A reanalysis of North Sea plaice spawning-stock biomass using the annual egg production method

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Uncertainty about the quality of current virtual population analysis-based stock assessment for North Sea plaice (*Pleuronectes platessa*) has led to various abundance indices. We compared biomass estimates from the annual egg production (AEP) method with current stock assessments based on catch-at-age to validate the current and historical perception of exploitation. The AEP method was also used to investigate the dynamics of the spatial components of plaice in the North Sea. We corrected for fecundity down-regulation and changes in sex ratio. Estimates from both methods were similar in trend and absolute biomass. On the Dogger Bank, there was a dramatic decline in biomass from 1948 and 1950 to 2004, and in the Southern Bight, the stock appeared to increase from 1987 and 1988 to 2004, although not reaching the historically high levels of 1948 or 1950. The timing of spawning of North Sea plaice does not appear to have changed throughout the period of high exploitation. We conclude that the AEP method is a useful way to hindcast the spatial dynamics of heavily exploited flatfish stocks.

Keywords: annual egg production, down-regulation, fecundity, North Sea, *Pleuronectes platessa*, spawning-stock biomass.

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Introduction

The annual egg production (AEP) method has been used successfully to estimate spawning-stock biomass (SSB) in determinant spawning fish (Lasker, 1985; Armstrong *et al.*, 1988, 2001). It is based on dividing the population's AEP by an average individual production. It has proven useful to investigate the trends in SSB in certain stocks (Lockwood *et al.*, 1981; Priede and Walsh, 1991), produce one-off SSB estimates (Zeldis, 1993; Bulman *et al.*, 1999), compare biomass estimates derived from catch-at-age-based stock assessments with fishery-independent assessments (Daan, 1981; Horwood, 1993; Zenitani *et al.*, 2001), and examine the spatial distribution of spawning components (Fox *et al.*, 2000; Heffernan *et al.*, 2004). A similar technique (the larvae production estimate, LPE) has been used to investigate the trends in stocks with attached or benthic eggs (Nichols *et al.*, 1987; Fossum, 1996; Briggs *et al.*, 2002). It can be argued that the SSB estimates from AEP are more useful for fish ecology or management than those derived from aged-based models because they are a fisheries-independent method, measure reproductive production directly, have a greater spatial resolution, and are not inferred from matrices of numbers- and weights-at-age derived from virtual population analysis (VPA). Moreover, the assumptions made when calculating SSB from an AEP estimate are often different from those made in a VPA

(Armstrong *et al.*, 2001). As the AEP method is fisheries-independent, it can be used in recovery situations where fishing effort must be reduced to rebuild SSB and no market samples are available. Further, the estimate of SSB obtained from the AEP method is not influenced by the movements of fish out of the management area after spawning. It does have some disadvantages: all spawning areas need to be sampled throughout the spawning season, and forecast possibilities are limited.

North Sea plaice (*Pleuronectes platessa*) are commercially important and exploited mainly by beam trawlers targeting both sole (*Solea solea*) and plaice (Daan, 1997). There is substantial discarding of plaice by beam trawlers, and this has complicated both the stock assessment and stock management (Casey, 1996; Rijnsdorp and Millner, 1996; Dickey-Collas *et al.*, 2007).

Spawning plaice are widely distributed throughout the English Channel and the southern and central North Sea (Buchanan-Wollaston, 1923; Houghton and Harding, 1976; Harding and Nichols, 1987), although rarely beyond the 50-m depth contour (Harding *et al.*, 1978). The nursery grounds are inshore on sandy flats (Zijlstra, 1972; van Beek *et al.*, 1989), and plaice gradually move offshore as they grow (Wimpeny, 1953). Spawning commences in December in the eastern English Channel and is progressively later north through the North Sea (Bagenal, 1966). Spawning peaks in mid-January in the

Southern Bight and in February/March in the more northern regions (Simpson, 1959; Harding *et al.*, 1978).

Plaice are determinate batch spawners (Urban, 1991; Armstrong *et al.*, 2001; Murua and Saborido-Rey, 2003). Fecundity is determined from the standing stock of advanced vitellogenic follicles, which are clearly separated from precursor previtellogenic follicles well before the onset of spawning. We use the term follicle here to refer to the developing oocyte and the maternal follicle granulosa and theca layers (Tyler and Sumpter, 1996). At the start of maturation, fecundity is high. During the maturation cycle, fecundity is down-regulated, i.e. the number of developing oocytes decreases (Kjesbu, 2009) through follicular atresia according to the energy reserves of the female (Kennedy *et al.*, 2007, 2008). Atresia is not thought to cause further loss after spawning commences (Nash *et al.*, 2000). During spawning, pelagic eggs are released in batches (Rijnsdorp, 1989; Urban, 1991). Individual females spawn over a period of 4–6 weeks (Rijnsdorp, 1989). Fecundity varies between spawning areas, and in the North Sea, fecundity decreases from the eastern English Channel to the German Bight, though interannual variation in fecundity can be considerable (Horwood *et al.*, 1986; Rijnsdorp, 1991).

The spatial distribution of plaice has reportedly changed in recent years (van Keeken *et al.*, 2007), and there is anecdotal evidence coming from the fishery that the relative distribution of the adults may also have changed. Plaice in the southern North Sea are managed partly through spatial closures designed to protect juveniles (Rijnsdorp and van Beek, 1991; Pastoors *et al.*, 2000). There are also predictable patterns in the seasonal and spatial distribution of the population, which relate to the migration patterns between spawning and feeding areas and recruitment (Rijnsdorp *et al.*, 2005). Plaice in the North Sea and the English Channel are managed as different stocks, and it is assumed that there is no mixing (ICES, 2003a) between the stocks. Recent studies, however, show considerable mixing (Hunter *et al.*, 2003; Bolle *et al.*, 2005), and it can influence the stock assessments (Kell *et al.*, 2004). The spatial components of spawning can be investigated by the AEP method (Bannister *et al.*, 1974). Therefore, within this spatial context of fish and fleet behaviour, the AEP method can provide evidence for changes in relative importance of plaice spawning grounds.

We considered a new estimate of plaice SSB by AEP necessary in light of the uncertainty in the VPA estimates. There have been large retrospective changes in the estimated absolute levels of plaice SSB in the North Sea (Pastoors, 2005). Moreover, the stock assessment methodology for North Sea plaice has changed greatly in recent years. Now the assessment incorporates discards of plaice, information obtained by raising discard estimates from fleet samples in recent years, and using an interannually varying growth model that simulates the potential discarding behaviour of the fleets back in time (van Keeken *et al.*, 2003; ICES, 2006). This new method has never been tested for its sensitivity to the assumptions in the model or the different variance associated with the data sources (STECF, 2005), and more information is required to support its use (Dickey-Collas *et al.*, 2007).

In 2004, a series of ichthyoplankton surveys covered the whole North Sea (Taylor *et al.*, 2007), targeting cod and plaice egg production with the primary aim of mapping the spawning grounds. In the southern North Sea, there were sufficient repeated surveys conducted during the spawning season to allow estimating the plaice SSB by AEP. With this in mind, the fecundity of plaice in the southern North Sea was also evaluated in 2004. Data from previous ichthyoplankton surveys of the southern North Sea (Simpson, 1959; Heessen and Rijnsdorp, 1989; van der Land, 1991) were reanalysed using the same method as for the 2004 data to explore the relative trends in the North Sea plaice stock and the variability in the spatial pattern of spawning.

Methods

Ichthyoplankton surveys

From December 2003 to April 2004, 11 ichthyoplankton cruises were carried out (Table 1). Data from two cruises were not used in this investigation, however, because they covered the area outside that considered important for plaice spawning ($<55.5°N$) and are therefore not included in the table. A detailed description of those surveys is given by Taylor *et al.* (2007), but briefly, plankton was collected at each station by deploying the sampler in a double-oblique manner down to 2 m from the

Table 1. Ichthyoplankton survey dates and gears deployed.

Cruise	Country/ ship	Start date	End date	Gear	Number of hauls	Area surveyed
1	Netherlands "Tridens II"	15 December 2003	18 December 2003	Gulf III, 20 cm nose-cone diameter, 270 μm mesh	77	A and B
2	Netherlands "Tridens II"	12 January 2004	16 January 2004	Gulf VII, 53 cm length, 28 cm nose-cone diameter, 270 μm mesh	66	C and D
3	Germany "Alkor"	08 January 2004	19 January 2004	Gulf III, 53 cm length, 20 cm nose-cone diameter, 270 μm mesh	108	A and B
4	Netherlands "Tridens II"	19 January 2004	23 January 2004	Gulf III, 20 cm nose-cone diameter, 270 μm mesh	92	A and B
5	Netherlands "Tridens I"	11 February 2004	16 February 2004	Gulf VII, 53 cm length, 28 cm nose-cone diameter, 270 μm mesh	69	B, C, and D
6	Germany "Heincke"	16 February 2004	23 February 2004	Bongo, 60 cm diameter, 500 μm mesh	52	B, C, and D
7	England "Corystes"	18 February 2004	08 March 2004	Gulf VII, 76 cm length, 40 cm nose-cone diameter, 270 μm mesh	136	C
8	Netherlands "Tridens II"	01 March 2004	04 March 2004	Gulf VII, 53 cm length, 28 cm nose-cone diameter, 270 μm mesh	66	B, C, and D
9	Germany "Alkor"	06 April 2004	13 April 2004	Bongo, 60 cm diameter, 500 μm mesh	54	B, C, and D

The areas surveyed are shown in Figure 2. Note that two of the cruises within this programme were dropped from the analysis and this table because they were outside the area of plaice spawning ($<55.5°N$).
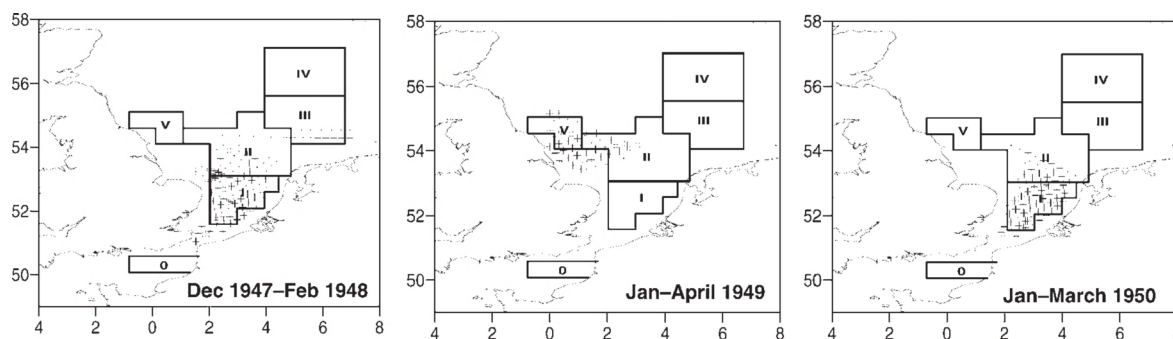
Figure 1. Positions of recovered plaice egg distribution data, after Simpson (1959), from December 1947 to March 1950, and the survey area and divisions used by Heessen and Rijnsdorp (1989).

seabed. Hydrographic data were collected at each station, although during cruise 1, no temperature data were collected owing to failure of the CTD. Based on data from earlier years in the ICES oceanographic database, 9°C was assumed to be the temperature for all samples from that first cruise.

Plankton samples were fixed and stored at sea in 4% formaldehyde solution buffered with sodium acetate trihydrate (Tucker and Chester, 1984). Eggs were later sorted from the samples and counted, samples containing large quantities of eggs being subsampled using a Folsom splitter, following agreed protocols (ICES, 2003b). The eggs were identified to species level using the criteria described by Russell (1976). Plaice eggs were identified based on their size (>1.75 mm diameter) and their thick chorion, and their development stage was assigned according to the description of Simpson (1959).

The raw data from the 1948, 1949, and 1950 egg surveys reported on by Simpson (1959) and the 1987 and 1988 egg surveys reported on by Heessen and Rijnsdorp (1989) were used to re-estimate AEP and SSB for those years using the same methods, for comparison with the 2004 data. However, owing to incomplete coverage in 1949 (Figure 1), it was not possible to compare data for the whole of the southern North Sea in that year.

Estimating North Sea plaice fecundity

In December 2003 and January 2004, female plaice were collected from three areas of the southern North Sea (Figure 2) by the Dutch beam trawler "ARM 44" and the RV "Tridens II" (Table 2). The fish were kept on ice before collecting fecundity samples. Only fresh, mature, and ripening (Walsh *et al.*, 1990) females were used for fecundity estimation. The fish were measured and sampled within 24 h of being caught. Biological parameters collected were total length, total weight, maturity stage, and ovary

weight. From each fish, duplicate (one of each ovary) fecundity samples with a known volume of 100 μl (corresponding to a weight of 0.105 g) were taken with a solid displacement pipette (Kennedy *et al.*, 2007), then preserved separately in 2 ml of 3.6% buffered formaldehyde.

The opaque oocytes were coloured using Periodic Acid-Schiff reagent staining to aid counting and measurement of follicle diameter with an auto image-analysis system (GFA, PIAS; Thorsen and Kjesbu, 2001; van Damme *et al.*, 2005). The threshold to include vitellogenic or to exclude smaller previtellogenic follicles in the fecundity count was set at 450 μm. Before image analysis, the samples were examined manually, under a dissecting microscope, to identify and reject samples containing spawning markers (hyaline or post-ovulatory follicles; Witthames *et al.*, 2009). The means of the follicle count and the diameter in the pair of samples taken from each fish were used to determine the fecundity and to correct for down-regulation during maturation, respectively.

Fecundity of individual plaice was calculated using the formula

$$F = \frac{N(O/s)}{W}, \tag{1}$$

where F is the relative fecundity, N the number of vitellogenic follicles in the pipette subsample, s the subsample weight, O the ovary weight, and W the total weight of the fish.

Fecundity was estimated for each of the three areas separately and for the whole of the southern North Sea (Figure 2). For the whole North Sea, fecundity estimates from the separate areas were pooled. For each area, female size-specific relative fecundity was estimated from a linear regression of relative fecundity against total body weight predicted from the mean area-specific female weight (Armstrong *et al.*, 2001). An age-specific fecundity was not applied.

Down-regulation of fecundity was estimated for the Southern Bight and Dogger Bank areas. Differences in fecundity and down-regulation between areas were estimated using generalized linear models in R (R Development Core Team, 2008). Linear regression was determined between relative fecundity and mean follicle diameter. Using the relationship between oocyte diameter and fecundity, down-regulation was estimated using the mean oocyte diameter in December and January. Fecundity was corrected for down-regulation, but to be able to compare the estimates with earlier studies, uncorrected fecundity data for 2004 were used too.

Table 2. Sampling of female plaice for estimating fecundity from December 2003 to January 2004.

Sample	Sample area	Sample date	Number of females
1	Southern Bight (B)	3 December 2003	17
2	Dogger Bank (C)	2 December 2003	19
3	German Bight (D)	11 December 2003	21
4	Dogger Bank (C)	11 December 2003	34
5	Southern Bight (B)	18 December 2003	23
6	Southern Bight (B)	07 January 2004	19
7	Dogger Bank (C)	06 January 2004	26

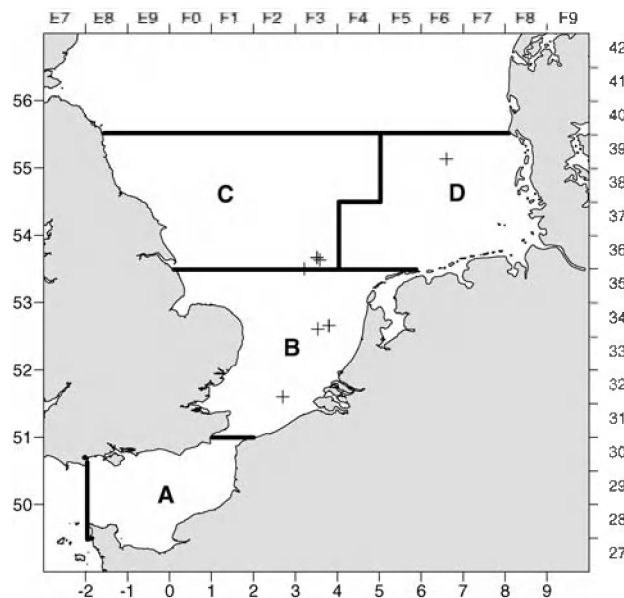The sample areas referred to are shown in Figure 2.

Figure 2. The southern North Sea, showing the location of plaice sampling for fecundity estimation (plus symbols) in December 2003 and January 2004, and the area division for the 2004 egg survey. A, Eastern Channel; B, Southern Bight; C, Dogger Bank; D, German Bight. Degrees shown on the bottom and the left axes, ICES rectangle descriptors on the top and the right axes.

As plaice fecundity changes over time (Rijnsdorp, 1991), separate fecundity values were used for each of the earlier periods (Simpson, 1959; Rijnsdorp, 1991) rather than using the 2004 estimates. To be able to compare data between periods, all estimates were also made using the area division of Heessen and Rijnsdorp (1989; Figure 1).

Estimating AEP

The method we used for this was developed from those described by Heessen and Rijnsdorp (1989) and Armstrong *et al.* (2001); for the assumptions made in estimating AEP and SSB, see Table 3. AEP estimation requires rates of egg development and mortality. To test the sensitivity of the estimates of AEP to assumptions on rates of egg development, two models of development rates at various temperatures were compared. Development rates were calculated using the equations

$$D = [100/(aT + b)] + D_0 \text{ (after Ryland and Nichols, 1975),} \quad (2)$$

and

$$D = a + b \times \ln(T) \text{ (after Fox } et\ al.,\ 2003), \quad (3)$$

where D is the development time up to the end of the development stage, T the temperature (°C), and D_0, a, and b the constants (Table 4).

The rate of egg mortality must be assumed or calculated to estimate the numbers of eggs at the immediate time of spawning (i.e. time = 0). To investigate the sensitivity of assumptions about egg mortality, we assumed rates of egg mortality similar to those described previously (e.g. Harding *et al.*, 1978; van der Land, 1991; Dickey-Collas *et al.*, 2003). Assuming that instantaneous daily mortality $Z = 0$ results in the minimum AEP, and

Table 3. Assumptions used in the AEP and SSB estimates.

Step	Assumptions
Egg sampling	The plankton samplers provide an unbiased estimate of the abundance at a station
	Egg identification and staging were not biased
	Flowmeter and CTD measurements were calibrated and unbiased
	The cline in abundance between stations is linear
	The seasonal trend between surveys can be linearly interpolated
	The first and last cruise (unless otherwise stated) occur at almost zero egg production
Fecundity estimation	For comparison with previous studies, there is no loss of fecundity through atresia in the North Sea population during spawning in assessment years
	Realized fecundity is fertilized eggs produced on a one-to-one basis
	Fecundity samples collected in each area refer to the spawning population producing the eggs
Egg mortality	Mortalities were assumed to have similar orders and distributions to those described in previous studies (e.g. Harding *et al.*, 1978; Heessen and Rijnsdorp, 1989; van der Land, 1991; Dickey-Collas *et al.*, 2003)
Estimation of AEP	The age of the eggs was the median of an egg stage (1A, 1B, 2, 3, 4, and 5)
	Mean development duration of stage 1A eggs indicated the half-way point of the 1A stage duration
	Rates of egg development determined for Irish Sea plaice were applicable to plaice in the North Sea
Estimation of SSB	The ratio of female weight to total SSB was estimated to be 0.37 in 1987 and 1988, and 0.60 in 2004; the time-series does not go back as far as 1948, so 0.54 (the mean of the early 1960s) was applied

Table 4. Constants used for the calculation of development time up to the end of each stage, using models 2 and 3.

Stage	Ryland and Nichols (1975)			Fox *et al.* (2003)	
	a	*b*	D_0	*a*	*b*
1A	0.6203	8.9372	−5.5639	5.186	−1.612
1B	2.3629	4.6528	−1.2662	8.002	−2.540
2	2.1274	0.9166	−0.2867	12.819	−4.098
3	1.0642	1.5260	−1.7543	25.398	−8.078
4	0.7299	1.3619	−2.7171	29.880	−9.313
5	0.3150	1.3153	−10.4479	43.853	−14.427

$Z = 0.29$ (approximately the maximum estimated for plaice eggs; Dickey-Collas *et al.*, 2003) results in the likely maximum estimate of AEP. In addition to fixed mortalities, Z was also calculated based on temperature using the equation

$$\ln(Z) = 0.40T - 4.79 \text{ (after Dickey-Collas } et\ al.,\ 2003), \quad (4)$$

where Z is the instantaneous daily mortality and T the temperature (°C) for each haul.

It is also possible to use the decline by stage in an empirically estimated egg production (Fox *et al.*, 2003). However, this

would lead to great variability in the estimates of Z (Dickey-Collas *et al.*, 2003) but no great change in the likely maximum or minimum estimates of Z, so we did not use the method in calculating daily mortality.

For each haul, the abundance (numbers m^{-2}) of eggs was calculated and converted to the daily production of plaice eggs by stage (numbers $m^{-2}\,d^{-1}$), using the integrated water-column temperature (°C) and egg development time. The daily production was back-calculated to the daily production at the time of spawning (development stage 1A):

$$P_{t_0} = P_{t_{1A}} e^{-Z_t}, \qquad (5)$$

where P is the egg production, t the time between t_0 (spawning) and t_{1A} (median time of egg development stage 1A), and Z the coefficient of daily mortality. Although sampled numbers of stage 1A eggs reflected the mean abundance for that stage, their age was assumed to be the median age of stage 1A eggs.

For each survey (Figure 2), the egg production per cruise was calculated by taking the mean production of all ICES rectangle productions weighted by area. Variance in the egg production was calculated by ICES rectangle, and these were raised to the areas. The raised variance was used to estimate the *CV* for all egg productions. Annual production curves by area were estimated following Armstrong *et al.* (2001). The production curves by area were then integrated using the equation

$$\text{AEP} = \Sigma(t_{\text{cruise}} \times P_{\text{cruise}}), \qquad (6)$$

where P is the egg production per cruise and t the duration (in d) of this production, equal to half the number of days between the midpoint of the cruise and the midpoint of the previous one, plus half the number of days between this cruise and the midpoint of the following one. For the first and last cruises, the duration was assumed to be equal to the number of days between the midpoint of the first or last cruise and the midpoint of the adjacent cruise. The variance in the egg productions was summed as described for the AEP in Equation (6), and this variance was used to estimate the *CV* for the AEP.

Estimating SSB

Female SSB was calculated for the various areas using the area-specific population fecundity estimates and the estimated AEP and the equation

$$\text{SSB}_f = \frac{\text{AEP}}{F}, \qquad (7)$$

where SSB_f is female SSB and F the relative population fecundity. The standard stock assessment total SSB includes both males and females, so a sex ratio R was applied to raise SSB_f to total SSB. For this, the female-only stock assessment (A. D. Rijnsdorp, IMARES, unpublished) was used to estimate the sex ratio by weight between mature males and females. The maturity ogive for males was taken from Rijnsdorp (1989). The ratio of female weight to total SSB was estimated for the years 1982–1985 and 2004. The time-series does not go back as far as 1948, so 0.54 (the mean of the early 1960s; ICES, 2006) was applied. As no down-regulation estimates are available for the earlier periods, it was assumed to be zero then. However, for 2004, an SSB estimate was also calculated with a corrected fecundity to show the impact of down-regulation. Summing

all areas yielded a total SSB. To investigate the sensitivity of applying area-specific fecundity estimates, the total SSB was also estimated by summing the annual productions by area and dividing this by the mean fecundity for the whole region. The variance in SSB was estimated by scaling the AEP variance, but not accounting for the variance in *F*.

Age-based SSB from stock assessments

To compare the SSB estimates derived from the AEP method with stock assessment SSB estimates, current estimates derived from extended survivor analysis (XSA) were taken from the ICES Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (ICES, 2007). These included estimates of discard mortality (see the Introduction). The ICES stock assessment assumes a constant maturity ogive and is not sex-specific. The time-series from 1957 to 2006 is for the North Sea only (i.e. not the eastern English Channel). There are no reliable absolute SSB estimates available for plaice in the eastern English Channel at present (area A, Figure 2; ICES Area VIId; see ICES, 2007), but an assessment indicative of trends is available.

Another time-series of the population dynamics of North Sea plaice was available to the current study. This was a newly developed female-only XSA stock assessment (A. D. Rijnsdorp, IMARES, and L. T. Kell, Cefas, pers. comm.). This used sex-specific catch matrices adjusted for sexual dimorphism in growth and maturation (Rijnsdorp and Ibelings, 1991). Although this method did not use discard data, the estimation of SSB without discards is relatively robust (Dickey-Collas *et al.*, 2007) because most discarded fish are not mature.

Results

Spatial and temporal coverage of surveys

Areas B and C (Figure 2) had sufficient surveys to carry out full AEP estimates for plaice, providing seven and six daily egg production estimates, respectively. The surveys had good temporal coverage, so the onset and decline of spawning were covered. There were fewer surveys of areas A and D, and just three daily egg production estimates were possible in area A and five in area D. The end of spawning was missed in area A (last estimate 21 January 2004) and the beginning was missed in area D (first estimate 15 January 2004). If spawning is assumed to be similar to previous years, as described in earlier studies, then the dates for zero production can be assumed, allowing AEP estimates to be derived.

Estimating North Sea plaice fecundity

Fecundity in the Southern Bight and Dogger Bank was the same, but fecundity in the German Bight was lower, though not significantly so (ANOVA, for both slopes and intercepts, $p = 0.7$; Figure 3). Relative fecundity was higher in 2004 than in the years 1947–1949 (Simpson, 1959) and 1982–1985 (Rijnsdorp, 1991; Table 5). For the Southern Bight and Dogger Bank areas, temporal variation in sampling was large enough to allow estimation of down-regulation of fecundity. Mean oocyte diameter in December was 1.0 mm and in January 1.1 mm. The down-regulation in fecundity between December and January is therefore 10% in both areas. The data show that before the onset of spawning, there is still a clear down-regulation of fecundity in North Sea plaice (Figure 4), but down-regulation was different
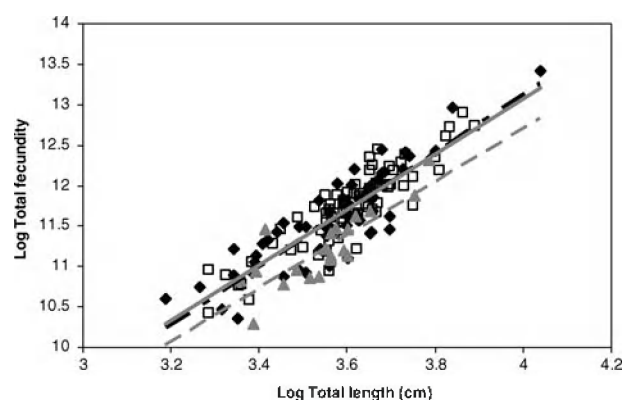
Figure 3. Plaice total fecundity for the three different areas sampled: Southern Bight (filled diamonds and grey line), Dogger Bank (open squares and dotted line), and German Bight (filled triangles and grey dotted line). The areas are shown in Figure 2.

Table 5. Plaice relative fecundity estimates (oocytes g^{-1} female) for the three different areas sampled and the total southern North Sea, for comparison with Simpson (1959) and Rijnsdorp (1991).

Area	Year	Relative fecundity	Standard deviation
Southern Bight (B)	2004	255	63
Dogger Bank (C)	2004	235	51
German Bight (D)	2004	185	43
Total southern North Sea	2004	238	58
Southern Bight (Simpson, 1959)	1947–1949	163	
Total southern North Sea (Rijnsdorp, 1991)	1982–1985	171[a]	

To be able to compare between the periods, the 2004 estimates are not corrected for down-regulation.
[a]Population fecundity was recalculated from the 1989 data using the method described.
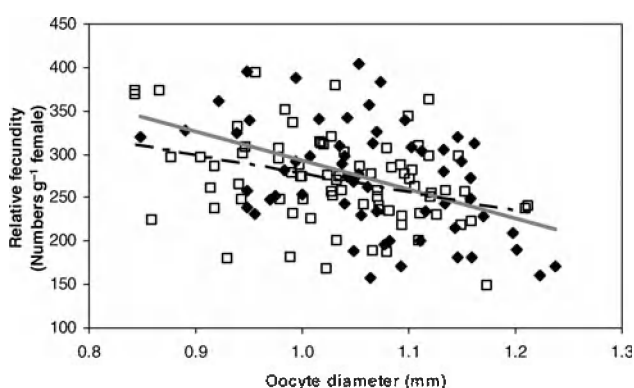

Figure 4. Down-regulation of fecundity in plaice for the different areas, December 2003 and January 2004: Southern Bight (filled diamonds and grey line), Dogger Bank (open squares and dotted line). The areas are shown in Figure 2.

in the two areas. Although the slopes did not differ significantly (ANOVA, $p = 0.4$), there is a significant difference between the two areas in the intercepts (ANOVA, $p < 0.01$).

Table 6. Mean difference in the estimation of stage 1A egg daily production at median age using the Fox *et al.* (2003) and Ryland and Nichols (1975) methods by survey area.

Area	Mean difference in estimate of daily egg production dependent on model choice	Mean sea temperature (°C)
A	0.72	9.57
B	0.89	7.38
C	0.97	6.90
D	0.98	6.37

Estimates were not weighted by egg abundance, but were based on the unweighted mean of cruises in each area.

Table 7. Assumed daily rate of egg mortality (based on Dickey-Collas *et al.*, 2003) and its impact on the estimate of egg production at spawning from back-calculations of production at median developmental stage 1A.

Area	Mean sea temperature (°C)	Mean assumed daily Z	Mean difference between median age stage 1A production and production at spawning (%)
A	9.57	0.38	37
B	7.38	0.16	21
C	6.90	0.13	14
D	6.37	0.11	13

Estimates were not weighted by egg abundance, but were based on the unweighted mean of cruises in each area.

Effect of temperature on development rate

The study of Fox *et al.* (2003) was on the eggs of Irish Sea plaice, but it did use many more fish and different methods to investigate maternal effects than the study of Ryland and Nichols (1975), whose results were based on a single batch of eggs from a single female. It is clear that although the new relationships from Fox *et al.* (2003) do affect the estimation of production, it is small. For example, in area B, the Southern Bight, using the Fox *et al.* (2003) relationship, production of stage 1A at median age is estimated to be 89% of that using the Ryland and Nichols (1975) relationship (Table 6). Owing to the different sea temperatures at the time of sampling in area A, this area shows the biggest difference. As the Fox *et al.* (2003) relationship was based on a larger sample size and takes maternal effects into account, however, it was decided to use that method for estimating AEP.

Effect of assumptions about egg mortality (Z)

To investigate the difference in the estimates of daily production at median age of stage 1A and at spawning (i.e. time = 0), a range of mortality rates was assumed and applied (see above). The estimated egg production at spawning increased by 16% in area A, by 21% in area B, and by 24% in areas C and D if the assumed Z was increased from 0 to 0.29. When Z was assumed to be related to sea temperature, following Dickey-Collas *et al.* (2003), the differences between the areas were greater (Table 7). The higher temperatures in area A resulted in a 37% increase in production when back-calculated from stage 1A to spawning. The back-calculated increase in production, and hence the impact of assuming Z to be related to temperature, rather than $Z = 0$, was less in the other areas (Figure 5). The variations in estimated egg production at spawning caused by different assumptions of Z
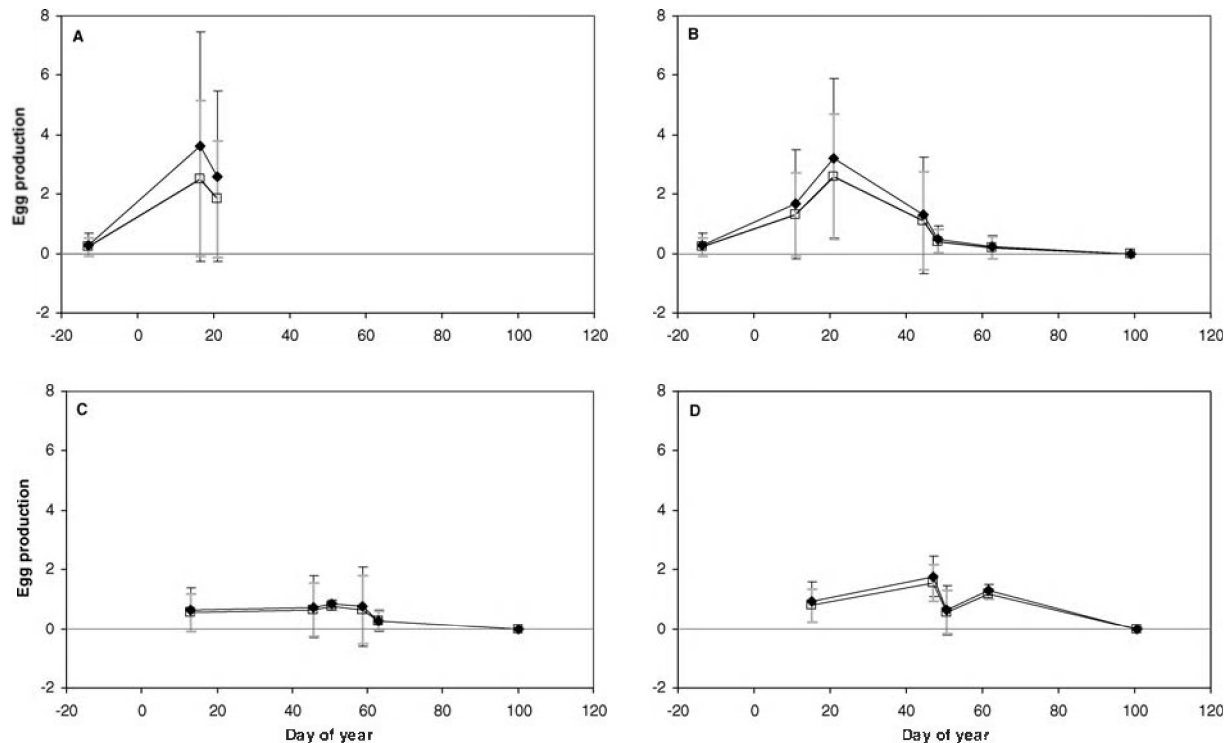
Figure 5. Comparison of the seasonality in daily egg production in numbers m^{-2} d^{-1} of North Sea plaice in 2004 in survey areas A–D (Figure 2). Day of year = 0 is 1 January 2004, and egg development is based on Fox *et al.* (2003). Daily production is estimated from daily mortality (filled diamonds) $Z = T$, the temperature to egg mortality relationship of Dickey-Collas *et al.* (2003), and (open squares) at the time of capture (i.e. $Z = 0$, median developmental stage 1A). Error bars denote 1 s.d., grey for $Z = 0$, and black for Z being temperature-dependent.

are well within the overall variability of the production estimates, as reflected by the standard deviations in Figure 5. For the calculation of EAP and SSB, $Z = 0$ was used for a minimum estimate, then compared with Z dependent on sea temperature.

Egg production

The seasonal trend in egg production varied by area (Figure 5). The smaller area A (Figure 2) had equivalent maximum egg production per square metre to that of area B. Areas C and D had lower production per square metre. The coverage of area A ended at day 20, when egg production was still high (Figure 5). From the results for the other areas, however, it is clear that egg production declines gradually. Another survey in area A around day 40 would have been useful in allowing a better estimate of the end of egg production there. Likewise, a survey in early January in areas C and D would also have provided useful data to allow a better estimate of the start of the egg production. The peak in production appeared earlier in areas A and B than in C and D (Figure 5), and A and B appeared to have a more marked peak than C and D. The dip in egg production in area D (Figure 5) is probably a consequence of sampling constraints. During cruises 5 and 8, just four stations were sampled there.

The curves in daily egg production were summed and raised by area to determine the AEP (Table 8). The Southern Bight and German Bight (areas B and D) appeared to have been the most important for the production of plaice spawning products in the southern North Sea.

As the current study (2004) had greater spatial coverage than that of Simpson (1959) and Heessen and Rijnsdorp (1989), the estimates from 1948, 1950, and 2004 were reworked into the survey areas of Heessen and Rijnsdorp to allow direct comparison (Figure 1). The Fox *et al.* (2003) relationships for temperature to egg development were also applied to all 20th century data to obtain comparable daily production estimates at median developmental stage 1A (Figure 6). Unfortunately, the raw data from van der Land (1991) have been lost, so for the results of that study no thorough comparisons with similar methods could be made, other than comparing the maps of production.

It is remarkably clear that in some of the sampling areas, the production of plaice eggs appears not to have changed greatly between 1987, 1988, and 2004 (Figure 6). Areas 0 and 1 of Heessen and Rijnsdorp (1989) show no marked changes in magnitude or timing of spawning, the areas corresponding to the eastern Channel and Southern Bight. In the Dogger Bank and German Bight areas (Heessen and Rijnsdorp's areas II and III), the picture is less clear, however. The data appear more variable, and the lack of an earlier survey in area II in 2004 apparently prevent more robust comparisons on magnitude and timing of spawning in the Dogger Bank area, but the estimates of declining production in February appear similar. More obvious differences are seen when the 2004 data and the 1980s data are compared with those from around 1950. Egg production in Heessen and Rijnsdorp's area I (the Southern Bight) was much higher around 1950, and the peak was later in 1948, though in 1950 the peak may have been slightly earlier than in 2004. It also appears that spawning on or south of the Dogger Bank was earlier and more intense around 1950. There was no sampling by Simpson (1959) in the eastern Channel or the German Bight.

Table 8. AEP (*CV* in parenthesis) and SSB estimates for North Sea plaice in 2004.

Parameter	A	B	C	D	Total
AEP estimate $Z = 0$ ($\times 10^{12}$)	1.82 (0.85)	6.08 (0.53)	3.27 (0.63)	5.11 (0.23)	–
AEP estimate $Z = T$ ($\times 10^{12}$)	2.58 (0.60)	7.50 (0.43)	3.76 (0.58)	5.78 (0.27)	–
Fecundity (eggs g^{-1} female)	255[a]	255	235	185	–
Female-only SSB estimate $Z = 0$ (t)	7 126 (0.85)	23 832 (0.53)	13 917 (0.67)	27 615 (0.31)	72 489 (0.29)
Female-only SSB estimate $Z = T$ (t)	10 103 (0.87)	29 395 (0.54)	16 006 (0.67)	31 268 (0.31)	86 771 (0.30)

The relationship between egg development and temperature is from Fox *et al.* (2003). Atresia during spawning was assumed to be 0, although down-regulation was found in areas B and C.
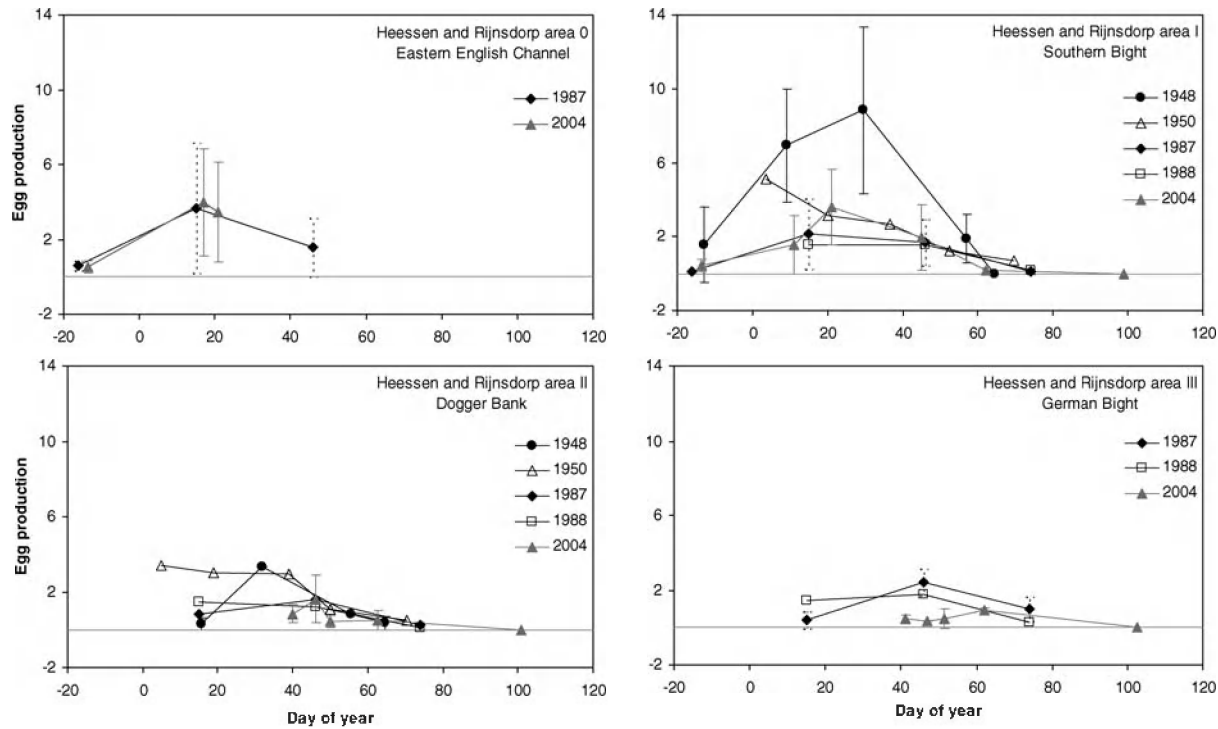[a]Taken from area B.

Figure 6. Seasonality in the daily egg production of North Sea plaice in 1948, 1950, 1987, 1988, and 2004 in four Heessen and Rijnsdorp (1989) areas. Estimates are based on median stage 1A egg production and Fox *et al.* (2003) egg development. The areas are shown in Figure 1. Only a maximum of three series per graph show error bars (denoting the standard deviation), for ease of viewing.

The female-only SSB associated with these AEP estimates shows a marked change over time (Table 9). Different estimates of fecundity were used for 1948 and 1950, 1987 and 1988, and 2004. These estimates of SSB are minimum estimates, because the production at median development stage 1A was used. As apparent in the comparison of the seasonal production curves (Figure 6), spawning in the Southern Bight declined from 1948 to 2004, but remained at the same level between 1987/1988 and 2004. In the eastern Channel, though, the lower SSB estimate by the AEP in 2004 (45% lower) could be attributable to the failure to survey throughout the spawning season, and the large variability in the estimates for that area in 2004 (Table 9). When the Southern Bight is combined with the Dogger Bank estimates (Figure 7), a substantial decline in female spawning biomass is apparent, from ~48 000 to 17 000 t, a decline to 35% of the post-war spawning stock. In the German Bight, the 2004 survey did not find the peak spawning recorded by Heessen and Rijnsdorp (1989), and this is reflected in an apparent decline in

female SSB from ~16 000 t in 1987/1988 to 5000 t in 2004 (Table 9).

Comparing AEP estimates of SSB with aged-based stock assessments of North Sea plaice

Combining the AEP estimates with fecundity estimates resulted in a minimum female spawning biomass of North Sea plaice in 2004 of 72 500 t (*CV* = 0.29), based on the production of stage 1A eggs, and a maximum of 86 800 t (*CV* = 0.30) when accounting for egg mortality. When taking down-regulation of fecundity into account, this resulted in a minimum female SSB estimate of 80 600 t. If a sex ratio of 1:1 is assumed, this results in a SSB of 145 000–174 000 t.

The AEP-derived estimates of SSB for plaice in the southern North Sea in 1987 and 1988 were similar to both the female-only assessment and the SSB from the ICES stock assessment. It is clear that the large proportion of males in the stock in 1987 and 1988 led to the total SSB appearing more productive in terms of eggs than it

Table 9. Comparison of AEP estimates of female SSB from 1948 to 2004 by Heessen and Rijnsdorp (1989) area (Figure 1).

Parameter	0	I	II	III	Total
AEP estimate 1948 ($\times 10^{12}$)	–	9.29 (0.32)	3.73 (0.05)	–	–
AEP estimate 1950 ($\times 10^{12}$)	–	4.18 (0.40)	6.79 (0.17)	–	–
AEP estimate 1987 ($\times 10^{12}$)	1.60 (0.68)	2.68 (0.58)	3.11 (0.34)	3.18 (0.27)	–
AEP estimate 1988 ($\times 10^{12}$)	–	1.93 (0.50)	3.13 (0.44)	2.83 (0.30)	–
AEP estimate 2004 ($\times 10^{12}$)	0.88 (0.55)	3.10 (0.41)	1.24 (0.51)	0.99 (0.15)	–
Female-only SSB 1948 (t)	–	36 413	15 886	–	52 299
Female-only SSB 1950 (t)	–	16 382	28 879	–	45 261
Female-only SSB 1987 (t)	6 274	10 519	13 241	17 173	59 202
Female-only SSB 1988 (t)	–	7 565	13 306	15 299	54 352
Female-only SSB 2004 (t)	3 450	12 159	5 276	5 354	26 736

Production of median developmental stage 1A eggs was estimated using the egg development to temperature relationship of Fox *et al.* (2003). Rijnsdorp (1991) estimates of fecundity were applied to 1987 and 1988. Area I fecundity was applied to area 0 in 2004 (*CV* in parenthesis).
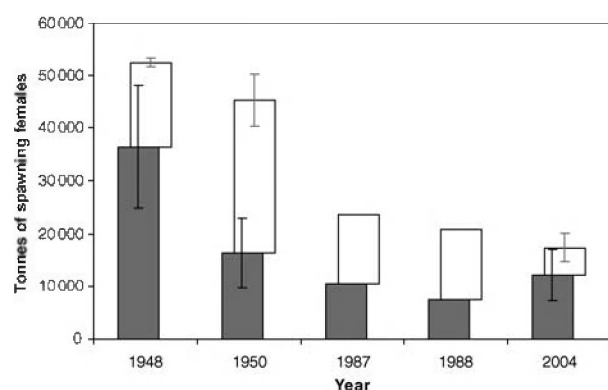

Figure 7. Estimated spawning biomass of female plaice in two areas of the North Sea over 5 years. The areas are shown in Figure 1, and the fecundities applied are described in Table 9. Filled histograms, Heessen and Rijnsdorp area I, Southern Bight; Open histograms, Heessen and Rijnsdorp area II, Dogger Bank. Error bars denote the standard deviation.

actually was (Figure 8). The confidence interval of the AEP estimate of females (Table 9) in 2004 covers the female-only assessment, but the difference from the total stock assessment made by ICES is rather larger (Figure 8). The Simpson (1959) data were from one region only, and when comparing them with the later survey data covering the whole area, their inclusion shows the relative decline in the plaice SSB in the latter half of the 20th century. Here, though, we note that temporal coverage was much less in 1950 than in 1948. This is the first time that an XSA-derived estimate of SSB for plaice has the same magnitude as an AEP (Armstrong *et al.*, 2001; Kennedy, 2006). It should be remembered, however, that both assessment time-series are for the North Sea only, whereas the AEP methods ($\geq$1987) include the eastern English Channel.

Discussion

Our study shows the utility of using the AEP method for estimating SSB and that the AEP method is a useful way to hindcast the spatial dynamics of heavily exploited flatfish stocks. In 2004, egg production was highest in the Southern Bight and production peaked earlier in the eastern Channel and Southern Bight. The lower fecundity in the German Bight resulted in the highest SSB estimate for that area. The egg production in 2004 was similar

to the egg production in 1987 and 1988. However, in 1948 and 1950, egg production was higher in the Southern Bight and around the Dogger Bank. There appears to have been no major change in the timing of spawning since 1948. The total female SSB seems to have declined over time, but the SSB estimates from AEP show the same magnitude as the VPA estimates.

The AEP method depends on the spatial and temporal coverage of sampling, but despite the intensive sampling during all surveys reported, here it was not possible to cover all spawning areas (Simpson, 1959; Bagenal, 1966) and the whole spawning season of plaice in the North Sea. Hence, we would expect some under-estimation of North Sea plaice AEP and SSB. Moreover, it was not possible to standardize the gear for the collection of eggs (Table 1). The differences between Gulf III and Gulf VII samplers are small and tested (Nash *et al.*, 1998), but with the bongo net the differences are larger. The use of the different nets may have resulted in further bias of the estimates.

It is clear that there are still many assumptions in current methods of AEP that still need to be adequately evaluated (Hunter and Lo, 1993; Armstrong *et al.*, 2001). The current work did not investigate the empirical evidence for *Z*, or errors introduced by mistakes in staging the eggs. The "pseudo-synoptic" nature of the surveys was not accounted for, and no geostatistical or GAM method was used (Fox *et al.*, 2000). However, because the methods broadly followed those of earlier similar studies (Daan, 1981; Horwood, 1993; Armstrong *et al.*, 2001), the estimates are considered to be robust for comparison with the results of previous studies. The 2004 ichthyoplankton survey of the North Sea provided excellent coverage of the Southern Bight and allowed acceptable comparisons with previous studies. As mentioned above, the temporal coverage was poor in the eastern English Channel and German Bight, but still allowed comparisons with earlier studies.

The sensitivity analysis of using the Fox *et al.* (2003) rates of egg development compared with those of Ryland and Nichols (1975) show that, as expected, when temperatures were higher, there was a greater influence in the choice of model, particularly in the eastern Channel. Therefore, the choice of model is important for future testing of climate-change scenarios. Although Fox *et al.* (2003) argue that there may be stock differences in development rate, comparison with the Ryland and Nichols (1975) development rates here results in just minor differences. As the Fox *et al.* (2003) study was based on more experiments and on many more crosses of parents, it is therefore considered to give the better relationship, although it is based on Irish Sea material.
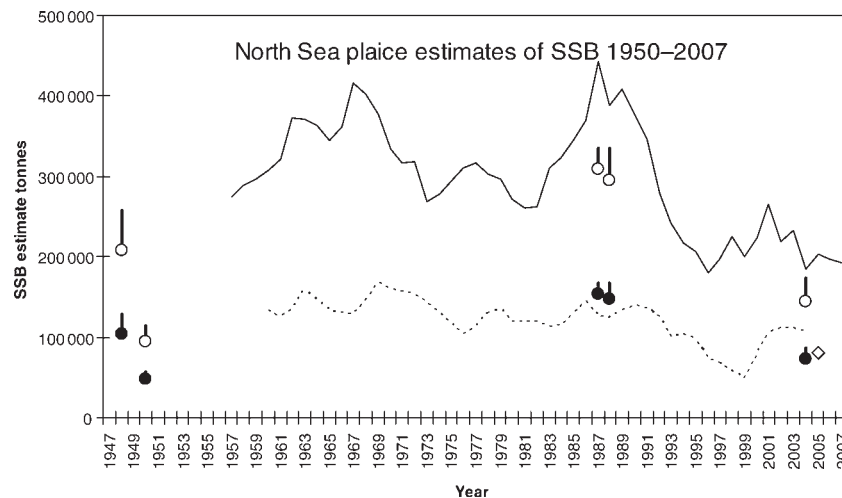
Figure 8. Comparison of AEP SSB with (solid line) the ICES stock assessment using XSA (ICES, 2007), and (dotted line) a "females-only" assessment of SSB (after A. D. Rijnsdorp, IMARES, pers. comm.). Circles denote the AEP estimate of SSB using egg production at the median age of egg stage 1A, and the top of the vertical bars denotes the AEP estimate of SSB using the egg production at spawning (derived by varying mortalities with temperature; Dickey-Collas *et al.*, 2003). Filled circles denote "females-only" estimates, open circles total SSB using a sex ratio of females to males by weight, and the diamond the "females-only" estimate with down-regulation of fecundity.

The fecundity of North Sea plaice has gradually increased since 1948. In flatfish species in the Northwest Atlantic, fecundity either increased or decreased over time (Rideout and Morgan, 2007). Variation in fecundity depends on the condition of the fish. As plaice are capital spawners, their condition in winter depends on feeding conditions during summer. Data are not available on feeding conditions in the years over the period studied here, but a large increase in prey and hence condition would be required to explain the increase in fecundity we found. North Sea plaice now mature earlier and smaller (Rijnsdorp, 1993) but this change would not necessarily result in increased fecundity, in fact should result in reduced fecundity per gramme of SSB.

Our study has also revealed down-regulation in North Sea plaice fecundity before spawning. The sampling for fecundity could have been more extensive, and we do not know how representative the German Bight sample was of the whole population in that area, because a replicate sample was not collected. However, if the fecundity was higher in the German Bight, then the estimates of SSB would be even lower than the current approach suggests. Although fecundity samples were only taken in December and January, just before spawning, the results did show a down-regulation of fecundity. In Atlantic herring (*Clupea harengus*), down-regulation of fecundity increases towards the end of the maturation period (Kurita *et al.*, 2003). The down-regulation is comparable with that found in Irish Sea plaice (Kennedy *et al.* 2007). When accounting for down-regulation, the SSB estimates increased by 11%. This shows the importance of sampling for fecundity just before the onset of spawning, or taking the stage of maturation and subsequent down-regulation into account.

This study shows no apparent change in the timing of spawning of North Sea plaice between the years 1948–1950, 1987–1988, and 2004. In the Irish Sea, the spawning peak changes considerably between years, depending on water temperature (Nash and Geffen, 1999). The variation in water temperature between years in the North Sea was small (1948, 4–10°C; 1950, 5–10°C; 1987, 2–11°C; 1988, 4–9°C; 2004, 3–11°C), suggesting that if temperature was the causative mechanism, we would not be able to detect a change in the timing of peak spawning.

For back-calculating to egg production at spawning, it was considered that because sampling was continuous throughout day and night, the mean development duration of stage 1A eggs indicated the median of the 1A stage duration. This assumption is actually incorrect because of the exponential decline in fish egg numbers after spawning, which would result in an overestimate of egg production, depending on Z (Dickey-Collas *et al.*, 2003). However, the median stage duration was used for simplicity.

The plaice SSB time-series from 1957 to 2006 is for the North Sea only (i.e. not the eastern English Channel). There are no reliable absolute SSB estimates available for plaice in the eastern English Channel at present (area A, Figure 2; ICES Area VIId; see ICES, 2007), but an assessment indicative of trends is available. This shows broadly the same trends as for plaice in the North Sea. Therefore, it is likely that any AEP estimate that includes the English Channel should have a positive bias when compared with the assessment of the North Sea population only.

The results of our study were compared with a newly developed female-only XSA stock assessment (A. D. Rijnsdorp, IMARES, and L. T. Kell, Cefas, pers. comm.). This used sex-specific catch matrices adjusted for sexual dimorphism in growth and maturation (Rijnsdorp and Ibelings, 1991). Although that assessment did not use discard data, the estimation of SSB without discards is relatively robust (Dickey-Collas *et al.*, 2007) if the majority of discarded fish are not mature.

The current AEP estimate of North Sea plaice SSB broadly agrees with the current ICES standard XSA stock assessment. When the AEP method was used in other areas, SSBs from empirical ichthyoplankton data were found to be higher than the standard XSA results. In the Irish Sea, this has consistently been by a factor of 3 (Armstrong *et al.*, 2001) and attributed to a range of possible factors, including the selection pattern at age assumed in the assessment, the lack of discard estimates in the catch-at-age matrix of the assessment, changes in natural mortality, and the spatial mismatch of the fishery and the spawning of plaice. None of these has been proved thus far to be the cause of the discrepancy.

In the North Sea, the estimates from AEP and XSA appear to be similar. The decline in SSB from 1988 to 2004 was ~60% when

estimated by XSA and 50% when estimated by AEP. The AEP method supports the current ICES XSA stock assessment both in terms of the relative trend in SSB and the current absolute biomass. The AEP also suggests that most of the decline was in the Dogger Bank and German Bight areas. There appears to have been no major shift in the timing of spawning of North Sea plaice throughout the period of heavy exploitation. In the Southern Bight, SSB appears to have increased between the years 1982–1985 and 2004, but it is still lower than the biomass calculated for 1948 and 1950. However, the decline in SSB on the Dogger Bank seems to suggest a switch in the location of spawning areas from the Dogger Bank to the Southern Bight. During the past century, there were changes in the North Sea plankton community attributable to climate change (Fromentin and Planque, 1996; Beaugrand, 2003; Reid *et al.*, 2003), as well as changes in the benthic and fish community shown to be caused by fishing effects (Jennings *et al.*, 1999; Frid and Clark, 2000; Daan *et al.*, 2005). These factors probably also affected the North Sea plaice stock and its spawning, but it is difficult to disentangle the specific mechanisms.

Conducting an AEP is expensive in terms of ship and staff time. This may reflect the paucity of other studies that use AEP on flatfish. The AEP method can provide a useful validation of the trends in the outputs from age-based methods. In addition, it can provide the improved spatial resolution that tends to be lost when catch-and-effort data are amalgamated across large management areas. Because of the high cost of egg-based methods, they are probably most useful when applied periodically to validate trends in age-based stock assessments or in cases, such as North Sea or Irish Sea plaice, where there are particular uncertainties, such as the level of unrecorded discarding.

Acknowledgements

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