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Enhancing stock-recruitment models for North Sea cod by including climate and zooplankton

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EXTENDED ABSTRACT

Background

The "recruitment problem" - trying to understand what regulates recruitment variability in marine fish populations - has been the number one issue in fisheries science since the early twentieth century. Intuitively, the size of the spawning stock should influence recruitment. In practice, however, the relationship is most often weak, complicating fisheries management and causing much controversy. Thus, the value of fitting stock-recruitment relationships for marine fish populations could be questioned. Nonetheless, the weak connections found may be due to insufficient data or models, and a general denial of meaningful stock-recruitment relationships would have rather alarming consequences on the science of fish population dynamics. A more constructive approach is to expand upon the established knowledge, both

by introducing refined models and by including other sources of data. Specifically, theoretical work suggests that the shape and the position of the stock recruitment curve will be influenced by the environmental conditions experienced by the fish larvae. Pioneering work by Cushing and Horwood showed unexpected support for strong density-dependent mortality of fish larvae, even with low observed larval densities. Their model suggests a positive link between the number of food organisms and the slope of the stock-recruitment relationship, with potentially important implications for population dynamics. More recent work suggests that a Ricker-type stock-recruitment relationship, i.e. overcompensation, could be expected at limited food levels, while as food availability improves the recruitment curve becomes monotonically increasing towards an upper limit, i.e. a Beverton-Holt type stock-recruitment relationship. In both of these modelling approaches, the time to metamorphosis appears important for recruitment. Lack of food will slow down the growth of the larvae and delay the time to metamorphosis. This may cause the larval cohort to experience density-dependent mortality to the extent that the recruitment curve becomes overcompensatory.

Results

Building upon the work described above and the unique Continuous Plankton Recorder (CPR) zooplankton data, we here employ a novel approach to the recruitment problem to the once large North Sea cod (*Gadus morhua*) stock. We fitted a combined Ricker-Beverton-Holt model incorporating food availability (zooplankton) and climate (sea temperature) (Table 1: model 1). For recruitment we use numbers at age 1. This is the stage where the fish first enter the fisheries and the earliest measure of year class strength available for the full time period. The statistical support for model 1 is compared with that of three alternative candidate models: a combined Ricker-Beverton-Holt model including the zooplankton covariate but excluding the sea temperature covariate, and the traditional Ricker and Beverton-Holt models (Table 1: models 2-4). Model selection was based on the Akaike Information Criterion, where the model with the lowest AIC value represents the best compromise between bias (including too few parameters) and lack of precision (including too many parameters). The model with the lowest AIC value will therefore have most support. Specifically, the support of each model refers to its normalized Akaike weight, based on a comparison of the AIC values of all a priori candidate models.

Table 1. A-priori set of stock (*S*) and recruitment (*R*) models: (1) a combined Ricker-Beverton-Holt model including zooplankton (*Z*) and temperature (*T*) effects, (2) a combined Ricker-Beverton-Holt model including a zooplankton effect only, (3) a traditional Ricker model, and (4) a traditional Beverton-Holt model.

Model	Structure
1	$\log(R/S) = a0 - a1T + \log((1-Z)(\exp(-b\cdot S) + Z/(1 + \exp(c)S/maxS))$
2	$\log(R/S) = a0 + \log((1-Z)\exp(-bS) + Z/(1 + \exp(c)S/maxS))$
3	$\log(R/S) = a0 + \log(\exp(-bS))$
4	$\log(R/S) = a0 - \log(1 + \exp(c)S/maxS)$

The data strongly support the combined model 1 (Table 2). When the zooplankton index was low, the model indicated a positive relationship between spawning stock biomass and recruitment until the stock reached about 50.000 tonnes; above this level the model predicted a negative relationship between spawning stock and recruitment (i.e., a Ricker type relationship: Fig. 1). At intermediate to high zooplankton levels, the model indicated a Beverton-Holt type stock-recruitment relationship, where the recruitment curve levelled out more slowly as zooplankton abundance improved (Fig. 1). Overall, high sea temperatures were associated with poor cod recruitment, and vice versa (Fig. 1). Removing the effect of sea temperature from the model led to an increased AIC value and a corresponding decrease in model support (Table 2). The traditional Ricker and Beverton-Holt models received virtually no support when compared with the combined model (Table 2).

Table 2. Model selection. The number of parameters to be estimated (K), the AIC value ($-2\times$ log likelihood $+2\times$ K) and the relative support in favour of each of the four candidate models (Table 1) calculated as normalized Akaike weights, $w_i = (\exp(-(AIC_i-AIC_1)/2)/\sum(\exp(-(AIC_i-AIC_1)/2))$. The models were fitted using the R-software (version 2.6.0, www.r-project.org).

Model	*K*	AIC	*w*
1	4	62.3	0.76
2	3	64.6	0.24
3	2	80.4	0
4	2	80.6	0

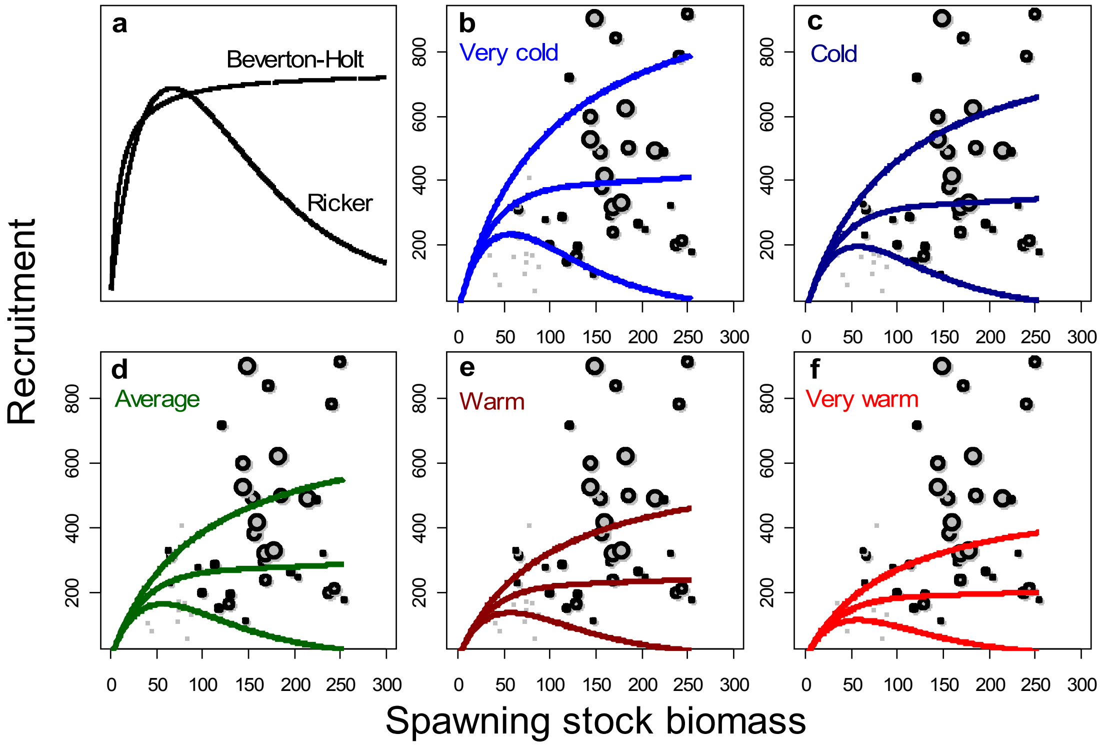

Figure 1. Spawning stock and recruitment. Traditional Beverton-Holt and Ricker models (a), and the combined effects of spawning stock biomass (1000 t), food availability (zooplankton index) and climate (sea surface temperature, °C) on North Sea cod recruitment at age 1 (x1000), as predicted from our combined Ricker-Beverton-Holt model at low zooplankton level (solid line), intermediate (dashed line) and high (dotted line), and five different temperatures: very cold (b), cold (c), average (d), warm (e) and very warm (f); corresponding to standardized temperatures of −2, −1, 0, 1 and 2. Observations of stock and recruitment are shown as grey circles; with diameter indicating the corresponding zooplankton index.

Conclusions

We find that a model combining the Ricker and Beverton-Holt stock-recruitment models has considerably more explanatory power than any of the two in isolation. In essence, food availability (zooplankton) determines whether the Ricker or Beverton-Holt model applies. Furthermore, we find evidence for an effect of temperature displacing the recruitment curve upwards (good recruitment) during cold years and downwards during warm years (poor recruitment). These findings shed new light on the recruitment problem in general, and specifically support earlier studies in that full recovery of the North Sea cod stock should not be expected until the environmental conditions become more favourable.