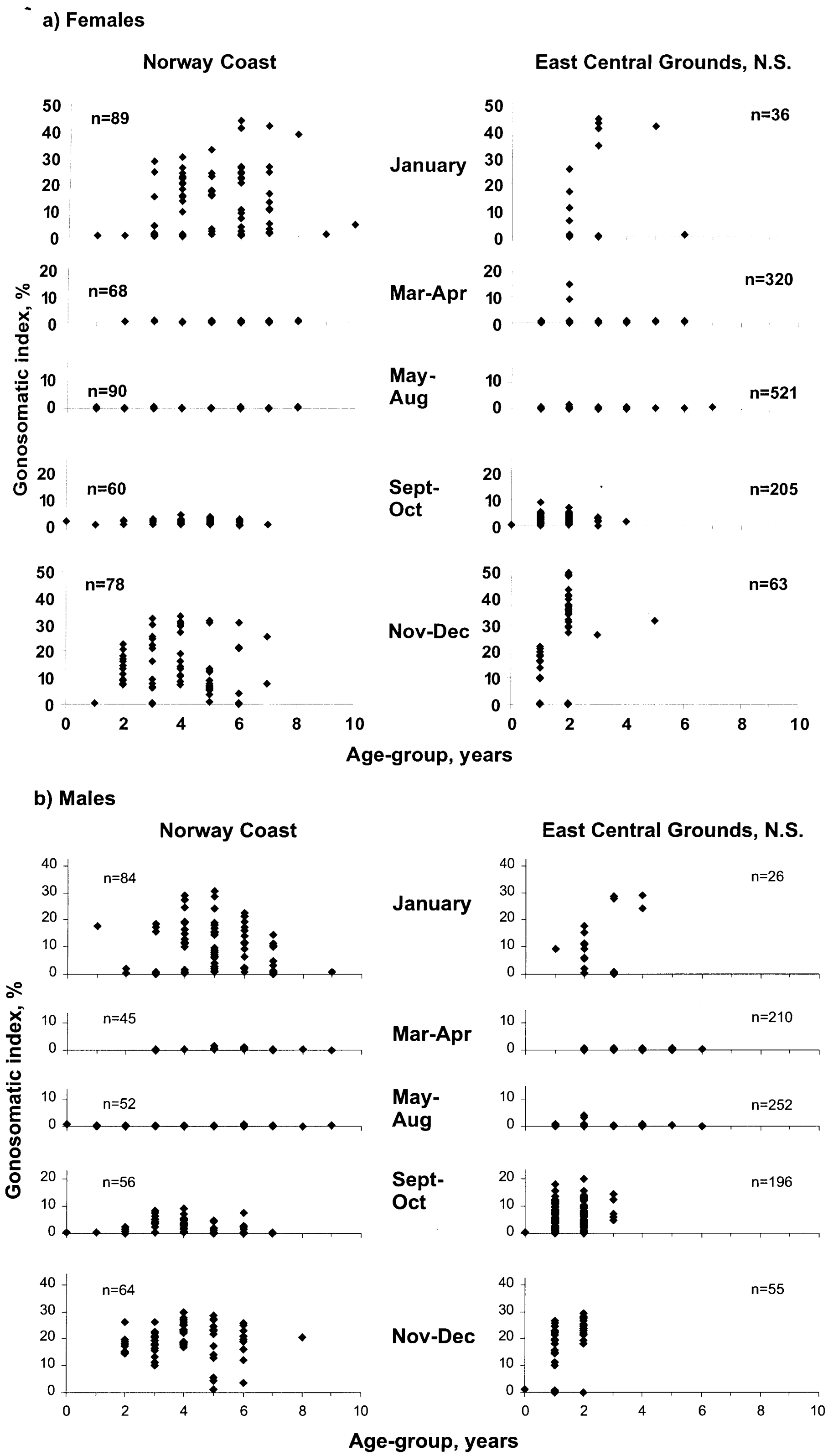

Figure 2. The gonosomatic index of individual (**a**) female, and (**b**) male sandeel, from the two sampling areas by time of year. n: number of specimens.

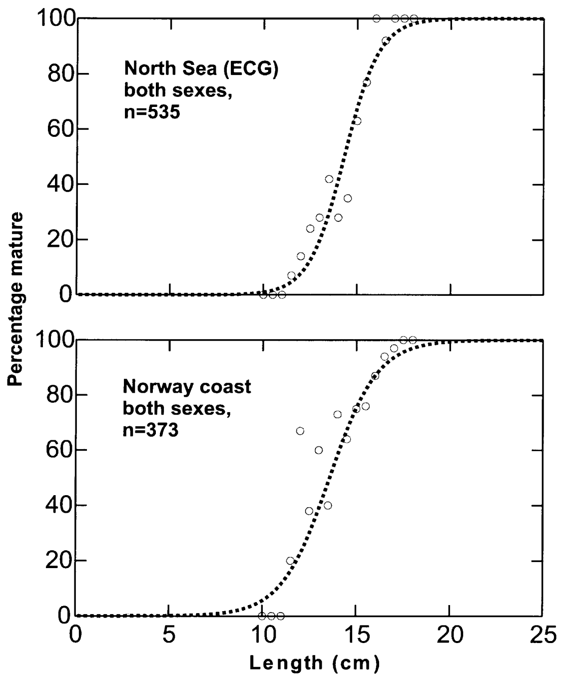

Figure 3. Proportion of mature sandeel in relation to total body length, and maturity ogive fitted by probit analysis. n: numbers of specimens staged. Only data from December-January were used in this analysis, and sexes were pooled.

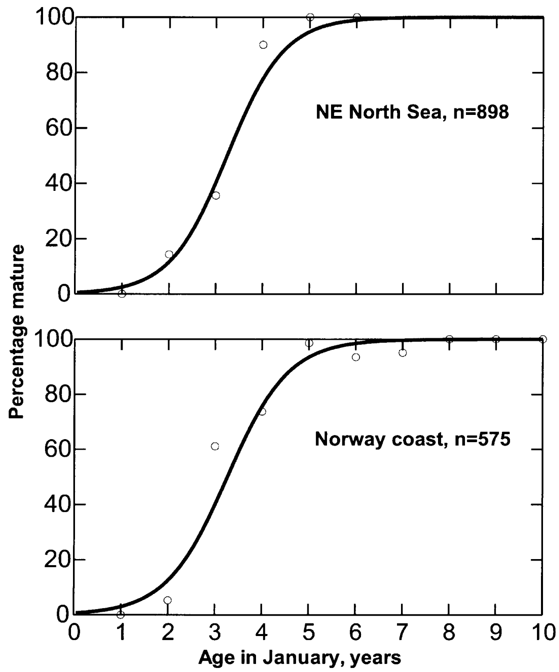

Figure 4. Proportion of mature sandeel in relation to age (past 1 January), and the associated maturity ogives. n: number of specimens staged. Only data from December-January were used, and sexes were pooled.

proportions of females. In the coastal area, the mean proportion of females across age-groups was 0.52 (range 0.46–0.59, number of pairs = 6).

3.4. Fecundity

Estimates of fecundity for the 27 and seven specimens from ECG and the Norway coast, respectively, were plotted against fish length in *figure 6*. Also included for comparison are lines corresponding to published power functions based on datasets of 35, 156, and 50 specimens from the southern North Sea/the Faroes (Macer, 1966), the Shetlands and Fair Isle (Gauld and Hutcheon, 1990), respectively. Statistical comparisons cannot readily be made between any of these results, and the datasets from our study areas became smaller than planned. The results must therefore be interpreted with caution. However, it is noteworthy that all the points from the Norway coast were found below, and a high proportion of the ECG points above the curves published previously.

The mean oocyte diameter was 841 μm (SE = 14.1, n = 29). There were no differences between areas and no apparent variation with body weight or length.

3.5. Proportion of adults at spawning time

To analyse the spatial and temporal variation in the fraction of the population that was mature prior to or at

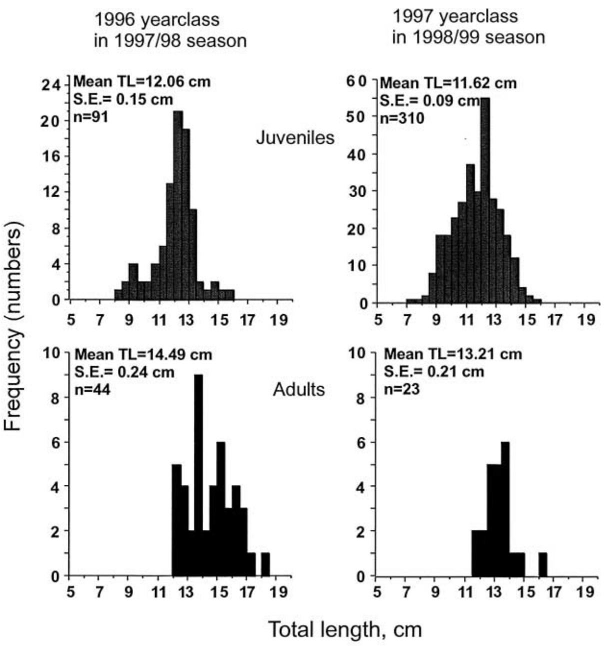

Figure 5. Size distributions of mature and immature sandeel from the 'East Central Grounds'. Data for the two year classes 1996 and 1997, n: sample size, S.E.: standard error.

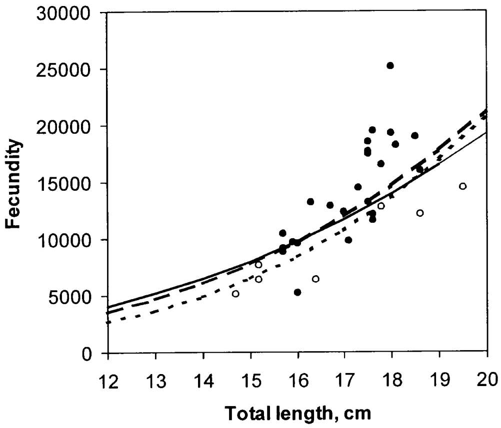

Figure 6. Estimates of the absolute fecundity of individual sandeels in relation to total length. The lines represent published fecundity-length relationships included for comparison. Dots: ECG (n = 27); empty circles: Norway coast (n = 7); line: Macer, 1966; hatched lines: Shetland and Fair Isle data from Gauld and Hutcheon (1990).

spawning time, we applied the maturity ogives to the age-distributions presented in a previous paper (Bergstad and Høines, 2001). Choosing a somewhat conservative approach, we assumed that 10 % of the age-group 1 (becoming age-group 2 in January) and all subsequent age-groups were adults. We only included observations from the September–January period and compared data for the spawning seasons 1997/98 and 1998/99 (*figure 7*). Because trawl and benthic samples were not pooled, there were sometimes several estimates for the same area and month.

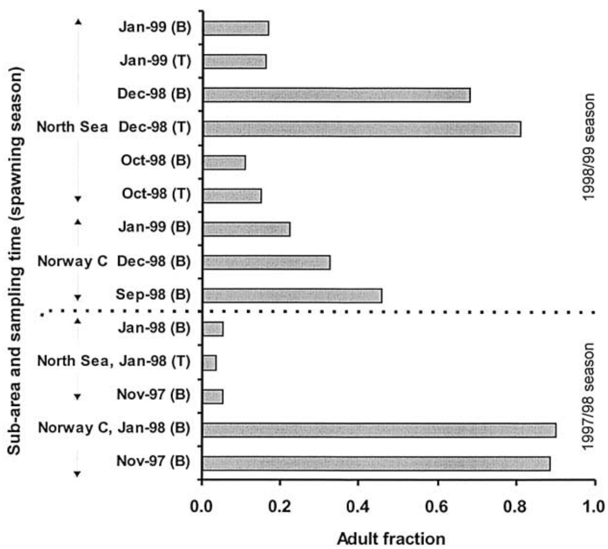

Figure 7. Estimates of the proportion of adults in the sandeel catches from the two sampling areas, in the spawning seasons 1997/98 and 1998/99. Gear type is indicated in brackets: B: benthic samplers; T: bottom trawl.

Within the 1997/98 spawning season, there was reasonable consistency between the estimates for the same sub-area. The adult fraction was around 5 % on the ECG, compared with the approximately 90 % on the coastal ground. A similar inter-site difference, although not as pronounced, was found in September-October 1998 and January 1999, i.e. in the 1998/99 spawning season. In that spawning season, however, the Dec 1998 samples from the ECG showed very high adult fractions, inconsistent with the observations immediately before and after. During the short cruise conducted in December, there was only opportunity to sample a single sub-area of the ECG. The samples obtained may thus only be representative for a particular aggregation, evidently with an elevated proportion of adults.

4. DISCUSSION

The seasonal pattern of the gonosomatic index showed that sandeel in the two sampling areas underwent gonad development and spawned in the same period of the year. This was expected since the distance between the areas is limited and the seasonality in environmental conditions probably very similar. The results are also similar to those reported from the southern North Sea (Macer, 1966; Reay, 1970) and Shetland (Gauld and Hutcheon, 1990). No spent specimens were found in November-December, but many in January, suggesting that the spawning activity was strongest in January. At spawning time, there were no indications of strong deviations from a 1:1 ratio of females:males in any of the areas. This contrasts somewhat with a previous report of a surplus of males (Macer, 1966), but that observation was based on a single sample only. Among the youngest spawners there was a surplus of males, however, and this corresponds with findings at Shetland and in the Moray Firth (Gauld and Hutcheon, 1990). In September-October, males with elevated GSIs tended to have higher indices than females, suggesting that the males either develop faster or start developing somewhat earlier than the females.

The size and age at 50 % maturity and in the size and age ranges during which maturation occurred was the same or very similar in the two study areas. Thus we could not on the basis of our observations reject the null-hypothesis of no differences between exploited and unexploited areas. We have no historical data from the 'East Central Grounds', hence we cannot strictly conclude with certainty that no changes in these traits have occurred during the decades when the sandeel fishery expanded. According to Rochet (1998), a common response to enhanced adult fishing mortality is a decrease in age at maturity and an increase in the length at maturity. Sandeels in the southern North Sea (Macer, 1966) and off Scotland and Shetland (Gauld and Hutcheon, 1990), evidently start to spawn already as 1-group (i.e. as 12–14 months old), and the age at 50 % maturity appears to be 1 year earlier than in our study areas. This shows that it is possible for the sandeel to spawn at an earlier age than that observed on ECG and the Norway coast. The enhanced mortality due to fishing on the ECG does, however, not seem to have caused any such change. If a change towards earlier maturation had occurred, one would have to assume that the pre-fishery age at maturity was higher than 3 years. In view of results from other areas, this does not seem very likely. The highest age at maturity reported previously was 3 years, for sandeel from the Barents Sea (Kirillov (1936) as cited by Reay, 1970). The smallest maturing fish in both our study areas were 11.5 cm, and the length at 50 % maturity was about 14 cm. In Shetland and Moray Firth, the minimum length was less, i.e. 95–100 mm, and all fish > 135 mm were maturing (Gauld and Hutcheon, 1990). The somewhat higher length on the ECG might suggest that an increase had occurred in that area due to exploitation. However, given the observed similarity with sandeel on the Norway coast, this conclusion cannot be drawn.

Our results suggest that not only the age but also the length of maturity differs between sub-areas of the North Sea. In another paper (Bergstad et al., 2001) where we analysed the growth of sandeel, we found both spatial and temporal variation, and also variation between year-classes. These results suggest that, although major spatial patterns may be persistent, the sandeel shows considerable plasticity in both growth and size-age at maturity. A clear link between growth variation and variation in age and size at maturity has yet to be established, hence a study of this aspect would seem an interesting task for the future.

The size distributions of mature and immature 2-group fish showed that the mature fish were the larger within the age-group. Whether a 1-group sandeel will become a spawner at the age of 2 (past 1 January), probably depends on the length and condition attained during the preceding growth season. The fraction of the 1-group population that reaches this stage may vary between years and year-classes as suggested by the differing proportions of mature observed for the 1996 and 1997 year-classes on the ECG (32 against 7 %).

Our dataset for comparative studies of fecundity became smaller than intended, partly because too small subsamples were collected and because few of the females in the samples were at the appropriate maturity stage. No definite conclusions can be drawn from comparisons between the sampling sites or between the present datasets and published data. The large ECG sandeel tended to have higher fecundities than what has been observed in the southern North Sea (Macer, 1966) and at Shetland (Gauld and Hutcheon, 1990), but analyses based on a larger dataset are needed to analyse this further.

In a previous paper (Bergstad and Høines, 2001), we contrasted age-distributions from the ECG and from the same coastal area as studied in this paper. There were differences between the areas consistent with expectations in unexploited and exploited populations, respectively. The distributions on the exploited grounds essentially consisted of only 1–3 age-groups, whereas those on the coastal ground were much wider. The age compositions of our catches on the ECG were similar to those resulting from the North Sea wide stock assessments (ICES, 2000). Using the age-distributions from our previous paper and the maturity ogives from the present work, we could estimate area-specific fractions of adults in the two spawning seasons sampled. With the exception of the high fractions in the few samples from the ECG in December 1998, the main pattern was that of much lower fractions of adults on the ECG than on the coastal ground. In the 1997/98 spawning season, the adult fraction on ECG was only about 5 %. In the following season it was somewhat higher, but still lower than on the coastal ground. The same sampling gears were used in both areas, i.e. bottom trawl and benthic samplers. These observations point to a potentially important effect of the enhanced mortality due to fishing, i.e. the reduction of the portion of the stock which is mature and which can contribute to the reproductive capacity of the population. Indeed, the proportion of adults in the North Sea samples appeared surprisingly low compared with what would seem necessary to sustain the population. A possible explanation may be that adults are found in greater densities in more marginal areas that cannot be trawled efficiently. If so, such small but numerous sandy patches may to some extent serve as refugia for the stock. This is a hypothesis that should be explored further in the future.

In most years, between 30 and 50 % of the sandeel landings from the North Sea come from the ECG or adjacent grounds. Catches from that area thus have significant impact on the results of the North Sea wide stock assessments. In the estimation of spawning stock in terms of numbers and biomass as currently conducted by ICES, a knife-edge maturity ogive is applied which assumes that 100 % of the 2-group and older (at the beginning of the year) are considered adults. We have shown that this is not the case in the ECG and on the coast off Norway, where the age at 50 % maturity is 3 years. The likely consequence of this error is a bias toward too high spawning stock estimates.

The apparently exceptionally high adult fractions found in December 1998 on the ECG could be a sampling artefact, but may also indicate that some degree of concentration of spawners may occur during the peak of the spawning season. This is a phenomenon which should be studied in greater detail, in particular because it may be relevant to some much debated issues concerning the sustainability of the sandeel stock as a whole and the existence of self-sustaining local stock units (ICES 1999, 2000, Pedersen et al., 1998).

5. CONCLUSION

Sandeel in exploited areas of the east central North Sea and in unexploited Norwegian coastal waters spawned in December-January. In both areas, length and age at 50 % maturity was 14 cm and 3 years, respectively, higher than previous estimates from other parts of the North Sea. Fecundity was similar in both areas and comparable to published data. The proportion of adults in catches on the main fishing banks was usually appreciably lower than on the coast where the age-distributions were wider.

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