Bayesian Assessment of Northeast Atlantic Spurdog Using a Stock Production Model, with Prior for Intrinsic Population Growth Rate Set by Demographic Methods

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Abstract

Schaefer-model stock assessments can be imprecise when they are fitted to catch rate data (CPUE) because a large, unproductive stock can often explain CPUE trends as well as a small, productive one. However, consideration of life-history characteristics can improve parameter estimates by constraining maximum productivity. Therefore, we applied the methods of McAllister *et al.* (2001) to Northeast Atlantic spurdog (*Squalus acanthias)* by using demographic techniques to convert prior distributions for age-specific fecundity and natural mortality (the latter based on published estimates from tagging studies) to prior distributions for the intrinsic rate of population growth (*r*). The priors for *r* generated in this manner were then used in a Bayesian, Schaefer-model assessment of spurdog, fitted to bottom trawl survey CPUE data. Results suggest the stock is depleted to about 5% of virgin biomass.

Key words: age, assessment, biomass, catch, effort, fecundity, growth, population, spurdog

Introduction

Distribution

Spurdog (*Squalus acanthias* Linnaeus, 1758) is a relatively small (<120 cm total length) squaliform shark that occurs in temperate and boreal waters of the Northwest Atlantic (Cuba to Greenland), Northeast Atlantic (Barents Sea to Morocco, Mediterranean and Black Seas), Southwest Atlantic (Uruguay to Argentina) and Southeast Atlantic (South Africa). It also occurs in the North Pacific (Japan to Mexico, including the Bering Sea) in the South Pacific (Chile, New Zealand and southern Australia) (Compagno, 1984). *Squalus acanthias* have been caught at depths down to 900m (Compagno, 1984), although they tend to occur in waters of 10–200 m in the Northeast Atlantic (McEachran and Branstetter, 1989).

Life-history

Squalus acanthias is aplacentally viviparous, with embryos reliant on the yolk sac during development, and the reproductive biology is well documented (Hisaw and Albert, 1947; Gilbert and Heath, 1972; Tsang and Callard, 1987). Length at sexual maturity is reported for several areas (Table 1) and, within the Northeast Atlantic, female *S. acanthias* start to mature at 69–73 cm, and 50% are mature at 74–83 cm. Gauld (1979) recorded maximum fecundity values of 16 (oocytes), 14 (candled embryos) and 13 (free embryos). Elsewhere, fecundity estimates range from 1–16 for New Zealand waters (Hanchet, 1988)

and 4–32 (average = 14) in the Black Sea (Kirnosova, 1989), with fecundity increasing with size. Gestation lasts about 22–24 months and the sex ratio of pups is about 1:1 (Gauld, 1979; Hanchet, 1988). Estimates of mean size at birth are 27.5 cm (Holden and Meadows, 1964) and 26 cm (range = 19–30 cm, Gauld, 1989) in the Northeast Atlantic; 24 cm (range = 18–30 cm) off New Zealand (Hanchet, 1988), and 26–27 cm in the Northeast Pacific (Ketchen, 1972). Pup size increases with maternal length (Hanchet, 1988).

Several investigators have used the annuli on the second dorsal spine for estimating age and growth parameters (Table 2), and such data are available for Northwest Atlantic (Soldat, 1982), Northeast Atlantic (Holden and Meadows, 1962; Tucker, 1985) and Northeast Pacific stocks (Beamish and McFarlane, 1985; McFarlane and Beamish, 1987). Recent tag returns have cast doubt on the precision of reading annuli on the spines, at least for Atlantic specimens (Martin Vince, CEFAS, pers. comm.), so caution should be used when using age data. Other methods of ageing *S. acanthias* include x-ray spectrometry (Jones and Geen, 1977a) and the size of the eye lens (Siezen, 1989). The observed maximum sizes of male and female *S. acanthias,* reviewed by Ketchen (1972), were 100 and 135cm (Northwest Pacific), 107 and 130 cm (Northeast Pacific), 86 and 108 cm (Northwest Atlantic) and 83 and 110 cm (Northeast Atlantic). Market sampling in the UK has recorded female spurdog up to 124 cm long.

TABLE 1. Size at maturity of female and male *Squalus acanthias*.

Area	Length at maturity (cm)			Author
	First	50%	100%	
Females				
NE Atlantic	60–64	–	–	Hickling (1930)
	73	82	96	Holden and Meadows (1964)
	71	83	94	Gauld (1979)
	69	74	86	Fahy (1988, 1989)
NW Atlantic	76	77.9	86	Nammack *et al.*, (1985)
Black Sea	97.7–116.3	–	–	Kirnosova (1989)
New Zealand	65	71.5–74	82	Hanchet (1988)
NE Pacific	76	93.5	118	Ketchen (1972), Jones and Geen (1977b)
Males				
NE Atlantic	55	59–60	64	Hickling (1930)
NW Atlantic	58	59.5	63	Nammack *et al.* (1985)
Black Sea	81.7–96.3	–	–	Kirnosova (1989)
New Zealand	53	57.5	64	Hanchet (1988)
NE Pacific	–	78.5	–	Jones and Geen (1977b)

TABLE 2. Von Bertalanffy growth parameters for *Squalus acanthias* .

Region	Sex	L_∞ (cm)	K	t_0 (years)	Author
Ireland	Male	79.9	0.16	-1.69	Fahy (1988, 1989)
	Female	98.8	0.19	-1.57	
British Isles	Male	79.9 (86.0)	0.21 (0.14)	-2.0 (-3.13)	Holden & Meadows (1962)[1]
	Female	101.4 (104.0)	0.11 (0.11)	-3.6 (-3.28)	
North Sea	Male	81.7	0.19	-1.47	Sosinski (1977)
	Female	137.1	0.05	-4.71	
	Total	101.5	0.10	-3049	
NE Pacific	Male	99.8	0.070	-4.70	Ketchen (1975)
	Female	125.3	0.048	-4.88	
NW Atlantic	Male	82.49	0.148	-2.67	Nammack *et al.* (1985)
	Female	100.5	0.1067	-2.90	

[1] Original data and recalculated values (as given by Fahy (1989)) in parentheses.

Movements and migrations

Extensive tagging studies conducted by British and Norwegian scientists since the late 1950s have tagged several thousand spurdog (e.g. Holden, 1967; Gauld and MacDonald, 1982). Initial tagging programmes focused on populations in the northern North Sea and off Northwest Scotland, and fish tagged off Scotland were regularly recaptured off the Norwegian coast (Aasen, 1960), suggesting a winter migration from Scotland to Norway, with a return migration in summer (Aasen, 1962). Whereas there were some recaptures from outside the area, including the Barents Sea and west of Ireland (Aasen, 1963), and southern North Sea, English Channel and northern Bay of Biscay (Holden, 1966, 1967), the majority of returned fish were from Scottish and Norwegian waters, where the major fisheries occurred, and may reflect spatial differences in fishing activity. Hence, Scottish-Norwegian and Channel stocks were originally distinguished (Holden, 1965, 1967, 1968). Although fewer fish were tagged in the south, fish tagged in the Irish Sea were recaptured from northern Scotland to the Celtic Sea (Holden, 1962), and fish tagged in the Celtic Sea were recaptured all around the British Isles (Vince, 1991). Hjertenes (1980) also reported that migration patterns of *S. acanthias* in the North Sea had changed, and that they were more frequent in the southern North Sea. Furthermore, the most recent analyses of tagging studies suggested a single Northeast Atlantic

stock (Vince, 1991). Although transatlantic migrations have occurred (Templeman, 1954, 1984), such cases are infrequent and Northeast and Northwest Atlantic stocks should be treated independently.

Fisheries

Spurdog are the most commercially important shark species in Northwest Europe. During the early 1900s, they were of little economic value and landings were small. During the 1950s and 1960s, landings of spurdog in the North Sea increased rapidly and total annual landings rose to 58 000 tons (t) during the 1960s. During the 1980s, longline fisheries for spurdog became relatively important in the Irish Sea, with boats targeting shoals of large females, with this fishery subsequently declining. Spurdog are currently taken in mixed demersal fisheries (e.g. otter trawls), and are also targeted in localised longline and gillnet fisheries (Fahy and Gleeson, 1990; Fahy, 1992). Since the late 1980s, total landings of spurdog have declined, and recent catches (1997–99) are around 15 000 tons per year.

The major European fishing nations for spurdog are the UK, Norway, Ireland and France, with Germany, Denmark, Poland, Belgium and Portugal landing smaller quantities. ICES landings data indicate that *S. acanthias* is caught primarily in the Norwegian Sea, Kattegat, Skagerrak, North Sea, Hebridean Sea, Irish Sea, English Channel, Bristol Channel, Celtic Sea and west of Ireland. There are some landings from the Bay of Biscay and Iberian waters, but it is possible that these landings also include *S. blainvillei*. Small quantities are also taken from off Greenland and Barents Sea, though these areas are considered to be outside the main stock area.

The primary aim of this paper is to incorporate published biological information into a Schaefer-model stock assessment for spurdog in the Northeast Atlantic using Bayesian priors, as recommended by McAllister *et al.* (2001). Incorporating such information can be important in situations where data are not very informative about model parameters, a common occurrence in fitting biomass dynamics models. It is especially important to prevent the data from leading to high estimates of productivity for species that are probably K selected.

Methods

The first step in this analysis was to convert prior distributions for age-specific fecundity, maturity and natural mortality to prior distributions for the intrinsic rate of population growth (r). This conversion was done using a demographic method, namely the numerical Leslie matrix projection approach described in McAllister *et al.* (2001) and reproduced below. While converting three prior distributions into one might seem to complicate the problem, the task was actually facilitated by available life history data, which were used to construct the additional priors.

Demographic analyses require age-specific estimates of length, fecundity and maturity. They also require information on mortality, which is discussed below. The measurements behind these estimates should be obtained from a depleted population, in which density dependent effects may be considered negligible. Here, the information was based on published estimates of mean length at age, length at 50% maturity (L_{50}) and fecundity at length. The sources of these biological parameters are listed in Table 3, and all data were assumed to arise from a depleted population, as few data were available for before the 1950s (when landings increased dramatically). Adjustments can be made for less depleted stocks, but these corrections assume that the level of depletion is known. For example, if the stock were at half the carrying capacity, estimates of r would need to be increased by a factor of 2.

The general strategy for obtaining priors from the life-history information in Table 3 was to use the variability in published studies as an index of prior uncertainty: the more variability between studies the broader the prior would be. This approach has the advantage of capturing some of the significant uncertainty due to variations in ageing technique between studies. It also assumed that the studies were broadly comparable, and that there were few important spatial and temporal differences between data for Atlantic spurdog. Moreover, the life history parameters in Table 3 were not a perfect match for the requirements of demographic analysis, so certain assumptions were made. These assumptions were made in order to use data-driven priors rather than arbitrary ones, though they are not without their own subjectivity, as discussed below.

Firstly, the proportion of mature fish at each age was obtained from L_{50}, using age-specific estimates of the proportion of fish longer than L_{50}. The latter were obtained by assuming a lognormal distribution for length at a given age (x), with mode given by a published dataset (from the Von Bertalanffy growth curve evaluated at x), and dispersion parameter estimated from the variability in published lengths at each age across studies. So, for example, if 3 studies showed expected lengths at age $x = 10$ of 87, 78, and 71 cm, then we might take the standard deviation of the logarithms of these three lengths as the lognormal dispersion parameter, giving a lognormal

distribution with μ = *log* (87) (for the fist study) and σ = 0.1 for length at age 10. We constructed one lognormal for each age and study, though each study at a given x shared the same σ. By taking the proportion mature at age x to be the same as the probability that the mean length of age x fish is above L_{50} (from the lognormal) we ensured that 50% of the fish are mature at the age when most of them reach L_{50}. To continue the example with L_{50}= 83 cm, the cumulative distribution function for a lognormal (*log* (87), 0.1) evaluated at 83 cm would suggest that about 32% of the fish are mature at age 10. So, the more studies differed about length-at-age, the greater was the range of ages over which maturation was said to take place.

Secondly, fecundity at age for mature females was calculated by taking the mean length at age and computing the fecundity at that length. The effective fecundity at age x (m_x) was computed by multiplying the fecundity and proportion mature at age and dividing the result by 4 to account for the two-year gestation period and the 1:1 sex ratio of pups.

Uncertainty in m_x was modelled using the variability in estimates of it obtained by employing data from different studies. More specifically, we modelled estimates of m_x (as calculated above) from each of five sources: Holden and Meadows (1962, 1964, UK waters), Gauld (1979, Scotland), Nammack *et al.* (1985, Northwest Atlantic), Fahy (1988, 1989, Irish waters) and Jones and Ugland (2001, Norway). We assumed that each source would use their own data, when available, and an average of other sources when not. We took a weighted average of the m_x estimates from these sources, wherein the weight assigned to each study was independent and lognormal (μ = 0, σ = 2). In other words, if the m^x values for each source were 4, 7, 2, 0, and 9, respectively, we would repeatedly draw five weights w_1, w_2, w_3, w_4, w_5 from that lognormal and take $m_x = (4w_1+7w_2+2w_3+9w_5)/(w_1+w_2+w_3+w_4+w_5)$ for each draw.

The probability of surviving to age x (l_x) was estimated from the tagging studies (on females > 80 cm) of Aasen (1964) and Holden (1968). These researchers converted tagging study estimates of total mortality (*Z*) to estimates of natural mortality (*M*) by subtracting estimates of fishing mortality (*F*) from stock assessments. Resulting estimates were converted to a prior for natural mortality, which was lognormal (μ = –1.76, σ = 0.54). Then, l_0= 1 and $l_x = l_{x-1}$exp(-*M*).

The resulting estimates of l_x and m_x were then converted to estimates of the intrinsic rate of population increase (*r*), using the numerical Leslie matrix projection method described in McAllister *et al.* (2001). In that approach, estimates of l_x and m_x were drawn randomly from their prior distributions. As shown above, each m_x value was drawn by selecting random weights w_1, w_2, w_3, w_4, w_5 while the l_x values were determined by a single draw of *M* from the natural mortality prior. Then, taking each of the resulting l_x and m_x values, and assuming a maximum age of 40, we initialised a vector of female numbers at age by:

$$N_{x,o} = 10000 l_x \qquad (1)$$

The number of female pups for the next time-step is then given by:

$$N_{0,t+1} = \sum_{x=0}^{40} m_x N_{x,t} \qquad (2)$$

and the numbers of older females at the next time-step is governed by:

$$N_{x,t+1} = S_{x-1} N_{x-1,t} \qquad (3)$$

where in S_{x-1} is the probability of surviving through age x-1. Using equations (2) and (3), the population was projected forward until the age structure stabilized (to within <0.00001%), which took a few hundred steps. Then, defining total abundance with

$$P_t = \sum_{x=0}^{40} N_{x,t} \qquad (4)$$

TABLE 3. Source data for life history parameters for *Squalus acanthias.*

Parameters	Source
Length-at-age	Fahy (1988, 1989), Holden and Meadows (1962, 1964), Nammack *et al.* (1985), Soldat (1982), Jones and Ugland (2001), Aasen (1964)
Fecundity-at-length	Fahy (1988), Gauld (1979)
Natural mortality	Aasen (1964), and Holden (1968)
Length at 50% maturity	Jones AND Ugland (2001), Fahy (1988), Gauld (1979), Holden and Meadows (1964), Nammack *et al.* (1985)

we computed

$$r = log\left(\frac{P_t}{P_{t-1}}\right) \qquad (5)$$

at the equilibrium t.

Computing a sample of more than 5000 such r estimates and discarding any negative values (which McAllister *et al.* 2001 also obtained) led to the prior distribution shown in Fig. 1. Negative values of r result from generating l_x and m_x values independently of one another, as sometimes very low simulated survivorship values were coupled with very low production values. This combination can lead to a population that could not sustain itself, giving a negative r. The fact that this technique used numbers and not biomass (as in our assessment model) was shown by those authors to make no difference.

A Bayesian Schaefer-model assessment of spurdog was fitted to survey data from England, Scotland and Northern Ireland (Table 4). Figure 2 shows the time-series of landings used in fitting this model. It was assumed that the population started from the carrying capacity K in 1906.

In fitting the model, we assumed that each index i had its own catchability q_i and its own dispersion parameter σ_i^2. In accordance with precedent (McAllister *et al.* 2001, Walters and Ludwig 1994), these parameters were assigned non-informative priors, uniform in log space. The same approach was adopted to obtain a prior distribution for the Shaefer production model parameter K.

Each index $O_{i,y}$ value in Table 4 was assigned a lognormal distribution, with mode equal $q_i B_y$, (where B_y is the predicted biomass in year y) and with dispersion parameter

$$\sigma_{i,y}^2 = c_i CV_{i,y}^2 \sigma_i^2 \qquad (6)$$

\where the $CV_{i,y}$ entries come from Table 5 and where

$$c_i = \left(\sum_y CV_{i,y}^2\right)^{-1} \qquad (7)$$

As usual, each index value $O_{i,y}$ was assumed to be conditionally independent of all others, given q_i, σ_i^2 and B_y.

Equation (6) implies that we are doing an inverse CV^2 weighting of survey index values, so years with high between-haul CV in catch weight get less weight in the model fit.

This specification allows nuisance parameters q_i and σ_i^2 to be integrated out, using a slight generalization of equations in Walters and Ludwig (1994). If, for each index

i, we define the statistics

$$\qquad (8)$$

$$log(\hat{q}_i) = \frac{\sum_y \left(log(O_{i,y}) - log(B_y)\right)CV_{i,y}^{-2}}{\sum_y CV_{i,y}^{-2}} \qquad (9)$$

and

$$SS_i = \sum_y \left(log(O_{iy}) - log(B_y)\right)^2 CV_{i,y}^{-2} \qquad (10)$$

then, upon integrating out both q_i and σ_i^2, the likelihood kernel for index i becomes

$$\left(SS_i - log(\hat{q}_i)^2 \sum_y CV_{i,y}^{-2}\right)^{\frac{-(n-1)}{2}}$$

where n is the number of years of data in index i. If the $CV_{i,y}$ values were all 1, this result would be proportional (and therefore equivalent) to equation (18) of Walters and Ludwig (1994). The joint posterior distribution is readily obtained from equation (10), up to a constant of proportionality, by multiplying in the priors for r and K.

With the nuisance parameters thus eliminated, the only remaining estimated parameters were r and K. We explored uncertainty in these by creating a grid of parameter values. In so doing we departed from the prescription of McAllister *et al.* (2001), who used the sampling importance/resampling (SIR) algorithm to
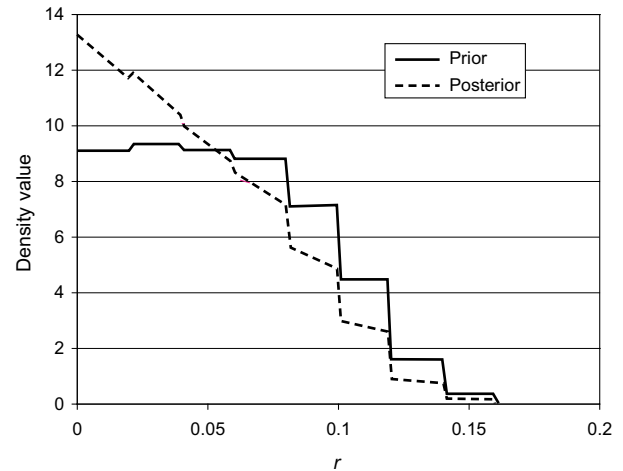

Fig. 1.   The prior for maximum rate of increase (r) resulting from demographic computations.

TABLE 4. Mean catch per unit effort (kg per hour) of *Squalus acanthias* from UK groundfish surveys.

| Vessel Gear	Cirolana GOV	Cirolana Granton	Cirolana PHHT	Corystes Granton	Explorer Aberdeen Trawl	Lough Foyle Rockhopper Otter Trawl	Scotia Aberdeen Trawl	Scotia GOV
1977		2.50			147.19			
1978		10.23			11.35			
1979		2.41			11.54			
1980		9.44			0.54			
1981		7.53			12.53			
1982		5.72	12.67				1.21	
1983		6.15	2.66				0.66	6.22
1984		3.30	16.25				0.69	2.84
1985		4.95	13.82				1.66	35.95
1986		28.56	11.23				1.08	9.20
1987		13.54	22.83				7.62	0.35
1988		4.69	5.68	8.36			2.55	8.91
1989		1.20	5.26	0.39			0.71	2.97
1990		2.30	5.14	3.55			0.78	7.04
1991	3.58	0.49	1.30	3.53		6.03	0.10	5.75
1992	3.14		0.83	3.70		3.74	0.24	4.67
1993	0.96		1.24			7.30	0.35	4.47
1994	2.56		1.10			1.48	0.12	5.50
1995	1.44		0.58			3.85	0.04	3.48
1996	0.26					3.22	0.07	2.78
1997	0.53		1.18			2.54	0.19	1.61
1998	0.32		0.81			5.04		1.97
1999	0.18		14.44			3.61	0.00	1.80
2000	0.06		0.94			3.42		6.25
2001	0.47		1.26			1.65		0.42
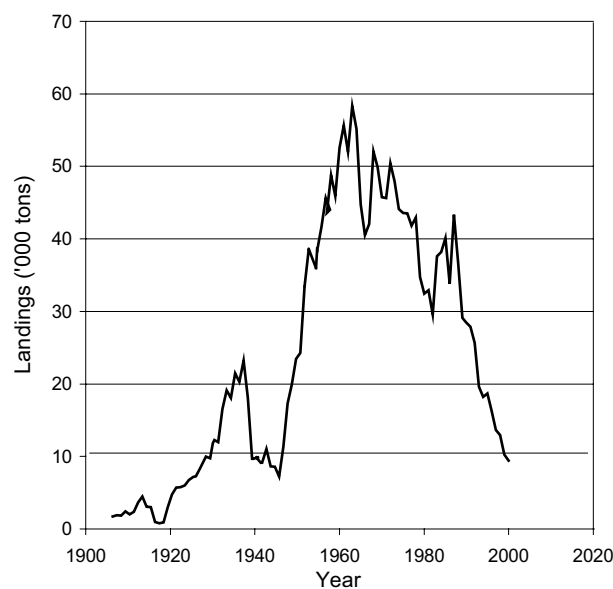
Fig. 2. ICES landings data for North-east Atlantic spurdog.

compute posterior results. Using a grid allowed us to avoid any convergence issues that might have arisen with SIR, but that is not to say that this algorithm could not have been applied. For each value of parameter r in the grid, we determined the value of K at which the likelihood kernel was maximized ($Kmax(r)$). Because parameters r and K were very highly correlated (Fig. 3), we created a grid of parameter values composed of r values and multipliers (δ) of $Kmax(r)$, such that $K = \delta\, Kmax(r)$, an approach based on recommendations in Walters and Ludwig (1994).

A number of estimation scenarios were examined to explore the impact of model assumptions. We explored the effect of ignoring both the demographic results and the prior for K, the effect of replacing the demographic prior for r with one that is uniform on the interval from 0 to 0.15, the impact of changing the prior for natural mortality (M) to lognormal ($\mu = -2.3$, $\sigma = 0.54$) (which has a median of 0.1 instead of 0.17) and the impact of assuming the $CV_{i,y}$ values were all 1 for equation (10)

TABLE 5. The coefficient of variation (CV, just standard error/mean) in survey CPUE (Table 2), for the survey indices used.

Vessel Gear	Cirolana GOV	Cirolana Granton	Cirolana PHHT	Corystes Granton Trawl	Explorer Aberdeen Trawl	Lough Foyle Rockhopper Otter Trawl	Scotia Aberdeen Trawl	Scotia GOV
1977		0.26			0.68			
1978		0.57			0.72			
1979		0.27			0.37			
1980		0.39			0.42			
1981		0.65			0.40			
1982		0.49	0.51				0.34	
1983		0.50	0.44				0.35	0.54
1984		0.39	0.37				0.34	0.44
1985		0.40	0.45				0.38	0.36
1986		0.89	0.38				0.50	0.58
1987		0.53	0.45				0.74	0.36
1988		0.77	0.26	0.52			0.77	0.89
1989		0.36	0.45	0.79			0.39	0.58
1990		0.32	0.44	0.95			0.62	0.72
1991	0.28	0.48	0.48	0.54		0.60	0.35	0.64
1992	0.46		0.34	0.76		0.28	0.28	0.63
1993	0.27		0.41			0.76	0.36	0.27
1994	0.21		0.58			0.30	0.42	0.47
1995	0.31		0.54			0.57	0.52	0.62
1996	0.44					0.30	0.54	0.29
1997	0.64		0.49			0.37	0.45	0.21
1998	0.46		0.53			0.69		0.27
1999	0.73		0.89			0.31	0.00	0.22
2000	1.00		0.41			0.28		0.85
2001	0.67		0.48			0.51		0.54

(which assigns equal weight to the index values in a survey series). We also investigated the evidence for a change in the value of parameter K by splitting the time-series into two equal portions, each with their own K parameter. A lognormal($\mu = 0$, $\sigma = 0.4$) prior for the ratio of the two K values ($K2/K$) was used.
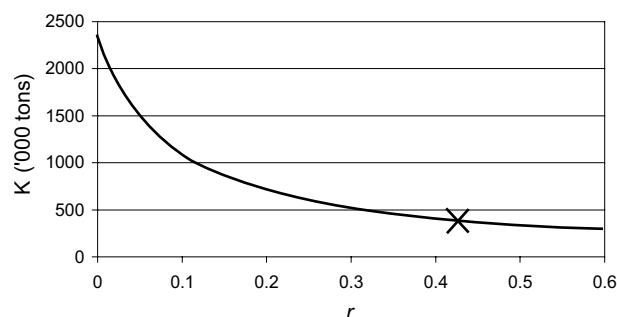

Fig. 3.   The likelihood kernel for the IBTS survey data has a sharp ridge (solid line), along which it is virtually flat (the maximum value along it is twice the minimum). The maximum likelihood estimates of r (0.416) and K (406, 400) are indicated (X).

Results

Figure 3 gives a plot of r against $Kmax(r)$ in which no account was taken of any priors for r and K. Thus, this plot illustrates the parameter values favoured by survey data. Essentially, the CPUE data cannot discriminate between a large, unproductive stock and a small, productive one. The maximum likelihood-kernel estimate was at $r = 0.416$ and $K = 406\ 400$ tons, at which values the 2001 biomass would be at 39% of K. Below this curve, the likelihood surface drops off to zero within 1% of $Kmax(r)$. Above it, the surface drops off much more gradually.

Figure 4 shows the main assessment result: the base-case population time-series estimated by incorporating the priors for r and K. It suggests a stock that was depleted to below 5% of K in 2001 (Table 6). The posterior result for parameter r (using the base-case demographic priors) is shown in Figure 1. Under base-case assumptions, most landings since 1946 were definitely above MSY (maximum sustainable yield, c.f. Fig. 2) and there were probably (i.e. probability 95%) < 150 000 tons of spurdog

left in 2001. There was a 5% chance that the population was depleted below 2% of *K*.

Table 6 gives the results for other scenarios described above. All suggested that the stock had declined to about 2–9% of *K*. Altering the prior on natural mortality (by lowering its median) had the largest effect on results, giving a less pessimistic assessment. The Bayes factor (a Bayesian analogue of a likelihood ratio) comparing the change in *K* model to the base-case scenario was 0.2 (below 1), evidence against the model with a change in *K*.

Discussion

This assessment highlights the contrast between Bayesian and classical estimation. According to the classical approach (as exemplified in Fig. 3), the spurdog stock is at about 39% of *K*. While this is below the biomass that will yield MSY, recovery would be rapid because the method suggested that *r* is 0.42. The Bayesian approach excluded the possibility that *r* could be as high as 0.42 on the basis of a demographic analysis and suggested that the stock is depleted to about 5% of *K*. Under this scenario, decreased fishing mortality would be required to achieve recovery, as median *r* is 0.04–0.07 (Table 6).

While we consider this Bayesian approach to be more biologically realistic than the classical one, a number of assumptions and difficulties remain. The main issues are as follows:

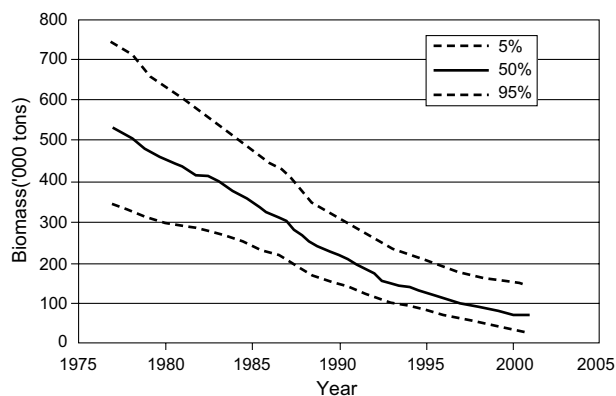- The base-case model assumes that parameters *r* and *K* have remained constant since 1906.

Fig. 4.   The estimated biomass time-series suggests a downward trajectory, which is uninformative about population parameters.

- The variability in published studies was used as an index of prior uncertainty.

- The estimates of natural mortality were based on published accounts of tagging studies of large females as an indication of mortality of females of all ages.

- The ageing data (used in computing growth and maturity ogives) are uncertain.

- The demographic parameters are supposed to represent growth and mortality under optimal conditions (at low density). Had the stock not appeared so depleted, this assumption might have posed awkward problems.

There is a trade-off between two of our assumptions: that the population starts at *K* in 1906 and that *r* and *K* have remained constant. In going back to 1906, we can use more landings data in calculating depletion, but we lengthen the time-series and hence the likelihood that conditions have changed. When we compared a model with a change in parameter *K* to one without, the Bayes factor suggested that the constant model was superior.

Our demographic analysis used inter-study variability in spurdog life-history parameters in creating the priors. This approach assumed similarity between life-history traits in different areas and independence between studies. It is not difficult to imagine how these assumptions might have been violated to a degree; however, this approach reduces the effect of possible ageing errors in any one study. This approach was chosen because we had only point estimates of biological parameters from various studies. With access to the raw data from individual fish, more realistic computations could have been attempted.

This assessment also examined the effects of a number of changes in the model. It addressed uncertainty about the prior for natural mortality by showing that depletion results were relatively insensitive to it. The level of uncertainty about natural mortality in spurdog, and the absence of data on ontogenetic changes in their mortality is typical for most elasmobranch stocks.

The base-case model down-weighted survey catch rates with a high *CV*, an approach we copied from McAllister *et al.* (2001). Since spurdog are a shoaling species with a patchy distribution, this may have had an impact on the model predictions. Therefore, we examined the impact of assigning equal weights to CPUE observations and found that this had virtually no effect on depletion estimates, which remained <9% (Table 6).

TABLE 6. Results for selected parameters under different estimation scenarios.

Scenario	Quantiles		
Base case	5%	50%	95%
K	1.05E+06	1.60E+06	2.29E+06
r	0.002	0.041	0.108
MSY	1896	16845	28525
Biomass in 2001/*K*	2.04%	4.37%	8.84%
Change in *K*			
K	1.09E+06	1.69E+06	2.31E+06
K2	1.01E+06	1.49E+06	2.53E+06
r	0.002	0.040	0.104
MSY	1894.15	16744	30649
Biomass in 2001/*K*	1.98%	4.26%	8.85%
Different M prior			
K	945751	1.31E+06	2.14E+06
r	0.009	0.070	0.129
MSY	4896.16	23089.4	30774
Biomass in 2001/*K*	2.18%	4.65%	9.27%
Different r prior			
K	918293	1.47E+06	2.27E+06
r	0.003	0.052	0.136
MSY	2558	19690	31307
Biomass in 2001/*K*	2.10%	4.46%	9.08%
No inverse CV weighting of indices			
K	1.07E+06	1.64E+06	2.30E+06
r	0.002	0.038	0.104
MSY	1871	15833	28061
Biomass in 2001/*K*	1.96%	3.96%	7.81%

In summary, the incorporation of life-history characteristics prevented the Schaefer assessment from producing unrealistic estimates of *r* and, therefore, also of *K*. Hence, this method is considered to be a useful approach to the assessment of fish stocks that are known to be unproductive.

Acknowledgements

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