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The use of market sampling to generate maturity ogives and to investigate growth, sexual dimorphism and reproductive strategy in central and south-western North Sea sole (*Solea solea* L.)

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The influence of body size, age, geographical distribution, year and season on the sexual maturation of Dover sole (*Solea solea* L.) in the North Sea was investigated using market sampling data collected from fish landed by commercial fishing vessels at English ports on a monthly basis since 1983. A comparison was made with maturity estimates for sole derived from research vessel survey data. The market sampling data were summarized using general linear modelling and used to generate maturity ogives for sole. There are a number of uncertainties with this approach, stemming from the use of the commercial fishery to provide the fish samples and reliance on visual (macroscopic) staging to ascertain the stage of sexual maturation of the gonads. Despite the inability to resolve all uncertainties, it was felt that it should be feasible to derive general-purpose maturity ogives from market sampling data, and that these should be sufficiently reliable for use in assessing the spawning stock biomass of North Sea Dover sole. Male and female sole were shown to have different growth and reproductive strategies, with the emphasis being directed towards maximizing egg production.

Current stock assessments for sole assume that sexual maturation is knife-edged, with all fish maturing at 3 years of age. Evidence is presented to show that this approach is likely to inflate estimates of spawning stock size, since not all 3-year-olds spawn, and the proportion that do spawn varies annually. Size selection pressures resulting from commercial fishing practices are also likely to further inflate estimates of the spawning stock size. In addition, reproductive investment in first time spawning females was found to be substantially lower than in older established spawners, and it is the latter which are the first to become depleted through the pressure of sustained size-selective fishing. As a consequence, the current view of the state of well being of the North Sea sole spawning stock is likely to be overly optimistic.

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Introduction

One of the main criteria for judging the status of an exploited fish population is the size of the spawning stock. In the case of North Sea sole (*Solea solea* L.), the spawning stock biomass (SSB) is currently assessed analytically on an annual basis (ICES, 2001a). For this, a knife-edge maturity ogive is presently used, where all sole are assumed to fully mature at 3 years of age. This paper explores the possibility of deriving reliable maturity ogives based on samples of sole derived from the catch landed by the commercial fishery. This has the

potential to enable annual variability in maturity to be incorporated into stock assessments without the need for costly annual fishing surveys to measure maturity.

The study concentrates on data from the English North Sea sole fishery, which operates in the central and south-western North Sea and covers the principal range of distribution of Dover sole, apart from the south-eastern North Sea, where there is a substantial international sole fishery (CEFAS, 2001). Ideally, for stock assessment purposes, it is desirable to combine data from all the major North Sea sole fisheries. The present study is aimed at establishing the principles of the general approach to generating maturity ogives from market data. The main uncertainties with this approach relate to the appropriateness of attempting to apply results based on commercial landings to the wild stock, and to the reliability of implementing the visual (macroscopic) 7-stage key used to measure the stage of development of the gonads.

Fishing tends to deplete the proportion of the larger, older, sexually mature fish in the stock (Jennings *et al.*, 2001), leading to a smaller broodstock comprising of predominantly younger individuals. The relative reproductive investment and reproductive potential of young fish generally tends to be low compared to that of older fish (Oosthuizen and Daan, 1974; Ware, 1980; Trippel, 1999; Bromley, 2000; Cardinale and Arrhenius, 2000). This adds to the risk that the spawning stock might drop below a sustainable level in the face of continuing exploitation. Under these circumstances, errors in estimating the maturity ogive can bias the estimates of spawning stock biomass and distort the stock and recruitment relationship. This in turn affects the validity of the reference points based on spawning biomass, on which biological criteria for managing fisheries are largely founded (Murawski *et al.*, 2001).

For many years, age, length, weight and sexual maturity statistics for North Sea sole have been routinely collected at Lowestoft and other fishing ports along the east coast of England, as well as on research vessel surveys. These data were used to investigate the factors that influence sexual maturation, such as body size, age, geographical distribution, and their seasonal and annual trends. The reliability of using market-sampling data to generate maturity ogives to estimate spawning stock biomass is discussed.

Materials and methods

The study is based primarily on market sampling data collected from fish landed by commercial fishing vessels at English ports since 1983. Some of the methods used were similar to those applied to North Sea plaice (Bromley, 2000) and these are only summarized here. Most of the sole sampled were caught by trawling and

netting using a variety of gears with mesh sizes ranging from 80–110 mm. The minimum legal landing size of sole throughout the period of study was 24 cm. The fish were gutted at sea, with the gonads left *in situ*. The stage of sexual maturity of the gonads was ascertained for a length-stratified subset of approximately 100 fish per month. The total length of each fish was measured and, as far as possible depending on availability, equal numbers of fish were sampled for each 2 cm size category over the length range 23–44 cm, with fish of 45 cm and over being lumped into a single category. The fish were sexed and the stage of sexual maturation was ascertained by visual inspection of the exposed anterior region of the gonad using a seven-stage key (Table 1) modified after Winpenny (1953). Otoliths were removed for age determination, and the fish carcasses, which included the gonads, were individually weighed (W in g) and the total length of each fish was measured to the nearest cm below (L in cm). The condition factor of each fish carcass was calculated as $100*(W/L^3)$. Data from the fishing logbooks were used to identify the ICES rectangle where the fish were most likely to have been caught.

For statistical analysis purposes the data were not raised by catch rates since the location of the commercial fishing effort was variable and neither random nor in accordance with a pre-determined grid. Instead, a generalized linear model (GLM) was used to summarize the data and standardize for the impact of the main variables influencing sexual maturation. The form of the GLM used to investigate sexual maturation was:

$$\text{Logit } (E[y]) = I + R_i + Y_i + M_i + \beta_1 A + \beta_2 W \qquad (1)$$

In the model, the maturity status of each individual fish was input in binary form, taking the value 0 for immature gonads (MAT_1, i.e. gonads at maturity stage 1) and 1 for maturing or mature gonads (MAT_{2-7}, i.e. gonads at maturity stages ranging from 2 to 7). E[y], the estimated maturity level, represents the number of maturing and mature fish expressed as a proportion of the total (maturity level = nos. MAT_{2-7}/nos. MAT_{1-7}) for each class of predictor variable fitted in the GLM. E[y] is determined using a logit link function (Collett, 1991), where I = intercept and R_i, Y_i and M_i are fitted parameters for the class variables ICES square, year and month respectively. Co-variables in the model are A = fish age in years and W = body weight in g, with β_1 and β_2 being their respective fitted constants. The sexes were analysed separately.

Based on the monthly market sampling data, it was possible to monitor the sexual maturation cycle of sole, which is a serial spawner (Houghton *et al.*, 1985; Urban, 1991), on a seasonal basis. This enabled the construction of maturity ogives based on the spawning fraction of sole, which was assumed to be equivalent to the peak in the proportion (%) of fish with gonads that ranged from half-full to spent (Max MAT_{3-7}) over the course of the

Table 1. Sexual maturity stages of sole (modified after Winpenny, 1953).

Stage	Males	Females
1. Immature	Testes tight up against back of gut cavity and very small, usually not larger than about 0.2 cm	Ovaries small, normally extending less than 6 cm down side of body, thin walled and internally yellowish-orange in colour
2. Spent, recovering	Testes thin, redness lost. Occasionally a little sperm remaining in the ducts can be extruded under moderate pressure	All eggs reabsorbed, little or no slime inside ovaries
3. Half full	Testes filling, roughly half full, no sperm in ducts	Ovaries roughly half full with developing oocytes
4. Full	Testes fully swollen, but will not run, even with moderate pressure	Ovaries full, but no sign of hyaline eggs
5. Hydrated eggs	No stage 5 in males	Ovaries contain from few, to many hyaline eggs, but will not run, even under heavy pressure. Ovaries full varying to part full depending on the progress through spawning. Red colour appears in nearly spent ovaries
6. Running	A little sperm can be extruded under pressure	Eggs can be extruded under light pressure – females cycle between stage 5 and 6 as the spawning season progresses until spent
7. Spent	Testes thin, flabby and often red in places. Any remaining sperm in the gonoducts can be extruded under fairly light pressure	Ovaries contain a few, mainly opaque eggs, in a state of being reabsorbed, with much slime

spawning season (i.e. Max MAT_{3-7} is the maximum monthly value of nos. MAT_{3-7}/nos. MAT_{1-7}). Attempts were made to adjust the spawning fraction estimates to account for two sources of bias. The first entailed identifying adolescent females that had initiated ovarian recrudescence but which where unlikely to reach spawning condition. The second was to account for differences between the average maturity level of the sole landed commercially compared with the average maturity level of fish in the wild stock. Fishing, particularly for young sole that are not fully recruited into the fishery, is size selective and the average weight at age of the fish landed is likely to be higher than in the wild stock population (ICES, 2001a). Since the propensity to mature tends to be positively correlated with body size (Rijnsdorp and Iberlings, 1989), it is likely that maturity levels in the landings will be biased upwards. Males grow at a slower rate than females, and the size selection pressures are likely to be greater on males.

A comparison was made between the maturity estimates for 3-year-old sole derived from commercial landings in the 3rd quarter of the year (July–September) with those sampled on English Summer Groundfish Surveys in August–September from 1983–2000. This survey provides good spatial coverage of the North Sea as a whole.

The Grande Ouvriture Verticale trawl (GOV) used for surveys is a large otter trawl with a 20mm stretched mesh liner in the cod end, which retains fish of well below the minimum landing size. This should substantially diminish any impact of size selection and provide maturity estimates that are more representative of the situation in the wild sole stock. The survey trawl uses lightweight ground gear and is not as efficient at catching sole as are commercial trawls. However, sufficient 3-year-old sole were caught on the surveys to make a comparison with the average maturity level of sole landed commercially since 1983. Ideally, such a comparison is best made during the spawning season, but in lieu of available data, the comparison was made during the 3rd quarter of the year.

After adjustment for bias, the estimated mean spawning fraction for 3-year-old sole derived from market data was applied to annual ICES stock abundance estimates (ICES, 2001a) to ascertain the size of the North Sea sole spawning stock. A comparison was made with the spawning stock estimates derived by ICES, based on the assumption of knife-edged maturation at the age of 3 years. The impact of inter-annual variation in the maturity level of 3-year-old sole on the estimated size of the spawning stock was also investigated.
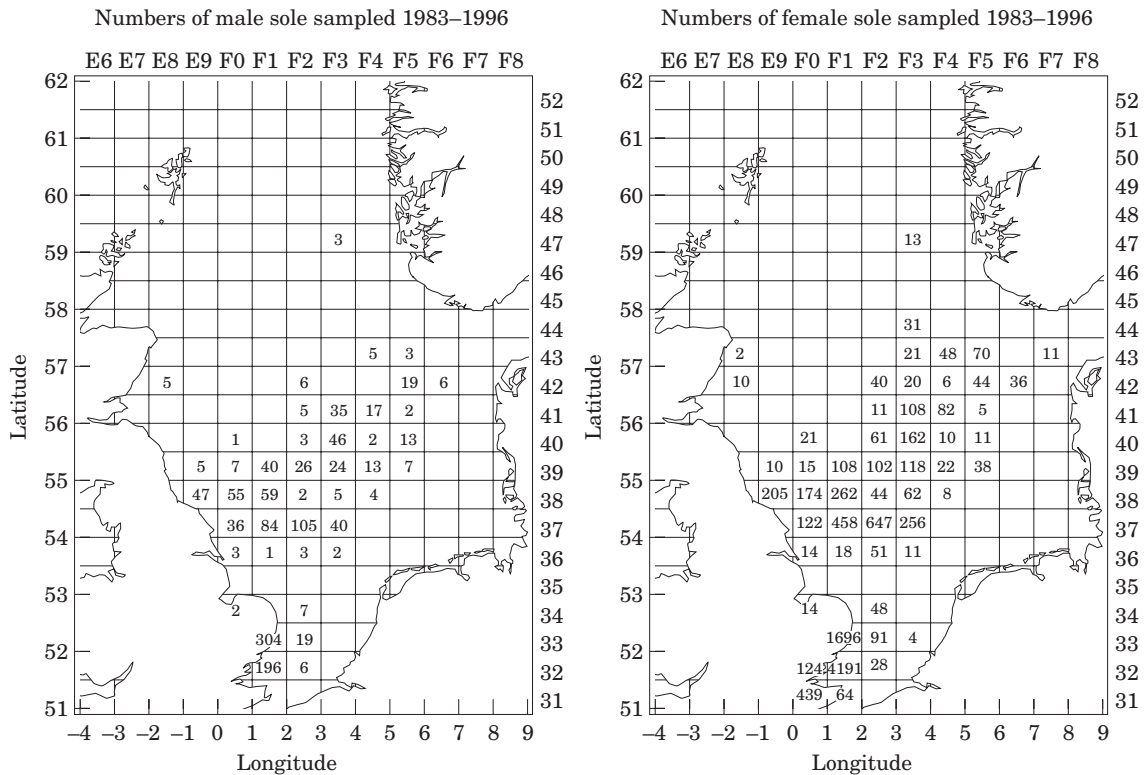
Numbers of male sole sampled 1983–1996

Numbers of female sole sampled 1983–1996

Figure 1. The numbers of North Sea sole sampled and their location of capture by the English fishing fleet over the period 1983–1996.

Results

Sampling

Of the sole sampled on English markets, 60% were landed at Lowestoft and the rest were from east coast ports between Lowestoft and West Mercia in the Blackwater estuary. The English fishery has an inshore and offshore component, the latter being restricted to the more central regions of the North Sea. The numbers of market sole sampled and their location of capture is shown in Figure 1. In total, 10 261 females were sampled at a rate of 29–97 fish per month, and 1288 males were sampled at a rate of 4–12 fish per month over the 14 years from 1983–1996. The number and age of the sole sampled are shown in Table 2. Though spawning takes place in the spring, the birth date of sole is regarded as 1 January for stock assessment purposes. During the first half of the year, which includes the spawning season, the 2-year-old males were too small to be landed and only 55 2-year-old females were available for sampling.

In addition to the market sampling data, maturity information was available for plaice caught on the North Sea annual English Summer Groundfish Surveys since 1983.

Sexual maturation cycle

Most of the 2-year-old females examined were immature, and although 20% showed signs of ovarian recrudescence, none of the ovaries were found to contain hyaline eggs and none were running with eggs, with only

Table 2. The number of North Sea sole sampled for age, weight, length and maturity on English fish markets over the period 1983–1996.

Age in years	Sex	
	Females	Males
2	524	80
3	1660	227
4	1961	258
5	1585	215
6	1046	137
7	848	104
8	605	49
9	495	46
10+	1537	172

one individual being classed as spent. This is consistent with the earlier findings (De Veen, 1970, 1976; Van Beek, 1985) for North Sea sole, and is indicative that most 2-year-old females showing signs of ovarian recrudescence were probably non-spawning adolescents. These are fish in which the ovaries abort development before reaching spawning status (Ramsay and Witthames, 1996), probably through atretic resorbtion of the vitellogenic oocytes (Hunter and Macewicz, 1985; Horwood, 1993; Witthames and Walker, 1995; Bromley *et al.*, 2000). Later in the year, after the spawning season, a third of the 2-year-old females sampled (Figure 2a) were classed as spent-recovering (stage 2). However, this is not proof of spawning since it is doubtful if the ovaries of resorbing virgins can be reliably distinguished from spent-recovering ovaries other than by histological investigation, as found for sea bass (Pawson *et al.*, 2000). The sole fishery lands only the largest 2-year-olds, and because of the strong positive correlation between maturity and body weight (Figure 3a), it is unlikely that significant numbers of smaller 2-year-olds, which were beneath the minimum landing size, would have matured.

Since the 2-year-old males were too small to be landed during the spawning season, it is not known what proportion matured. Later in the year, half of the 2-year-old males sampled were classed as spent-recovering, but, as was the case for females, it is uncertain if this reliably reflects the spawning fraction.

The progressive stages of gonad maturation are shown in Figure 2. Ovary recrudescence started around October in the year prior to spawning. Although, proportionally fewer 3-year-old females matured compared with older females, the timing of the maturation process was similar for all age groups (Figure 2a and b). By December the ovaries of most fish were classed as half-full (stage 3), becoming full (stage 4) by March, and reaching the hyaline egg phase (stage 5) in April, with the peak in running females (stage 6) occurring in April–May. By June, most females were spent or entering the spent/recovering phase (stage 2). Although in sole the testes are small in comparison with the ovaries, the timing of testes maturation spanned a similar time scale to that for ovarian development (Figure 2c). The proportion of males with full testes (stage 4) peaked in April, at the same time as the peak in the hyaline egg phase in females. Males produce small amounts of milt and, even in the case of live fish in hatchery conditions, they do not run freely if an attempt is made to strip them manually. As a consequence, males were rarely identified as running with sperm. It has generally been assumed that fish with enlarged testes are mature, but this does not appear to have been verified histologically, so that maturity estimates for males must be regarded as provisional.

Cyclical fluctuations in body weight and condition factor during the reproductive cycle

By 3 years of age, the first time spawning females were larger than the males (Figure 4). Female body weight followed an annual cycle, peaking at the start of the spawning season, and declining during spawning and beyond, before increasing again in the autumn. The amplitude of the decline in body weight increased with age. Overall, fewer males were sampled and the annual cycle of weight change was less distinct. In females, mean body length also tended to decline during and after the spawning phase. The amplitude of the decline in length ranged from 1–4 cm (Figure 4), being greatest in larger/older fish. A GLM of body length against ICES square, month and year showed significant ($p<0.05$) variations in length on a regional, seasonal and annual basis over the period March–June. Having standardized for the effects of year and ICES square, the monthly least-square mean lengths predicted by the GLM showed less variability than the unadjusted means, and provided no evidence of a consistent decline in length over the course of the spawning season. For example, in the case of 4-year-old females the predicted monthly least-square mean lengths ($\pm$ s.e.) over the period March–June were 27.3 cm (0.5), 27.3 cm (0.4), 28.4 cm (0.3) and 28.9 cm (0.3) respectively. The corresponding values for 9-year-old females from March–June were 40.2 cm (0.7), 40.5 cm (0.5), 40.0 cm (0.5) and 40.0 cm (0.5). The most likely explanation is that the dip in the unadjusted mean length-at-age of the females probably reflects seasonal shifts in the location of fishing effort into areas where the fish tended to be smaller. The predicted least square mean weight of the fish declined during and immediately after spawning, which can be expected due to the shedding of spawning products, but the dip was less pronounced than for the unadjusted means.

The average seasonal fluctuation in condition factor of sole is shown in Figure 5. The condition factor of the females followed an annual cycle, peaking prior to spawning as reproductive investment built up to a maximum, and then declined during spawning and beyond. The condition factor increased again later during the feeding phase in the summer and autumn. For females, the post-spawning hiatus in condition factor was fairly stable, ranging from 0.90–0.92. This indicates that as the females increase in size, the weight gain up to a condition factor of around 0.9 can be regarded as somatic growth, whilst the weight gain associated with the build up of the condition factor in excess of 0.9 can be regarded as "reproductive growth". This is destined either to be metabolized or shed as eggs during the spawning season (Rijnsdorp and Ibelings, 1989). In males, the decline in condition factor started earlier than for females – before spawning commenced. Whether this
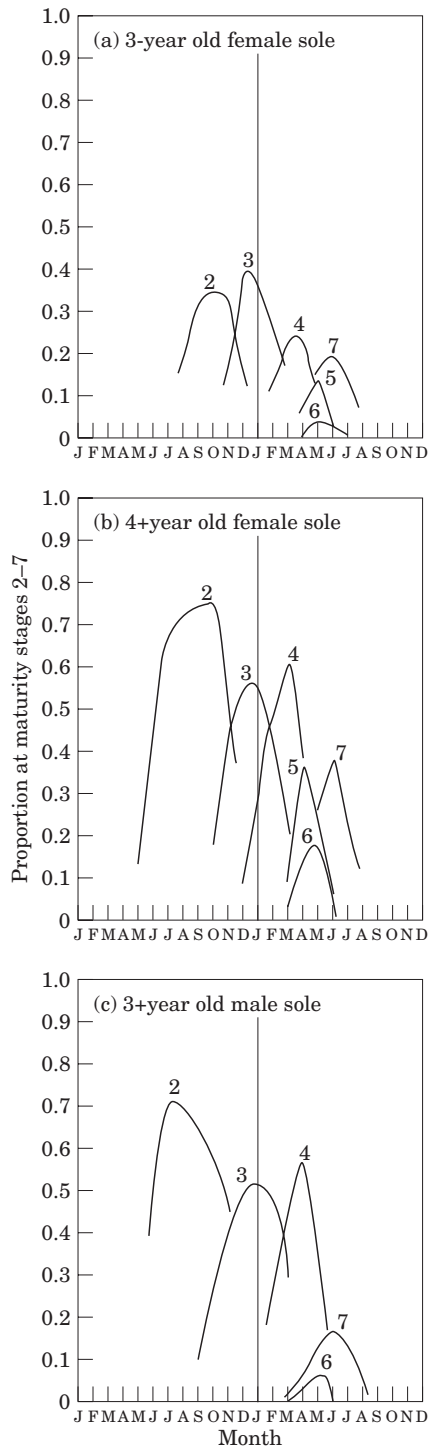
Figure 2. The progressive stages of sexual maturation in North Sea sole, (a) 3-year-old females, (b) females of 4-years-old and above, (c) males of 3-years-old and above. The vertical dotted line marks the transition from one age group to the next, and the age of the fish is in the year of spawning. In all cases, gonad recrudescence was initiated during the year prior to spawning. Based on English market sampling data from 1983–1996.
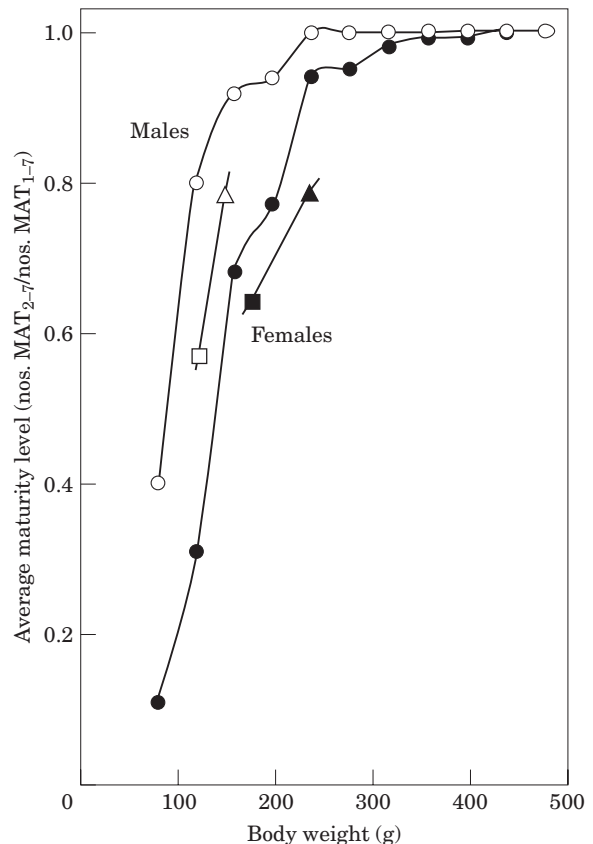

Figure 3. The relationship between average maturity level (nos. MAT_{2-7}/nos. MAT_{1-7}) and the body weight of North Sea sole for the period 1983–1996, (a) based on English market sampling data (males = ○, females = ●) collected during the spawning season, (b) 3-year-old fish sampled on English markets in summer (males = △, females = ▲) and on the English Summer Groundfish Surveys (males = □, females = ■)

relates to differences in feeding patterns or behavioural activities between the sexes is not known.

In 3-year-olds, the pre-spawning peak in condition was of similar magnitude in males and females. In older fish, the pre-spawning peak in condition was greater in females than in males, as was the drop in condition during the spawning season, indicative of greater reproductive investment in females compared with males. In females, the amplitude of the annual fluctuation in condition factor increased with age: in first time spawners the drop in condition during spawning was only about half the level observed in older established spawners. This indicates that reproductive investment in older females was higher, not only in absolute terms, but also in relative terms, compared with first time spawners. In males, the amplitude of the fluctuation in condition factor appeared to remain fairly stable with age, indicative that relative reproductive investment was independent of age. In males the post spawning hiatus in
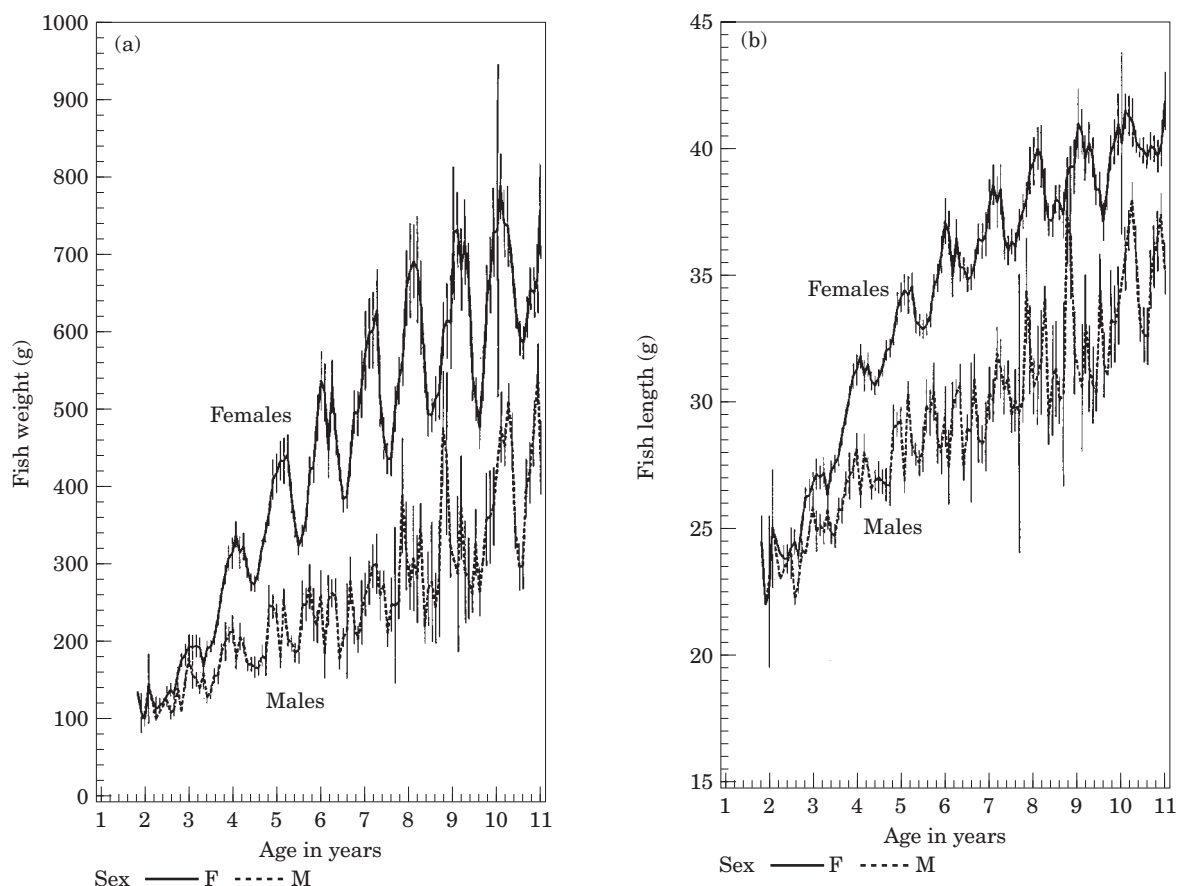
Figure 4. The average (a) weight $\pm$ s.d. and (b) length $\pm$ s.d. at age on a monthly basis for North Sea sole. This is for fish that were either maturing or mature (MAT_{2-7}), based on English market sampling data from 1983–1996.

condition factor was slightly lower than in females, averaging around 0.88, which suggests that as well as investing less on reproduction, the males also invest less on somatic growth than do females. Overall, the reproductive strategy in sole seems to be aimed at maximizing egg production in females and minimizing somatic growth and reproductive investment in males.

Since the fish length and weight data used in the above analysis were based on market samples they are liable to be subject to sampling bias, for example, in relation to where the fish were caught. Therefore, although the trends in growth and condition outlined above probably reflect those of fish in the wild stock, there are likely to be differences in the detail.

Factors influencing sexual maturity

General linear modelling (GLM, equation 1, Table 3) accounted for 52% of the deviance in the maturity level (nos. MAT_{2-7}/nos. MAT_{1-7}) of females and 33% in the case of male sole landed by the English fishery. The

chi-square test and fitted constants β_1 and β_2 (Table 3) indicated that the maturity level was primarily a positive function of body weight (as can be expected from Figure 3a), but, after standardizing for the influence of body weight, the GLM indicated that older individuals were more likely to mature than younger ones of equivalent weight. In males of equal weight, by contrast, the maturity level did not vary significantly with age. Obviously, body weight and age are strongly correlated and if body weight was omitted from the full GLM, age was strongly correlated with the maturity level in both females and males (p<0.0001). The full GLM showed significant inter-annual variability in maturity level (Table 3), particularly in 3-year-olds, where mean annual maturity level ranged from 59–82% in females and 60–100% in males over the 14 year study period. The parameter estimates derived from the GLM for the effect of year (Yi) on maturity level were not significantly correlated between the sexes (p=0.15), indicating that factors influencing the maturation of females did not appear to impact on the males in the same fashion.
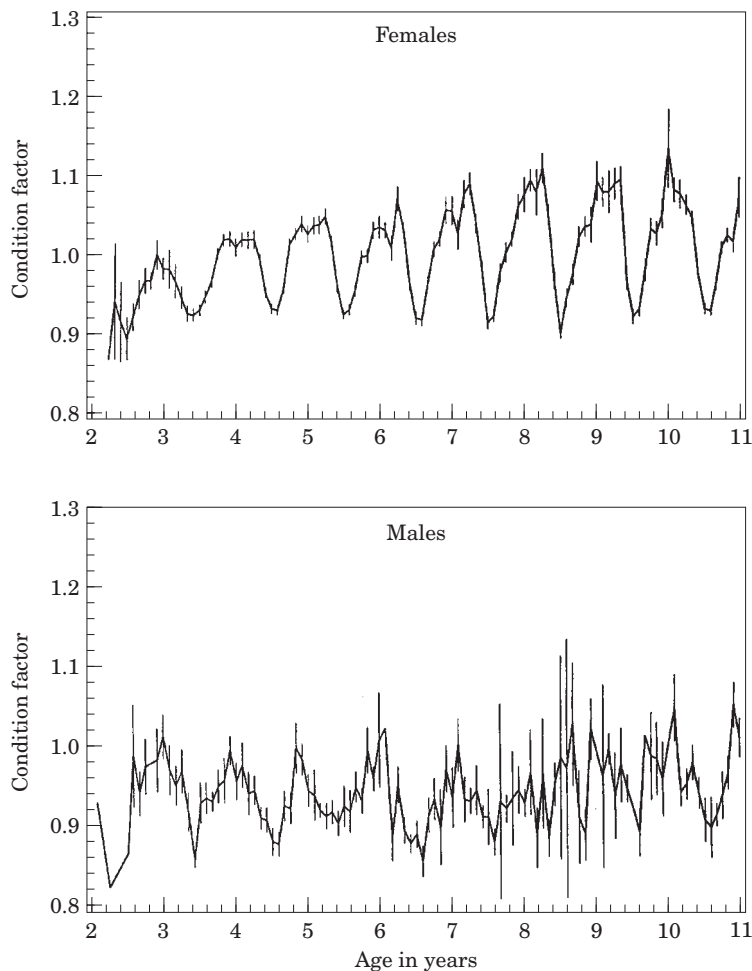
Figure 5. The average condition factor ± s.d. at age on a monthly basis for North Sea sole. This is for fish that were either maturing or mature (MAT$_{2-7}$), based on English market sampling data from 1983–1996.

The GLM parameter estimate Mi, for the impact of month on maturity level (Table 3), showed that average maturity levels varied significantly on a seasonal basis (Figure 6). Changes in the maturity level of 3-year-olds during the year can be expected as increasing proportions of virgin fish start to mature for first time as the spawning season approaches. However, there was evidence of a general post-spawning decline in the proportion of sole classed as mature (Figure 6), which was manifest across the age groups: the significance of which is uncertain and is discussed later. In females, but not males the maturity level varied significantly in relation to the ICES square where the fish were caught (Table 3), indicative of regional variations in the rate at which North Sea sole mature. Based on the proportion of running females in the fish sampled on the markets in the spring, a principal sole spawning site is located off the Thames estuary in ICES squares 31F0 and 32F1 in the Southern Bight (Figure 1).

The construction of maturity ogives from market data

For the purposes of constructing a maturity ogive, it was assumed that 2-year-old female sole were predominantly adolescents that did not spawn. The spawning fraction of 2-year-old males was impossible to ascertain with any certainty.

Because the maturity level varied seasonally and because of doubts over the reliability of visual staging when the gonads are in the inter-spawning phase, only observations made around the time of spawning were used to generate maturity ogives based on estimates of the spawning fraction (the proportion of fish that spawn) of sole. The market sampling data enabled changes in maturity to be tracked on a monthly basis, facilitating the build up a cumulative picture of the proportion of mature fish in the landings over the course of the spawning season. The peak in the proportion of

Table 3. Analysis of deviance of GLM of sole maturity using Lowestoft market sampling data for the period 1983–96, based on equation 1. Type III (Wald) tests show the significance of removing individual variables from the full model.

Source of deviance	Degrees of freedom	Deviance	Deviance ÷ degrees of freedom	p
Females				
Analysis of deviance				
Proportion of deviance accounted for by the model=52%				
Model	78	3316	42.5	0.0001
Error	10 188	3015	0.29	
Total	10 266	6332		

Source of deviance	Degrees of freedom	Chi-square	p	
Type III (Wald) tests				
ICES square	52	334.5	0.0001	
Year	13	62.9	0.0001	
Month	11	72.4	0.0001	
Age	1	14.1	0.0002 ($\beta_1=0.214$, s.e. ± 0.057, p=0.0002)	
Fish weight	1	558.5	0.0001 ($\beta_2=0.023$, s.e. ± 0.001, p=0.0001)	

Source of deviance	Degrees of freedom	Deviance	Deviance ÷ degrees of freedom	p
Males				
Analysis of deviance				
Proportion of deviance accounted for by the model=33%				
Model	90	282	4.1	0.0001
Error	7781	516	0.42	
Total	7871	798		

Source of deviance	Degrees of freedom	Chi-square	p	
Type III (Wald) tests				
Square	43	23.0	0.99	
Year	13	22.7	0.05	
Month	11	38.8	0.0001	
Age	1	0.06	0.80 ($\beta_1=-0.02$, s.e. ± 0.09, p=0.80)	
Fish weight	1	53.1	0.0001 ($\beta_2=0.024$, s.e. ± 0.003, p=0.0001)	

fish with gonads classed as ranging from half-full to spent (Max MAT_{3-7}) occurred at the end of the spawning season in May for both sexes and all age groups, and this value provided an initial estimate of the average spawning fraction for sole. In 3-year-old females Max MAT_{3-7} was 60% and in males it was 82%. However, in May, the ovaries of 3% of the 3-year-old females were classed as half-full, and since it is doubtful if the vitellogenic oocytes in such ovaries would have had time to fully develop into eggs before the end of the spawning season (Ramsay and Witthames, 1996), it was assumed that such fish were probably non-spawning adolescents. The estimate of the spawning fraction based on Max MAT_{3-7} was adjusted downwards accordingly. By 4 years of age, most females (Max $MAT_{3-7}=97\%$) and virtually all males (Max $MAT_{3-7}=100\%$) appeared to be fully mature.

Because of incomplete recruitment of young sole into the fishery, estimates of maturity level (nos. MAT_{2-7}/nos. MAT_{1-7}) based on landings of the younger age groups of sole are liable to be biased upwards compared to the average maturity level of fish in the wild stock. A comparison of the average length, weight and maturity level of 3-year-old sole landed commercially during the summer with fish caught on the North Sea English Summer Groundfish Surveys (Woolner and Pope, 1983)
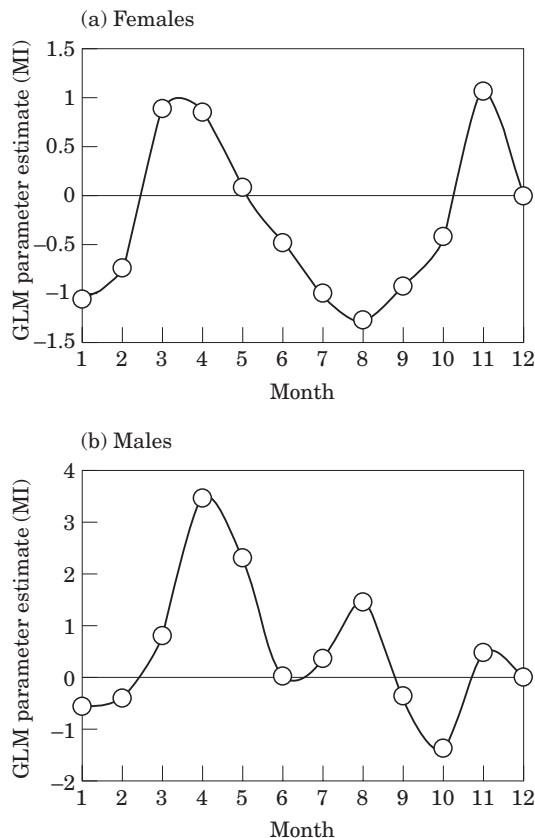
Figure 6. Seasonal trends in North Sea sole maturity, as exemplified by fluctuations in the parameter estimate Mi derived from GLM for the impact of month on maturity level (see equation 1, and Table 3), based on English market sampling data from 1983–1996.

is shown in Table 4. Most of the sole were caught in the southern half of the North Sea, corresponding with ICES area IVc, and the comparison made in Table 4 is for fish caught in this area. The 3-year-old sole landed commercially were on average larger and the maturity level was on average 15% higher for females and 21% higher for males compared with the fish caught on the surveys (Figure 3b). The maturity level of fish caught in the summer was lower than at the time of spawning earlier in the year (Figure 3b), but the slope of the relationship between maturity level and body weight in the summer was similar to that during the spawning season. This suggests that the difference in maturity level between market and survey fish in the summer probably stemmed from differences in the mean body size of the fish being sampled. On the assumption that the difference in maturity level between the market and survey data in the 2nd quarter of the year was of the same order as in the summer (3rd quarter), the spawning fraction estimates (max MAT_{3-7}) for 3-year-old sole were adjusted downwards to account for the impact of size

selection associated with commercial fishing practices. The adjusted estimate of the spawning fraction was 42% for 3-year-old females and 61% for 3-year-old males.

Current stock assessments of North Sea sole are for sexes combined (ICES, 2001a). Based on data for 3-year-old sole sampled on English markets since 1983, which includes fish which were not subjected to maturity staging, the sex ratio of females to males was 2.6:1 (13 200 fish sampled). This compares with a sex ratio of 1.3:1 (total of 4400 fish sampled) on the English Summer Groundfish Surveys, where the impact of size selection on the sex ratio in favour of females should be substantially diminished. In practice, it is likely that the sex ratio of 3-year-old sole in the wild stock is probably fairly close to unity, and assuming a 50:50 sex ratio, the average proportion of spawning 3-year-old sole in the wild stock would be 51% by numbers for the sexes combined.

If, as in current North Sea sole stock assessments, it is assumed that maturation is knife-edged at the age of 3 years (ICES, 2001a), but only 51% of 3-year-olds actually spawn, the spawning stock size will be overestimated. In the case of North Sea sole from 1960–2000 (ICES, 2001a), the annual number of spawning sole would be overestimated by 2–53% compared with fish in the wild stock (Figure 7). The extent of the bias appears to be largely dependent on the size of the 3-year-old yearclass; the larger the yearclass, the greater the discrepancy. There is some evidence of an upward trend in the overestimation of the spawning fraction over time (Figure 7), possibly related to the increase in the ratio of young to old fish in the stock due to the preferential depletion of older sole through the sustained pressure of size-selective fishing (ICES, 2001a).

In some years, too few 3-year-olds were sampled on the English markets in May to get a reliable annual update of the spawning fraction based on Max MAT_{3-7}. In order to get an indication of the annual variability in maturity on estimates of sole spawning stock size, average annual maturity levels for 3-year-olds (nos. MAT_{2-7}/nos. MAT_{1-7}) were used. Based on these values, which were not adjusted for seasonal variation in maturity, bias due to non-spawning adolescents nor for the impact of size selection, the resultant overestimation of the size of the sole spawning stock size on a year by year basis from 1983–1996 (Figure 7) showed a fairly similar trend to that based on the average spawning fraction (Figure 7). The big difference in the absolute values between the two datasets was largely because the annual maturity levels were not adjusted for sampling bias.

Discussion

North Sea sole appear to share many similarities with North Sea plaice (*Pleuronectes plattessa* L.) (Bromley,

Table 4. Comparison of the mean length, weight and maturity level of southern North Sea sole (ICES area IVC) for fish landed from the commercial fishery in the 3rd quarter of the year (July–September) and fish caught on the English Summer Groundfish Survey (August/September) from 1983–2000.

	Market sampling data ± s.e.		Fishing survey data ± s.e.		Difference	
Females						
Length (cm)	28.5 ± 1.1	(N=975)	27.0 ± 0.2	(N=154)	1.5 cm	(5%)
Weight (g)	237[a] ± 2		182 ± 4		55 g	(30%)
Maturity level (%)	78 ± 1		63 ± 4		15%	
Males						
Length (cm)	25.7 ± 0.2	(N=199)	23.8 ± 0.2	(N=94)	1.9 cm	(8%)
Weight (g)	166[a] ± 4		118 ± 3		48 g	(41%)
Maturity level (%)	78 ± 5		57 ± 5		21%	

[a]The gut-free landed weight was adjusted upwards by multiplying by a correction factor of 1.05 (Bedford *et al.*, 1986) to provide an estimate of the whole body weight of fish landed on the market for comparison with the fish caught and weighed whole on the English Summer Groundfish Surveys.
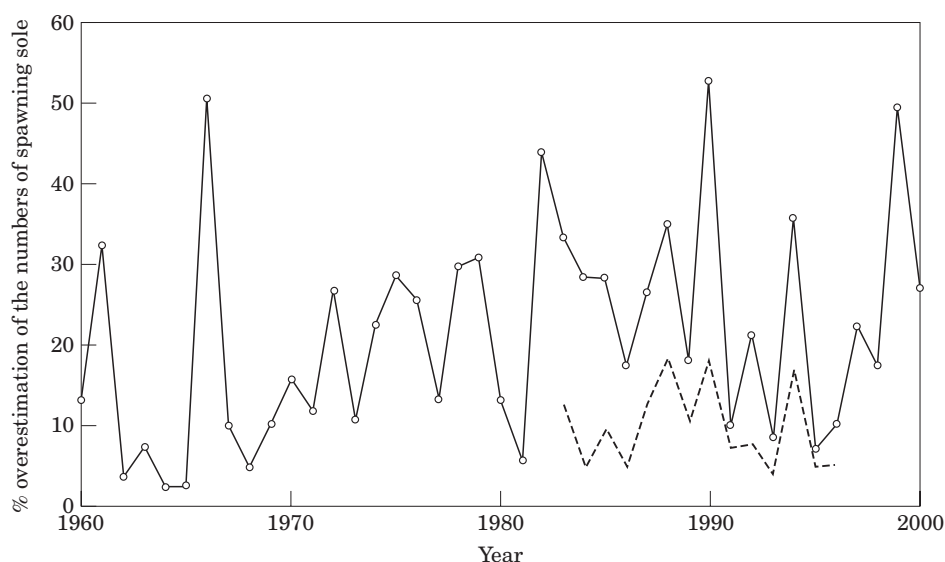

Figure 7. The percentage overestimation of the total number of spawning North Sea sole for the period 1960–2000 (solid line and open circles) if it is assumed that 100% rather than 51% of 3-year-olds spawn (i.e. after the market data had been adjustment for sampling bias). The dotted line represents the overestimation of the size of the sole spawning stock based on the annual mean maturity levels for 3-year-olds derived from English market sampling data for individual years from 1983–1996 (these data were not adjusted for sampling bias).

2000). The males tend to mature earlier and at a smaller size, whereas females grow larger, mature later and tend to invest relatively more resources on reproduction. In females, but not males, the relative reproductive investment also increases with age, as in plaice (Rijnsdorp and Iberlings, 1989) and turbot (*Scophthalmus maximus* L.), where relative realized fecundity has been observed to increase with age (Bromley *et al.*, 1986). At the population level, the strategy is likely to have the advantage of maximizing the proportion of the available food resources that can be diverted into egg production, whilst reducing the amount of food that needs to be

allocated for somatic growth and reproductive investment in males. This might give flatfish a reproductive advantage compared with fish that do not practice sexual dimorphism to a comparable degree.

An apparent decline in the length-at-age of females during the spawning phase has also been observed in market sampling data for North Sea plaice (Bromley, 2000). Whilst some shrinkage in length might accompany the loss of body reserves and spawning products, the magnitude of the decline in length points to a possible sampling problem. The inshore English sole fishery tends to target spawning fish and if the largest

individuals within cohorts spawn first, followed by smaller individuals spawn later, as observed in plaice (Horwood, 1990; Arnold and Metcalfe, 1995), this would be manifest as an apparent decrease in length at age as the spawning season progressed. The least square mean lengths predicted by the GLM after standardizing for regional variation in the location (ICES square) of fishing effort tended to be fairly stable over the course of the spawning season, suggesting the apparent decline in fish length might be caused by the location of fishing effort shifting to sites where the fish were somewhat smaller towards the end of the spawning season. However, more research is needed to verify if this is the case.

There was also evidence of a post-spawning decline in maturity level in the landed catch (Figure 6). Possibly, when spent gonads progress to the spent/recovering phase there might be a bias towards classifying them as immature. Alternatively, if immature sole move towards the spawning areas later in the season, as observed in plaice (Arnold and Metcalfe, 1995) and cod (Trout, 1957), this would be manifested as an apparent decline in the maturity level at the end of the spawning phase. Alternatively, fishing effort might shift to areas where not only are the fish smaller, but maturity levels are lower. Further research is needed to clarify the situation.

If there are significant numbers of non-spawning fish dispersed away from the areas of fishing activity, the maturity estimates based on the landings are liable to be biased upwards compared with the stock as a whole. Additional fishing surveys away from the spawning areas fished commercially are needed to quantify the extent of any such bias in the case of North Sea sole.

In addition to the uncertainties outlined above, the spawning fraction of 2-year-old male sole, which were too small to be landed commercially, could not be ascertained and requires further investigation. Most 2-year-old females were either immature or else if they started maturing they probably ended up as non-spawning adolescents, which is consistent with earlier findings (De Veen, 1970, 1976; Van Beek, 1985). Even though there is evidence of climatic warming in the North Sea in recent years (Reed *et al.* 2001), this does not appear to have had a significant impact on the proportion of 2-year-old females reaching spawning condition. Since male sole only produce small amounts of milt and are rarely found in running condition, other techniques, such as histological screening, are needed to help resolve the question of how many reach spawning condition. In greenback flounder, for example, macroscopic changes in maturity stage may not always be accompanied by significant changes in proportions of gamete types in the testis (Barnett and Pankhurst, 1999).

Size selective pressures associated with the commercial fishing practices include the selectivity of the fishing gear itself, the necessity to discard under-sized fish, and,

because of the limited regional coverage of the commercial fishery, the fish sampled might not be representative of the wild stock as a whole. If the impact of size selection pressures operating in the commercial fishery and also the bias associated with the presence of non-spawning adolescents are not taken into account, the spawning faction and consequently, the size of the spawning stock risks being overestimated. There have been a number of recent studies of sole maturation (Van Beek, 1988; Millner *et al.*, 1991; Witthames and Walker, 1995), but with apparently little attention paid towards quantifying the impact of size selection during fish capture. Van Beek (1985) analysed Dutch market sampling data for sole from 1962–1984. He found an average maturity level of 60% in 3-year-old females, which is similar to the spawning fraction in the present study, prior to it being adjusted downwards to account for bias. Van Beek (1985) obtained an average maturity level of 95% in 4-year-old female North Sea sole, which is also close the estimate of the spawning fraction found in the present study. As a consequence, it would appear that data derived from the English sole fishery can be regarded as reasonably representative of the North Sea in general. In a histological study (Ramsay and Witthames, 1996), using material gathered on a research vessel survey, which is less likely to be susceptible to size selection than market data, it was concluded from the potential growth rate of sole vitellogenic oocytes that 60% of 3-year-old female sole spawn in the English Channel, which is on a par with the unadjusted estimate of the spawning fraction for the North Sea, but greater than for the adjusted estimate of the spawning fraction of 42% obtained in the present study for North Sea females. Possibly, sole in the Channel benefit from the warmer winter temperatures during the sexual maturation phase.

As in the present study, Van Beek (1985) and Rijnsdorp and Vethaak (1997) found annual variation in the maturity of 3-year-old females, which was of similar magnitude to that found in the present study. Experiments on first time spawning turbot pointed to food availability as a factor influencing the proportion of females maturing for the first time (Bromley *et al.*, 2000), but not for males. If food availability varies inter-annually, this might explain why inter-annual variability in maturity levels in the two sexes did not show parallel trends through time in sole.

Some uncertainties remain on the reliability of maturity data derived using visual staging. In females, as well as males, quality control measures and histological screening (Ramsay and Witthames, 1996) offer the possibility of verifying the precision of visual staging and the possibility of generating reliable confidence limits for the maturity estimates.

Applying knife-edged maturity ogives inappropriately can cause serious bias in estimates of the number of

spawning fish in the stock. Assuming 100% maturity for 3-year-old North Sea sole, when on average only 51% spawn, led to the total number spawning sole being overestimated by from 2–53% between years, depending on the yearclass strength. If the mean weight of the 3-year-old sole landed by the commercial fishery is 30% greater for females and 41% higher for males compared with fish in the wild stock, as implied by the survey data, the numbers of spawning sole and the spawning stock biomass estimates are liable to be considerably over inflated. The overestimation of the sole spawning stock size in the stock assessments stems mainly from the knife edged maturity ogive which assume that all 3-year-old sole spawn and from size selection pressures associated with commercial fishing practices.

Any tendency to overestimate the spawning stock size is exacerbated by the observation that reproductive investment in first time spawning females appeared to be only about half that of older, established spawners. The differential removal of older mature sole though fishing is likely not only lead to a drop in spawning stock biomass, but also to a drop in the relative reproductive fitness of the residual spawning stock. A similar scenario has been observed in cod (Marshall *et al.*, 2000; Marteinsdottir and Thorarinsson, 1998). In this situation, applying a fixed maturity ogive, particularly one that overestimates the maturity level and does not accommodate the poorer reproductive fitness of young fish could seriously overestimate the egg production capacity of the stock, leading to an underestimate of the impact of fishing and to a false sense of security over the well being of the sole spawning stock. In terms of managing the sole fishery (and other heavily exploited stocks) an expedient approach would be to ascertain as precisely as possible the spawning fraction of young fish in the stock and scale down their biomass in proportion to any reduction in their reproductive potential.

An increase in the condition factor of sole is feeding related and is accompanied by the laying down of both protein and lipid reserves (Bromley, 1971, 1974). In pre-spawning sole, the degree of elevation of the condition factor above the somatic growth baseline (condition factor ca. 0.9) can be regarded as a measure of reproductive investment. This in turn is likely to be a reflection of the reproductive potential of the fish, since the more reserves a fish has the greater its likely potential for producing eggs (Marshall *et al.*, 1998), either in terms of numbers or size, or a combination of the two. It might be possible, therefore, to use the amplitude of the spawning related fluctuation in condition factor as an index of reproductive potential in order to scale the contribution each age group of sole makes to the spawning stock in terms of its egg production capacity. This would be advantageous for the purposes of investigating stock and recruitment relationships, since the resulting spawning stock biomass estimate should provide an improved index of the potential capacity of the stock to procreate. Current stock assessment methods have tended to simply sum the total biomass of spawning fish across size groups on a pro-rata basis, which in effect is the same as making the assumption that reproductive investment/potential does not vary with age. The present findings for sole do not support such an assumption, which is in line with a number of other studies on a variety of fish species (Rijnsdorp *et al.*, 1991; Marshall *et al.*, 1998). Only recently has there been a concerted effort to rectify this situation for stock assessment purposes (ICES, 2001b).

In conclusion, it is presently feasible to quantify some, but not to eliminate all likely sources of biases in the maturity estimates of sole based on market sampling data. However, given that stock assessments based on virtual population analysis are themselves likely to contain bias, the magnitude of which is uncertain (Hilborn and Walters, 1992), the adjusted estimates of the spawning fraction of sole derived from market sampling are probably acceptable for use in estimating the spawning stock biomass of North Sea sole. The advantage of deriving estimates of the spawning fraction from market sampling is that the maturity ogive could be updated on an annual basis, without the need for costly annual research vessel surveys. The market sampling effort should be concentrated during the spawning season, particularly on fish under 5 years of age, at the time of peak spawning in May, rather than during the inter-spawning phase when the reliability of visual staging of maturity appears to be somewhat problematical. This would open up the potential for incorporating greater biological and dynamic realism into efforts aimed at improving the efficacy of stock assessment procedures. However, it has to be borne in mind that biases in market sampling data can have such a big impact on the perceived size of the spawning stock that there is little point in updating the maturity estimates annually if the major sources of bias cannot be identified and quantified.

Acknowledgements

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