Spawning stock and recruitment in North Sea cod shaped by food and climate

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In order to provide better fisheries management and conservation decisions, there is a need to discern the underlying relationship between the spawning stock and recruitment of marine fishes, a relationship which is influenced by the environmental conditions. Here, we demonstrate how the environmental conditions (temperature and the food availability for fish larvae) influence the stock–recruitment relationship and indeed what kind of stock–recruitment relationship we might see under different environmental conditions. Using unique zooplankton data from the Continuous Plankton Recorder, we find that food availability (i.e. zooplankton) in essence determines which model applies for the once large North Sea cod (*Gadus morhua*) stock. Further, we show that recruitment is strengthened during cold years and weakened during warm years. Our combined model explained 45 per cent of the total variance in cod recruitment, while the traditional Ricker and Beverton–Holt models only explained about 10 per cent. Specifically, our approach predicts that a full recovery of the North Sea cod stock might not be expected until the environment becomes more favourable.

Keywords: North Sea cod; climate; modelling; stock–recruitment; zooplankton

1. INTRODUCTION

For both fisheries and conservation purposes, a major challenge is to understand how environmental change influences marine ecosystems [1,2]. For instance, climate change may influence recruitment of marine fishes directly through physiological processes and also indirectly through temperature-induced shifts in the zooplankton community, representing the main food items for newborn fishes [3,4]. Theory suggests that such effects may modify the quantitative relationship between the mature population and the recruits, i.e. the stock–recruitment curves [5]. Unfortunately, discerning the underlying stock–recruitment relationship has remained a central and long-lasting problem in fisheries science [6]. Although there is good evidence showing that high recruitment tends to occur when spawner abundance is high, and vice versa [7], the value of fitting specific stock–recruitment relationships in marine fishes has been questioned owing to the weak associations that are frequently observed [6,8]. A poor fit may be simply owing to insufficient data and/or inadequate models, and a general denial of meaningful stock–recruitment relationships

would have rather alarming consequences on the science of fish population dynamics [9]. A more constructive approach would be to expand upon the established knowledge, both by introducing refined models and by including other sources of data [10,11]. The work presented here is intended to be a contribution towards this means.

In their pioneering study, Cushing & Horwood [12] found unexpected support for strong density-dependent mortality of fish larvae, even with low observed larval densities. The model indicates that there is a positive link between the number of food organisms and the slope of the stock–recruitment relationship, with potentially important implications for population dynamics [13]. Chaotic-like dynamics may exist depending on food availability for fish larvae and fishing pressure on the recruited individuals [14]. More recently, a theoretical study by Johansen [5] found that under abundant food availability, the recruitment curve might become monotonically increasing towards an upper limit, i.e. a Beverton–Holt type stock–recruitment relationship [6,15], whereas a Ricker-type stock–recruitment relationship incorporating the feature of overcompensation [6,16] was expected at limited food levels. Specifically, Johansen [5] suggested that lack of food will slow down the growth of the larvae and delay the time to metamorphosis (the end of the larval stage), and that this may cause the larval cohort to experience density-dependent mortality to the extent that the recruitment curve becomes over-compensatory (see also [17]).
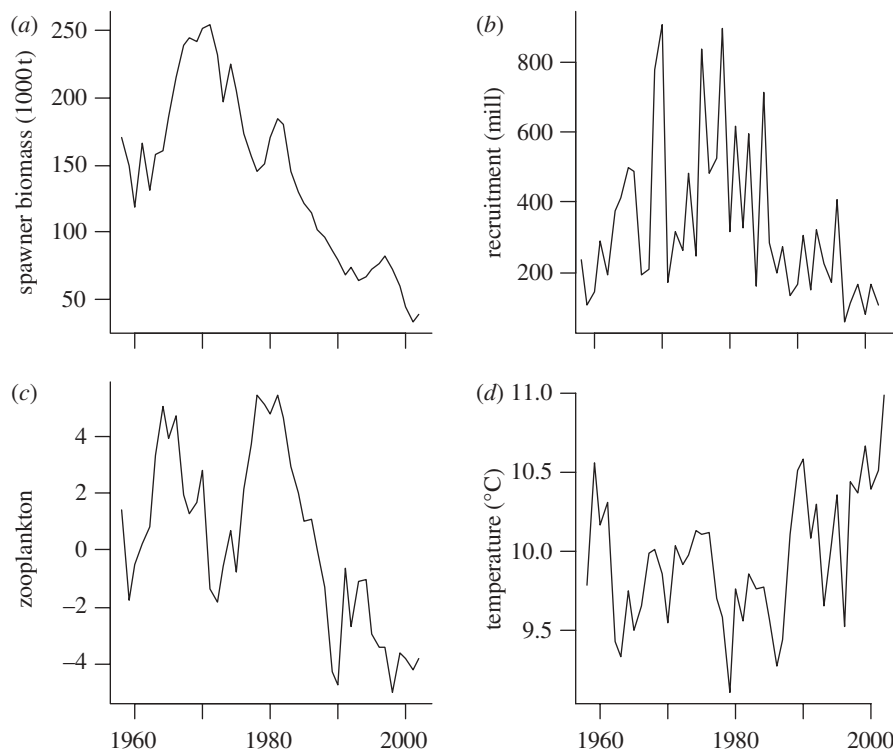
Figure 1. Data series. Temporal variation in (*a*) North Sea cod spawning stock biomass, (*b*) recruitment at age 1 year, (*c*) zooplankton index, and (*d*) sea surface temperature (SST).

Here, we test this expectation by developing a modelling approach linking the traditional Ricker and Beverton–Holt stock–recruitment models so that the Beverton–Holt model will have most weight when food availability for fish larvae is good and the Ricker model will have most weight when food availability is sparse (see §2; electronic supplementary material). We apply this model to long-term data on cod (*Gadus morhua* L.) in the North Sea, where excellent long-term data on zooplankton (i.e. food for fish larvae) are available [18]. The North Sea cod has been in a poor state for several years, partly owing to overfishing and partly owing to environmental change [19,20]. Furthermore, North Sea cod is at the southern edge of this species distribution and plausible scenarios of future climate change are expected to slow the recovery of the stock [21]. Recent empirical studies provide evidence that shifts in the composition of the zooplankton community, linked to shifts in the temperature regime, have had a clear influence on cod recruitment [4,20,22]. Sea temperature may also act directly on recruitment [3,23] and indirectly via the spatial distribution of the spawning stock [24]. The current understanding suggests a particularly strong effect of climate through plankton during the larval stage of cod development [4]. Here, we test for both a plankton effect and a temperature effect on cod recruitment.

We find evidence that both the shape and the position of the underlying stock–recruitment relationship are not fixed. Instead, a family of recruitment functions may result from variability in environmental conditions. This has implications for the management of harvested species such as the North Sea cod because it strongly suggests that recruitment effects of harvesting (i.e. reducing the spawning stock) and climate change will not be independent.

2. MATERIAL AND METHODS

(a) *The Atlantic cod*

The Atlantic cod is an important food fish found along both the western and eastern parts of the North Atlantic Ocean. Many of the historically large populations have been severely depleted by harvesting, including cod in the North Sea basin [19]. The Atlantic cod is a highly fecund bet-hedging species with no parental care [25,26]. Spawning typically occurs during February to May, depending on the location [27], and involves complex behaviour within and between sexes [28]. In the North Sea, the peak of the spawning period is usually in March [29]. The offspring of Atlantic cod spend from several weeks up to five months as pelagic eggs and larvae and then settle towards the bottom as age 0 juveniles [30]. During the pelagic stage, the larvae feed on energy-rich zooplankton such as *Calanus finmarchicus* [31].

(b) *Datasets*

We used data series from the available period of overlap 1958–2002 (figure 1; see also electronic supplementary material). Data on North Sea cod spawning stock biomass and recruitment were obtained from www.ices.dk, following the procedure described by Beaugrand *et al.* [20]. These data were derived from virtual population analysis [32]. Recruitment refers to the estimated numbers of fishes at age 1. This is the stage where the fishes first enter the fisheries and the earliest measure of year class strength available for the full time period. Zooplankton data are from the Continuous Plankton Recorder survey, where samples were collected by merchant ships continuously towing a plankton recorder on their regular routes in the North Atlantic and the North Sea [18,33]. A plankton index was developed using the procedure proposed by Beaugrand *et al.* [20]. This index represents the first principal component performed on key zooplankton indicators of

Table 1. Stock (S) and recruitment (R) models fitted to North Sea cod and environmental data (figure 1): (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, (4) a traditional Beverton–Holt model, (5) a Ricker model including a zooplankton effect and (6) a Beverton–Holt model including a zooplankton effect. (Model formulation is on the logarithmic scale because this ensures that the constant-variance and normal error distribution assumptions are better met (see electronic supplementary material). (The term max$S$ refers to the maximum observed spawning stock biomass (included in order to normalise the spawing stock biomass and avoid problems of colinearity), while a_0, a_1, b and c are parameters to be estimated.))

model	structure
1	$\log(R) - \log(S) = a_0 - a_1 T + \log((1 - Z)\exp(-bS) + Z(1 + \exp(c)S/\max S)^{-1})$
2	$\log(R) - \log(S) = a_0 + \log((1 - Z)\exp(-bS) + Z(1 + \exp(c)S/\max S)^{-1})$
3	$\log(R) - \log(S) = a_0 + \log(\exp(-bS))$
4	$\log(R) - \log(S) = a_0 - \log(1 + \exp(c)S/\max S)$
5	$\log(R) - \log(S) = a_0 + \log(\exp(-b(1 - Z)S))$
6	$\log(R) - \log(S) = a_0 - \log(1 + \exp(c(1 - Z))S/\max S)$

food for larval cod [20]. A positive value reflects high total calanoid copepod biomass, large mean size of calanoid copepods, high abundance of abundance of *C. finmarchicus* and euphausiids and low abundance of *Calanus helgolandicus*. The plankton index was scaled to range between zero and one. Sea surface temperatures (SSTs) were obtained from the International Comprehensive Ocean–Atmosphere DataSet (ICOADS, 1-degree enhanced) provided by the NOAA-ESRL Physical Sciences Division, Boulder CO, USA (http://www.cdc.noaa.gov/). Annual averaged values (°C) were calculated for the North Sea–Skagerrak area (from longitude -3.5–$11.5°$ E and latitude 51.5–$61.5°$ N). SST is standardized to a mean of zero and a standard deviation of one.

(c) *Stock–recruitment modelling*
We fitted a combined Ricker–Beverton–Holt model incorporating food availability (zooplankton, Z) and climate (sea temperature, T) to the available stock (S) and recruitment (R) data on North Sea cod (table 1, model 1). On the original scale, this model can be expressed as:

$$R = S\exp(a_0 - a_1 T)((1 - Z)\exp(-bS) + Z(1 + \gamma S)^{-1}),$$

where $\gamma = \exp(c)/\max S$, and $\max S$ is the maximum observed spawning biomass. The reproductive rate equals $\exp(a_0 - a_1 T)((1 - Z)\exp(-bS) + Z(1 + \gamma S)^{-1})$, with $\exp(a_0 - a_1 T)$ as the maximum reproductive rate at temperature T. The rescaling of the spawning biomass by its observed maximum value makes the variables comparable in their scales, which avoid multi-collinearity [34]. For interpretation, it can be absorbed into $\exp(c)$. The parameterization $\exp(c)$ ensures that the coefficient γ is positive, which prevents numerical problems in fitting the model. While the parameter b is also postulated to be positive, it does not create numerical problems in fitting by not constraining it to be positive, and hence no such constraint was imposed. Note that the term $((1 - Z)\exp(-bS) + Z(1 + \gamma S)^{-1})$ represents the density dependence, which is now a function of the zooplankton index Z. As Z tends to 1, the density dependence approaches the form of Ricker model with an exponential decay in the density, namely $\exp(-bS)$, whereas as Z tends to 0, the density dependence is asymptotically Beverton–Holt, namely $(1 + \gamma S)^{-1}$. For a fractional Z, the density dependence is a weighted mean of these two types of density dependence with weight Z for the Beverton–Holt density dependence. In particular, when $Z = 0$, the model becomes the Ricker model but it reduces to Beverton–Holt model when $Z = 1$.

A model formulation on the logarithmic scale (table 1, model 1) is, however, preferred because after the log transformation, the assumption of a constant-variance normal error distribution appears to be met (see electronic supplementary material). In turn, this allows us to estimate the model by minimizing the nonlinear least-squares objective function. For this purpose, we used the *nls* function provided in program R [35]. Here, a Gauss–Newton algorithm is used to determine the nonlinear least-squares estimates of the model parameters. Note also that the term $\log(S)$ is not moved to the right side of the equation for the subtle technical reason that the *nls* function does not have an offset option.

The statistical support for this model is compared with that of several alternative candidate models. First, we tested a combined Ricker–Beverton–Holt model including the zooplankton covariate but excluding the sea temperature covariate (table 1, model 2). Second, we fitted each of the traditional Ricker and Beverton–Holt models (table 1, models 3 and 4). Finally, we added two models to the list in order to explore whether a more parsimonious explanation is for food availability to directly affect either of the traditional Ricker or Beverton–Holt models. We hypothesized that low food availability (1—zooplankton) might lead to increased overcompensation (table 1, model 5), or it might lower the carrying capacity of the system (table 1, model 6). Additional models involving for instance a temperature effect within each of the Ricker and Beverton–Holt models might also be formulated, but following the model selection philosophy outlined by Burnham & Anderson [36], we include only a restricted set of *a priori* defined models needed for testing our hypotheses. Model selection was based on the Akaike Information Criterion (AIC; [36]), 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 and was used in making inferences about North Sea cod recruitment.

3. RESULTS
The combined Ricker–Beverton–Holt model, where the North Sea cod stock–recruitment relationship is influenced by both zooplankton abundance and sea temperature, had the lowest AIC value and therefore the most support from the available data series (table 2; $a_0 = 2.06$, s.e. $= 0.40$, $p < 0.001$; $a_1 = 0.18$, s.e. $= 0.09$,

Table 2. Model selection. (The number of parameters to be estimated (K), the AIC value ($-2\log$ likelihood $+ 2K$), the residual sum of squares (RSS) and the proportion of the variance explained (r^2) by each of the candidate stock–recruitment models (table 1).)

model	K	AIC	RSS	r^2
1	4	62.3	8.43	0.45
2	3	64.6	9.27	0.39
3	2	80.4	13.77	0.10
4	2	80.6	13.81	0.097
5	2	66.6	10.12	0.34
6	2	65.6	9.90	0.35

$p = 0.05$; $b = 0.018$, s.e. $= 0.007$, $p = 0.01$; $c = 0.96$, s.e. $= 0.58$, $p = 0.10$). This model fitted the data reasonably well (Shapiro–Wilk test of normality: $p = 0.89$, see also electronic supplementary material). 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: figure 2). 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 (figure 2). In addition to the zooplankton effect, model selection also supported a negative effect of increasing sea temperature on cod recruitment (table 2 and figure 3). 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). Including a zooplankton effect in each of the traditional Ricker and Beverton–Holt model increased their r^2-value and decreased the corresponding AIC (table 2, models 5–6). Of the two, the Beverton–Holt model containing a zooplankton effect had the most support, indicating that the maximum recruitment would be negatively affected by low food availability (results not shown). The differences in AIC among the four best models were not very large (1–4 units, table 2). Still, the combined Ricker–Beverton–Holt model (with or without a temperature effect) had the most support from the data (table 2, model 1–2).

4. DISCUSSION

In this study, we have developed a modelling approach that—when applied to the North Sea cod—demonstrates how the underlying relationship between the population of spawners and recruit fish can be shaped by food availability for fish larvae and sea temperature. We find empirical support for the theoretical prediction [5] stating that the classical Ricker model involving overcompensation [16] may apply when food availability is poor while the classical Beverton–Holt model without overcompensation [15] may apply when food is abundant. We acknowledge that our results, as is generally the case for statistical data-driven models, only are valid within the
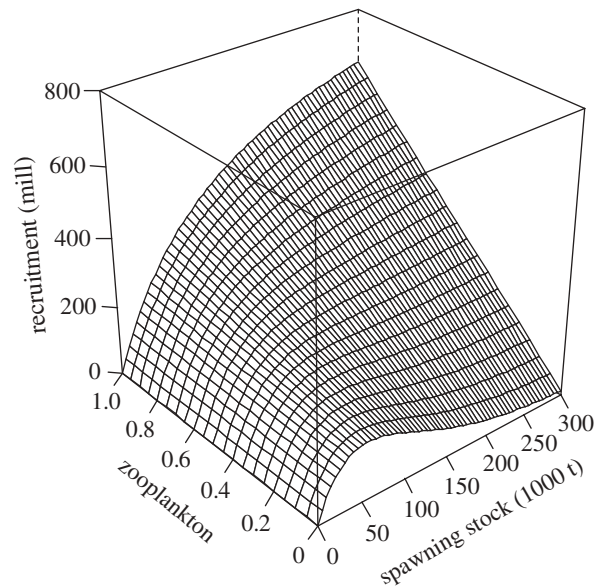

Figure 2. Influence of spawning stock biomass and pelagic food availability (zooplankton) on North Sea cod recruitment at age 1, as predicted from a combined Ricker–Beverton–Holt model (table 1, model 1). Predictions are shown for the average annual SST of 10°C.

range of observed values. It follows that future values of environmental conditions (e.g. owing to climate change), spawning stock biomass or recruitment could fall outside this range and that the model then would need to be re-parametrized to remain valid. Future values might also prove helpful in discerning the stock–recruitment relationship at combinations of very low food abundance and very high spawner biomass, and vice versa, where the current data availability was relatively sparse.

Although studies of environmental effects on cod recruitment are numerous, North Sea cod was until very recently probably the only stock for which correlations between time series of planktonic prey and recruitment are established [37]. Thanks to Russian zooplankton data recently being made available such relations have now also being studied for Arcto-Norwegian (Barents Sea) cod [38]. Cushing [39] suggested that successful recruitment of North Sea cod was dependent on a match between the first-feeding larvae and their prey known as the match–mismatch hypothesis. Later, Beaugrand *et al.* [20]. found strong evidence that changes in the plankton community lead to improved recruitment of North Sea cod during the 1960s and 1970s, known as the 'gadoid outburst' [39], and that later unfavourable changes in the plankton community intensified the impact of overfishing and caused a marked reduction in recruitment since the mid-1980s. These unfavourable changes involved a reduction in the abundance of the large calanoid copepod *C. finmarchicus*, largely being replaced by its more temperate–water affiliated co-gener, *C. helgolandicus* [40,41]. While nauplii stages of *C. finmarchicus* are the preferred and often dominant prey of larval North Sea cod [31], the less nutritious nauplii of the autumn-spawning *C. helgolandicus* have never been found in the diet records of larval cod [37]. In later years, the distribution of *C. finmarchicus* has
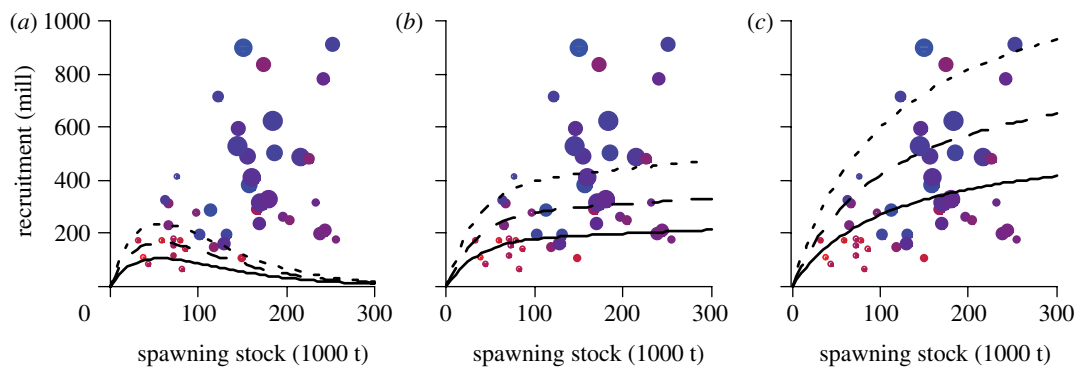
Figure 3. Recruitment of North Sea cod at the historical maximum SST (solid line), average temperature (dashed line) and historical minimum temperature (dotted line) for the corresponding historical (*a*) low food abundance (*b*) average food abundance and (*c*) historical top food abundance as predicted from a combined Ricker–Beverton–Holt model (table 1, model 1). Colour symbols refer to observed combinations of stock and recruitment. The size of the symbols is scaled to reflect annual variation in zooplankton abundance, while the corresponding colour reflects annual SST (red: warm, blue: cold).

shifted northwards and the diet of larval cod in the North Sea tends to be more dominated by smaller copepod species [37]. In the neighbouring Irish Sea, where the abundances of *Calanus* species are low and highly variable, cod still shows a preference for *Calanus*, not only at the onset of external feeding, but also after metamorphosis [42].

The preferred food of early life stages of cod gradually progresses from mainly copepod eggs to copepod and euphausiid nauplii, then to a copepod dominated diet and finally to a progressive replacement of the copepod-based diet by euphausiids and fish larvae [22]. Although the zooplankton index we apply was designed to reflect the potential prey of larval cod, the size-spectrum also includes food suitable for older stages, notably euphasiids and copepodite stages of *Calanus* species. Admittedly, the use of a composite index, covering several species and months, poses challenges when we want to assess effects on the slope of the stock–recruitment curve. For example, one could expect rapid depletion of zooplankton nauplii to lead to over-compensatory effects, while ongoing competition for euphasiids by later stages of young cod would probably be a more purely compensatory process.

Few studies have suggested density-dependent survival of marine fish larvae. The dominating paradigm is that the larvae are too sparsely distributed to influence the abundance of their planktonic prey and thus cause food limitation at high densities. Density-independent environmental controls are thought to account for most of the variability in the early life [43]. However, there is some observational evidence of density dependence occurring at the larval stage (e.g. on bluefin tuna, [44]; walleye pollock, [45]; cod [38]).

Literature giving empirical support for effects of variability in availability of zooplankton prey on larval cod growth is also sparse. This should by no means be taken as evidence that such a connection does not exist, but rather that such investigations are difficult to conduct under both field and culture conditions. A mesocosm (outdoor enclosure system) study by Van der Meeren & Naess [46] showed that cod larvae which lacked sufficient amounts of energetically favourable prey had low-specific growth rates, while the larvae on the other hand realized

their high potential for growth when copepod nauplii were abundant. Furthermore, there is convincing support for survival of a cohort (of both cod and other marine fish) being directly related to growth rates during the pre-recruit period [47–49]. A rapid growth rate through the larval and juvenile stages is thought to increase the probability of survival owing to an enhanced ability to feed and avoid predators [12,50]. In this context, our results of zooplankton regulating larval fish growth and survival and ultimately year class strength indeed make sense.

Our results of North Sea cod recruitment being weak during warm periods finds support in earlier work. Evidence suggests that cod stocks towards the northern limit of the species geographical range tend to produce strong year classes during anomalously warm years while southerly stocks are favoured by temperatures below average [51,52]. The North Sea stock is the southernmost of the large stocks of Atlantic cod in the northeast Atlantic. Its recruitment would thus be expected to be negatively correlated with temperature [52–54]. Furthermore, a critical review of environment–recruitment relations points to one generalization that stands out: 'correlations for populations at the limit of a species' geographical range have often remained statistically significant when re-examined' [55]. Temperature could affect recruitment directly through juvenile survival and growth performance [3,21]. Temperature may also limit the available habitat [21,24]. Also, there is good evidence that recent warming of the North Sea is affecting the survival of juvenile cod via its effects on the plankton along a critical thermal boundary [2,4,20]. Our study strongly suggests that if warming continues at the rate projected by the Intergovernmental Panel on Climate Change, it will considerably limit larval cod survival and thereby recruitment, making the reconstitution of the stock difficult. Rising temperatures are expected to lead to an increased rate of decline in North Sea cod abundance as compared with model simulations without climate change [56].

Recruitment modelling is a vital component of the assessment and management of marine fish populations, such as the North Sea Atlantic cod. Nevertheless, our understanding of what regulates the number of young fishes has remained opaque since the birth of fisheries

science itself [57]. We certainly do not claim that our study will perfectly clarify the mechanisms underlying stock–recruitment relationships, but it reveals how the underlying recruitment dynamics need not be fixed (i.e. described by one specific stock–recruitment curve), but instead shaped by the prevailing environmental conditions (i.e. food availability and sea temperature). In terms of fishery management and conservation, the most important implication of this finding is probably that there will be interaction effects between harvesting and climate change on population dynamics.

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