

Spatial and temporal patterns in age and size at maturity and Spawning Stock Biomass of North Sea Gadoids

by
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Abstract

Demographic traits like growth, maturity and fecundity are plastic in fish. The question is how their variability affects recruitment and population dynamics, and whether it should be taken into account in stock assessment.

This paper focuses on variations of age and size at maturity in time and space in four North Sea Gadoid species: cod, whiting, haddock and Norway pout. Data from the International Bottom Trawl Survey (IBTS) in the nine Standard Roundfish Areas of the North Sea for the period 1983-1998 are used. It is shown that there is significant spatial variation in age and size at maturity for cod, haddock and whiting. An index of Spawning Stock Biomass (SSB) is estimated, which takes into account this variability, along with the spatial and temporal variation of fish abundances (also provided by IBTS data). These estimates of SSB are much more variable than those obtained through VPA by stock assessment working groups. In addition, for cod, haddock and whiting, the decreasing trend in SSB is steeper when spatial variations are included. Taking into account the location of spawners improves the prediction of recruitment.

Keywords

Age at maturity; length at maturity; Spawning Stock Biomass; spatial patterns; cod; haddock; whiting; Norway pout; North sea.

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1. Introduction

There is increasing awareness that Spawning Stock Biomass (SSB) is not a good index of spawning potential (*e.g.* Trippel *et al.*, 1997; Marshall *et al.*, 1998; Marteinsdottir and Thorarinsson, 1998). There are two possible reasons. Firstly, SSB might be estimated with low precision in many cases. SSB estimates usually result from the combination of numbers at age (VPA output) and a maturity ogive (probability of being mature at age). The reported variations of the latter in time (*e.g.* Trippel, 1995) and space (Morgan and Bowering, 1997; Tomkiewicz *et al.*, 1997) are not always taken into account. Using as precise as possible maturity ogives for estimating SSB might be a way to improve SSB precision; a more precise estimate of SSB might be a better predictor of recruitment. Secondly, all SSB is not equivalent in terms of egg production (Murawski *et al.*, In Press). There is increasing evidence that spawner size and condition and spawning time influence recruitment success (*e.g.* Trippel *et al.*, 1997; Marshall and Frank, 1999). The spawning location may also affect recruitment patterns, because the place where eggs are released will determine the conditions for larval development and their drift to favourable environments; this has been reported for Baltic cod (MacKenzie *et al.*, 1998). Sampling eggs and larvae is a way to map the spawning areas in detail, but requires a huge sampling effort for large populations. Another approach is to combine local abundance indices with local maturity ogives, sampled during the spawning season.

Hence there are two reasons for portraying the spatial patterns in maturity ogives and Spawning Stock Biomass. Gadoids in the North sea are large populations, with a wide enough distribution to potentially show spatial variation. This study uses a time-series of survey data for the following purposes:

- i) Examine how the probability of being mature at length (or age) varies in space and time for North sea cod, haddock, whiting and Norway pout;
- ii) Combine these probabilities with local abundance indices to map spawning stock biomass;
- iii) Compare the resulting SSB estimates with those from VPA
- iv) Examine whether the incorporation of additional information on spawner location and size into stock-recruitment relationships improves the prediction of recruitment.

2. Materials and methods

Length frequency distributions and maturity-age-length keys from the International Bottom Trawl Survey (IBTS) were used for this study. IBTS is an coordinated survey conducted in the North Sea since 1978 (Anonymous, 1996). Since 1983 the coverage is homogeneous over the whole North Sea. The data from the first quarter (February) survey were used as all four species under study have their peak of spawning in February-March (Daan *et al.*, 1990). Each survey consists of 350 to 550 30-minutes tows performed with the 36/47 GOV-trawl. Length distributions are recorded for all fish species caught. Otolith samples of selected species, together with sex and maturity data, are collected in 9 areas (Figure 1) with a fixed sampling design.

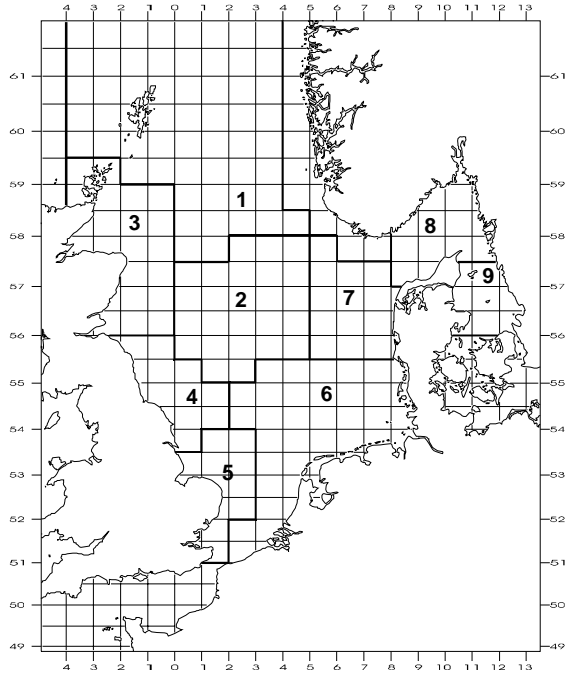


Figure 1: IBTS Standard Roundfish Areas

Abundance indices at length were raised by the ratio of total area to trawled area for each Standard Roundfish Area (SRA). The global abundance index of fish of length l in year i is

$$\hat{N}_{l,i} = \sum_j \frac{A_j}{a} \bar{n}_{l,i,j}$$

where a is mean trawled area, A_j area of SRA j and $\bar{n}_{l,i,j}$ mean number

caught per haul. The variance of this index is $V(\hat{N}_{l,i}) = \sum_j \frac{A_j^2}{a^2} \text{var}(n_{l,i,j})$. Skagerrak and

Kattegat areas 8 and 9 were excluded from the analysis due to poor coverage of maturity data until 1990. The estimated total number of fish is $\hat{N}_i = \sum_l \hat{N}_{l,i}$. An *ad hoc* recruitment

index was estimated as the number of fish in the first length mode. For each year and SRA a length threshold $l_{l,i,j}$ was defined as length at the first minimum of the length distribution, and recruitment is $\hat{R}_{i,j} = \sum_{l < l_{l,i,j}} N_{l,i,j}$, with raising factors and variance estimators as before.

A logistic model was used for the probability of being mature p_l as a function of body length

or age (l), year (i) and area (j): $\log\left(\frac{p_{l,i,j}}{1-p_{l,i,j}}\right) = \mu + a_i + b_l + c_j + d_j l + e_l$ (model 1). The terms of

this model were tested sequentially by an analysis of deviance. An alternative model without

any interaction ($\log\left(\frac{p_{l,i,j}}{1-p_{l,i,j}}\right) = \mu + a_i + c_j + e_l$: model 2) was also defined. Only SRAs with enough data were included.

The selected model was used to predict median length (or age) at maturity L_{50} for each Year \times Area combination. The mean annual length at maturity for whole North Sea was estimated as the average L_{50} across areas, weighted by the total abundance in each area:

$$\bar{L}_{50,i} = \frac{1}{\hat{N}_i} \sum_j L_{50,i,j} \hat{N}_{i,j}$$

This is an index of size at first reproduction, and was compared to the

$$\bar{l}_{S,i} = \frac{1}{\hat{N}_i} \sum_j \sum_l \hat{p}_{l,i,j} \hat{N}_{l,i,j} l$$

Predicted proportions mature at length and abundance indices were combined to estimate Spawning Stock Biomass (SSB) in each cell: $\hat{SSB}_{i,j} = \sum_l \hat{p}_{l,i,j} \hat{N}_{l,i,j} b l^c$, where b and c are the

coefficients of the length-weight relationship (Dorel, 1986). We assume that abundance indices and proportions mature are estimated independently to estimate the variance of SSB:

$$\hat{Var}(\hat{SSB}_{i,j}) = \sum_l \hat{SSB}_{l,i,j}^2 \left(\frac{Var(\hat{p}_{l,i,j})}{\hat{p}_{l,i,j}^2} + \frac{Var(\hat{N}_{l,i,j})}{\hat{N}_{l,i,j}^2} + \frac{Var(\hat{p}_{l,i,j})}{\hat{p}_{l,i,j}^2} \times \frac{Var(\hat{N}_{l,i,j})}{\hat{N}_{l,i,j}^2} \right) \quad (\text{Seber, 1982}),$$

where $Var(\hat{p}_{l,i,j})$ is estimated from the variance of the estimated coefficients. Proportions mature at length rather than at age were used for estimating SSB to avoid inflating the variance through the use of age-length keys. Analyses of length at maturity were performed on females only, avoiding inaccuracies due to potential sexual dimorphism in maturation; females were preferred because they are more determining for population dynamics. SSB were estimated as if all fish were female. Abundance and recruitment indices, as well as SSB estimates, were compared to estimates obtained by Virtual Population Analysis (Anonymous, 2000).

The geographic co-ordinates of the centre of gravity for spawners in year i were estimated as:

$\begin{pmatrix} \bar{x}_i \\ \bar{y}_i \end{pmatrix} = \frac{1}{M_i} \sum_j M_{i,j} \begin{pmatrix} x_j \\ y_j \end{pmatrix}$, where x_j and y_j are the longitude and latitude of the centre each SRA, and M_{ij} the number of mature fish. To detect whether the location of spawners affects recruitment, these co-ordinates were correlated with the time series of recruitment \hat{R}_i .

The performance of these estimates of SSB in predicting recruitment was compared to that of VPA estimates by fitting Ricker-type stock-recruitment relationships (Ricker, 1954; Iles, 1994). The improvement of incorporating information on location and size of spawners was also examined. GLM were used to predict recruitment as a function of $\log(SSB)$ and SSB with a log-link and Gaussian distribution: $R = \exp[\log(SSB) + \alpha SSB + \beta + \gamma_k X_k]$ where X_k are additional predictors and α , β and γ_k are parameters. VPA recruitment estimates were predicted from i) VPA SSB estimates, ii) IBTS stratified SSB estimates, iii) IBTS single area SSB estimates, or an improved model including IBTS or VPA SSB estimates and additional predictors, selected among mean length of spawners and the co-ordinates of their centre of gravity by an automated forward stepwise method (Venables and Ripley, 1994). Residual deviance was used as criterion to compare models.

3. Results

3.1. Maturity at age and length

The probability of being mature at age and at length significantly varies between areas and years for all four species. Year and area effects and their interactions with length were significant for maturity at age and at length for all species (model 1). However, this model was used only for cod and whiting. For haddock and Norway pout, data were insufficient to properly estimate all parameters and model 2 was estimated instead. The model explains 90% of variability for haddock, whiting and Norway pout, and 75% for cod. Table 1 shows the analysis of deviance for the models of the probability of being mature at length; patterns at age are similar.

Table 1: Sequential analysis of deviance for logistic regression models of the proportion mature at length (L_t) with Year and Area effects. Differences in residual deviance are tested by a Chi2 test, appropriate for the logistic model (Venables and Ripley, 1994).

		Df	Deviance	Resid.Df	Resid.Dev	Pr(Chi)
Cod	Null model			5846	17526.7	
	+ Area	6	177.26	5840	17349.45	0
	+ Year	15	593.65	5825	16755.80	0
	+ L_t	1	11848.25	5824	4907.55	0
	+ Area \times L_t	6	150.35	5818	4757.20	0
	+ Year \times L_t	15	122.48	5803	4634.72	0
Haddock	Null model			3115	27038.6	
	+ Area	4	799.97	3111	26238.62	0
	+ Year	15	343.34	3096	25895.29	0
	+ L_t	1	23012.59	3095	2882.70	0
Whiting	Null model			2290	27219.9	
	+ Area	6	491.67	2284	26728.27	0
	+ Year	15	889.23	2269	25839.04	0
	+ L_t	1	22870.54	2268	2968.50	0
	+ Area \times L_t	6	112.98	2262	2855.52	0
	+ Year \times L_t	15	139.99	2247	2715.53	0
Norway pout	Null model			546	5384.8	
	+ Area	3	266.02	543	5118.80	0
	+ Year	15	173.51	528	4945.29	0
	+ L_t	1	4230.91	527	714.38	0

Average age and length at maturity decreased in cod and haddock from 1983 to 1998 (Figure 2). Average length of spawners decreased more steeply than mean length at maturity in cod. For haddock there was a drop between 1988 and 1990; age at maturity then recovered slowly, but not length. Mean age at maturity increased slightly in Norway pout during this period. There was no trend in age neither in length at maturity for whiting (Figure 2).

Cod, haddock and whiting show the largest size at maturity in areas 1 and 7, and the smallest in area 3. In contrast, Norway pout size at maturity is larger in area 4 and smaller in area 1.

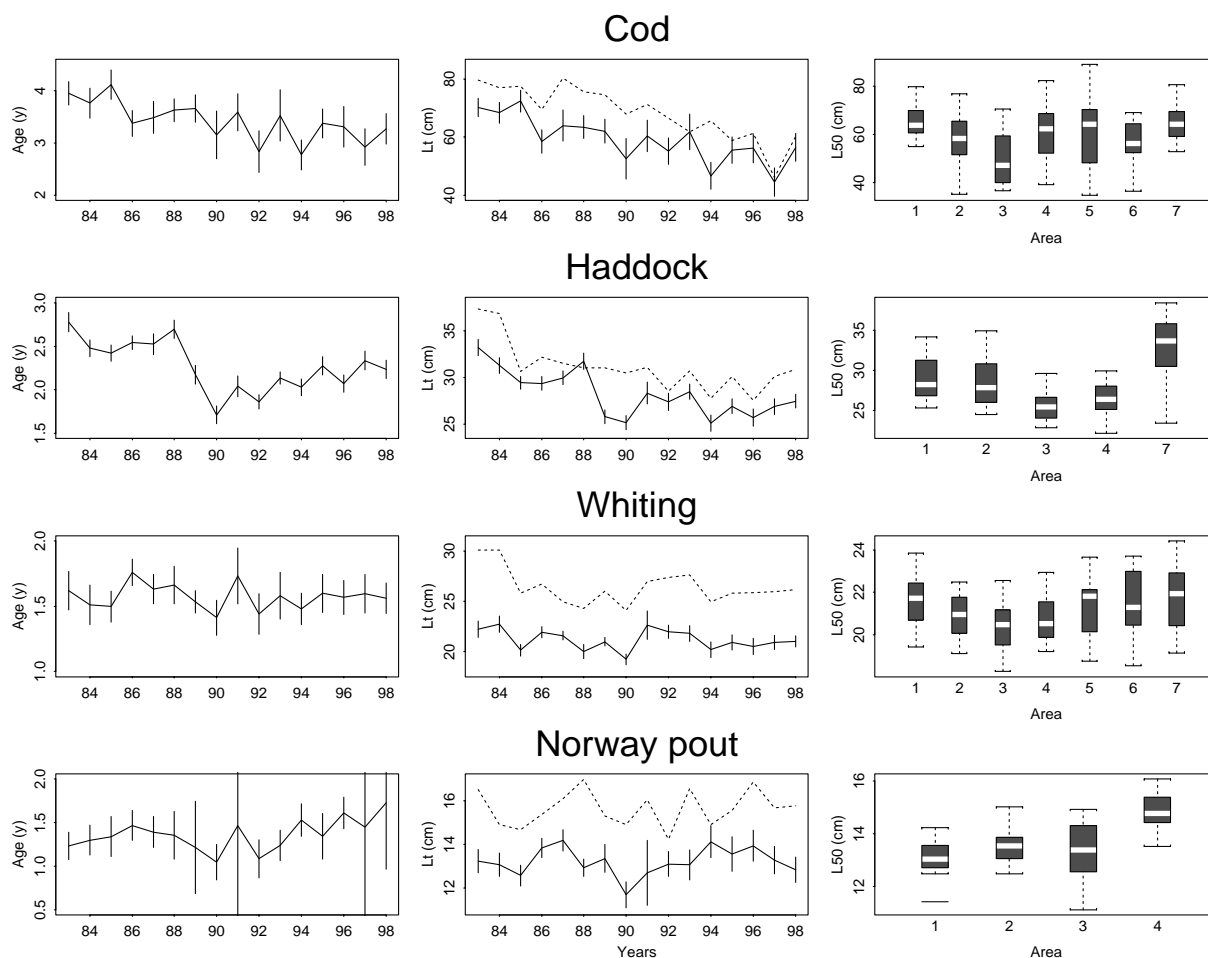


Figure 2: Left: Time variations of estimated average age at 50% maturity of four Gadoids in the North sea, 1983-1998. Bars indicate 95% confidence intervals. Middle: Time variations of estimated average length at 50% maturity (continuous line) and estimated mean length of spawners (dashed line). Right: Box plots of length at 50% maturity by area (boxes: quartiles, whiskers: extremes).

3.2. Spawning Stock Biomass

Spawning areas change from year to year. The distribution of total biomass also varies between years; both are not as linked as expected if length distributions and maturity ogives were spatially homogeneous (see the example of Cod in Appendix 1). This implies that a stratified estimate of SSB, taking account of spatial variation of biomass and of maturity at length, is useful. The stratified IBTS estimates of SSB show more year to year variation than the VPA estimates for all four species (Figure 3). On the whole the orders of magnitude of both SSB estimates are consistent, except for cod where the IBTS estimate is lower by 30% on average. The decrease in SSB for cod, haddock and whiting appears steeper when estimated from IBTS data than by VPA. For cod, VPA indicates a slight stock rebuilding in 94-98, which does not appear in the IBTS stratified estimates. The precision of the stratified IBTS SSB estimates is high for cod, haddock and whiting. In Norway pout a lower precision in both the estimated probability of being mature (fewer length classes) and abundance indices (higher variability) causes a lower precision in the SSB estimates.

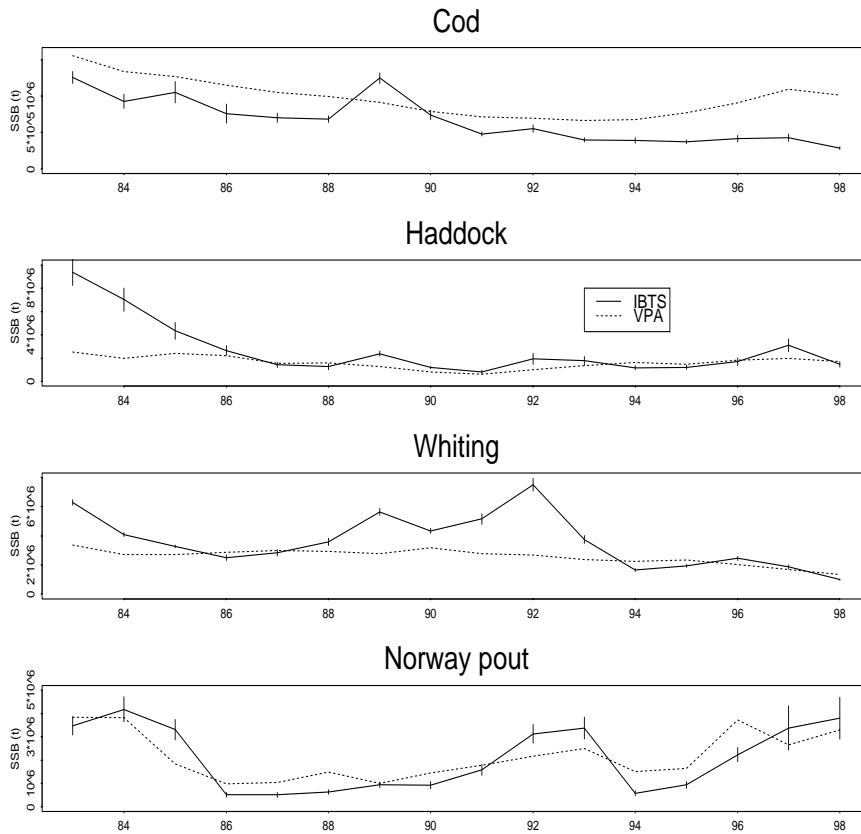


Figure 3: Variation of Spawning Stock Biomass from 1983 to 1998, as estimated by the stratified estimator from IBTS survey data (continuous line) and by VPA (dashed line) (Anonymous, 2000). Bars indicate 95% confidence intervals.

3.3. Does it improve the prediction of recruitment?

There exists a link between the location of spawners and subsequent recruitment (Figure 4, Table 2). This is especially true for cod, for which both average longitude and latitude of spawners are correlated with recruitment. Recruitment is significantly correlated with SSB in areas 1 and 3 for cod and area 1 for haddock, whereas it is not correlated with total SSB, which would seem reasonable for these highly depleted stocks.

Table 2: Correlations between recruitment and SSB by area, total SSB, and the longitude and latitude of the centre of gravity of spawners. Coefficients of correlation (R) and their P-value (P). Significant correlations at the 0.1 level are in bold (n=15 years).

	Cod		Haddock		Whiting		Norway pout	
	R	P	R	P	R	P	R	P
SSB Area 1	0.52	0.05	0.50	0.06	-0.04	0.87	0.42	0.12
SSB Area 2	-0.19	0.49	-0.26	0.36	0.37	0.18	-0.29	0.29
SSB Area 3	0.57	0.03	0.17	0.54	0.35	0.20	-0.07	0.80
SSB Area 4	0.20	0.47	-0.34	0.21	-0.11	0.68	-0.22	0.43
SSB Area 5	-0.14	0.63			-0.19	0.49		
SSB Area 6	-0.27	0.33			0.03	0.92		
SSB Area 7	0.13	0.65	-0.28	0.31	0.38	0.17		
Total SSB	0.30	0.28	0.39	0.13	0.17	0.55	-0.28	0.30
Mean longitude	-0.49	0.06	-0.09	0.76	0.38	0.16	-0.22	0.44
Mean latitude	0.48	0.07	0.48	0.07	-0.50	0.06	0.55	0.03

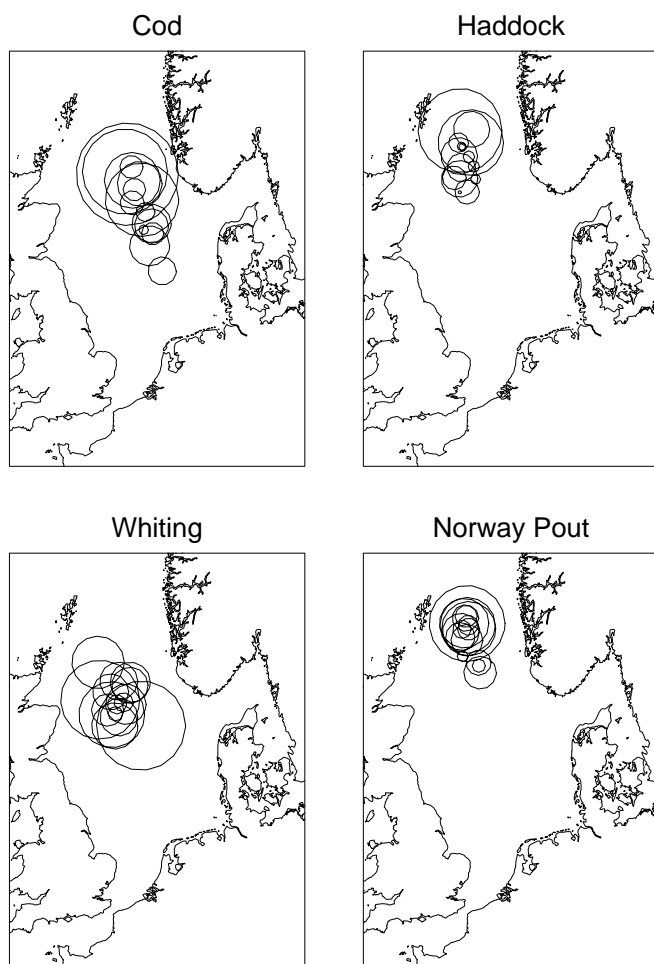


Figure 4: Recruitment at the mean location of spawners. A circle with radius proportional to recruitment (estimate from Anonymous, 2000) is plotted as the centre of gravity of SSB for each year.

Only for Norway pout does the stratified IBTS estimate of SSB perform better than the VPA estimate for predicting recruitment in terms of residual deviance (Table 3). However, the shape of the fitted curve seems more reasonable, especially for low stock sizes (Figure 5). For cod, haddock and whiting, both SSB and recruitment decreased during the 1983-98 period. The stratified IBTS SSB estimate, decreasing more steeply than the VPA estimate, results in a steeper slope at the origin: for all three species the coefficient α of SSB in the model is negative with IBTS estimates and positive with VPA estimates. Addition of information on

mean latitude of spawners (cod and Norway pout) and average length of spawners (cod) significantly improves the prediction. For haddock, a good fit (although residual deviance is not lower) is also obtained with SSB in area 1 instead of total SSB. For whiting, none of the alternative models tested was found to have a similar fit. The advantage of IBTS SSB estimates over VPA estimates is that it is easy to estimate their variance; higher SSB estimates have a higher variance, but not high compared to the scatter of the stock-recruitment plot (Figure 5). Haddock and Norway pout recruitments (estimated as the number of fish in the first length mode) have surprisingly low variances.

Table 3: Estimates of coefficients of Ricker-type models to predict recruitment as estimated by VPA from i) VPA SSB estimates, ii) IBTS stratified SSB estimates, iii) SSB in area 1 (haddock) or a stepwise selected model (cod and Norway pout).

Model	Variable	Coeff.	Std.Error	Residual Deviance
Cod i	(Intercept)	5.58	0.65	4.14E+17
	VPA SSB	1.03E-07	5.56E-07	
Cod ii	(Intercept)	6.53	0.48	4.65E+17
	IBTS SSB	-6.35E-07	5.47E-07	
Cod iii	(Intercept)	1.90	2.25	2.75E+17
	VPA SSB	-6.28E-07	6.69E-07	
	\bar{l}_s	0.02	0.03	
	Mean lat.	5.08E-04	2.63E-04	
Haddock i	(Intercept)	13.88	0.90	5.35E+23
	VPA SSB	1.77E-06	4.42E-06	
Haddock ii	(Intercept)	14.16	0.37	5.68E+23
	IBTS SSB	-1.19E-06	6.90E-07	
Haddock iii	(Intercept)	14.80	0.33	6.12E+23
	SSB Area 1	-2.13E-06	7.80E-07	
Whiting i	(Intercept)	6.09	0.82	1.02E+19
	VPA SSB	2.26E-07	2.87E-07	
Whiting ii	(Intercept)	7.27	0.32	1.30E+19
	IBTS SSB	-2.19E-07	7.51E-08	
Norway pout i	(Intercept)	14.04	0.38	4.91E+22
	VPA SSB	-4.10E-06	1.54E-06	
Norway pout ii	(Intercept)	12.47	0.23	4.06E+22
	IBTS SSB	-6.83E-07	1.10E-07	
Norway pout iii	(Intercept)	4.54	3.82	2.80E+22
	IBTS SSB	-7.71E-07	9.88E-08	
	Mean lat.	1.05E-03	4.95E-04	

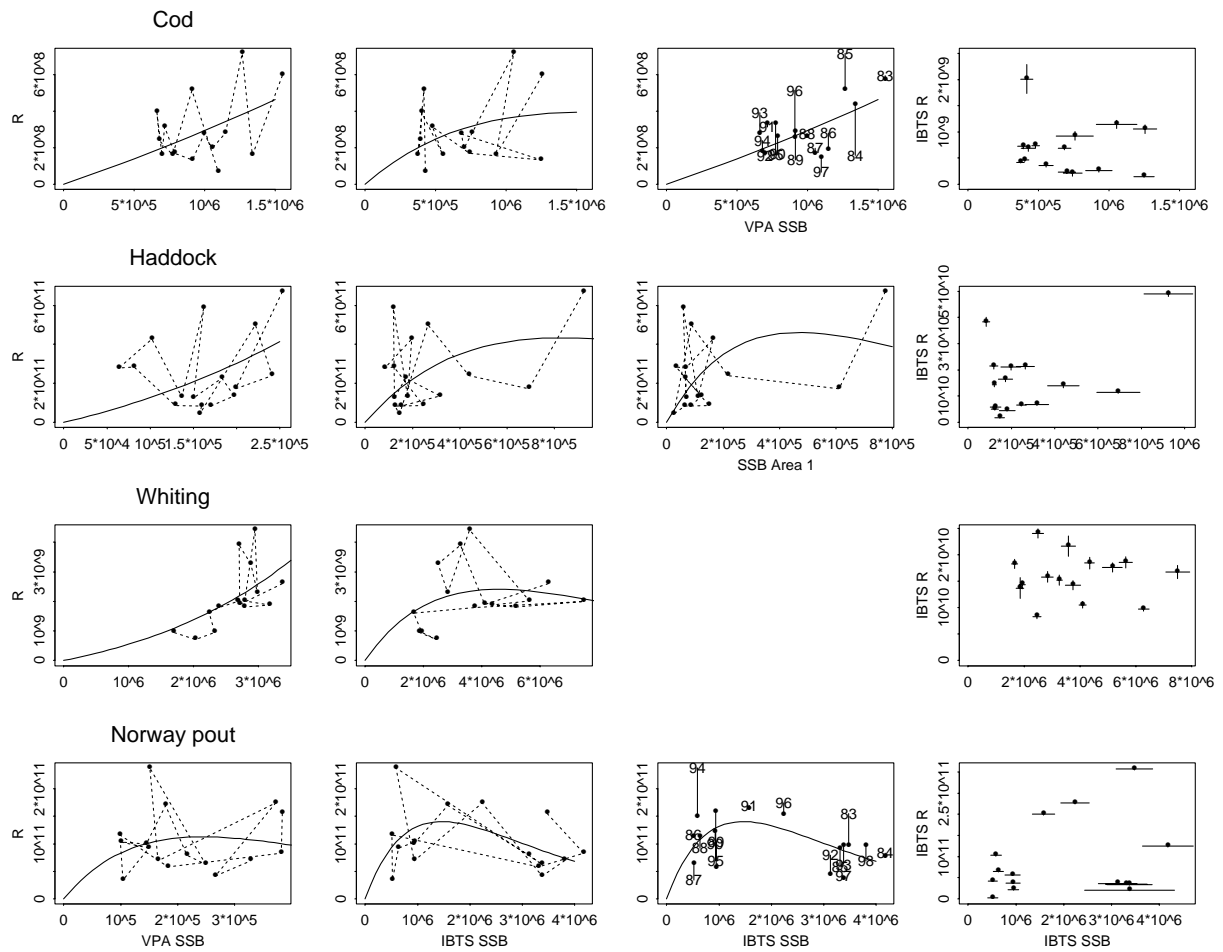


Figure 5: Ricker-type stock-recruitment relationships as fitted in Table 3. Points: "observed" data. Dashed lines link subsequent years, continuous lines show the best fit model. First column: VPA estimated SSB. Second column: IBTS estimated SSB. Third column: alternative models using Area 1 SSB (haddock) or including additional variables (cod and Norway pout: numbers indicate years, the fitted model is the same as in the second column, each fitted value is joined with the corresponding observed point). Fourth column: IBTS estimates of SSB and R with their 95% confidence intervals.

4. Discussion

Age and length at maturity of cod and haddock decreased during the 1983-1998 period. This is often interpreted as an effect of fishing (Trippel, 1995; Rochet, 1998). Indeed fishing mortality was steadily high until 1995 for these two stocks, whereas it decreased by 50% for whiting and more for Norway pout (Anonymous, 2000). Moreover, in cod average length of spawners and mean length at maturity became similar in recent years, indicating a preoccupying decrease in reproductive life-span. This is an additional index of overexploitation, consistent with the alarming assessment by Cook *et al.* (1997).

The probability of being mature at length varies in space and time. As a consequence, the distribution of spawning stock biomass varies between years. Taking account of this spatial variability for estimating SSB yields much more variable SSB estimates than VPA. The assumption of constant maturity ogives in many stock assessments probably leads to underestimate the variability in SSB. In cod, haddock and whiting, a decrease in total numbers of fish occurred, but less than in SSB (not shown). Earlier maturity did not compensate for the decrease in stock size. Variations in SSB result from complex interactions

between the number of fish, where they are and the probability of being mature there. Understanding the reasons of this variability would be of great interest (see *e.g.* Tomkiewicz *et al.*, 1998). VPA estimates decline less steeply than survey estimates. This discrepancy may be due to changes in sex-ratio, which were not examined in the present study; this should be done using IBTS data. Alternatively, VPA can overestimate stock sizes when certain assumptions of the model are not met (Walters and Maguire, 1996).

SSB in some areas (area 1 for haddock) might be more determining for recruitment than in others. In addition, taking account of SSB location improves the prediction of recruitment for cod and Norway pout. This was done here in an exploratory way. Processes explaining how spawner location influences recruitment through larval drift should be investigated.

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Appendix 1: Maps of total abundance (squares) and Spawning Stock Biomass (circles) of Cod by Roundfish Area of the North Sea, 1983-98.

Radii or circles are proportional to SSB, sides of squares to total number of fish.

