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Spawning stock characteristics and cod recruitment success in the southern Gulf of St. Lawrence

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Abstract

Recruitment rate (defined here as R, the abundance of 3 yr old cod, divided by SSB, the biomass of the spawning stock that produced them) has varied widely for cod in the southern Gulf of St. Lawrence. In particular, the rate of recruitment was remarkably high from the mid 1970s to the early 1980s. Variation in the quantity or quality of eggs produced by a unit of SSB will contribute to variation in the recruitment rate when it is estimated by R/SSB. We tested effects of spawning stock characteristics (age and size structure) on the recruitment rate of southern Gulf cod. Over the 1950-1994 period, there was no tendency for high recruitment rates to be associated with an older or more diverse age structure of the spawning stock, or with a spawning stock composed of larger fish in better condition (as measured by growth rate or weight at age). Mean age of spawners, their age diversity and the proportion of older fish in the spawning stock all declined to their lowest levels in the mid to late 1970s, when recruitment rates were at their highest. Size and growth of spawners were high both during the period of high recruitment rates in the mid to late 1970s and in the 1950s and 1960s when recruitment rates were unremarkable. Effects of indices of spawner age and size composition were not significant when included as covariates in the stock-recruitment relationship, even accounting for the effect of pelagic fish biomass on the recruitment rate. It appears that effects of characteristics of the spawning stock on recruitment success of southern Gulf cod are overshadowed by other sources of variation in recruitment rate, at least in the case of the spawning stock characteristics that we have measured.

Résumé

Le taux de recrutement (défini dans le présent document comme R, l'abondance de morue de 3 ans, divisé par BSS, la biomasse du stock reproducteur à son origine) de la morue a fortement varié dans le sud du golfe du Saint-Laurent. Par exemple, il était remarquablement élevé du milieu des années 70 au début des années 80. La variation de la quantité ou de la qualité des œufs produits par unité de BSS entraînera une variation du taux de recrutement lorsque le facteur R/SSB est utilisé pour estimer ce dernier. Un examen des effets des caractéristiques du stock reproducteur (structure par âge et longueur) sur le taux de recrutement de la morue du sud du golfe n'a pas révélé une tendance, pendant la période 1950-1994, vers une association de taux de recrutement élevés à des âges plus avancés ou plus variés dans le stock reproducteur ou à un stock reproducteur composé de grosses morues en meilleure santé (telle qu'indiquée par le taux de croissance ou le poids selon l'âge). L'âge moyen des reproducteurs, la diversité de leur âge et la proportion de vieilles morues dans le stock reproducteur ont tous tombé à leurs plus bas niveaux du milieu à la fin des années 70, lorsque les taux de recrutement ont atteint un pic. La taille et le taux de croissance des reproducteurs étaient de même élevés pendant la période de taux de recrutement forts s'échelonnant du milieu à la fin des années 70, ainsi que dans les années 50 et 60, lorsque les taux de recrutement étaient médiocres. Les effets des indices de la distribution des âges et des longueurs des reproducteurs n'étaient pas significatifs lorsque ceux-ci ont été inclus comme covariables dans la relation stock-recrutement, même lorsque l'effet de la biomasse des poissons pélagiques sur le taux de recrutement était pris en compte. Il semble que d'autres sources de variation du taux de ecrutement, au moins dans le cas des caractéristiques du stock reproducteur mesurées, obscurcissent les effets de certaines caractéristiques de celui-ci sur le succès du recrutement de la morue du sud du golfe.

Introduction

Spawner biomass may not be a sensitive measure of reproductive potential (Marshall et al. 1998). The quantity and quality of progeny has been linked to spawner characteristics in gadoids (see references in Marshall et al. 1998, Marteinsdottir and Steinarsson 1998). Relative fecundity (fecundity per unit of body weight) tends to be greater in larger cod, so that the same spawner biomass will lead to greater egg production if it is composed of larger fish. Cod in poor condition have reduced fecundity. Egg quality (e.g., survivorship, egg size, hatching success) has been reported to increase with maternal size, condition, age and spawning experience. Positive correlations have been reported between egg size and larval viability parameters (e.g., age at first feeding, larval growth rates). Marteinsdottir and Thorarinsson (1998) reported a positive correlation between recruitment and age diversity of spawners in Icelandic cod, presumed to reflect the influence of female characteristics like the number of old/large fish and the duration and timing of spawning. Marshall and Frank (1999) reported positive correlations between haddock recruitment and spawner condition and size-at-age.

Recruitment rate (defined here as R, the abundance of 3 yr old cod, divided by S, the biomass of the spawning stock that produced them) has varied widely for cod in the southern Gulf of St. Lawrence (Fig. 1). In particular, the rate of recruitment was remarkably high from the mid 1970s to the early 1980s. Variation in the recruitment rate, R/S, may reflect variation in early survival of cod, or variation in the quantity or quality of eggs produced by a unit of spawning stock biomass. In this paper, we test two predictions related to effects of spawner characteristics on recruitment rate. First, we predicted a positive correlation between recruitment rate and measures of the age of spawners (i.e., mean age, proportion older fish, age diversity). Second, we predicted a positive correlation between recruitment rate and measures of the mean size and condition of spawners.

Data

Recruitment Rate

Calculation of the index of recruitment rate of southern Gulf cod is described by Swain and Chouinard (2000). Analyses presented here use the SPA-based index (to maximize time series length), using the formulation accepted in the most recent assessment of this stock (Chouinard et al., 1999) updated to include 1999 data. This SPA assumed an increase in M from 0.2 to 0.4 in 1986, and was calibrated using research survey catch rates, fishery catch rates and five sentinel survey catch rate series. Results were similar using estimates from the SPA calibrated using only the research survey catch rates.

Spawner characteristics

Statistics describing the age composition of spawners were based on the SPA described above. Age composition was based on age-specific abundance at the beginning of the year. Spawning in this stock is in spring and early summer. As in the calculation of spawner biomass, the same maturity ogive, based on data collected in spring and early summer of 1991-1995, was used for all years. Four measures of age composition were calculated: the mean age of spawners, the proportion 7 yrs and older or 10 yrs and older, and age diversity of spawners. We used the Shannon diversity index (see Marteinsdottir and Thorarinsson 1998 for details). These indices of age composition were strongly correlated (R 0.65 – 0.96). We summarized variation in these indices using principle component analysis (*PCA*). The first component accounted for 86% of the variation in the measures of age composition. All these measures had strong positive loadings of similar magnitude on *PC*1 (Table 1). High values of *PC*1 thus indicated a spawning stock with a high mean age, high age diversity, and high proportions of older fish.

Size distribution and growth rate of spawners was characterized by the mean individual weight of all spawners, mean weights at ages 5 and 6 yrs, and the weight increment from age 5 to age 6. Weights at age were for the beginning of the year, estimated from the mean weights at age i-0.5 in year t-0.5 and at age i+0.5 in year t+0.5. Size composition was based on research survey data for 1960-1999 and fishery data for 1950-1959. Mean weights at age were closely correlated between these two sources of data for the 1971-1999 period.

Seasonal variation in condition has been monitored for this stock only since the early 1990s (see Chouinard et al. 1999 for details). Estimates for September are available since 1971. However, due to the strong seasonal cycle in condition and phase shifts in the cycle between years, interannual variation in condition in September is not a good indicator of interannual variation in either maximum condition (achieved in late fall) or in minimum condition in spring. Thus, we did not include any direct measures of condition in the analysis. However, growth rate and condition might be expected to be correlated. A measure of condition in September (weight at 55 cm) is positively correlated with both weight at age 6 in September (R^2=0.27) and the weight increment from age 5 in September t-1 to age 6 in September t (R^2=0.36).

We summarized variation in the indices of spawner size composition and growth using *PCA*. The first component accounted for 78% of the variation in the measures of size and growth (88% in the 1963-1994 period). All these measures had strong positive loadings of similar magnitude on *PC*1 (Table 2). High values of *PC*1 thus indicated a spawning stock with a high mean individual weight, a high mean weight at ages 5 and 6, and a high growth increment from age 5 to 6.

Time trends in spawning stock characteristics

Mean age of spawners was high in the 1950s, declined to lower values in the late 1950s and early 1960s, returned to high values in the mid1960s and then declined to the lowest values seen as the stock collapsed in the 1970s. Mean age then increased, achieving high values in the late 1980s, then declined in the early 1990s as the stock again collapsed and has recently returned to high values (Fig. 2). The other measures of age composition of spawners show similar patterns. Thus, in the mid to late 1970s, when the recruitment rate was at very high levels, the spawning stock had a low mean age and low age diversity, with small proportions of older fish. This age composition is opposite to that predicted to be associated with high recruitment success.

Mean individual weight of spawners was high throughout the 1950s, 1960s and early 1970s, but declined beginning in the mid1970s, reaching its lowest level in the early 1990s (Fig. 3). Mean individual weight of spawners has been relatively low since the mid 1970s, reflecting a combination of variations in mean age of spawners and mean weight at age. Mean weights at age 5 and age 6 were high in the 1950s, but declined briefly to lower values in the early 1960s. Mean weights were relatively high from the mid1960s to the late 1970s, but declined sharply from the late 1970s to the mid 1980s. Weights at age have remained low since the mid 1980s. Weight increments from age 5 to 6 were high in the late 1960s and mid to late 1970s, but have been relatively low since 1980. Thus, weights at age and growth increments were at high levels in the mid to late 1970s, when the recruitment rate was at very high levels. This supports the prediction of high recruitment success when size and condition of spawners is high. However, the recruitment rate was much lower throughout the 1950s and 1960s, when size and/or growth of spawners was as high or higher.

Time trends in the first *PC*s of the age and size compositions of the spawners conform to those expected on the basis of the trends in the individual age and size variables (Fig. 4). *PC*1 of spawner age composition reached its lowest values during the period of remarkable recruitment rates in the mid to late 1970s. *PC*1 of spawner size composition was at a relatively high level during this period of high recruitment success, but was as high or higher during earlier periods when recrutiment rate was unremarkable and was low in recent years when the recruitment rate appeared to be above average.

Statistical Methods

We tested for effects of characteristics of the spawning stock on the stock-recruitment relationship of southern Gulf cod. We assumed a Ricker relationship with lognormal error. We fit the relationship using linear regression, with $\log_e(R/S)$ as the dependent variable and S and the first PCs of the spawner age and size compositions as the independent variables. Pre-recruit survival of southern Gulf cod appears to be strongly influenced by the biomass of pelagic

fishes in the southern Gulf (Swain et al., 2000). Effects of characteristics of the spawning stock on recruitment rate could be obscured by this apparent effect of pelagic fish biomass. We performed a second analysis for the 1963-1994 period including the biomass of pelagic fishes (herring and mackerel) as a covariate in the model. We used the following procedure, recommended by Bence (1995), to account for autocorrelation (see Pyper and Peterman 1999). After fitting the regression using ordinary least squares, we tested for autocorrelation in the residuals using a Durbin-Watson test. In all cases, this test rejected the hypothesis of zero lag-1 autocorrelation (at $\alpha<0.05$). We thus simultaneously computed maximum likelihood estimates of the regression parameters and the first-order autoregressive parameter for the error. *S* and pelagic fish biomass were standardized to a mean of 0 and a standard deviation of 1 for these analyses.

Results

Strong compensation is evident in the stock-recruit relationship of southern Gulf cod, with higher pre-recruit survival at low spawning stock biomass (Fig. 5). No strong relationships are evident between residuals from the stock-recruit relationship and the first PCs of the spawner age and size compositions (Fig. 5).

There was no indication of an effect of either the age or size/growth characteristics of the spawners on the stock-recruitment relationship for the 1951-1994 period (Table 3). When the effect of pelagic fish biomass was included in the model (1963-1994), the effect of spawner age composition remained insignificant, but the effect of spawner size/growth characteristics approached significance (P=0.059) according to a two-sided test. However, this effect was in the negative direction, opposite to the predicted direction of effect. The tendency for high recruitment rates to be associated with small spawner size/growth rate after accounting for effects of *S* and pelagic fish biomass was due to the relatively high recruitment rates in recent years according to the accepted SPA calibration. The calibration using only the research vessel indices indicates less spectacular recruitment rates for recent years, and tests using the results of this calibration do not indicate any effect of spawner size/growth on recruitment success (b=-0.0848, P=0.13).

Conclusions

The recruitment rate of southern Gulf cod has varied widely, with a period of remarkably high recruitment success from the mid 1970s to the early 1980s. Characteristics of the spawning stock have also varied widely since 1950. However, despite this wide variation in both recruitment rate and spawning stock characteristics, we were unable to detect any significant relationships between these variables. Weight at age and growth did tend to be high in the mid1970s when recruitment success was unusually great, but they were also high in the 1950s and 1960s, when the recruitment rate was unremarkable. Mean age and

age diversity of spawners were at their lowest levels in the mid to late 1970s when the recruitment rate was at its highest, opposite to the predicted relationship. It appears that effects of characteristics of the spawning stock on recruitment success of southern Gulf cod are overshadowed by other sources of variation in recruitment rate, at least in the case of the spawning stock characteristics that we have measured.

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Table 1. First principle component of spawner age composition of southern Gulf cod.

	1950-1994	1963-1994
% variance	85.6	80.6
Eigenvector:		
Mean age	0.510	0.517
Proportion 7+ yr	0.501	0.506
Proportion 10+ yr	0.473	0.449
Shannon index	0.515	0.524

Table 2. First principle component of spawner size composition of southern Gulf cod.

	1951-1994	1963-1994
% variance	78.1	87.8
Eigenvector:		
Mean weight	0.490	0.452
Mean weight at age 5	0.534	0.526
Mean weight at age 6	0.548	0.519
Weight increment 5-6 yr	0.416	0.499

Table 3. Stock/recruitment analysis for southern Gulf of St. Lawrence cod, incorporating effects of characteristics of the spawning stock on recruitment success ($\log_e R/S$). *R* is abundance of 3 yr old cod, *S* is cod spawning stock biomass, *PF* is the biomass of pelagic fishes (herring and mackerel), *PA* is the first principle component of variables describing the age composition of spawners (high values of *PA* indicate a spawning stock with a high mean age, high age diversity, and high proportions of older fish), and *PS* is the first principle component of variables describing the size composition of spawners (high values of *PS* indicate a spawning stock with a high mean individual weight, a high mean weight at ages 5 and 6, and a high growth increment from age 5 to 6). *S* and *PF* were standardized to a mean of 0 and a SD of 1. Significance levels of the partial regression coefficients *b* are given in parentheses. *A*(1) is the first-order autoregressive parameter for the error. R^2 gives the proportion of the variation explained by *S* and *C* after transformation to adjust for the estimated autocorrelation.

	1951-1994		1963-1994	
b(*S*)	-0.4001	(0.012)	-0.4057	(0.0004)
b(*PF*)	—	—	-0.4543	(0.0005)
b(*PA*)	0.0429	(0.52)	0.0282	(0.63)
b(*PS*)	-0.0900	(0.26)	-0.1159	(0.059)
A(1)	0.7551	(0.0001)	0.4821	(0.014)
R^2	0.20		0.58	

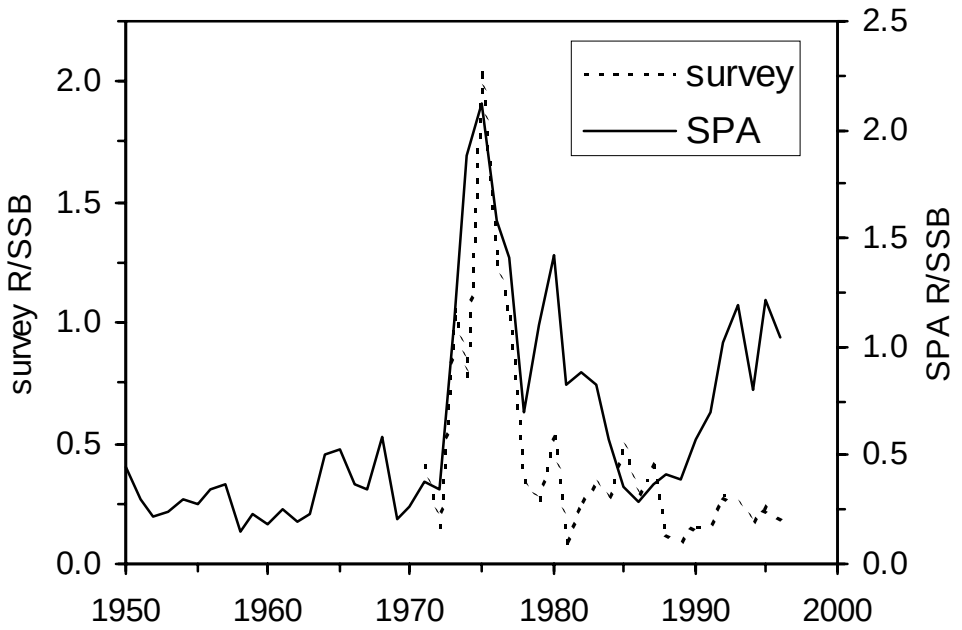

Figure 1. Recruitment rate of southern Gulf of St. Lawrence cod.

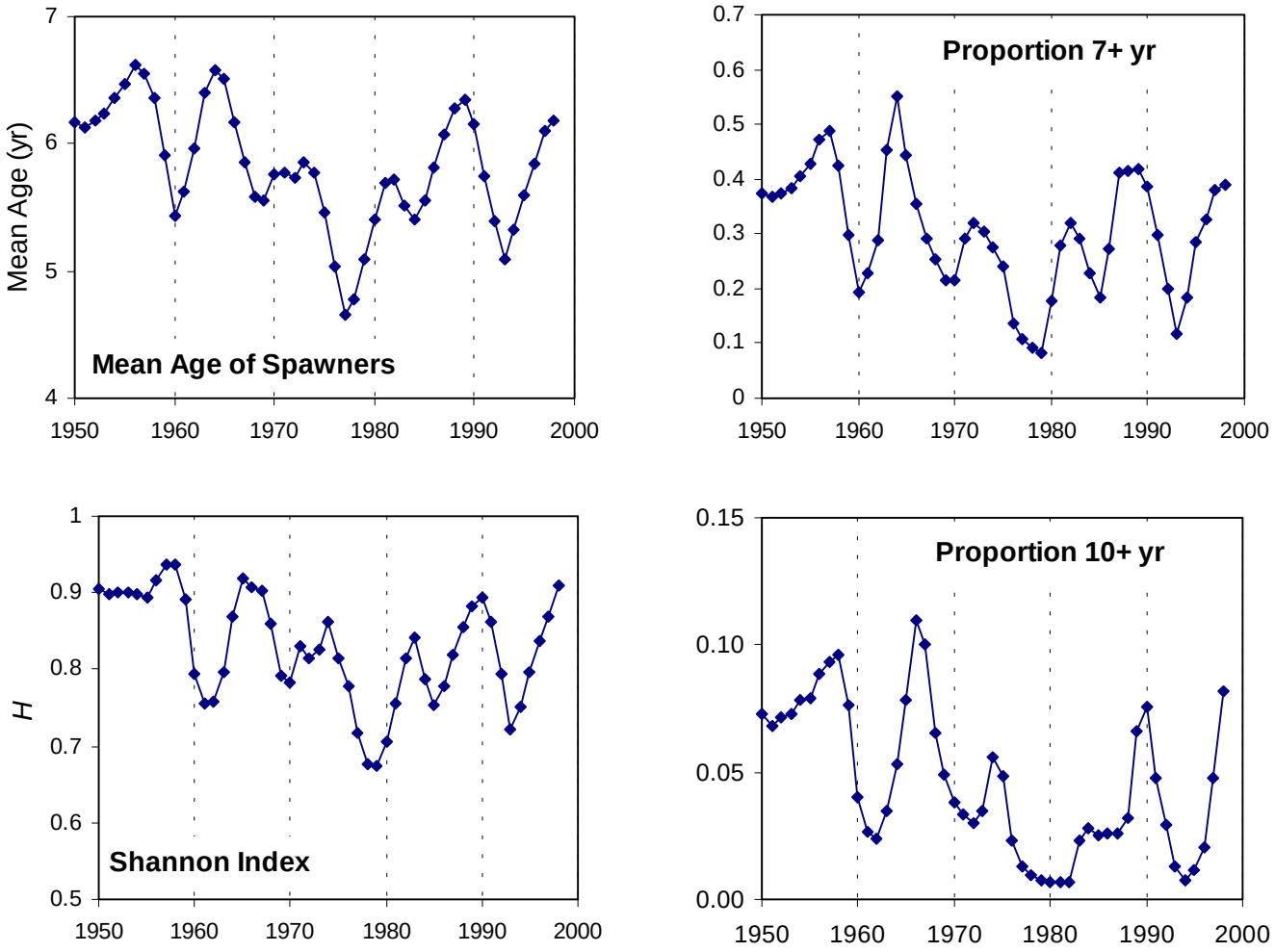

Figure 2. Interannual variation in measures of the age composition of the spawning stock of southern Gulf of St. Lawrence cod.

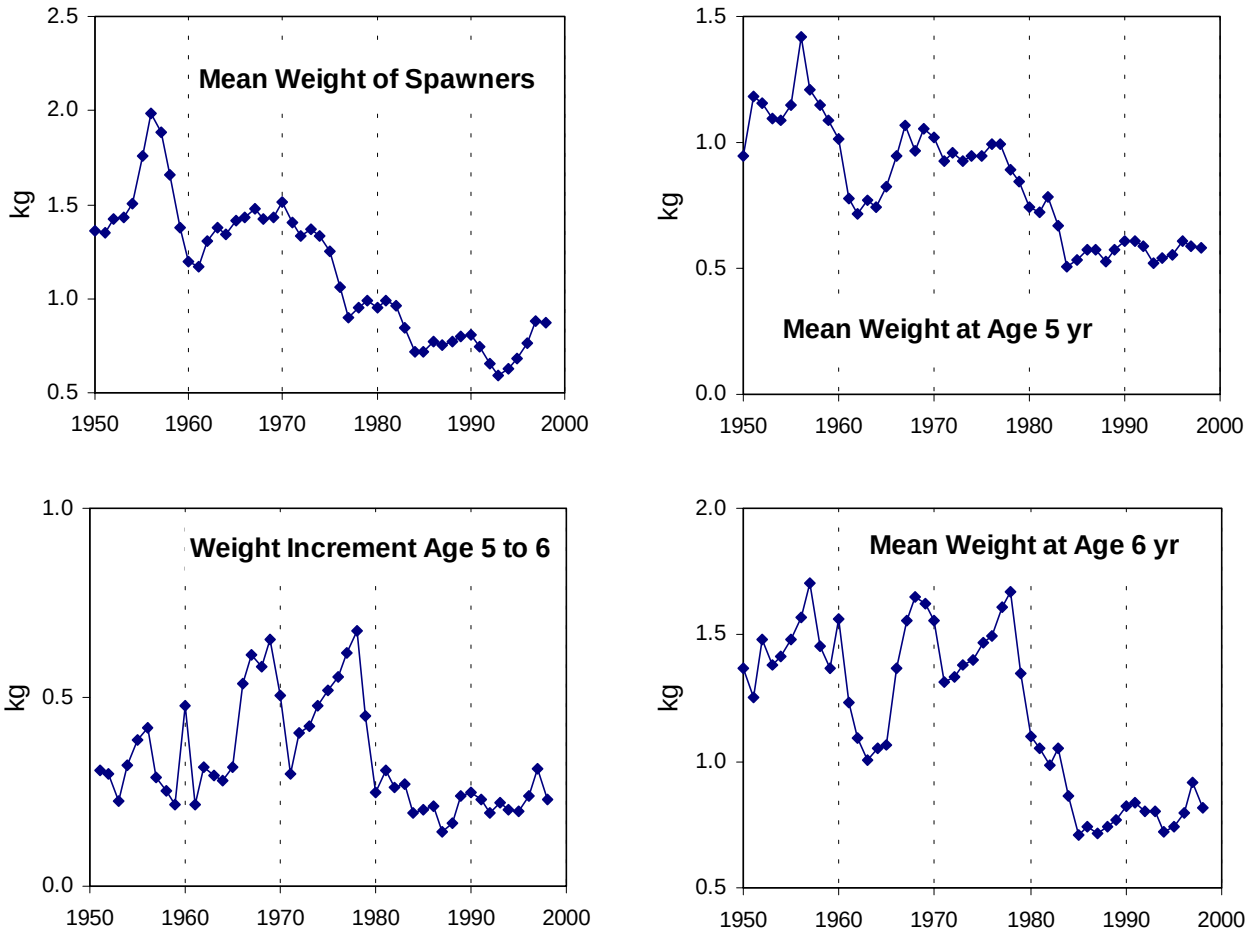

Figure 3. Interannual variation in measures of the size composition and growth rate of the spawning stock of southern Gulf of St. Lawrence cod.

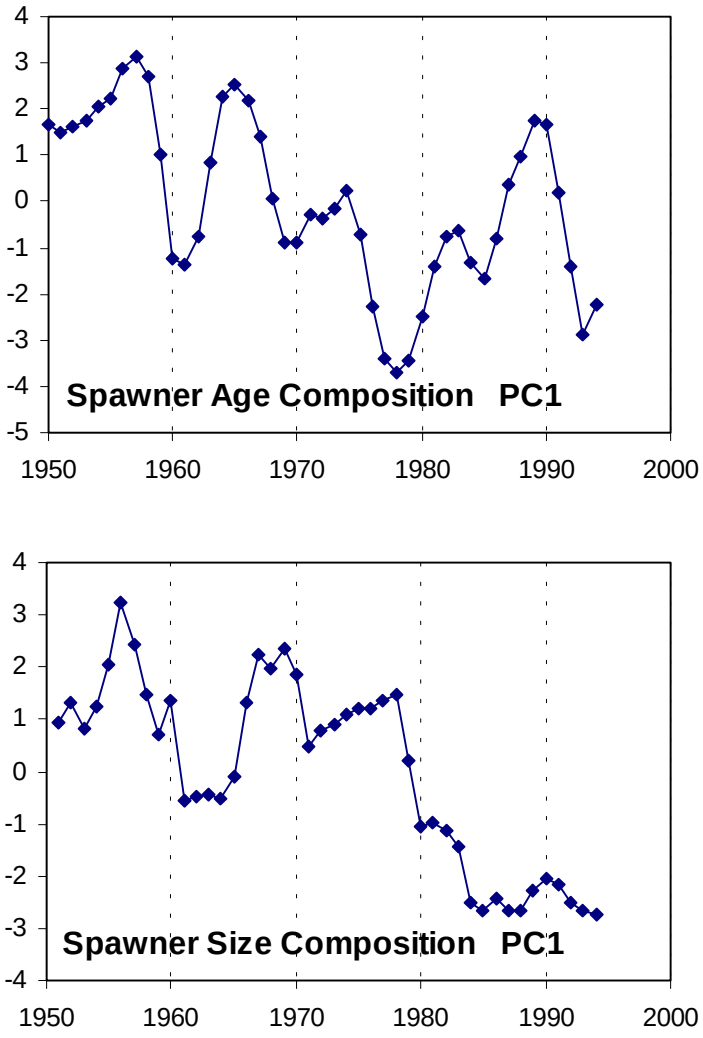

Figure 4. Interannual variation in the first principle components of the age and size composition of the spawning stock of southern Gulf cod.

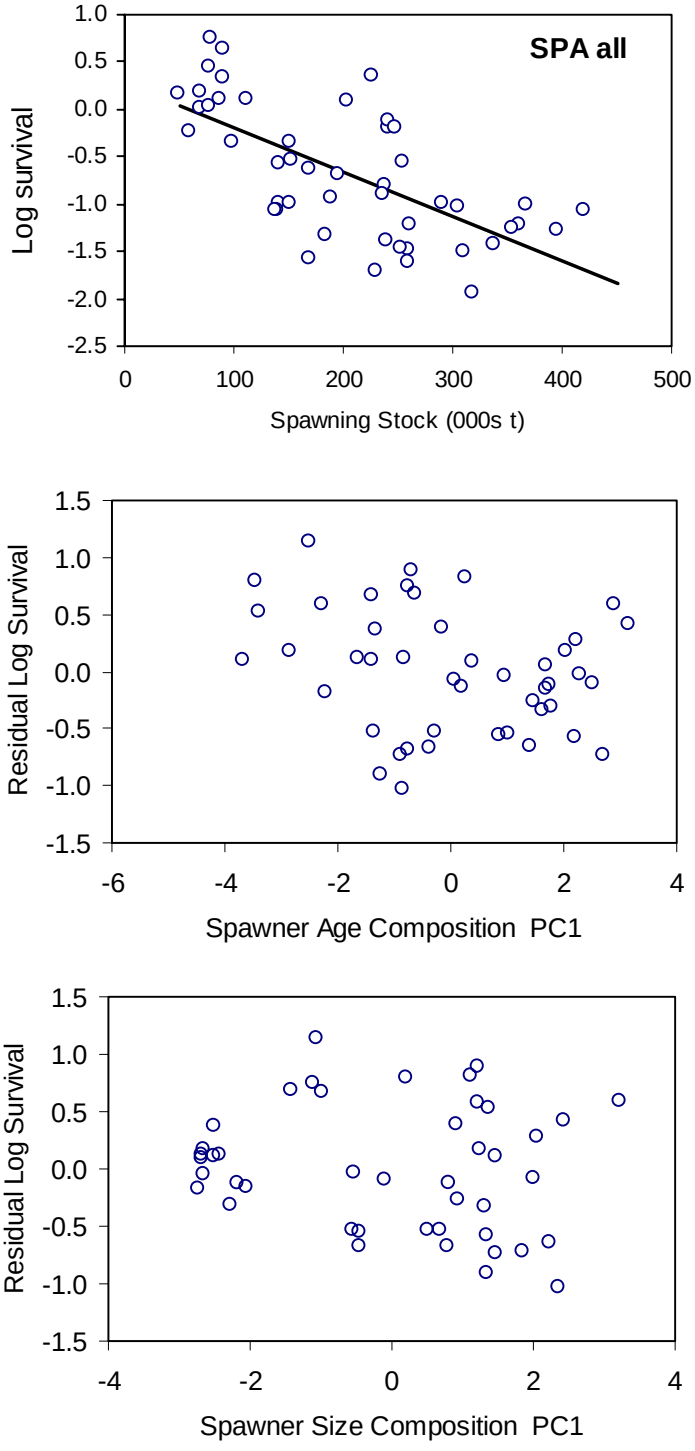

Figure 5. Relationship between spawning stock biomass and log recruitment rate for southern Gulf cod, and between the residuals from this relationship and characteristics of the spawning stock.