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NOTE

The relationship between stock and recruitment: are the assumptions valid?

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ABSTRACT: The management of exploited fish populations is, at present, based on stock assessment methods which assume that spawning biomass is proportional to the reproductive potential of the stock. This implies that the survival rates of offspring do not substantially change with the age or size of the spawner. However, the commercial extinction of many fish stock worldwide has provoked concern about the techniques used in stock assessment. Is the contribution of different age classes to recruitment equal, irrespective of the age of the fish? Here we show that not only do older individuals contribute the largest amount of eggs to the reproductive potential of cod *Gadus morhua*, but that they also have the largest number of recruits likely to produce offspring with higher rates of survival. This important effect of population structure on recruitment should be taken into account in fisheries science and fisheries management.

KEY WORDS: Stock assessment · Recruitment · Parental age · Population strucure · Generalized Additive Model

Quantifying the reproductive potential of fish populations represents a high priority in fisheries science (Trippel et al. 1997). The most important and usually most difficult task in the assessment of fisheries resources is the establishment of the relationship between stock and recruitment (SR) (Hilborn & Walters 1992). The Beverton & Holt model (Beverton & Holt 1995) and Ricker functions (Ricker 1957) are among the 2 most widely accepted approaches for describing the SR relationship. They assume that spawning biomass is proportional to reproductive potential, which implies that survival rates of progeny do not vary substantially with adult age or size (Trippel et al. 1997). Although the classical models provide important insights into SR dynamics, they may not include other key factors or specific situations that may contribute significantly to explaining the observed recruitment variability in fish stocks (Clark 1976, De Angelis 1988, Fogarty 1993). The assumption that spawning biomass is proportional to the number of potential recruits (reproductive potential) produced by the stock remains one of the largest untested assumptions in fisheries science, and different authors have recently challenged this paradigm (Trippel et al. 1997, Marshall et al. 1998, Marteinsdottir & Thorarinsson 1998).

The overexploitation of marine fish populations typically results in the loss of the large members of the stocks (Policansky 1993, Garrod & Schumacher 1994). The depletion of large individuals may not only affect the quantitative reproductive potential of the population but, if poorer gamete quality is exhibited by younger fish as compared to older fish, the qualitative reproductive output of the stock may also be seriously depleted (Trippel et al. 1997).

The influence of parental size or age on the viability of eggs and larvae is an open question. The effect of parental age on the offspring has been defined as strong, multidirectional and manifested in a long-lasting way in various aspects of the progeny's life (Kamler 1992). The age of a parental fish influences the chemical composition of ovaries, egg size, egg metabolism, fertilization and larva and juvenile survival (Kamler 1992). As suggested by Kjesbu et al. (1996), larger cod larvae, derived from larger and older individuals, for both physiological and ecological (food availability) reasons should be in a better survival situation than smaller larvae. Previous management strategies have only considered the quantitative impact of age structure on recruitment, neglecting the importance of the age of the spawners on the quality of the offspring (survival rates). Yet, population structure may be a key factor in explaining recruitment variability; the aim of this study was to test this hypothesis.

Materials and methods. We analysed fishery-dependent and -independent data from the Kattegat, Arctic

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and North Sea cod stocks *Gadus morhua* from the ICES (International Council for the Exploration of the Sea) (Anonymous 1998, 1999a,b). To assess the contribution to recruitment of different age classes, we calculated the potential egg production for each age class of cod. The estimates were based on the number of fish in the stocks, sex ratios, proportion of mature individuals, sex ratios, weight at age in the stocks (Anonymous 1998, 1999a,b) and fecundity estimates (Kjesbu et al. 1991).

We used Generalized Additive Models (GAMs) (Hastie & Tibshirani 1990) to estimate and quantify the effect of stock age structure on recruitment. In nature, the relationship between a dependent variable and 2 or more biotic or abiotic factors is unlikely to be monotonic, linear or parametric (Maravelias & Reid 1997). The GAM is not limited by normality and linearity assumptions (Swartzman et al. 1992) and therefore it extends the power of conventional regression techniques by fitting nonparametric functions to the response and the predictors. Therefore, GAM is not tied to any particular functional relationship (i.e. linearity or normality of the residuals) or to any statistical distribution of the data (i.e. normality). The underlying probability distribution for the data can be any distribution from the exponential family (e.g. the normal, Poisson, Gamma and binomial distribution). In this study we used the Gamma distribution, since in testing different distributions we discovered that the Gamma gave better fit with the data and the minimum residual deviance in the models. In the GAM the dependent variables are assumed to be affected by the predictors through additive, unspecified smooth functions, and thus the nonparametric functions are estimated from the data using smoothing operations. Cod recruitment (response variable) was expressed as a sum of smooth functions of the covariates (predictors). We used cubic B-splines to estimate the smoother (Hastie & Tibshirani 1990, Swartzman et al. 1992). The hypothesized covariates were: the number of eggs produced by first spawners (FS), second spawners (SS) and repeated spawners (RS) and their first interaction terms. In North Sea and Kattegat cod, FS were the age classes 1 to 3, SS the age classes 4 and 5 and RS the age classes 6+. For Arctic cod, FS were the age classes 3 to 6, SS the age classes 7 and 8, and RS the age classes 9+. All the variables and their first order interaction terms were initially included in the model. Successively, a backward stepwise elimination was used to select significant predictors in the analysis. Different models were compared using *F*-tests at 95% significance, making appropriate adjustments for the model degrees of freedom beforehand. The final models were selected based on the parsimonius principle, i.e. the minimum residual deviance and the minimum number of covariates. In order to calculate the 90% confidence limits of the significant covariates, a bootstrapping technique (percentile method) was applied (1000 samples) as in Swartzman et al. (1992).

Results. Results of the significance value of all the covariates initially included in the model are presented in Table 1. The final GAM included the following variables: Recruitment = s(SS) + s(RS) + s(FS × SS) for Arctic for and North Sea cod, and Recruitment = s(RS) + s(FS × SS) for Arctic and Kattegat cod. The effect of the significant covariate and their interaction terms on the recruitment is shown on the *y*-axis for different values of the covariate or predictor (*x*-axis). The *0*-line indicates the mean recruitment estimated by the model while the *y*-axis is a relative scale where the effect of different values of the predictors on the response variable (i.e. recruitment) is shown. Thus, negative values on the *y*-axis indicate that, at those levels of the predictors (*x*-axis), the model estimates a recruitment that is lower than the mean value while the opposite holds at positive values on the *y*-axis. The effect of FS on recruitment (10^6 individuals) is negligible (less than 5% of the explained model variance) in all the cod stocks (Table 1), and therefore this variable was excluded from the final models. In contrast, SS and mostly RS have significant effects on recruitment (Figs. 1 & 2). Importantly, when the reproductive contribution from RS is at its lowest level, recruitment is strongly depleted, while the effect on recruitment is positive when there are large numbers of RS eggs in all the cod stocks (Fig. 1). SS contribute significantly to the recruitment variability in North Sea cod, showing a trend somewhat similar to the RS (Fig. 2). The interaction between FS and SS is also important in explaining the variability of recruitment in all the cod stocks (Fig. 3). The highest positive effect on recruitment occurred in 'balanced' populations, i.e. with a large number of eggs produced by SS, while truncated age structures (small numbers of SS eggs) have a negative impact on recruitment irrespective of the FS contribution (Fig. 3). Therefore, it appears that the number of recruits is

Table 1. Significance values (p levels) for the GAM covariates. Level of significance was set to 0.05. ns = non significant. FS: first spawners, SS: second spawners, RS: repeated spawners

Covariates	Arctic cod	North Sea cod	Kattegat cod
FS	ns	ns	ns
SS	ns	<0.05	ns
RS	<0.01	<0.01	<0.01
FS-RS interaction	ns	ns	ns
FS-SS interaction	<0.05	<0.01	<0.01
RS-SS interaction	ns	ns	ns

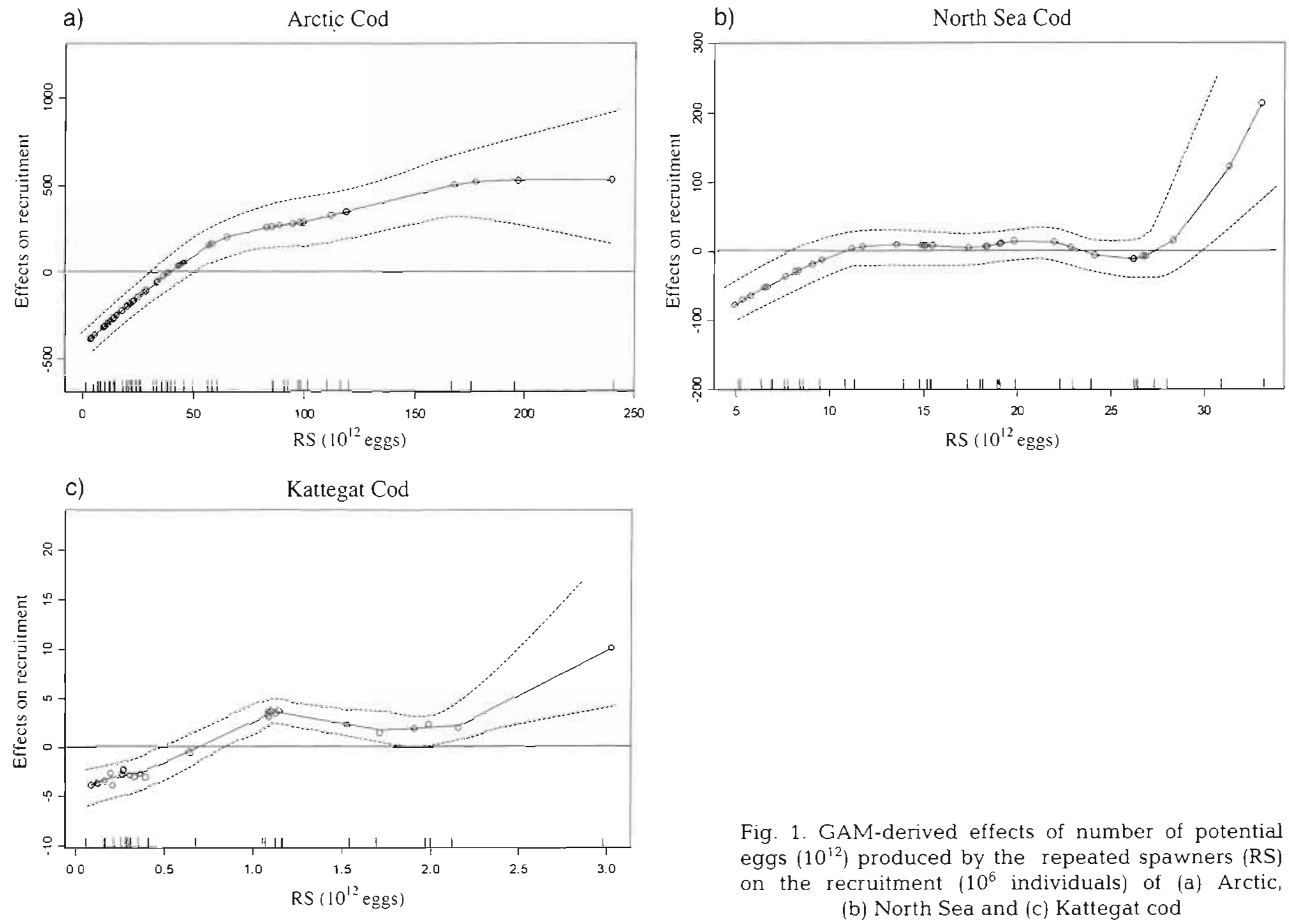

Fig. 1. GAM-derived effects of number of potential eggs (10^{12}) produced by the repeated spawners (RS) on the recruitment (10^6 individuals) of (a) Arctic, (b) North Sea and (c) Kattegat cod

dependent on the age population structure, with SS and, mostly, RS providing both the largest amounts of potential recruits and likely the highest offspring survival rates.

Discussion. The purpose of fisheries managment is to ensure sustainable production of fish stocks over time and to make quantitative predictions about the reactions of fish populations to alternative management choices (Hilborn & Walters 1992). A crucial assumption in fisheries science is that the spawning biomass is proportional to the reproductive potential of the stock. However, the commercial extinction of many marine fisheries worldwide (Cook et al. 1997, Myers et al. 1997) has raised concern about the management of renewable resources (Pitcher et al. 1998) and even that central assumption has been challenged (Gilbert 1997). Here we show that for cod the influence of parental age on recruitment is substantial and that population stock structure has a significant effect on recruitment. RS explained most of the variability of recruitment. Data from this study showed that recruitment is strongly depleted when the reproductive contribution from RS, in terms of number of produced eggs, is at its lowest level, while the effect on recruitment is positive when RS eggs are abundant. Our results agreed with the hypothesis of Kjesbu et al. (1996), who argued that the presence of a rich variety of age classes in the

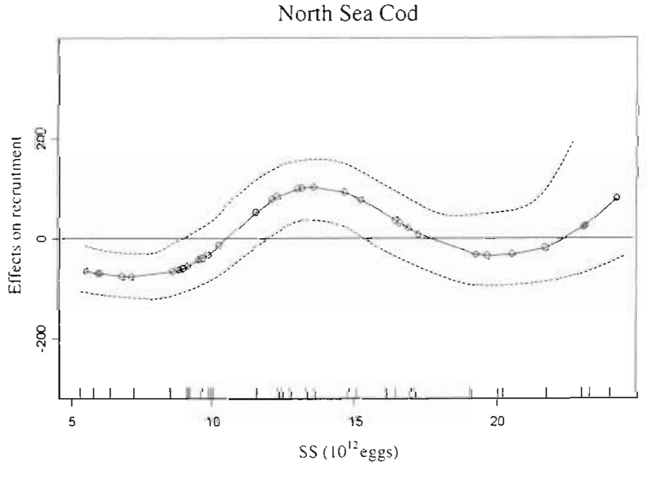

Fig. 2. GAM-derived effects of number of potential eggs (10^{12}) produced by the second spawners (SS) on the recruitment (10^6 individuals) of North Sea cod

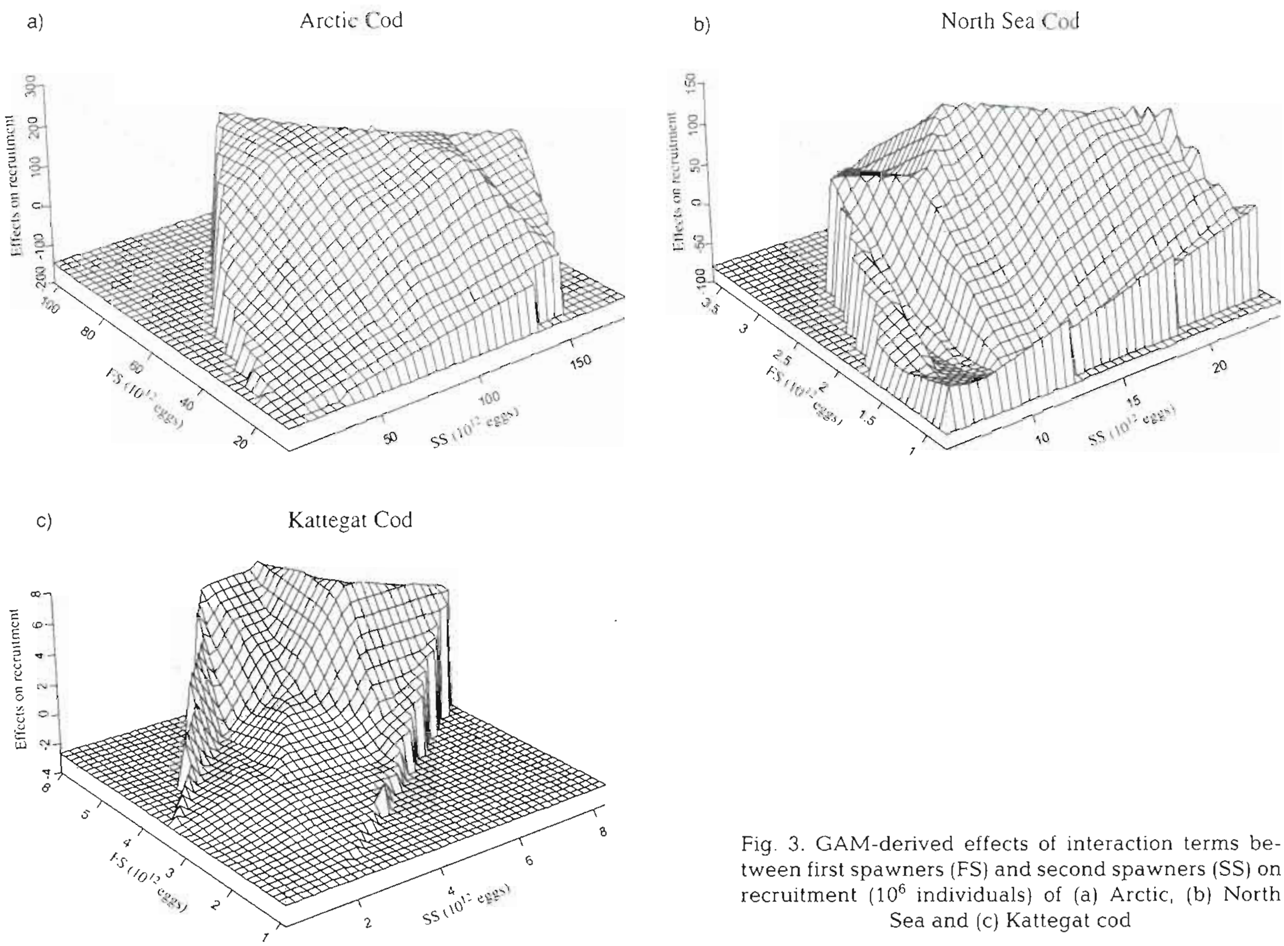

Fig. 3. GAM-derived effects of interaction terms between first spawners (FS) and second spawners (SS) on recruitment (10^6 individuals) of (a) Arctic, (b) North Sea and (c) Kattegat cod

spawning population should increase the probability of successful recruitment. The positive effect of older and larger individuals on cod recruitment is likely due to the production of larger larvae with higher rates of survival and the combination of more batches and a longer spawning period (Kjesbu et al. 1996). Nevertheless, other factors may influence cod recruitment, particularly temperature and salinity (Sparholt, 1996) or food availability, and they may also contribute significantly to explaining recruitment variability of fish stocks.

The implications for stock assessment and management are enormous. The risk of commercial extinction is high when population structure is truncated by fishing mortality and as a result the number of old, high-quality spawners is below a certain limit. Therefore, the protection of spawning biomass alone is not an adequate measure for optimal management of exploited fish populations. For example, for cod, a certain minimum number of SS and RS must be present in the population to ensure a large number of offspring with high rates of survival. It is time that the theory on recruitment take into account the qualitative influence of parental age on recruitment.

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