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Cod in a changing climate

Match-mismatch and Threshold for the North Sea cod recruitment

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ABSTRACT

Climatic changes are disrupting otherwise tight trophic interactions between predator and prey. Most of the earlier studies have primarily focused on the temporal dimension of the relationship in the framework of the match-mismatch hypothesis. Using a novel time-series model explicitly quantifying both timing and the abundance component for predator-prey relationship, we show that timing and abundance of food affect the north-sea cod (*Gadus morhua*) recruitment. The system shows a strong effect of match-mismatch; however, it does so in association with food abundance. The food abundance was shown to have a threshold effect on recruitment. This non-linear effect may explain the difficulties to reveal the mechanisms by which environment variability affects marine ecosystems. As such the quantification of the combined effect of abundance and timing of prey on predator dynamics will improve our ability to detect the effect of environmental changes on trophic interactions.

INTRODUCTION

Recent climatic changes have been reported to disrupt tight trophic interactions between predator and prey, in fish-plankton (Beaugrand *et al*., 2003; Cushing, 1990; Ottersen *et al*., 2001), insect-plant (Visser & Holleman, 2001) and bird-insect systems (Sanz *et al*., 2003; Thomas *et al*., 2001; Visser *et al*., 2003; Winkler *et al.,* 2002). However, earlier studies have primarily focused on the temporal dimension – that climate change creates a mismatch between timing of peak breeding of predator and prey (i.e., what might properly be referred to as the temporal match-mismatch hypothesis; Cushing, 1990), but typically ignoring variation in food abundance. The match-mismatch hypothesis (Cushing, 1990) was first proposed for marine systems and suggests that the inter-annual variability in fish recruitment is a function of the timing of the production of their food (Hjort, 1914). The match-mismatch hypothesis predict that predator's recruitment will be high if the peak of the prey availability temporally matches the most energy-demanding period of the predators breeding phenology, while a mismatch will lead to poor recruitment. The match-mismatch hypothesis is of great interest today when climate is changing the phenology of several species, changes which may be different for different species within an ecosystem (Forchhammer *et al.,* 1998; Stenseth *et al*., 2002). However, by ignoring food abundance component in the trophic interaction, our ability to discover ecological effects of climate change will certainly be reduced. In a first step we extend the match-mismatch hypothesis to also include the food abundance component of food availability and in a second step analyse the results of the model.

MATERIAL & METHODS

The data

We applied the model to time series data from three systems: Atlantic cod (*Gadus morhua* L.)/zooplankton (*Calanus spp*.) in the North Sea. We used time series between 1958-2002 (Beaugrand *et al.,* 2003) derived from a Virtual Population Analysis (VPA)(Lassen & Medley, 2001) based on the fisheries catch in the North Sea. As reproductive success we used the number of cod at age-1 derived from the VPA. As density index we used the spawning stock biomass (SSB) of cod in the North-Atlantic. For food abundance, we used the data on *Calanus spp*. abundance collected by the Continuous Plankton Recorder survey 1958-2002 (www.sahfos.org). The abundance of *Calanus* was estimated by the area below the graph of monthly means for the first five months. The timing of the seasonal *Calanus* peak for the five first months (the central tendency, T) was estimated using the month coordinate of the centre of gravity of this area: $T=\Sigma^{5}_{i=1} Mx_{m}/\Sigma^{5}_{i=1}x_{m}$ where x_m is the mean abundance in month M (January =1, …, May=5)(Colebrook & Robinson, 1965). Assuming a constant hatching date of cod, this peak was used to estimate the mismatch with the yearly *Calanus* bloom.

Exploration of the match-mismatch relationship (Durant *et al*., 2005)

Following the classical match-mismatch graphic representation (Cushing, 1990), we assumed that the requirement and abundance of the predator and its prey follow a unimodal bell-shaped distribution, and the area under the curve is a measure of the total food requirement and the total food abundance. The *Success* of the upper trophic level (e.g., survival or reproduction of the predator) is then proportional to the area of overlap between these curves. This overlap changes as a function of the timing of the peak abundance relative to the requirement (i.e., x = the degree of mismatch) as well as the total abundance relative to the total requirement (y = relative food abundance). If relative food abundance (y) is constant, the *Success* decreases with increasing mismatch (x) following a sigmoid (S-shaped) function, which may be approximated using the logistic function $\exp(a + bx)/[1+\exp(a + bx)]$. If mismatch ($x$) is constant, the expected *Success* increases linearly with relative food abundance (y) until a threshold value r is reached when the possible overlap is maximum. Thus, taking into account the mismatch as well as the relative food abundance surface, the overlap can be approximated by

$$F(x, y) = \begin{cases} e^{a+bx}/(1+e^{a+bx}) & \text{if } y \geq r \quad \textbf{(1a)} \\ \\ [e^{a+bx}/(1+e^{a+bx})][1+c(y-r)] & \text{if } y < r \quad \textbf{(1b)} \end{cases}$$

where $F(x,y)$ is proportional to the *Success* of the upper trophic level. That is, when $y \geq r$ *Success* depends only on the temporal match/mismatch (eqn 1a). If the relative food abundance is lower than this level, the *Success* is influenced by both the food abundance and the mismatch component (eqn 1b). The model is to be applied on annual data over many years. For more detail see Durant et al. (2005).

Before running the model on data we verified that no interaction between parameters was detected. We found that the reproductive success (cod age-1) was influenced by the cod density (spawning stock abundance; SSB). We removed this effect before analysis using a linear model for ln(SSB). Given the reproductive success (residuals of cod age-1), food abundance (y = *Calanus* abundance), and the time lag between the peak food requirement and the peak food abundance (x = peak of *Calanus* abundance), we estimated the parameters (a, b, c, r) for the various equations by minimizing the sum of squared errors of success using a parameter search procedure in S-plus (Venables & Ripley, 2002). Confidence limits and significance for the parameters were based on estimating the parameters by 1000 bootstrap samples for each of the three systems. To test the significance values we used one-sided tests with the alternative hypothesis being $b<0$ and $c>0$, as positive b and negative c are biologically nonsensical.

Analysis of the food threshold

To study effect of food abundance threshold on density-dependent cod survival to age-1across different environmental conditions we used variations of generalized additive model (GAM) formulations, as implemented in the mgcv library of R (Wood, 2000; Wood, 2001). Specifically, let SSB_t be the natural logarithm of the cod spawning stock biomass at time t. Let S_t the logarithm the cod age-1 at time t. Let $\mathbf{E}_t$ be a vector of environmental variables at time t whose single components are identified by the superscript j; let f and g_j be nonparametric, smoothing functions specifying the effect of population abundance (i.e., density dependence) and environmental forcing of the covariate $\mathbf{E}_j$ for the latest on the demographic variable S. The threshold nonadditive formulation (hereon referred to as TGAM, where T stands for "threshold interaction") is composed by two additive formulations. In particular, assuming a change of density dependence (i.e., nonadditivity) as a function of a linear combination of the environmental vector (**E**) the effect of external variable on cod age-1 survival can be modelled as follows:

$$S_t = \begin{cases} b_1 + f_1(\mathrm{SSB}_t) + \Sigma_j \; g_j(\mathbf{E}_t^j) + \varepsilon_t & \text{if } \mathbf{E} \leq r \qquad \textbf{(2a)} \\ b_2 + f_2(\mathrm{SSB}_t) + \Sigma_j \; g_j(\mathbf{E}_t^j) + \varepsilon_t & \text{otherwise} \qquad \textbf{(2b)} \end{cases}$$

where r is an environmental threshold across which the density-dependent function switches from f_1 to f_2, with possible changes in the intercept as well (from b_1 to b_2), with the additive environmental effects otherwise unaltered. b is an intercept and ε is a noise term.

The model selection was based on the GCV (generalized cross validation). Initially, we included all interacting terms; however, in the final formulation we only retained those that minimized the model GCV

RESULTS & DISCUSSION

Our analyses show that the food abundance is an important parameter and are stressing its limiting effect on recruitment (Durant *et al*., 2005). If we consider a fixed level of mismatch, the model-1 shows that recruitment is a function of the food abundance while in the previous match-mismatch hypothesis (Cushing, 1990) one mismatch corresponded to one recruitment level. The absence of the food abundance component in the previous match-mismatch hypothesis may to some extent explain the occurrence of negative results in the literature.

For the North-Sea cod/zooplankton system, recruitment is strongly linked to spawner abundance (i.e., population density of the predator, Fig. 1, Table 1), and a large part of the observed decreasing trend in cod recruitment may be explained by decreasing spawner biomass probably linked to over-fishing (Cook *et al*., 1997). However, after removal of this effect, we found that cod recruitment was affected by both the timing and the total annual abundance of zooplankton. In accordance with the literature (Cushing 1990), this system shows an effect of mismatch; however, it does so in association to food abundance that has an even more important effect below a certain threshold. This seems reasonable as the survival of the cod larvae depends on feeding condition but also on the level of cannibalism by older cod (Bromley *et al*., 1997; Hjermann *et al*., 2004). An increase of the zooplankton availability, which in turn increases the abundance of alternative prey for cod and hence reduces cannibalism, will be doubly beneficial for the young cod. In short, by taking into account both the time and quantity components of food availability, the model-1 improves our ability to detect effects of environmental changes on trophic interactions. The value of our model rests in its ability to separate (without constraints) a within-season temporal shift of trophic synchrony (the match-mismatch hypothesis) from an annual component linked to total food abundance.

The model-1 stressed the existence of a threshold in food availability, under which the recruitment, even during periods of match, can be greatly reduce with consequences on the population. Knowing this threshold will give a tool to predict trophic cascades due to climate change. Consequently, we explored this threshold using a TGAM technology and found similar results, in terms of prediction, to the one obtain with our first model, i.e., a negative effect of the degree of mismatch and a positive effect of food abundance on survival to age-1. More important, the TGAM analysis, while giving a somewhat less good model (Table 2), confirms the existence of a threshold in food abundance affecting the cod survival.

Our results add to the evidence that unfavourable changes in the plankton ecosystem can exacerbated the impact of over fishing (Cook *et al*., 1997; Beaugrand *et al*., 2003) in reducing recruitment of North Sea cod. We showed here that there is a threshold effect of food level on the relationship between spawning stock biomass and number of cod age-1 (index of first year survival). These are very important results as it will certainly have implication for fisheries management strategies, and for rates of stock recovery, which will be very dependant on the environmental conditions. Our theoretical and empirical analyse has extended the discussion on how environment variability affects trophic interactions in contrasting ecosystems.

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Table 1. The values of the parameters *b* (mismatch), *c* (food), and *r* (food threshold), as estimated in the three systems. In the case of cod/zooplankton the values of cod age-1 were corrected for the effect of the population size of the upper trophic level (SSB = ln(spawning stock biomass)) before the analysis. Confidence limits and significance values are based on 1000 bootstrap samples; the significance values are one-sided tests with the alternative hypothesis being $b<0$ and $c>0$. R^2 presented is the deviance calculated for cod age-1 uncorrected by SSB.

System	n	R^2	2.5 %	Estimate	97.5%	p-value
Cod/zooplankton	44	0.89				
x = Mismatch			-1.511	-0.729	0.094	0.037
y = Food – slope			0	0.067	0.084	0.038
– threshold			14.754	16.635	54.122	

Table 2. Final formulation of inspection models in the analysis of cod age-1 survival. SSB = ln(spawning stock biomass); *x* = degree of mismatch; *y* = *Calanus* abundance; *r* = food threshold; GCV = generalized cross validation

Formulation		R^2	GCV
$S_t = b_1 + f_1(SSB_t) + g_1(x_t) + g_2(y_t) + \varepsilon_t$	if $\{y_t\} \leq r$	0.45	0.281
$S_t = b_2 + g_1(x_t) + g_2(y_t) + \varepsilon_t$	if $\{y_t\} > r$		

Figure 1. Application of the theoretical overlap surface model on Cod/zooplankton system, with degree of mismatch (*x*) as month of the year, food abundance (y) as the zooplankton (*Calanus*) abundance, and success (*z*) as residuals number of cod at age-1. The grid represents the model, while the actual data are indicated by dots and their distance from the grid.