ELSEVIER

Fisheries Research 59 (2003) 343–362

FISHERIES RESEARCH

www.elsevier.com/locate/fishres

Spatial partitioning of relative fishing mortality and spawning stock biomass of Icelandic cod

Gavin A. Begg*, Gudrun Marteinsdottir

Marine Research Institute, Skulagata 4, P.O. Box 1390, 121 Reykjavík, Iceland

Received 29 March 2001; received in revised form 30 January 2002; accepted 8 February 2002

Abstract

Fishing mortality affects demographic characteristics of a population, and is a major determinant in loss of spawners from a fish stock; directly influencing stock productivity and recruitment variability. We investigated the effects of fishing on the composition of the spawning stock of cod (*Gadus morhua*) in Icelandic waters by partitioning relative fishing mortality and spawning stock biomass (SSB) into finer spatial components than those used previously. Geographic regions of reproductive importance were identified around the country, in contrast to traditional paradigms of cod stock structure in Icelandic waters. SSB and relative fishing mortality were unevenly distributed in waters around Iceland, where gill nets selectively removed larger spawners from inshore waters of the main spawning grounds, whose demographic characteristics were more conducive to progeny survival. Changes in stock structure and demographic characteristics caused by changes in spatially explicit exploitation patterns can significantly affect stock productivity through differential loss of reproductive potential. Our approach of partitioning SSB into finer spatial units than those used previously, enabled a more detailed analysis of the distribution of spawners and exploitation of the Icelandic cod stock, and will enable the development of spatially disaggregated models of total egg production, that in turn may assist in differentiating the inherent variability within stock–recruitment relationships.

Keywords: Cod; *Gadus morhua*; Iceland; Recruitment; Spawning composition; Maternal effects; Spatial distribution; Exploitation; Mortality; Population dynamics; Fisheries management

1. Introduction

Fishing mortality frequently represents a significant loss of spawners from a fish stock (Hutchings et al., 1993; Sinclair and Murawski, 1997; Sinclair et al., 1997), leading to the collapse of many historically important groundfish stocks (Hutchings, 1996; Myers et al., 1996; Cook et al., 1997). Common to these collapses is recruitment overfishing which occurs when the size of a spawning stock is reduced to a level at which subsequent recruitment to the stock is impaired (Myers and Barrowman, 1996; Sinclair and Murawski, 1997). In this study, we investigate the effects of fishing on spatially disaggregated estimates of spawning stock biomass (SSB) for the Icelandic cod (*Gadus morhua*) stock to evaluate spatial and temporal changes in stock structure and reproductive output. Over the past decade, the fishing mortality on Icelandic cod has generated an exploitation rate that has removed between 34 and 55% of the spawning stock each year, which is likely to have a large impact on egg

* Corresponding author. Present address: CRC Reef Research Centre, James Cook University, Townsville, Qld 4811, Australia. Tel.: +61-7-47815287; fax: +61-7-47814099.
E-mail address: gavin.begg@jcu.edu.au (G.A. Begg).

0165-7836/02/$ – see front matter
PII: S0165-7836(02)00025-5

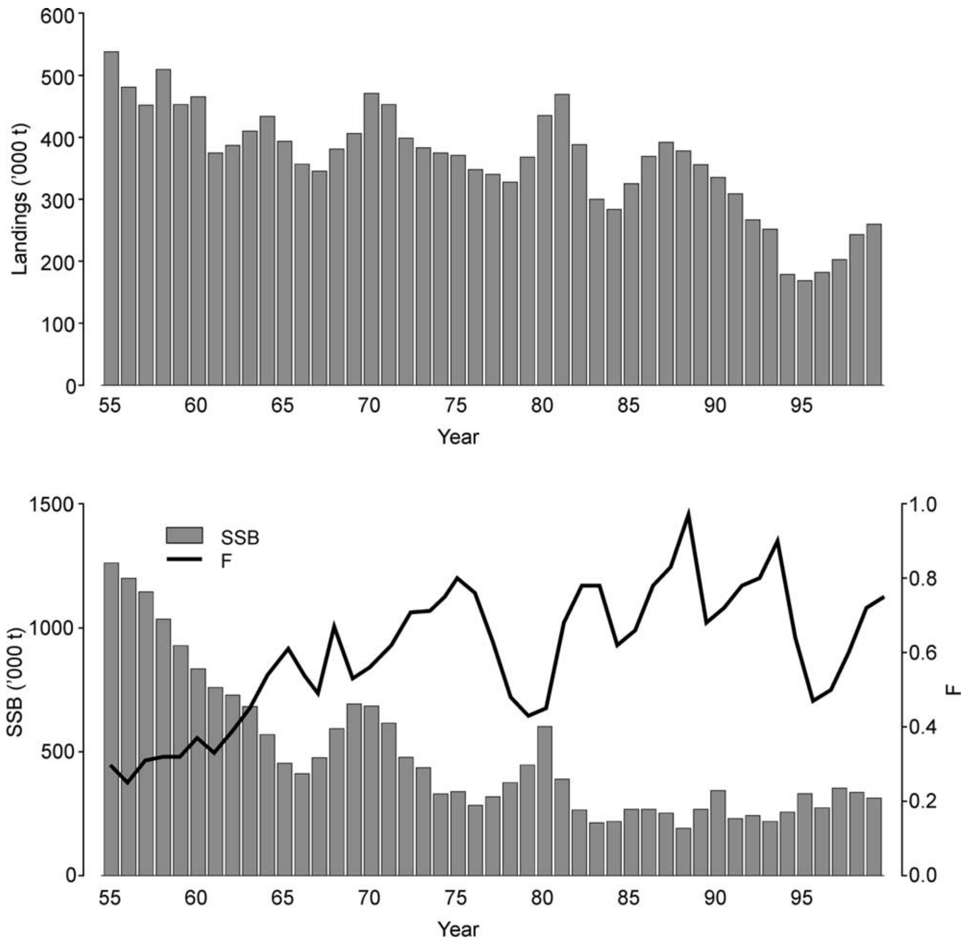

Fig. 1. Commercial landings ('000 t), spawning stock biomass (SSB; '000 t), and mean fishing mortality (*F*; ages 5–10) of Icelandic cod, 1955–1999 (Anonymous, 2001).

production, recruitment and the overall reproductive potential of the stock (Fig. 1).

The functional relationship between SSB and recruitment can be fundamental to understanding the population dynamics of exploited marine fish stocks (Ricker, 1954; Beverton and Holt, 1957; Myers and Barrowman, 1996), and is used for establishing biological reference limits (Cook, 1997). However, often this relationship is too poorly defined to identify precise limits needed to develop optimal harvesting strategies because of measurement error, use of inappropriate measures of stock and recruitment, unknown and variable effects of the environment, and diversity and structure of the spawning stock (Marshall et al., 1998; Scott et al., 1999). Furthermore, virtual population analysis (VPA)-derived estimates of SSB may not accurately estimate spawning biomass of a stock because of the spatially aggregated nature of the data. In contrast, partitioning SSB into finer spatial units than are typically used for stock assessments may enable a greater precision, on which estimations of reproductive potential can be based (Marteinsdottir et al., 2000a; Begg and Marteinsdottir, 2002a). Moreover, investigation into the effects of fishing on a spawning stock will enable a greater understanding of the processes responsible for the major reduction in reproductive outputs from a stock (Hutchings, 1996).

Fishing mortality influences the demographic characteristics of a fish stock that can have long-term detrimental effects on recruitment and yield. At high rates of exploitation, selective effects of fishing can truncate age and size distributions, eliminate spawning components, remove significant quantities of immature fish, induce changes in growth rate, maturation, fecundity, spawning duration and seasonality, and create "recruitment" fisheries; whereby a spawning stock is predominantly comprised of early maturing or "recruit" spawners (Hutchings and Myers, 1993; Cook et al., 1997; Sinclair and Murawski, 1997; Marteinsdottir and Thorarinsson, 1998). Fishing mortality can also influence breeding structure or "maternal" characteristics of a stock, that have direct implications on the quantity and quality of progeny produced, that in turn have implications for recruitment. Older, larger, and experienced (or "repeat") spawners produce not only greater quantities of eggs and larvae, but also produce progeny with greater viability and survival characteristics than those produced by younger, smaller, recruit spawners (Chambers and Leggett, 1996; Kjesbu et al., 1996; Marshall et al., 1998; Marteinsdottir and Steinarsson, 1998; Trippel, 1998; Marteinsdottir and Begg, 2002; Solemdal et al., 1995). Repeat spawners also tend to have a more protracted spawning season than recruit spawners; thereby increasing the probability that their progeny will encounter favourable environmental conditions for growth and survival (Trippel, 1998; Marteinsdottir and Bjornsson, 1999).

Historically, the Icelandic cod stock has supported significant fisheries, although in recent years it has been severely depleted, with SSB and recruitment having been low since the 1980s (Schopka, 1994; Fig. 1). During 1993–1997, a significant reduction in fishing mortality occurred on the stock in response to management reductions in total allowable catch (TAC) and diversion of fishing effort towards other species (Anonymous, 2001; Fig. 1). Although assessed as a single stock, the Icelandic cod stock is comprised of a major spawning component off the southwest coast (Jónsson, 1982), with additional spawning components located around the country (Begg and Marteinsdottir, 2000, 2002a; Marteinsdottir et al., 2000b). Peak spawning occurs from March to May, with older, larger cod spawning earlier and over a longer period than younger, smaller cod (Jónsson, 1982; Marteinsdottir and Bjornsson, 1999). Pelagic eggs and larvae derived from the main spawning component off the southwest coast (Fig. 2), during April and May, drift clockwise around the country with the coastal and offshore currents to the main nursery grounds off the north coast (Astthorsson et al., 1994; Begg and Marteinsdottir, 2000, 2002b). Currently, the status of the stock is assessed using a VPA approach (Anonymous, 2001), although there is arguably a need to disaggregate the data derived from this approach into finer spatial units, particularly if the spawning components comprising the stock contribute unequally to total reproductive potential of the stock.

In this study, we attempted to partition the Icelandic cod stock into spatially disaggregated spawning components on which future estimates of exploitation and reproductive potential can be based. Relative fishing mortality and SSB were partitioned into finer spatial components than that of the traditionally used VPA approach to establish relationships between exploitation patterns and stock composition. Exploitation patterns of the different fishing gears were examined further to determine any evidence for selective removal of the spawning stock whose demographic characteristics may have been more conducive to progeny survival, and subsequent year–class strength and recruitment.

2. Materials and methods

2.1. Sample collection

Spatial distribution, abundance, length, weight, sex, and maturity data of cod were collected from the Icelandic spring groundfish surveys (1990–1999). Sampling occurred in March for 2–3 weeks using a stratified systematic survey, where the station locations were fixed around the country (Table 1; Pálsson et al., 1989). The survey coincided with the beginning of the spawning season for cod, and survey design was aimed at minimizing possible biases due to spawning migrations (Pálsson et al., 1989). The survey employed standardized fishing methods (40 mm codend mesh), where tows were generally taken at 3.8 knots for 4 nautical miles (nm). At each station, cod were measured (cm), and sex and maturity stage (1: immature; 2: developing; 3: spawning; or 4: spent) determined macroscopically. Data were separated into nine statistical regions based on hydrographical and ecological considerations of the ecosystem; similar to the BORMICON model used to evaluate multispecies

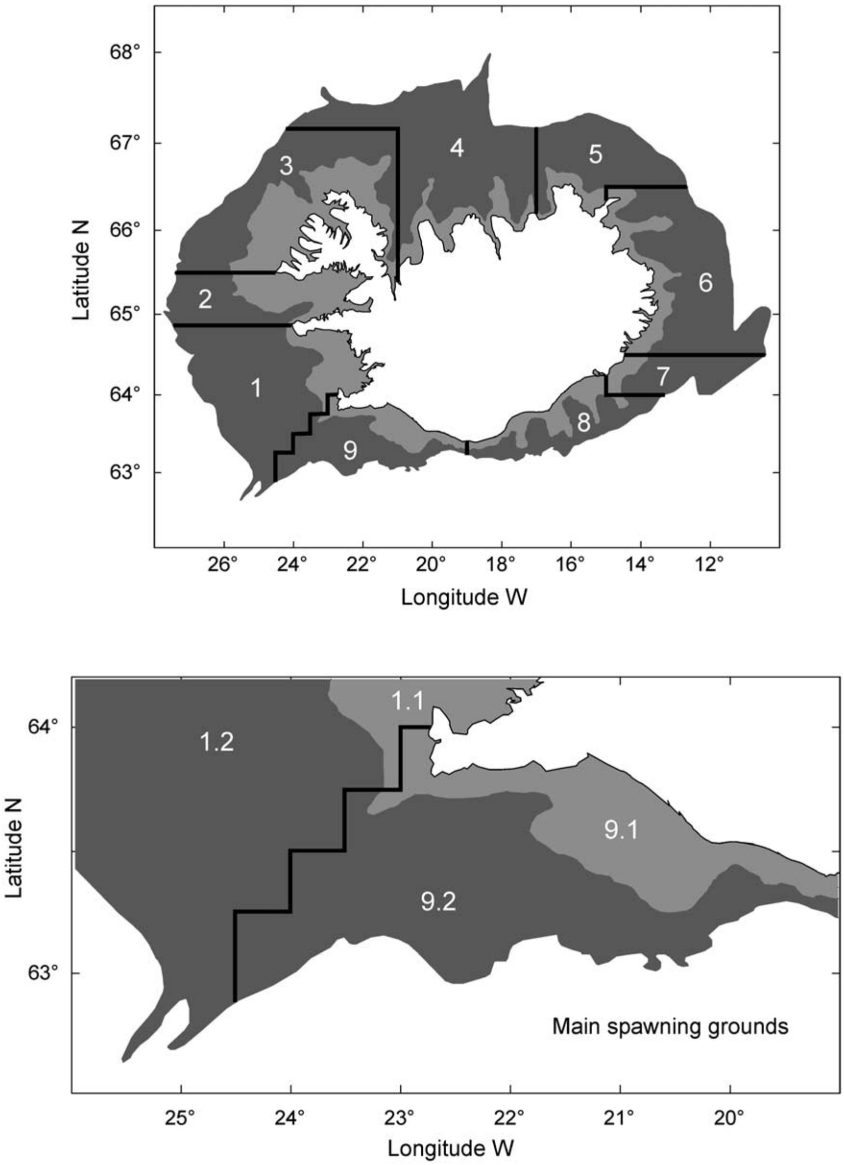

Fig. 2. Statistical regions (1–9) and main spawning grounds of Icelandic cod. Each statistical region is divided into two depth strata corresponding to 0–125 m (inshore: 1.1, . . ., 9.1), and 125–500 m (offshore: 1.2, . . ., 9.2), based on presumed hydrographic conditions and spawning behaviour of mature cod.

interactions in Icelandic waters (Stefánsson and Pálsson, 1997) (Fig. 2). These regions were further divided into two depth strata to account for individual spawning components of cod found on the main spawning grounds of southwest Iceland (Marteinsdottir et al., 2000a): 0–125 m (inshore 1.1, . . ., 9.1); and 125–500 m (offshore 1.2, . . ., 9.2) (Fig. 2).

2.2. Spatial and temporal spawning stock distribution

Spatial distribution and relative abundance of cod were examined to determine general aggregation patterns of cod at the beginning of the spawning season. Spawning biomass indices were then calculated from

Table 1
Number of stations sampled in each region and depth strata (1.1–9.2), 1990–1999

Region	Number of stations										Total
	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	
1.1	10	12	13	14	11	10	10	11	10	9	110
1.2	45	42	62	46	45	45	44	44	47	47	467
2.1	7	6	10	9	9	10	8	8	8	7	82
2.2	21	22	30	21	22	22	23	21	22	21	225
3.1	51	51	58	54	63	47	44	41	42	41	492
3.2	101	102	126	103	133	109	103	102	76	101	1056
4.1	11	10	16	16	17	17	13	12	10	10	132
4.2	72	73	92	71	74	73	68	68	70	69	730
5.1	4	5	7	5	6	5	6	5	5	4	52
5.2	44	43	56	44	43	44	42	43	43	44	446
6.1	8	9	14	16	14	15	6	6	8	8	104
6.2	75	72	90	74	74	73	71	71	68	68	736
7.1	3	3	5	3	4	4	3	3	3	4	35
7.2	32	34	35	32	33	33	26	25	25	25	300
8.1	9	9	11	9	10	11	8	9	8	7	91
8.2	17	17	25	17	17	17	17	18	17	17	179
9.1	9	7	14	14	14	18	14	13	15	16	134
9.2	30	32	38	31	31	30	31	30	30	38	321
Total	549	549	702	579	620	583	537	530	507	536	5692

the groundfish surveys (1990–1999) to provide annual estimates of relative stock size.

Measured length distributions were derived for each station, and scaled accordingly, where large tows required counting part of the catch (Pálsson et al., 1989). Initially, to enable spawning biomass indices to be calculated, annual length–weight relationships were estimated using generalized linear models (GLMs) with a log-link function and gamma distribution (MathSoft, 2000) for models of the form:

$$\log W = \alpha + \beta \log L \quad (1)$$

where W is the weight (g) and L the length (cm) of each cod sampled. GLMs avoid the use of correction factors when backtransforming typically used linear regression functions on log-transformed length–weight data, while the gamma distribution was selected partly because of increasing variation in the data with length (Gudmundsdottir and Steinarsson, 1997). The length–weight equations were estimated for cod sampled in waters off northern (Regions 3–6) and southern Iceland (Regions 1, 2, 7–9) separately, because of ecological considerations of the ecosystem and sample limitations with any given region (Begg and Marteinsdottir, 2002a). Horizontal gradients exist between these waters (as defined in Fig. 2), where the northern waters are colder and more variable than the southern waters (Malmberg and Kristmannsson, 1992), creating spatially diverse environments that may influence life history characteristics. Furthermore, owing to the disproportionate increase in weight of large cod, separate GLMs were estimated each year for cod $\leq$90 cm and for those >90 cm in length. In 1990–1992, the long-term mean (1993–1999) length–weight equations were used because of sample limitations in those years.

Logistic regression analysis (Sokal and Rohlf, 1995) was used to estimate annual maturity ogives (immature: stage 1; mature: stages 2–4) for cod sampled in waters off northern (Regions 3–6) and southern Iceland (Regions 1, 2, 7–9) separately. Likewise, annual mean lengths at age of recruitment (3 years) were estimated for cod sampled in northern and southern waters. Annual length–weight relationships and regional maturity ogives were then applied to the appropriate length distributions of cod sampled at each station to generate predicted weights, proportion mature, and corresponding relative spawning biomass estimates each year according to the following equation:

$$X_z = \frac{1}{T_z}\sum(C_l W_l M_l) \quad (2)$$

where at each station z, X_z is the relative spawning biomass (nm^{-1}) where catch was >0; T_z the tow distance (nm); C_l the number of cod measured at each length l (cm) > mean length at age of recruitment (3 years); W_l the predicted weight (g) of cod at each length l; and M_l the proportion mature at each length l. All cod below the annual mean lengths at age of recruitment were excluded from the relative spawning biomass estimates because those fish were not considered to be contributing to the spawning stock.

Annual spawning biomass indices (S_r) of cod in each region (1.1, ..., 9.2) were then calculated according to the following equations:

$$X_r = \frac{1}{N_r}\sum \log_e(X_z) \quad (3)$$

$$P_r = \frac{N_r}{N_t} \quad (4)$$

$$S_r = X_r P_r \left(\frac{U_r}{U_t}\right) \quad (5)$$

where in each region r, X_r is the logarithm of the mean spawning biomass; N_r the number of stations where catch was >0; P_r the proportion of non-zero tows; N_t the total number of stations; U_r the geographic area (km^2); and U_t the total geographic area of all the regions.

Spawning biomass indices were then used to partition spawning stock abundance (SSA) and SSB derived from the VPA-based stock assessment for Icelandic cod (Anonymous, 2001) to estimate the spatial distribution of the spawning stock. Relative spawning stock abundance (SSA_r) and spawning stock biomass (SSB_r) of cod in each region (1.1, ..., 9.2) were calculated each year according to the following equations:

$$S_t = \sum S_r \quad (6)$$

$$\text{SP}_r = \frac{S_r}{S_t} \quad (7)$$

$$\text{SSA}_r = \text{SP}_r\,\text{SSA} \quad (8)$$

$$\text{SSB}_r = \text{SP}_r\,\text{SSB} \quad (9)$$

where in each region r, S_r is the spawning biomass index; S_t the total spawning biomass index for all regions; SP_r the spawning biomass index proportion; SSA the total spawning stock abundance (millions; ages 3–14) from the annual VPA; and SSB the total spawning stock biomass ('000 t) from the annual VPA.

Regional estimates of SSA and SSB were then partitioned into the respective maturity-adjusted length frequency distributions for each region and year to describe the demographic characteristics of the spatially disaggregated spawning stock. Similar to the maturity ogives, annual sex ratios at length (20 cm intervals) were estimated for cod sampled in waters off northern (Regions 3–6) and southern Iceland (Regions 1, 2, 7–9) separately. The partitioned length (weight) frequency distributions of SSA and SSB were then multiplied by the proportion of female cod estimated for each length (weight) to determine the abundance and biomass of mature females comprising the spawning stock for each region and year.

2.3. Spatial and temporal fishing distribution

Commercial catches of cod were estimated from logbook data (1990–1999) to determine removal of potential spawners from the stock due to fishing mortality. Annual catch estimates for each of the major fishing gears used to target the stock were scaled according to the respective annual total landings, and partitioned into spatial and temporal components on the basis of individual years, months, and statistical regions. Measures of relative fishing mortality (F) in each year were then calculated according to the following equation:

$$F_r = \frac{C_r}{\text{SSB}_r} \quad (10)$$

where in each region r, C_r is the scaled catch estimate ('000 t); and SSB_r the spawning stock biomass ('000 t). Length frequency distributions of the landed catch were then derived for each of the major fishing gears to determine selective removal of the spawning stock.

2.4. Statistical analysis

GLMs were used to examine the effects of region, depth, and year on the composition of the spawning stock. Data for all of the response variables (except total length) were $\log_e$-transformed to stabilize the variance of the residuals and approximate normality. The Gaussian distribution was used for each model to examine each of the main effects and their first-order interaction terms. Residual plots were used to evaluate model fit. The final models used to examine spatial and temporal effects on the spawning stock of cod were:

$$\log_e(A+1) = \mu + R_i + Y_j + D_k + (\mathrm{RY})_{ij} + (\mathrm{RD})_{ik} + (\mathrm{YD})_{jk} \quad (11)$$

$$L = \mu + R_i + Y_j + D_k + (\mathrm{RY})_{ij} + (\mathrm{RD})_{ik} + (\mathrm{YD})_{jk} \quad (12)$$

$$\log_e(S) = \mu + D_k + R_i + Y_j + (\mathrm{DR})_{ki} + (\mathrm{DY})_{kj} + (\mathrm{RY})_{ij} \quad (13)$$

$$\log_e(\mathrm{SSA}) = \mu + D_k + R_i + Y_j + (\mathrm{DR})_{ki} + (\mathrm{DY})_{kj} + (\mathrm{RY})_{ij} \quad (14)$$

$$\log_e(\mathrm{SSB}) = \mu + D_k + R_i + Y_j + (\mathrm{DR})_{ki} + (\mathrm{DY})_{kj} + (\mathrm{RY})_{ij} \quad (15)$$

$$\log_e(\mathrm{SSA}f) = \mu + D_k + R_i + Y_j + (\mathrm{DR})_{ki} + (\mathrm{DY})_{kj} + (\mathrm{RY})_{ij} \quad (16)$$

$$\log_e(\mathrm{SSB}f) = \mu + D_k + R_i + Y_j + (\mathrm{DR})_{ki} + (\mathrm{DY})_{kj} + (\mathrm{RY})_{ij} \quad (17)$$

where A is the relative abundance (number nm^{-1}) at each station; μ the mean response; R_i the region effect; Y_j the year effect; D_k the depth effect; L the mean total length at each station; S the spawning biomass index for each region; SSA the total spawning stock abundance for each region; SSB the total spawning stock biomass for each region; SSAf the female spawning stock abundance for each region; and SSBf the female spawning stock biomass for each region. An additional effect of gear type was included in similar models used to examine relative F. Regions where there were no catch reported were excluded from statistical analysis. The final models used to examine the spatial and temporal effects on the relative F of cod were

$$\log_e(F) = \mu + D_m + G_n + R_i + Y_j + (\mathrm{DG})_{mn} + (\mathrm{DR})_{mi} + (\mathrm{DY})_{mj} + (\mathrm{GR})_{ni} + (\mathrm{GY})_{nj} + (\mathrm{RY})_{ij} \quad (18)$$

$$\log_e(F_s) = \mu + D_m + G_n + R_i + Y_j + (\mathrm{DG})_{mn} + (\mathrm{DR})_{mi} + (\mathrm{DY})_{mj} + (\mathrm{GR})_{ni} + (\mathrm{GY})_{nj} + (\mathrm{RY})_{ij} \quad (19)$$

where F is the total relative fishing mortality for each region; G the gear effect; and F_s the relative fishing mortality during the spawning months for each region. A posteriori multiple comparison of means ($\alpha = 0.05$) was conducted using Tukey's honestly significant difference (HSD) tests on the main effects for each model. All statistical analyses were performed using the version 6.0 S-PLUS software (MathSoft, 2000).

3. Results

3.1. Spatial and temporal spawning stock distribution

Generally, at the beginning of the spawning season in March, cod were distributed all around Iceland (Fig. 3). Relative abundance of cod was significantly affected by region, year and depth (Table 2), where greater concentrations of cod were found in waters off the north (Regions 3–6), and southeast (Region 7) coasts (HSD, $P < 0.05$). However, this may reflect the sampling coverage and selectivity of the groundfish survey as opposed to actual abundance patterns (Table 1). Corresponding to spatial differences in abundance of cod, were analogous differences in fish length (Fig. 3; Table 2), where larger cod were typically distributed each year in waters off the south coast (Regions 1, 2, 7–9) (HSD, $P < 0.05$).

Relative spawning biomass, SSA and SSB of cod were significantly affected by depth, region and year (Table 3). Reflective of the spawning biomass indices (Fig. 4), SSA and SSB were significantly greater in offshore waters off the southwest (Region 1) and north (Regions 3, 4 and 6) coasts (HSD, $P < 0.05$) (Table 4). Moreover, the maternal contribution to the spawning stock increased with fish length, where female cod were more abundant in the larger length groups (Fig. 5). Consequently, owing to known maternal effects on progeny survival and year–class success we estimated the abundance and biomass of spawning females in each region and year. Spatial and temporal trends in SSA and SSB of female cod were similar to

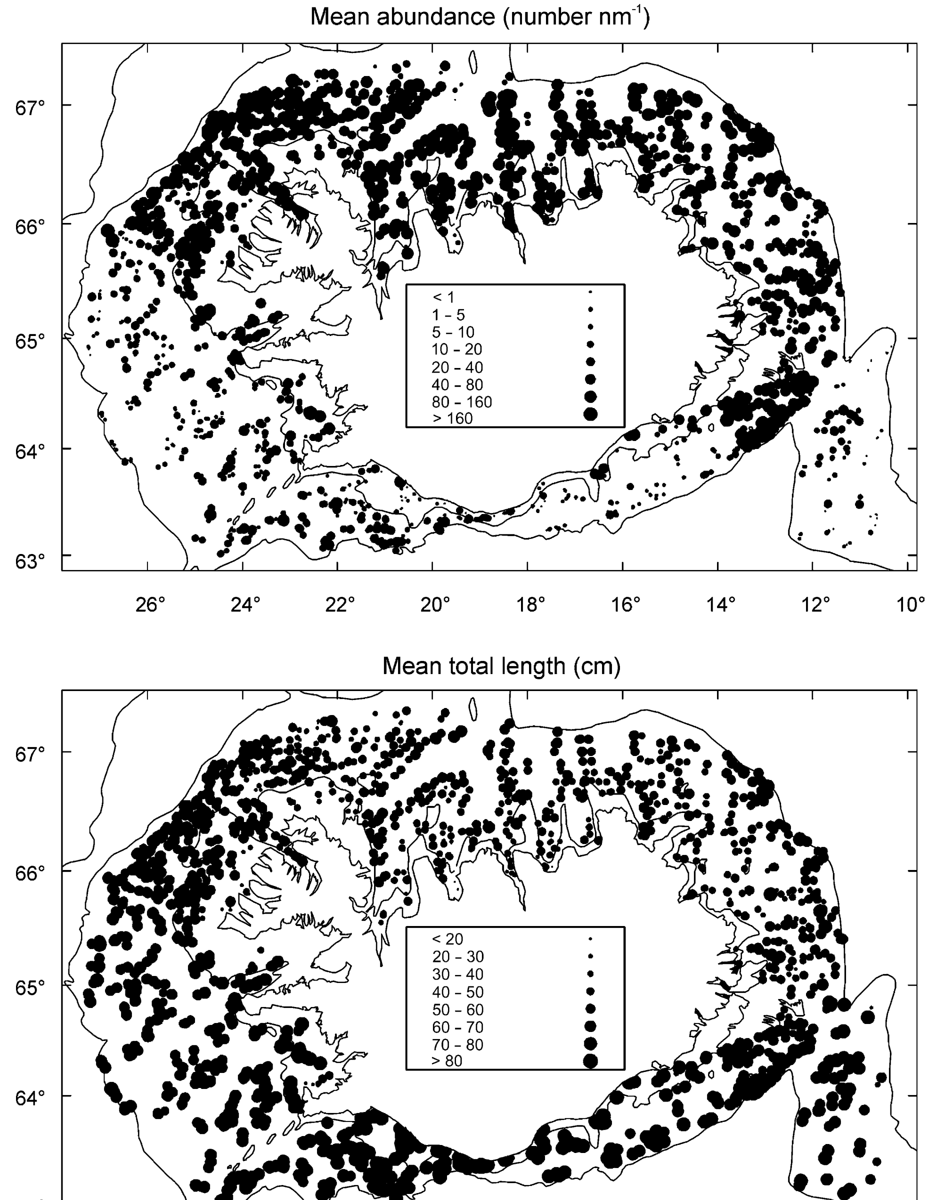

Fig. 3. Mean relative abundance (number nm^{-1}) and total length (cm) distributions of cod, 1990–1999.

the stock as a whole, albeit at a more reduced magnitude (Fig. 6; Table 5). SSA and SSB of female cod were significantly greater in offshore waters off the southwest (Region 1) and north (Regions 3, 4 and 6) coasts, respectively (HSD, $P < 0.05$).

3.2. Spatial and temporal fishing distribution

Commercial landings of cod have gradually declined since 1987, although in recent years have steadily increased with corresponding TACs (Fig. 1;

Table 2
Analysis of variance of relative abundance, $\log_e(\text{number nm}^{-1} + 1)$, and mean total length (cm) of cod for each station, 1990–1999, examining main effects and first-order interaction terms

Source	d.f.	SS	MS	F	P
Relative abundance					
Region	8	2388.7	298.6	247.9	<0.0001
Year	9	108.8	12.1	10.0	<0.0001
Depth	1	9.6	9.6	8.0	0.0047
Region × year	72	237.5	3.3	2.7	<0.0001
Region × depth	8	239.4	29.9	24.8	<0.0001
Year × depth	9	28.0	3.1	2.6	0.0058
Residual error	5584	6725.7	1.2		
Mean total length					
Region	8	836916.4	104614.6	751.5	<0.0001
Year	9	32420.6	3602.3	25.9	<0.0001
Depth	1	0.6	0.6	0.0	0.9496
Region × year	72	54768.6	760.7	5.5	<0.0001
Region × depth	8	17280.1	2160.0	15.5	<0.0001
Year × depth	9	4414.2	490.5	3.5	0.0002
Residual error	5444	757818.4	139.2		

Table 3
Analysis of variance of $\log_e$ relative spawning biomass, SSA (millions) and SSB ('000 t) of cod, 1990–1999, examining main effects and first-order interaction terms

Source	d.f.	SS	MS	F	P
Spawning biomass index					
Depth	1	49.79	49.79	3907.00	<0.0001
Region	8	31.89	3.99	312.78	<0.0001
Year	9	0.05	0.01	0.40	0.9331
Depth × region	8	20.36	2.54	199.68	<0.0001
Depth × year	9	0.06	0.01	0.52	0.8557
Region × year	72	1.01	0.01	1.10	0.3390
Residual error	72	0.92	0.01		
SSA					
Depth	1	49.79	49.79	3882.55	<0.0001
Region	8	31.92	3.99	311.11	<0.0001
Year	9	2.32	0.26	20.08	<0.0001
Depth × region	8	20.38	2.55	198.69	<0.0001
Depth × year	9	0.06	0.01	0.53	0.8452
Region × year	72	1.03	0.01	1.11	0.3279
Residual error	72	0.92	0.01		
SSB					
Depth	1	49.84	49.84	3933.06	<0.0001
Region	8	31.98	4.00	315.42	<0.0001
Year	9	5.06	0.56	44.37	<0.0001
Depth × region	8	20.37	2.55	200.98	<0.0001
Depth × year	9	0.06	0.01	0.52	0.8541
Region × year	72	1.01	0.01	1.11	0.3319
Residual error	72	0.91	0.01		

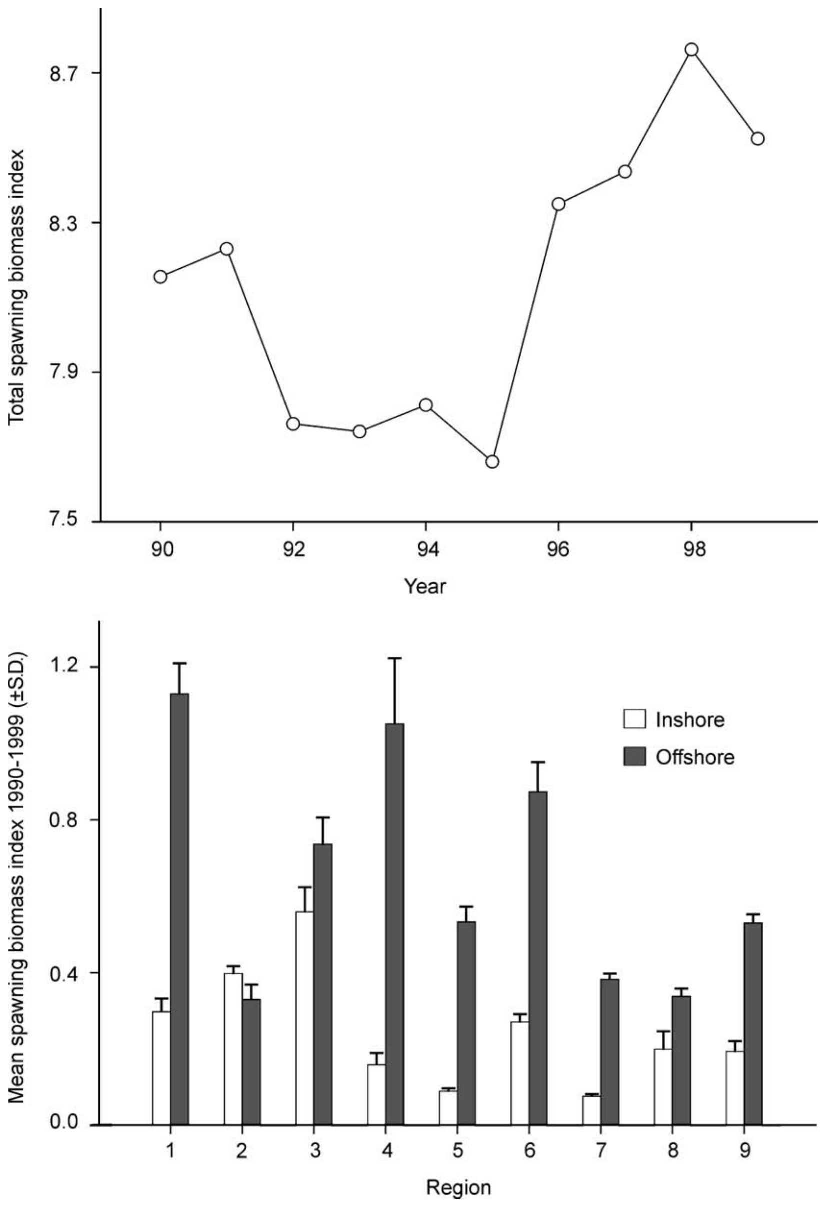

Fig. 4. Total spawning biomass index and mean (±S.D.) spawning biomass indices for cod in each region and depth strata, 1990–1999.

Anonymous, 2001). The catch reported in the commercial logbook data comprised 60–75% of the total landings, except in 1990 (26%) when the system was still being implemented. Consequently, we considered the logbook data to have adequately characterized the different fishing practices that have exploited the spawning stock of Icelandic cod over the past decade, except in 1990. Hence, further analyses were restricted to 1991–1999.

The commercial fishery for cod was comprised of five directed fishing gears (longline, gill net, handline, Danish seine and demersal bottom trawl), and two fishing gears (lobster trap and shrimp trawl) in which cod was caught as by-catch. Between 1991 and 1999,

Table 4
Relative SSA (millions) and SSB ('000 t) of cod in each region and depth strata (1.1–9.2), 1990–1999[a]

Region	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	Mean	S.D.
SSA (millions)												
1.1	18.1	13.7	15.3	13.5	9.4	10.5	14.8	13.5	12.9	9.8	13.2	2.7
1.2	63.9	53.7	51.1	50.6	39.9	51.7	51.9	41.5	50.7	41.8	49.7	7.1
2.1	20.6	17.8	18.5	19.5	14.2	15.9	18.4	18.1	17.4	14.1	17.5	2.1
2.2	20.1	14.7	15.7	13.4	10.8	11.5	15.1	14.5	15.0	13.6	14.4	2.5
3.1	25.7	23.8	25.9	25.2	19.1	21.9	24.9	23.6	29.4	24.8	24.4	2.7
3.2	32.5	32.2	31.2	30.6	26.9	32.5	37.7	33.2	36.8	28.3	32.2	3.3
4.1	6.8	6.7	6.9	5.4	6.3	6.8	7.5	6.2	7.7	8.3	6.9	0.8
4.2	42.7	42.1	45.7	50.8	36.1	36.1	52.2	53.2	60.5	40.4	46.0	8.0
5.1	5.0	3.9	3.3	4.3	3.5	3.9	4.1	4.1	3.9	3.1	3.9	0.5
5.2	27.1	21.5	21.1	24.5	20.0	23.3	26.5	23.9	26.6	19.1	23.4	2.9
6.1	15.7	11.6	11.0	12.7	9.7	12.6	12.2	12.4	11.4	9.6	11.9	1.7
6.2	51.5	36.3	41.1	34.7	30.4	35.2	41.0	36.4	43.8	33.8	38.4	6.1
7.1	4.3	2.7	3.6	3.7	2.7	3.4	3.8	3.0	3.7	2.6	3.4	0.6
7.2	20.2	16.4	17.1	17.0	13.5	17.2	17.9	16.0	18.4	14.1	16.8	2.0
8.1	13.0	10.2	9.8	9.2	8.6	6.5	11.4	8.9	5.3	5.1	8.8	2.6
8.2	18.4	12.9	16.2	15.7	11.7	15.8	15.3	15.1	16.2	11.5	14.9	2.2
9.1	9.8	6.8	9.8	9.5	6.0	7.7	9.4	8.3	11.5	6.6	8.5	1.8
9.2	29.8	22.8	23.7	23.7	19.3	23.5	25.8	21.1	23.7	19.5	23.3	3.1
Total	425	350	367	364	288	336	390	353	395	306	357.4	41.0
SSB ('000 t)												
1.1	14.6	9.0	10.2	8.1	8.4	10.3	10.4	13.5	11.0	10.0	10.6	2.1
1.2	51.6	35.3	33.9	30.5	35.6	50.9	36.5	41.6	43.2	42.7	40.2	7.1
2.1	16.6	11.7	12.3	11.7	12.7	15.7	12.9	18.2	14.8	14.5	14.1	2.2
2.2	16.2	9.7	10.4	8.1	9.7	11.3	10.6	14.6	12.8	13.9	11.7	2.6
3.1	20.7	15.6	17.1	15.2	17.0	21.5	17.5	23.6	25.0	25.4	19.9	3.9
3.2	26.3	21.2	20.6	18.4	24.0	32.0	26.5	33.3	31.3	28.9	26.3	5.2
4.1	5.5	4.4	4.5	3.3	5.6	6.7	5.3	6.2	6.6	8.4	5.7	1.4
4.2	34.4	27.7	30.3	30.6	32.2	35.6	36.6	53.4	51.4	41.3	37.4	8.8
5.1	4.0	2.6	2.2	2.6	3.1	3.8	2.9	4.1	3.3	3.2	3.2	0.6
5.2	21.9	14.1	14.0	14.7	17.8	23.0	18.6	23.9	22.6	19.5	19.0	3.8
6.1	12.7	7.6	7.3	7.7	8.7	12.4	8.6	12.4	9.7	9.8	9.7	2.1
6.2	41.6	23.9	27.2	20.9	27.1	34.6	28.8	36.5	37.3	34.6	31.3	6.6
7.1	3.4	1.8	2.4	2.2	2.4	3.4	2.6	3.0	3.2	2.6	2.7	0.5
7.2	16.3	10.8	11.4	10.2	12.1	16.9	12.6	16.1	15.6	14.4	13.6	2.5
8.1	10.5	6.7	6.5	5.5	7.6	6.4	8.0	8.9	4.5	5.2	7.0	1.8
8.2	14.8	8.5	10.7	9.4	10.4	15.5	10.8	15.1	13.8	11.8	12.1	2.5
9.1	7.9	4.5	6.5	5.7	5.4	7.6	6.6	8.3	9.8	6.7	6.9	1.5
9.2	24.0	15.0	15.7	14.3	17.2	23.1	18.1	21.1	20.1	20.0	18.9	3.4
Total	343	230	243	219	257	331	274	354	336	313	290.0	50.9

[a] Total SSA and SSB values are from the annual VPA (Anonymous, 2001).

cod comprised 22–87% of the total catch (all species) for the directed fishing gears. Although handlines were the most selective of these gears (mean proportion of cod in total handline catch $81 \pm 4\%$ S.D.); the relative mean removal of cod from the stock using handlines was insignificant (1%) compared to the other directed fishing gears (5–52%). Consequently, we only considered the effects of four fishing gears on the removal of spawners from the stock; longline (line), gill net (net), Danish seine (drag) and demersal bottom trawl (trawl), as these accounted on average for 97% of the total catch of cod in any given year.

Generally, cod were exploited each year all around Iceland, particularly off the northwest coast (Fig. 7).

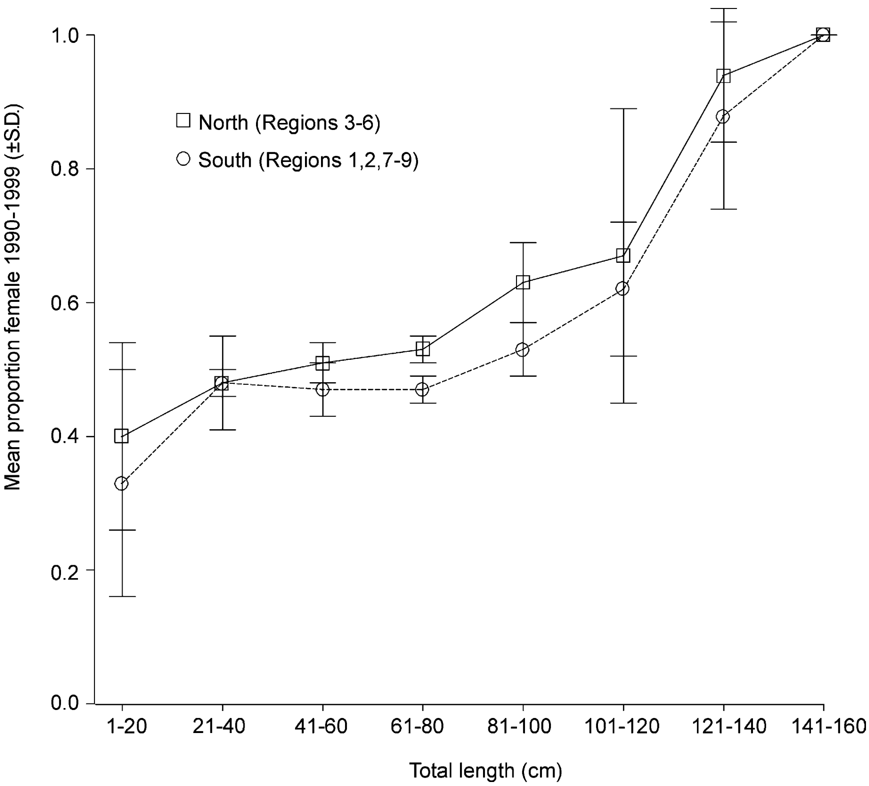

Fig. 5. Mean proportion of females in each length class for cod in the northern (Regions 3–6) and southern (Regions 1, 2, 7–9) statistical areas, 1990–1999.

Table 5
Analysis of variance of $\log_e$ SSA (millions) and SSB (’000 t) of female cod, 1990–1999, examining main effects and first-order interaction terms

Source	d.f.	SS	MS	*F*	*P*
SSA					
Depth	1	44.58	44.58	2961.13	<0.0001
Region	8	33.11	4.14	274.92	<0.0001
Year	9	2.61	0.29	19.28	<0.0001
Depth × region	8	20.39	2.55	169.34	<0.0001
Depth × year	9	0.11	0.01	0.81	0.6076
Region × year	72	1.32	0.02	1.22	0.1998
Residual error	72	1.08	0.02		
SSB					
Depth	1	42.33	42.33	2774.72	<0.0001
Region	8	32.97	4.12	270.19	<0.0001
Year	9	3.97	0.44	28.90	<0.0001
Depth × region	8	19.69	2.46	161.33	<0.0001
Depth × year	9	0.16	0.02	1.18	0.3237
Region × year	72	1.61	0.02	1.46	0.0546
Residual error	72	1.10	0.02		

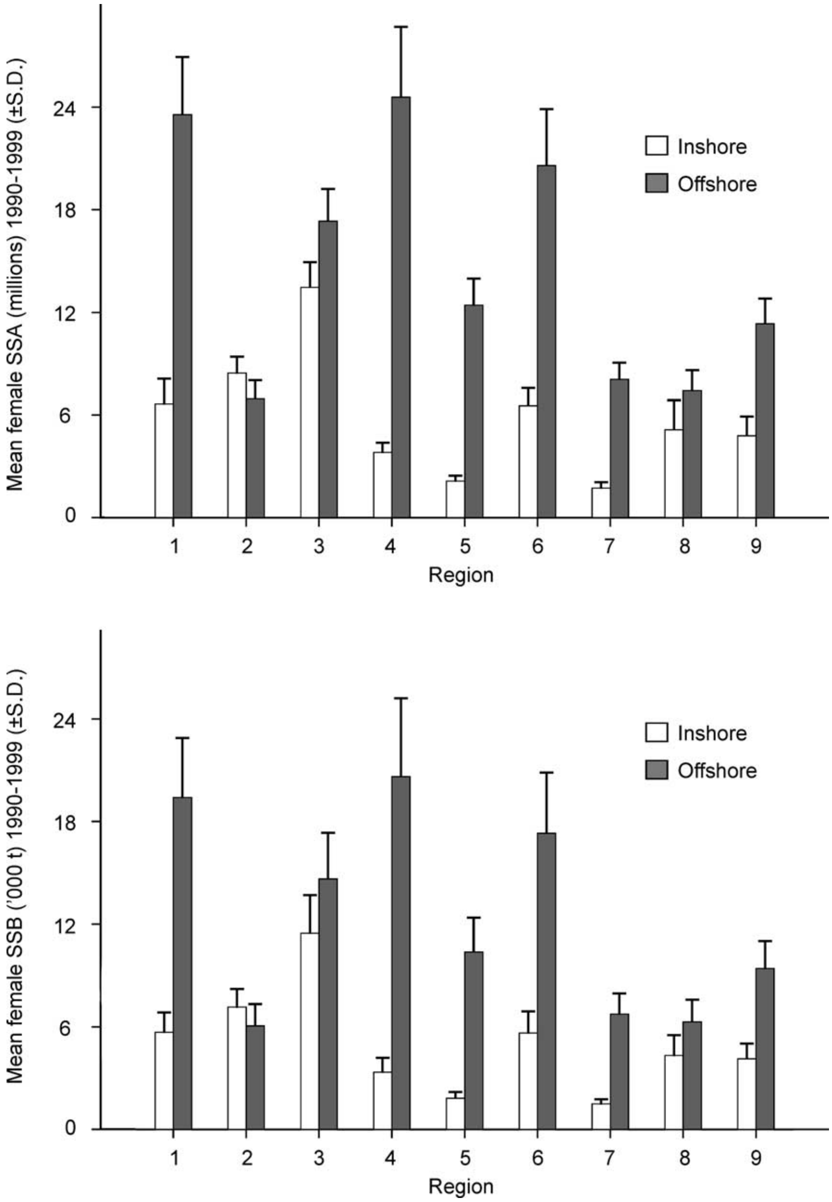

Fig. 6. Mean (±S.D.) spawning stock abundance SSA (millions) and biomass SSB ('000 t) of cod in each region and depth strata based on spawning biomass indices, 1990–1999.

Annual relative fishing mortality (*F*) of the spawning stock was significantly greater in inshore waters on the main spawning and feeding grounds off the southwest (Regions 1 and 9) and northwest (Region 3) coasts, respectively (HSD, $P < 0.05$) (Fig. 8; Table 6). Since 1993, annual total *F* has been significantly lower with the introduction of quota reductions, where trawl and net fishing gears have been responsible for most of the *F* of cod (HSD, $P < 0.05$). During the main spawning months (March–May), cod were mostly exploited each year on the main spawning grounds off the southwest coast (Fig. 7). Net fishing gear was responsible for most of the *F* of cod during these months, and was significantly greater in inshore waters on the main

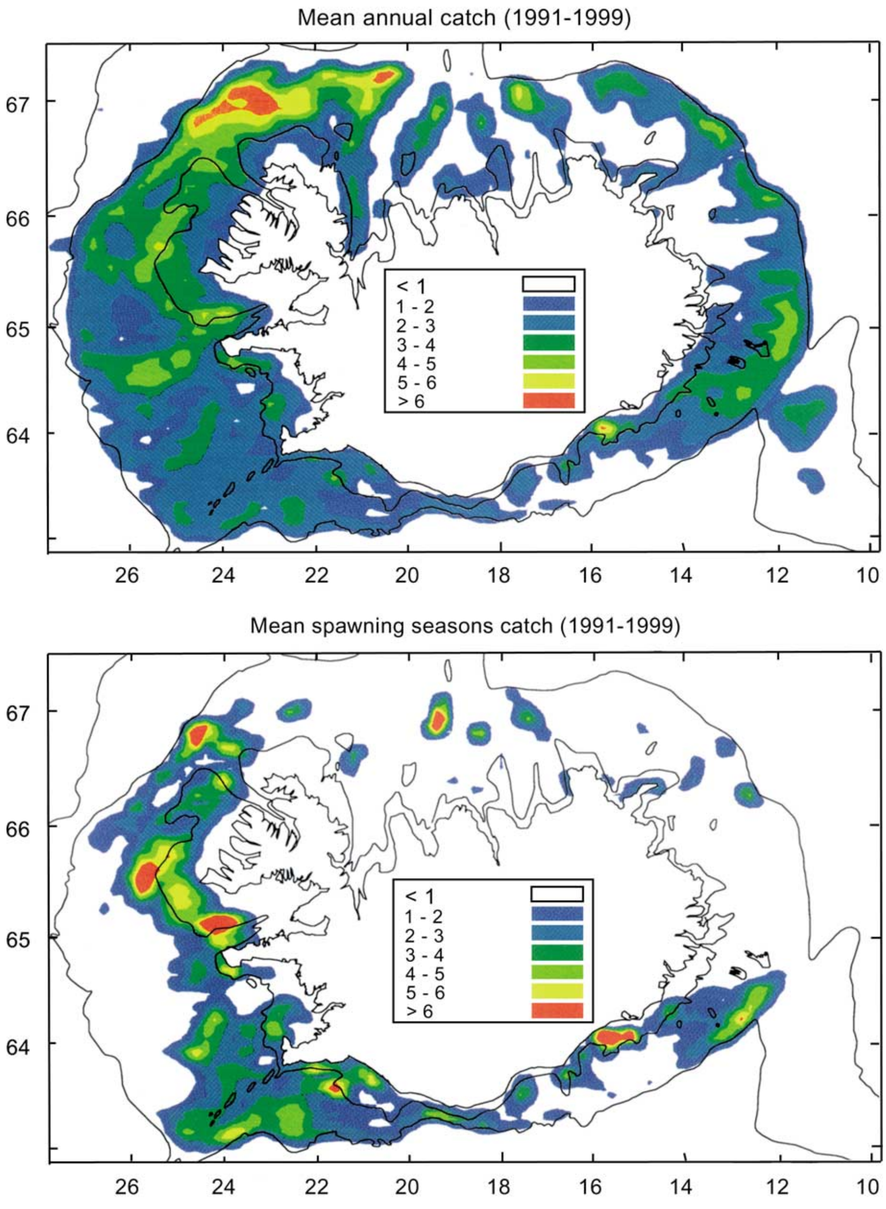

Fig. 7. Mean annual and spawning season (March–May) catch of cod (t nm^{-2}) for the main fishing gears (line, net, drag and trawl), 1991–1999.

spawning grounds (HSD, $P < 0.05$) (Table 6). Differential size-selection of cod was also apparent for each of the major fishing gears, where each year nets removed larger, and hence the most productive cod from inshore waters of the main spawning grounds (Fig. 9).

4. Discussion

Partitioning SSB into spatially explicit population components enabled geographic regions of reproductive importance to be identified that may influence the long-term viability and sustainable utilization of the

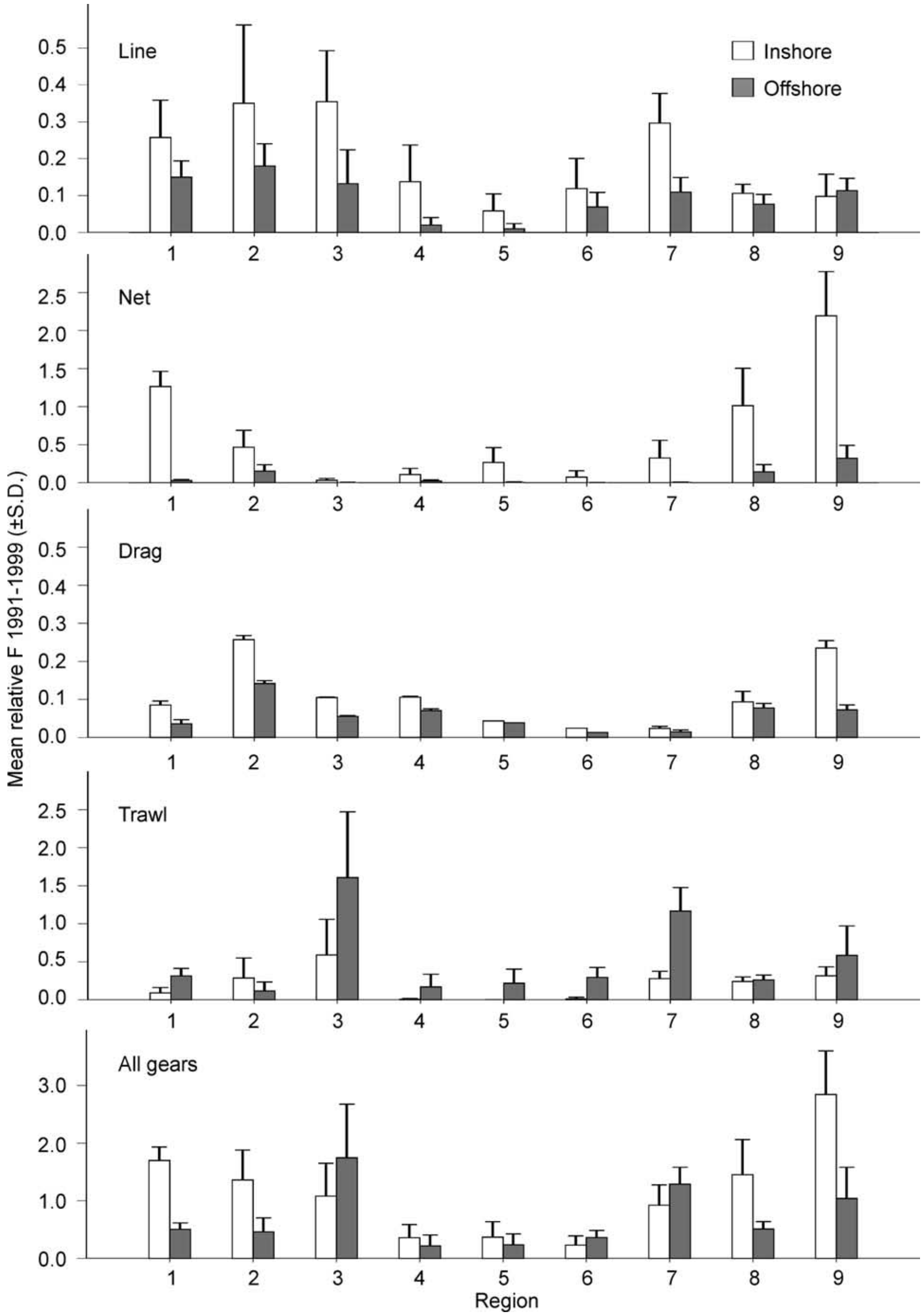

Fig. 8. Mean (±S.D.) relative fishing mortality (F) of cod for each of the major fishing gears (line, net, drag and trawl) in each region and depth strata, 1991–1999.

Table 6
Analysis of variance of $\log_e F$ (C/SSB) for the year and main spawning months (March–May), of cod, 1991–1999, examining main effects and first-order interaction terms

Source	d.f.	SS	MS	*F*	*P*
Annual *F*					
Depth	1	87.00	87.00	118.63	<0.0001
Gear	3	231.16	77.05	105.07	<0.0001
Region	8	310.18	38.77	52.87	<0.0001
Year	8	30.70	3.84	5.23	<0.0001
Depth × gear	3	377.24	125.75	171.46	<0.0001
Depth × region	8	16.85	2.11	2.87	0.0040
Depth × year	8	1.78	0.22	0.30	0.9648
Gear × region	24	355.68	14.82	20.21	<0.0001
Gear × year	24	46.11	1.92	2.62	<0.0001
Region × year	64	47.39	0.74	1.01	0.4611
Residual error	444	325.62	0.73		
Spawning months *F*					
Depth	1	67.53	67.53	86.35	<0.0001
Gear	3	318.77	106.26	135.87	<0.0001
Region	8	344.28	43.04	55.03	<0.0001
Year	8	75.16	9.40	12.01	<0.0001
Depth × gear	3	190.76	63.59	81.31	<0.0001
Depth × region	8	49.67	6.21	7.94	<0.0001
Depth × year	8	2.13	0.27	0.34	0.9501
Gear × region	24	187.41	7.81	9.99	<0.0001
Gear × year	24	55.33	2.31	2.95	<0.0001
Region × year	64	68.24	1.07	1.36	0.0427
Residual error	370	289.36	0.78		

Icelandic cod stock. The reproductive component of the stock was unevenly distributed in waters around the country, with significant concentrations located on the main spawning and feeding grounds off the southwest and northwest coasts, respectively (Fig. 6). Significant regional spawning grounds were also suggested in waters off the north and east coasts, in contrast to traditional paradigms of cod stock structure in Icelandic waters (Jónsson, 1982), although, it must be remembered that the regions where sexually mature cod were captured may not necessarily be the regions where spawning occurs. The groundfish survey is designed to coincide with the beginning of the spawning season for cod, and hence to minimize possible biases due to spawning migrations (Pálsson et al., 1989), but part of the spawning stock may still be migrating when the survey occurs, particularly those cod off the northwest coast in Region 3 (Jónsson, 1982). However, our results concurred with recent studies modelling back-calculated birth date distributions of 0-group cod that also indicated differential regional spawning components (Begg and Marteinsdottir, 2000; Marteinsdottir et al., 2000b). Moreover, tag-recapture studies indicated regional spawning components in waters off the north, northeast, and east coasts, with most tag returns in these waters occurring within close proximity to where the fish were tagged (Thorsteinsson and Marteinsdottir, 1992; Jónsson, 1996).

Spatial dispersal of spawning aggregations in the Icelandic cod stock may be partly responsible for maintaining the stock at viable levels of sustainability. An abundant, dispersed stock contributing to overall stock productivity, such as the Icelandic cod stock, is more likely to spawn in regions providing optimal environmental conditions for progeny survival than a single, isolated spawning stock, and may be a population strategy to counter years in which unfavourable environmental conditions exist for progeny survival (Begg and Marteinsdottir, 2000). Furthermore, there is relatively little exploitation on these other regional spawning components, particularly in the north

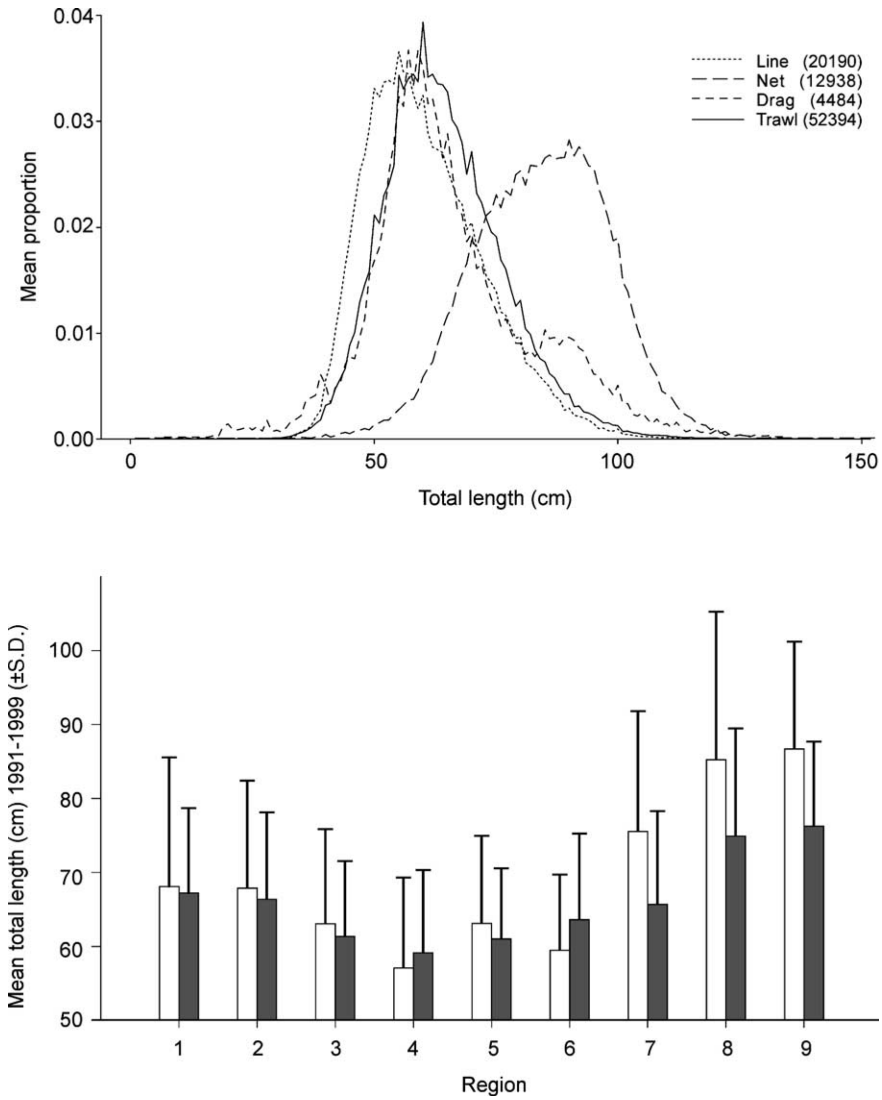

Fig. 9. Mean annual and regional (±S.D.) total length (cm) distributions of cod for the main fishing gears (line, net, drag and trawl), 1991–1999. Numbers in parentheses represent mean sample sizes for any given year.

(Regions 4 and 5) where the main nursery grounds are located (Begg and Marteinsdottir, 2000; Marteinsdottir et al., 2000b), indirectly ensuring relatively protected and undisturbed habitats for the juveniles, while maintaining a source of recruits for the main spawning component, and stock as a whole.

Fishing patterns were similar to distribution patterns of spawners, where high levels of exploitation occurred in regions containing high numbers of spawners. These patterns are of particular concern to the Icelandic cod stock, as fisheries that target concentrations of the most productive spawners are typified by stock declines and fishery collapses (Fulton et al., 1999). Significant proportions of cod were removed from waters off the northwest and southwest coasts, where the main feeding and spawning grounds were located respectively (Schopka, 1994; Marteinsdottir et al., 2000a). Historically, the most important fishing grounds were located between the northwest and southwest coasts in regions where cod came closest to the shore on their presumed spawning and feeding migrations (Jónsson, 1996). The northwest region is particularly important to the fishery, because as well as containing a resident population of cod, it is a transition zone through which large numbers of cod growing up on the north coast nursery grounds most likely pass on their way south to the main spawning grounds (Jónsson, 1996).

Besides differential removal of spawners from the stock in terms of *quantity*, there are also considerations of *quality*, where the different fishing gears comprising the fishery have differential size-selectivities that directly influence stock productivity. Differential removal of the spawning stock is particularly relevant for the gill net fishery, which removes significantly larger individuals, and hence greater reproductive potential in terms of both quantity and quality (i.e., older, repeat spawners) than the other fishing gears (Fig. 9). Older, larger, repeat spawners produce greater quantities of eggs and larvae, with greater viability and survival characteristics, than those produced by younger, smaller, recruit spawners (Kjesbu et al., 1996; Marteinsdottir and Steinarsson, 1998; Trippel, 1998). Likewise, in Icelandic waters older and larger cod have been found to produce greater quantities of eggs and more viable larvae than younger and smaller cod (Marteinsdottir et al., 2000a; Marteinsdottir and Begg, 2002). Consequently, the gill net fishery selectively removes adults from the spawning stock whose demographic characteristics are more conducive to progeny survival that can have direct implications on recruitment success and sustainability of the stock. Indeed, the dramatic increase in the use of commercial gill nets in the early 1960s has been suggested to be responsible for the decline in cod stocks throughout inshore waters of the northwest Atlantic (Hutchings et al., 1993). Hence, excessive removal of larger, older, repeat spawners from a stock may be more influential to recruitment success than simply removal of absolute biomass (Marshall et al., 1998; Murawski et al., 1999; Scott et al., 1999; Trippel, 1999); highlighting the importance of maintaining a broad and healthy age distribution within an exploited population (Marteinsdottir and Thorarinsson, 1998).

Generally, trends in our estimates of total biomass, concurred with trends in SSB derived from the annual stock assessment (Anonymous, 2001). However, our estimates based on finer spatial partitioning of the spawning stock (as well as those used in the VPA-based assessment) may be underestimating the relative proportion of older and larger spawners in the inshore waters of the main spawning grounds off the south coast because of catchability problems associated with the annual groundfish survey. Inshore waters off the south coast are characterized by untrawlable substratum (Marteinsdottir et al., 2000a), resulting in reduced sampling coverage, and potentially unrepresentative samples of the spawning stock being sampled by the groundfish survey in these regions (Pálsson et al., 1989). In 1996, an annual gill net survey was established to address these concerns, but results from this survey have yet to be incorporated into the assessment of the stock (Gudmundsdottir et al., 1998). Future studies need to integrate results from the groundfish and gill net surveys to examine the magnitude of the catchability problem, and to confirm the accuracy of our approach.

Our approach of partitioning SSB into finer spatial units than those used previously, enabled a more detailed analysis of the distribution of spawners and exploitation of the Icelandic cod stock. This study provides an important step in accurately describing the potential spawning components of the stock, that typically are not accounted for at such spatial units in most stock assessments (Murawski et al., 1999; Trippel, 1999). Future studies need to link results from this study with individual egg production models to enable spatially and temporally resolved reproductive potential to be estimated that will assist in explaining recruitment variability in the stock.

Acknowledgements

We would like to thank the survey leaders, Olafur K. Palsson, Sigfús A. Schopka, and Sólmundur T. Einarsson, as well as, all the cruise leaders and research scientists for collection of the survey data; Lorna Taylor, Gunnar Stefánsson, Asta Gudmundsdottir, and Höskuldur Björnsson for discussions and statistical advice; and two anonymous reviewers for their constructive comments. This study was part of the EU funded project, FAIR-PL98-4122, 'An operational model of the effects of stock structure and spatio-temporal factors on recruitment (STEREO)', and was supported by the Icelandic Research Council and the Ministry of Fisheries.

References

Anonymous, 2001. State of marine stocks in Icelandic waters 2000/2001. Prospects for the quota year 2001/2002. Hafrannsóknastofnun Fjölrit 80, 1–186.

Astthorsson, O.S., Gislason, A., Gudmundsdottir, A., 1994. Distribution, abundance, and length of pelagic juvenile cod in Icelandic waters in relation to environmental conditions. ICES Mar. Sci. Symp. 198, 529–541.

Begg, G.A., Marteinsdottir, G., 2000. Spawning origins of pelagic juvenile cod *Gadus morhua* inferred from spatially explicit age distributions: potential influences on year–class strength and recruitment. Mar. Ecol. Prog. Ser. 202, 193–217.

Begg, G.A., Marteinsdottir, G., 2002a. Environmental and stock effects on spatial distribution and abundance of mature cod *Gadus morhua*. Mar. Ecol. Prog. Ser. 229, 245–262.

Begg, G.A., Marteinsdottir, G., 2002b. Environmental and stock effects on spawning origins and recruitment of cod *Gadus morhua*. Mar. Ecol. Prog. Ser. 229, 263–277.

Beverton, R.J.H., Holt, S.J., 1957. On the dynamics of exploited fish populations. Fisheries Investigation London Series 2.

Chambers, R.C., Leggett, W.C., 1996. Maternal influences on variation in egg sizes in temperate marine fishes. Am. Zool. 36, 180–196.

Cook, R.M., 1997. The application of a sustainability criterion to demersal stocks in the ICES area. ICES C.M. 1997/V:7.

Cook, R.M., Sinclair, A., Stefánsson, G., 1997. Potential collapse of North Sea cod stocks. Nature 385, 521–522.

Fulton, E., Kault, D., Mapstone, B., Seaves, M., 1999. Spawning season influences on commercial catch rates: computer simulations and *Plectropomus leopardus*, a case in point. Can. J. Fish. Aquat. Sci. 56, 1096–1108.

Gudmundsdottir, A., Steinarsson, B.Æ., 1997. An attempt to model the length–weight relationship for saithe in Icelandic waters. ICES C.M. 1997/CC:08.

Gudmundsdottir, A., Þorsteinsson, V., Marteinsdottir, G., 1998. Gill-net survey of spawning cod in Icelandic waters in 1998. Hafrannsóknastofnun Fjölrit 71, 19.

Hutchings, J.A., 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. Can. J. Fish. Aquat. Sci. 53, 943–962.

Hutchings, J.A., Myers, R.A., 1993. Effect of age on the seasonality of maturation and spawning of Atlantic cod, *Gadus morhua*, in the northwest Atlantic. Can. J. Fish. Aquat. Sci. 50, 2468–2474.

Hutchings, J.A., Myers, R.A., Lilly, G.R., 1993. Geographic variation in the spawning of Atlantic cod, *Gadus morhua*, in the northwest Atlantic. Can. J. Fish. Aquat. Sci. 50, 2457–2467.

Jónsson, E., 1982. A survey of spawning and reproduction of the Icelandic cod. Rit Fiskideildar 6, 45.

Jónsson, J., 1996. Tagging of cod (*Gadus morhua*) in Icelandic waters 1948–1986. Rit Fiskideildar 14, 1–82.

Kjesbu, O.S., Solemdal, P., Bratland, P., Fonn, M., 1996. Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 53, 610–620.

Malmberg, S.A., Kristmannson, S.S., 1992. Hydrographic conditions in Icelandic waters, 1980–1989. ICES Mar. Sci. Symp. 195, 76–92.

Marshall, C.T., Kjesbu, O.S., Yaragina, N.A., Solemdal, P., Ulltang, Ø., 1998. Is spawner biomass a sensitive measure of the reproductive and recruitment potential of northeast Arctic cod. Can. J. Fish. Aquat. Sci. 55, 1766–1783.

Marteinsdottir, G., Begg, G.A., 2002. Essential relationships incorporating the influence of age, size, and condition on variables required for estimation of reproductive potential in Atlantic cod *Gadus morhua* stocks. Mar. Ecol. Prog. Ser. (in press).

Marteinsdottir, G., Bjornsson, H., 1999. Time and duration of spawning of cod in Icelandic waters. ICES C.M. 1999/Y:34.

Marteinsdottir, G., Steinarsson, A., 1998. Maternal influence on the size and viability of Iceland cod *Gadus morhua* eggs and larvae. J. Fish Biol. 52, 1241–1258.

Marteinsdottir, G., Thorarinsson, K., 1998. Improving the stock–recruitment relationship in Icelandic cod (*Gadus morhua*) by including age diversity of spawners. Can. J. Fish. Aquat. Sci. 55, 1372–1377.

Marteinsdottir, G., Gudmundsdottir, A., Thorsteinsson, V., Stefánsson, G., 2000a. Spatial variation in abundance, size composition and viable egg production of spawning cod (*Gadus morhua* L.) in Icelandic waters. ICES J. Mar. Sci. 57, 824–830.

Marteinsdottir, G., Gunnarsson, B., Suthers, I.M., 2000b. Spatial variation in hatch date distributions and origin of pelagic juvenile cod in Icelandic waters. ICES J. Mar. Sci. 57, 1184–1197.

MathSoft, 2000. S-PLUS 6.0 for Unix Guide to Statistics. Data Analysis Products Division, MathSoft, Seattle, WA.

Murawski, S.A., Rago, P.J., Trippel, E.A., 1999. Impacts of demographic variation in spawning success on reference points for fishery management. In: Restrepo, V.R. (Ed.), Proceedings of the Fifth National NMFS Stock Assessment Workshop: Providing Scientific Advice to Implement the Precautionary Approach Under the Magnuson-Stevens Fishery Conservation and Management Act. NOAA Technical Memorandum, NMFS-F/SPO-40, pp. 77–85.

Myers, R.A., Barrowman, N.J., 1996. Is fish recruitment related to spawner abundance? Fish. Bull. 94, 707–724.

Myers, R.A., Hutchings, J.A., Barrowman, N.J., 1996. Hypotheses for the decline of cod in the North Atlantic. Mar. Ecol. Prog. Ser. 138, 293–308.

Pálsson, O.K., Jonsson, E., Schopka, S.A., Stefánsson, G., Steinarsson, B.Æ., 1989. Icelandic groundfish survey data used to improve precision in stock assessments. J. Northw. Atl. Fish. Sci. 9, 53–72.

Ricker, W.E., 1954. Stock and recruitment. J. Fish. Res. Bd. Can. 11, 559–623.

Schopka, S.A., 1994. Fluctuations in the cod stock off Iceland during the twentieth century in relation to changes in the fisheries and environment. ICES Mar. Sci. Symp. 198, 175–193.

Scott, B., Marteinsdottir, G., Wright, P., 1999. Potential effects of maternal factors on spawning stock–recruitment relationships under varying fishing pressure. Can. J. Fish. Aquat. Sci. 56, 1882–1890.

Sinclair, A.F., Murawski, S.A., 1997. Why have groundfish stocks declined? In: Boreman, J., Nakashima, B.S., Wilson, J.A., Kendall, R.L. (Eds.), Northwest Atlantic Groundfish: Perspectives on a Fishery Collapse. American Fisheries Society Maryland, pp. 71–93.

Sinclair, M., O'Boyle, R., Burke, D.L., Peacock, G., 1997. Why do some fisheries survive and others collapse? In: Hancock, D.A., Smith, D.C., Grant, A., Beumer, J.P. (Eds.), Developing and Sustaining World Fisheries Resources. The State of Science and Management. CSIRO, Collingwood, Australia, pp. 23–35.

Sokal, R.R., Rohlf, F.J., 1995. Biometry, 3rd Edition. Freeman, New York.

Solemdal, P., Kjesbu, O.S., Fonn, M., 1995. Egg mortality in recruit- and repeat-spawning cod—an experimental study. ICES C.M. 1995/G:35.

Stefánsson, G., Pálsson, Ó.K., 1997. BORMICON. A boreal migration and consumption model. Hafrannsóknastofnun Fjölrit 58, 223.

Thorsteinsson, V., Marteinsdottir, G., 1992. Tagging of cod at spawning sites on the North and the East Coast in 1991. Ægir 2, 60–64 (in Icelandic).

Trippel, E.A., 1998. Egg size and viability and seasonal offspring production of young Atlantic cod. Trans. Am. Fish. Soc. 127, 339–359.

Trippel, E.A., 1999. Estimation of stock reproductive potential: history and challenges for Canadian Atlantic gadoid stock assessments. In: Restrepo, V.R. (Ed.), Proceedings of the Fifth National NMFS Stock Assessment Workshop: Providing Scientific Advice to Implement the Precautionary Approach Under the Magnuson-Stevens Fishery Conservation and Management Act. NOAA Technical Memorandum, NMFS-F/SPO-40, pp. 61–81.