The predictive potential of early life stage individual-based models (IBMs): an example for Atlantic cod *Gadus morhua* in the North Sea

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ABSTRACT: Using a spatially explicit individual-based model (IBM), we examined the potential larval survival (PLS) and growth of early life stages of Atlantic cod *Gadus morhua* in the North Sea ecosystem in response to changes in physical and biological forcing. We employed a 3-dimensional coupled model system that includes a hydrodynamic model, a physiologically based IBM and the lower trophic level ecosystem model ECOSMO, to provide related prey fields. The statistical analysis of a long-term (1949 to 2008) hindcast integration and the comparison to a set of 30-yr-long scenario experiments revealed a strong impact of atmospheric forcing on changes in PLS, where variations in transport processes and in the prey field are equally as important as temperature-dependent processes. Furthermore, the scenario experiments show that the different impacting environmental factors interact non-linearly and are non-homogeneous in time and space. A correlation analysis between estimated PLS and observed Atlantic cod recruitment in the North Sea indicated that time periods of high correlation alternate with periods of low or negative correlation. In the 1960s and from the end of the 1980s onwards, we identified high correlations between estimated PLS and recruitment and concluded that the model exhibits a significant predictive potential for cod recruitment during these periods. However, we also identified contrasting periods, e.g. during the 1970s and 1980s, for which we conclude that recruitment variability during these periods was significantly influenced by alternative processes, such as top-down or bottom-up controls during post-larval life stages.

KEY WORDS: Bio-physical modelling · Individual-based modelling · North Sea · Atlantic cod · Scenario modelling

INTRODUCTION

The North Sea, a highly productive sea adjacent to the North Atlantic, is characterized by strong co-oscillating tides and a dominant inflow of North Atlantic water. A major characteristic of the North Sea is the pronounced frontal regime that consists of a seasonal tidal mixing frontal system (Simpson & Hunter 1974) and, along the continental coast, a region of

freshwater influence (ROFI) frontal system (Simpson 1997). These fronts constitute the transition zone between shallow, well-mixed, highly productive coastal areas and the seasonally stratified central North Sea and have previously been identified to highly impact the North Sea ecosystem dynamics (e.g. Munk et al. 1995, Richardson et al. 2000), such as by bringing up nutrients to the euphotic zone or accumulating particles due to turbulence discontinuities.

Atlantic cod *Gadhus morhua* is a demersal gadoid that has traditionally been one of the most abundant predatory fish in the North Sea. Water temperatures in the North Sea lie in the upper range of Atlantic cod thermal tolerance. Cod spawning in the North Sea occurs in the Southern Bight, German Bight, Dogger Bank and the English Channel (Fig. 1), which constitutes the southernmost edge of Atlantic cod spawning distribution (Fox et al. 2008, Brander et al. 2010) in the Northeast Atlantic. Spawning appears to be not equally distributed in these areas but restricted to specific regions (Daewel et al. 2011). There are indications that cod avoid spawning in turbid waters (e.g. Rindorf & Lewy 2006) and that spawning is associated with the formation of frontal systems (Munk et al. 2009).

Since the 1980s, the abundance of Atlantic cod in the North Sea has markedly declined (Heath 2005, ICES 2005a, Nicolas et al. 2014). This was potentially caused by extensive (over-) exploitation of the stock, but several studies also indicate important changes in environmental factors potentially regulating the productivity (recruitment potential) of the North Sea cod stock. These include bottom-up, prey-driven changes (Beaugrand & Reid 2003); changes in water temperature (Brander & Mohn 2004); and food web interactions (Kempf et al. 2009, Minto & Worm 2012, Hjermann et al. 2013). Beaugrand et al. (2003) applied a principal component analysis to investigate the statistical relationship between cod recruitment strength and the abundance and species and size composition of dominant copepod species in the North Sea. Their results indicate a relationship between the decline in North Sea cod recruitment and the general change in the size (and species) composition of calanoid copepods in the North Sea, which would potentially lead to a mismatch of year 0 cod with their preferred prey.

Some studies (Planque & Frédou 1999, Brander & Mohn 2004, Drinkwater 2005) have shown negative relationships between cod recruitment and North Sea water temperature. For example, Drinkwater (2005) implemented potential temperature scenario tests based on estimates obtained from Intergovernmental Panel on Climate Change (IPCC 2001) multimodel scenarios. Those tests indicated that a water temperature increase of 3°C would collapse the North Sea cod stock, a result that agrees well with similar scenarios explored by Clark et al. (2003). In contrast, cod populations in areas with colder annual water temperatures such as the Barents Sea were predicted to remain unaffected or to benefit from climate warming (Drinkwater 2005). Observed trends of decreasing total stock biomass and recruitment of age 1 cod in the North Sea under increasing temperatures (ICES 2005a) support these projections. However, climate and coupled climate–ecosystem impacts on the survival of cod early life stages are manifold; in addition to direct temperature impacts on vital rates, climate modulates and controls
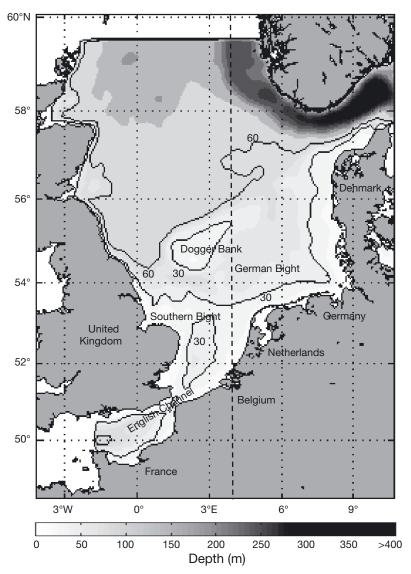

Fig. 1. North Sea bathymetry. Black isolines indicate the 30 and 60 m depth level. Vertical dashed line indicates division of the area into eastern and western North Sea

larval survival through transport processes (Hinrichsen et al. 2005), food availability and/or predation (Durant et al. 2007). Since temperature is a proxy for many other climatic variables, a pronounced temperature correlation does not necessarily indicate causality. Observational time series allow for statistical analysis of relevant factors and can allow for hypothesizing underlying processes for cod recruitment. Time series of relevant processes such as larval survival have previously been shown to be useful explanatory variables in statistical analysis (Köster et al. 2005). However, it is not possible to identify responsible processes and establish causality from statistical relationships. Hence, a more process-based understanding and predictive methods, which integrate and quantify the various effects, are required to improve confidence in assessments.

An appropriate tool to identify climate implications for fish is a spatially explicit, deterministic individual-based model (IBM). In contrast to stochastic models, which already consider cumulative mechanisms, mechanistic IBMs allow integration and quantitative assessment of various climate-influenced effects on individuals. So far, this kind of model has been used to understand species-specific consequences of regionally and seasonally varying climatic impacts (e.g. Shin & Cury 2004, Kristiansen et al. 2007, 2011, Megrey et al. 2007, Daewel et al. 2008a, 2011). Within the present study, we aim to explore the predictive potential of the method exemplarily for a cod IBM coupled to a North Sea ecosystem model (Daewel et al. 2011). We refer to the predictive potential of the model as the degree or extent that the model is able to predict variability in recruitment success when forced with ideal climate forcing. We present the first multidecadal integration of a spatially explicit IBM to assess both the impacts of bottom-up control on cod recruitment in the North Sea and the predictive capacity of IBM-based indicators for recruitment success for this period. We evaluate the predictive potential for this period and test the model output, potential larval survival (PLS), as a possible measure for recruitment against independent observational-based recruitment time series. Such an assessment is an essential prerequisite to identify the model's potential to be used for climate change studies or to predict recruitment variations on annual or multiyear time scales. Additionally, we present results from 30-yr-long scenario experiments, which allow disentangling single effects of environmental forcing to the bottom-up control of cod recruitment. The outcomes of various simulations that employ different biological and physical forcing allow

for identification of key processes impacting both individuals and populations and improve understanding of the complex interplay of environmental factors potentially regulating the survival of Atlantic cod early life stages.

The key questions addressed within this study are (1) What drives the interannual and spatial variability in cod larval survival? (2) What is the relevance of early larval survival for recruitment, and is it changing on multidecadal time scales? (3) What is the ability of the model to forecast and predict future changes in recruitment success, and what are the limitations of the IBM approach?

METHODS

Coupled model system

In this study, we employed a 3-dimensional (3D) coupled model system (Fig. 2) that was first presented by Daewel et al. (2008a) in an application for sprat *Sprattus sprattus*. The additional IBM submodule for North Sea Atlantic cod has been described in detail by Daewel et al. (2011). The model produces spatiotemporal variable fields of PLS (%), development time of non-feeding life stages (NFS; d) and larval growth rates (GR; mm d^{-1}). We refer to PLS as the percentage of larvae remaining above a critical minimum mass at the end of the individual's simulation (at 20 mm length) with respect to the spawning time and location (Daewel et al. 2011).

Hence, PLS is a function of the initial number of individuals spawned (N_{sp}) at a specific location (i,j,k) and time (t) and of the mortality related to these individuals $M(N_{sp})$. The latter is defined as the number of individuals that die of starvation before reaching 20 mm length.

$$\text{PLS}(i,j,k,t) = \frac{N_{sp}(i,j,k,t) - M[N_{sp}(i,j,k,t)]}{N_{sp}(i,j,k,t)} \times 100 \quad (1)$$

Four different modules are part of the coupled model system (Fig. 2); 3 of the modules (the hydrodynamics model, the Lagrangian transport model and the IBM) are solved simultaneously in our study. The advantage of the online coupling is the high time resolution at which the physical parameters are available for the IBM, which allows resolving the tidal cycle. In a highly dynamic, tidally influenced system like the North Sea, short-term changes in hydrodynamic processes such as currents and turbulence play an important role in larval survival. Addi-
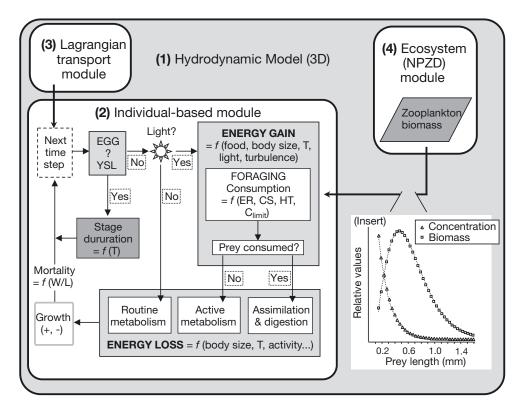
Fig. 2. (1) Coupled model structure (from Daewel et al. 2011). (2) The individual-based module (IBM) and (3) Lagrangian transport modules are implemented in the hydrodynamic core. The IBM consists of the egg, yolk sac and feeding larval stages. (4) The ecosystem model ECOSMO II (Daewel & Schrum 2013) provides zooplankton biomass that is converted into a size-specific prey field (insert) and utilized by the IBM foraging subroutine. YSL: yolk sac; T: temperature; ER: encounter rate; CS: capture success; HT: handling time; C_{limit}: maximum consumption; W: weight; L: length; NPZD: nutrient–phytoplankton–zooplankton–detritus
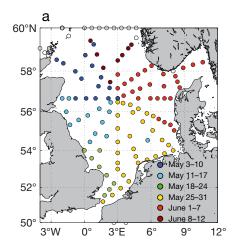
tionally, prey fields were received from a lower trophic level ecosystem model that was integrated over the required time period prior to the coupled model runs using the same configuration and forcing, such that the IBM exerts no predation pressure on the zooplankton. In contrast to the earlier model version presented by Daewel et al. (2011), we utilized ECOSMO II (Daewel & Schrum 2013), which is an updated version of the nutrient–phytoplankton–zooplankton–detritus (NPZD) model ECOSMO (Schrum et al. 2006a,b) that allows for long-term applications in the coupled North Sea and Baltic Sea system.

The hydrodynamic base of ECOSMO evolved from the 3D primitive equation Hamburg shelf ocean model (HAMSOM) that was described in detail by Schrum & Backhaus (1999). The model is able to simulate long-term climate variations in the North Sea (Janssen et al. 2001, Schrum & Siegismund 2002). The equations were solved on a staggered Arakawa C-grid with a horizontal resolution of 6 nautical miles (~10 km), 20 vertical levels and a 20 min time step. The hydrodynamic core provides, among others, estimates of seawater temperature, turbulence, transport and light conditions to be used in the spatially explicit IBM, the particle-tracking module and the lower trophic level module. In contrast to the earlier model version used by Schrum et al. (2006a) and Daewel et al. (2011) that was equipped with an

upwind advection scheme, the model version used here employs a less diffusive total variation diminishing (TVD) advection scheme. Its implementation is described in more detail by Barthel et al. (2012), who demonstrated that the choice of the advection scheme has large implications on the results of both the ecosystem model and the spatially explicit IBM in the North Sea, by improved spatial resolution of hydrodynamic features.

Individuals simulated by the IBM were treated as explicit entities, and their 3D location was estimated using a Lagrangian particle-tracking module. Both advective and diffusive velocities were accounted for when calculating the particle displacement. The advective velocity components were linearly interpolated to the particle location, and the vertical diffusion is described by a random diffusive velocity, which is scaled by the eddy diffusion coefficient calculated by the hydrodynamic model (Bork & Maier-Reimer 1978). Particles in the model were considered neutrally buoyant, and hence no additional vertical velocity component was considered for particle displacement.

The 3D ecosystem model ECOSMO II calculates zooplankton dynamics in the North Sea on the basis of 16 state variables. The model equations and a model validation exercise were presented in detail by Daewel & Schrum (2013), who found the model able to reproduce temporal and spatial variability of pri-
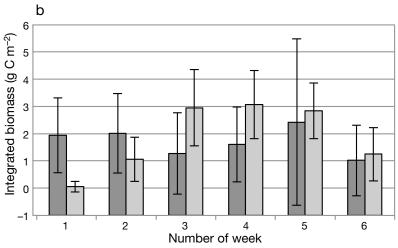
Fig. 3. (a) Experimental grid of the ZISCH field campaign in May to June 1986 (Krause et al. 1995) and (b) vertically integrated biomass in the upper 30 m, weekly averaged (±SD) according to the sampling time for ZISCH data (dark grey) and ECOSMO-estimated zooplankton (light grey) (observation and model were co-located in time and space prior to averaging)

mary and secondary production in the North Sea and Baltic Sea on intra- and interannual up to decadal time scales. In Daewel & Schrum (2013), the model was validated using nutrient data only because of the better availability and reliability of nutrient *in situ* data and the robustness of estimated nutrients. Phytoplankton and particularly zooplankton observations are much more difficult to undertake and are often associated with methodological uncertainties (Gutkowska et al. 2012, Dippner & Krause 2013). Since zooplankton are a crucial part of our model estimate, we here present a comparison of model-estimated zooplankton data with observed zooplankton data from the German BMBF ZISCH project experiment in summer 1995 (Krause et al. 1995) (Fig. 3). The comparison indicates that the model is able to estimate zooplankton in the right magnitude and with a reasonable spatial pattern, but the model appears to overestimate biomass in the southern North Sea and underestimate zooplankton in the northern North Sea. Estimates of average primary and secondary production in the North Sea and its seasonal dynamics are shown in Fig. 4, highlighting the highly productive areas in the well-mixed southern North Sea (figures from Daewel & Schrum 2013).

The NPZD module was designed to simulate different macronutrient limitation processes in the targeted ecosystems. Besides the 3 relevant nutrient cycles (nitrogen, phosphorus and silica), 3 functional groups of primary producers (diatoms, flagellates and cyanobacteria) and 2 zooplankton groups were resolved. The latter were divided, based on their feeding behaviour, into herbivorous and omnivorous zooplankton. Nonetheless, since the size attribution for the single zooplankton classes is too broad, we

developed an approach to convert integrated zooplankton biomass into an appropriate prey field required for the mechanistic IBM. Following Daewel et al. (2008b), the bulk zooplankton biomass (mg C m^{-3}) in each grid cell is divided into a prey size spectrum (using specific size bins) based on the assumption that the size spectrum of zooplankton in the North Sea follows an exponential decrease in abundance with increasing zooplankton size (Fig. 2 inset). Here, we used prey sizes ranging from 150 to 1600 µm, which covers the majority of zooplankton species in the North Sea (for more explanations, see Daewel et al. 2011) and a prey size increment of 40 µm.

The IBM contains formulations for both the non-feeding and the feeding early life stages of North Sea Atlantic cod as described earlier by Daewel et al. (2011). It is structured as an *i*-state configuration model as described by Caswell & John (1992), where some characteristic states that change depending on extrinsic and intrinsic conditions are assigned to each individual. In this model, an empirically derived, temperature-dependent formulation for development during the non-feeding stages (see Daewel et al. [2011] for equations) was chosen based on findings from Jordaan & Kling (2003) and Geffen et al. (2006).

The feeding larval stage, in contrast, was treated in a mechanistically formulated IBM, where larval weight-specific growth *G* is calculated as the difference between energy gain (by consumption *C*) and energy loss (by metabolic rate *R*) that comprises standard as well as active constituents of metabolic rates.

$$G = C\beta(1 - \text{SDA}) - R \qquad (2)$$

Consumption (µg dry mass) has been parameterized as functions of larval length and prey field struc-
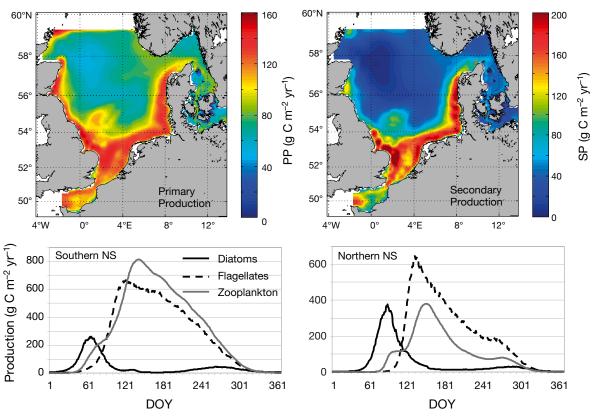
Fig. 4. Simulated spatial and seasonal dynamics of primary production (PP) and secondary production (SP) in the North Sea (NS). Seasonal dynamics were estimated for the southern North Sea and for the northern North Sea separately (southern and northern North Sea were divided at the 60 m isobath, see Fig. 1). Figure adapted from Daewel & Schrum (2013). DOY: day of year

ture and is reduced by assimilation efficiency (β), specific dynamic action (SDA) and metabolic rate. Limitations to consumption are given by tempera-ture-dependent gut evacuation rates as defined by Peck & Daewel (2007). Following Letcher et al. (1996), consumption rates also include mechanistic formulations for encounter rate, capture success and handling time.

As described by Lough et al. (2006), cod feeding larvae were considered pause–travel predators, with respective values for pause frequency and pause duration taken from the same study. Larval length (and length growth GR) was calculated using an allo-metric relationship between dry mass and standard length as proposed by Peck et al. (2005). Larval mortality has exclusively been incorporated into the model as a consequence of starvation to separate bottom-up and top-down impacts on larval survival. If not enough suitable food is available to com-pensate for metabolic losses, the individual larva loses weight until a critical minimum is exceeded, and the larva is removed from the simulation (Daewel et al. 2011).

Model setup

The coupled model system was applied to a 60 yr time period (1949 to 2008). Preceding the IBM model integration, a 61 yr model simulation with the cou-pled hydrodynamic–NPZD model compartment only (Daewel & Schrum 2013) was accomplished provid-ing the relevant prey fields. The hydrodynamic–IBM model simulations were performed as a series of sixty 1 yr simulations using initial fields for hydrodynamics and prey fields from the preceding simulation. Both ECOSMO and the IBM were parallelized and model runs were executed on multiple processors (for tech-nical details see Appendix).

The hydrodynamic–NPZD model configuration was described in detail by Daewel & Schrum (2013). For the required atmospheric forcing, we applied data from the National Center for Environmental Prediction–National Center for Atmospheric Re-search re-analysis (Kalnay et al. 1996) that are avail-able from 1948 onwards with a 6 hourly resolution. The model is initialized using climatological gridded data for the North Sea and Baltic Sea compiled by

Janssen et al. (1999) for temperature and salinity. At the open boundaries, sea surface elevation (from a coarser-scale diagnostic model), salinity (climatology modulated by annual anomalies from observations) and tidal variations are prescribed. For temperature, a Sommerfeld radiation condition is applied (Orlanski 1976). River loads and runoff used in the simulations were compiled from different sources. Details are described in Daewel & Schrum (2013).

To allow for long-term changes in spawning grounds, we did not restrict spawning to observed and reported spawning grounds but employed a setup first presented by Daewel et al. (2008a), where particles (eggs) are released homogeneously in every (horizontal and vertical) model grid point to avoid a bias towards present knowledge about spawning grounds. Only individuals that survived to a length of 20 mm are considered in the later analyses of PLS, GR and NFS. All others were excluded from the calculations. Therefore, the considered spawning grounds are limited to those areas supporting larval survival. As already discussed in Daewel et al. (2011), these areas agree considerably with observed spawning grounds (ICES 2005a). Our proposed method has the advantage that it does not introduce spurious variability due to undersampling of spawning grounds and allows consideration of climatic-induced variations of successful spawning grounds. Cod spawning in the North Sea has been observed to take place between January and April (ICES 2005b). Accordingly, eggs (over $110\,000\ d^{-1}$) were distributed homogeneously over the North Sea on each day during the spawning period. Since particles were released independently of spawning grounds and spawning stock biomass, the model does not allow for quantitative estimates of survivors but allows identifying spawning grounds that potentially support the survival of cod larvae and projecting changes in successful spawning grounds.

Scenario experiments

Understanding process interactions from the 4-dimensional model system is difficult since changes occur non-linearly and non-homogeneously and are difficult to analyse and trace back to single processes. Here, therefore, we chose to utilize a successive 30-yr-long (1949 to 1978) scenario experiments to disentangle single processes and their impact on larval fish survival. The simulation period was inten-

Table 1. Overview of scenario model experiments. IBM: individual-based model

Expt	Environmental change
Ia	Increase in temperature impacting egg and yolk sac development stage +1.2°C
Ib	Increase in temperature impacting all life stages +1.2°C
IIa	Increase in air temperature +1.2°C (reference prey field)
IIb	Increase in wind speed +16% (reference prey field)
IIc	Decrease in wind speed −16% (reference prey field)
IIIa	Increase in air temperature +1.2°C (on IBM and prey field)
IIIb	Increase in wind speed +16% (on IBM and prey field)
IIIc	Decrease in wind speed −16% (on IBM and prey field)

tionally chosen to exclude the regime shift period to prevent the regime shift response from artificially dominating the statistical relationships. Three sets of scenarios were performed (Table 1). In set I, temperature changes were applied only to the temperature-dependent equations of the IBM. In set II, environmental (air temperature and wind) changes were implemented by changing the atmospheric forcing for the coupled model system including physics and the IBM while prey fields were taken from the reference run. In set III, environmental (air temperature and wind) changes were applied to the spatially explicit IBM and concomitantly to the ecosystem model, providing consistent prey fields. The magnitude of changes in environmental conditions was derived based on the variation of the annually averaged time series and estimated using 2 times the standard deviation of the annual variations from the hindcast period (1949 to 2007). By chance, the values for air and water temperature were the same (1.2°C). This implies that the resulting water temperature change in Expts IIa and IIIa is not equal to the tested water temperature change in Expt I. The response to the water temperature in Expts IIa and IIIa would be variable in time and space, depending on actual hydrodynamic and atmospheric conditions. Wind, turbulence and stratification and radiation would modulate the oceanic response, and the experienced temperature change for the larvae (particles) could be very different depending on spawning time and location and corresponding drift pattern. However, the results can be compared since our analysis reveals that the standard deviation, which is a measure of the climatic-induced variability, is the same for air temperature and water temperature.

The evidence arising from the response of PLS to the different scenario experiments is fundamentally different from the indication provided by statistical analysis. The successive scenario experiments and

analysis of their consequences over all larvae (parti-cles) allow a mechanistic understanding of environ-mental processes and their impact on the bottom-up control of larval survival. The dedicated scenario experiments, which apply changes only to the larvae physiological rates (scenario set I) and separate the purely hydrodynamic-induced changes (scenario set II) from changes induced by hydrodynamics and consequent prey changes (scenario set III), allow for identification of key processes and quantification of their impacts.

Statistical methods and illustration

Kruskal-Wallis *H*-test: temporal pattern

To decide whether abrupt changes in PLS and the environmental conditions are statistically relevant and can be assumed to be associated with regime shifts, we applied the Kruskal-Wallis *H*-test, which is a non-parametric statistical test based on ranks instead of original observations. It was developed to decide 'whether several samples (in this case, 2 sub-sequent time periods of 20 yr) should be regarded as coming from the same population' (Kruskal & Wallis 1952, p. 584), whereas the null hypothesis is that the samples are from the same population. This means that if the p-value is below the significance level defined as 0.05, the null hypothesis can be rejected, and the change from one time period to another can be considered significant compared to the internal variability of the time series.

Empirical orthogonal functions: spatial pattern

Empirical orthogonal function (EOF) analysis is a statistical method to identify dominant modes in mul-tidimensional data fields and is widely used in cli-mate and ocean science (for a detailed discussion and method description, see e.g. von Storch & Zwiers [1999] or Venegas [2001]). The EOF analysis is also referred to as principal component analysis. Here, we apply the method to understand if long-term changes in PLS can be considered a North Sea-wide signal or whether spatial differences occur in the temporal variability and whether the single modes can be related to specific environmental conditions.

Here, we give a brief introduction into the main elements of the analysis with respect to the consid-ered application to clarify the terms used in the analysis. The annual values of the spatially explicit

PLS field form an $N \times M$ matrix χ (*N*: number of years; *M*: number of wet grid points). The empirical modes are given by the K eigenvectors of the covariance matrix with non-zero eigenvalues. Those modes are temporally constant and have the spatially variable pattern $p^k(m = 1,…,M)$ where $k = 1,…,K$. The time evolution $A^k(t = 1,…,N)$ of each mode can then be obtained by projecting $p^k(m)$ onto the original data field χ such that:

$$\chi(t, m) = \sum_{k=1}^{K} p^k(m)A^k(t) \qquad (3)$$

In the following sections, we will refer to $A^k(t)$ as the principal components (PCs) and to $p^k(m)$ as the EOF. The percentage of the variance of the field χ explained by mode k is determined by the respective eigenvalues and is referred to as the global explained variance $\eta_g(k)$.

Before using the method to analyse the spatiotem-poral dynamics of the field, the data were demeaned (to account for the variability only) and normalized (to allow an analysis of the variability independent of its amplitude). The identified modes are not neces-sarily equally significant in all grid points of the data field. Thus, the local explained variance $\eta_{local}^k(m)$ could provide additional information about the regional relevance of an EOF mode and the corre-sponding PC in percent:

$$\eta_{local}^k(m) = \left\{ 1 - \frac{\mathrm{Var}\left[\chi(m,t) - p^k(m)A^k(t) \right]}{\mathrm{Var}\left[\chi(m,t) \right]} \right\} \cdot 100 \qquad (4)$$
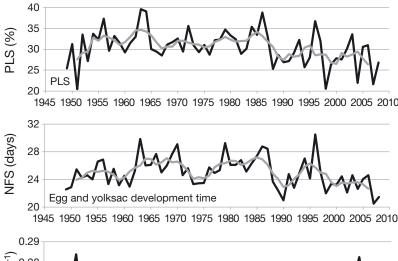
where $\mathrm{Var}(X) = \sum_{t=1}^{N} \left[\bar{X} - X(t) \right]^2$ denotes the variance of the field $X(t)$.

The decomposition of the field χ into principal modes is a purely mathematical approach and does not guarantee that the modes are related to dynami-cal processes or physically interpretable, especially because the EOFs are by definition orthogonal in space and time, while physical processes usually are not. However, a good resolution of characteristic spa-tial and temporal scales improves the potential for several dynamically relevant modes (Schrum et al. 2006b).

RESULTS AND DISCUSSION

Interannual variability

Long-term changes of all 3 parameters (PLS, NFS and GR) (Fig. 5) indicate pronounced year-to-year variability with relatively high correlations between
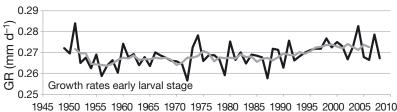
Fig. 5. Time series of annually averaged estimated potential larval survival (PLS), duration of the non-feeding life stages (NFS) and length-specific growth rates (GR) for feeding larvae (<10 mm) of Atlantic cod. Gray lines: 5 yr running means

the time series ($R_{PLS/NFS}$ = 0.63; $R_{PLS/GR}$ = −0.6). The negative correlation between GR and PLS appears to be a strange artefact, but indeed it is not. Because cod live at the edge of their thermal tolerance and spawn prior to the zooplankton bloom in the North Sea, it is vital for the cod larvae to match sufficient feeding conditions at first feeding. Additionally, higher temperatures demand higher energy intake by the larvae to compensate for higher metabolic rates. Low temperatures support longer NFS development rates and lower energy requirements for first-feeding larvae and, hence, increase the probability for larvae to match with suitable prey conditions. Simultaneously, growth rates under low temperatures are reduced. Since predation pressure is not considered in the model formulation, faster growth rates due to higher temperatures do not lead to increased survival but to fewer but faster-growing survivors among the individuals.

Additionally, the low-pass filtered time series indicate multidecadal variability, with a clear decrease in PLS and NFS between 1985 and 1990 and increasing growth rates between 1995 and 2000. The timing of the major change in PLS coincides with the earlier identified regime shift period in the North Sea in the late 1980s (Alheit et al. 2005). Both air temperature and wind field changes during this time period were

associated with larger-scale climate variations (indicated by the North Atlantic Oscillation [NAO]) (Siegismund & Schrum 2001, Pingree 2005, Holt et al. 2012), with consequent changes of the North Sea temperature, circulation and stratification. Warming resulted in increasing surface and bottom temperature and earlier establishment of stratification, and increased wind forcing led to intensified circulation (Schrum et al. 2003). The latter period is also characterized by a generally higher primary and secondary production as shown earlier by Daewel & Schrum (2013). The list of environmental factors potentially influencing the modelled PLS include seawater temperature (Tav); dispersion coefficient (DC); average current velocity (Cav); single current components (average U-current velocity [Uav], average V-current velocity [Vav], vertical current velocity at the surface [Wsur]); zooplankton biomass (ZOO); and production of diatoms (DIA), flagellates (FLA) and total phytoplankton (NPP). Other than recruitment, which is impacted also by long-term changes in external forcing (e.g. via the relation to the spawning stock biomass), mechanism chains relevant for the survival of early non-feeding and feeding life stages are usually rather short and accumulate environmental impacts of the respective year only. For early life stage survival, one of the major factors determining success and failure is the match–mismatch dynamic between feeding larvae and suitable prey (Beaugrand & Kirby 2010, Daewel et al. 2011, Kristiansen et al. 2011). Here, we estimated the correlation between average annual PLS and each of the aforementioned environmental parameters in addition to the winter NAO index and the Atlantic Multidecadal Oscillation (AMO) index (Fig. 6). The latter 2 indicators were chosen to evaluate the relation to the larger-scale climate state. A statistical comparison to environmental conditions can provide indications on relevant forcing parameters and potentially refer to causal processes. Nine of the parameters tested were found to be significantly (at the 5% level) correlated with the PLS. These comprise Tav, Uav, ZOO, DC, Cav, FLA, NPP and the NAO as well as the AMO, of which Tav, Uav, ZOO and NPP in winter (January to April) show the highest correlations with PLS (R > 0.5). Subsequently, we used this information to assess the relevance of the
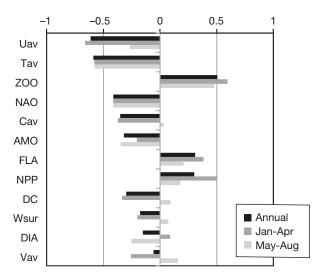
Fig. 6. Correlation coefficients between potential larval survival (PLS) (January to April) and the tested environmental parameter averaged over the North Sea area and averaged over the following time periods: annually (Annual), the winter and early spring period (Jan-Apr) and the late spring and summer period (May-Aug). Uav: average *U*-current velocity; Vav: average *V*-current velocity; Tav: average water temperature; ZOO: zooplankton biomass; NAO: North Atlantic Oscillation index; AMO: Atlantic Multidecadal Oscillation index; Cav: average mean current velocity; FLA: flagellate production; DIA: diatom production; NPP: net primary production; DC: dispersion coefficient; Wsur: vertical current velocity at the surface
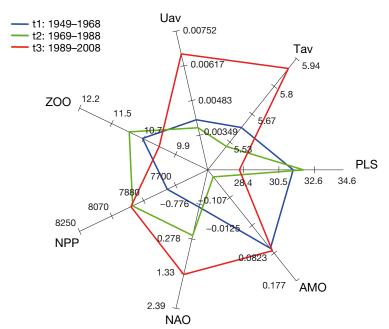
Table 2. P-values of Kruskal-Wallis ANOVA between 2 subsequent time periods (t1: 1949–1968 to t2: 1969–1988 and t2: 1969–1988 to t3: 1989–2008). **Bold** values are statistically significant at the 5% level. PLS: potential larval survival; Tav: average water temperature; Uav: average *U*-current velocity; ZOO: zooplankton biomass; NPP: total phytoplankton; NAO: North Atlantic Oscillation; AMO: Atlantic Multidecadal Oscillation

Parameter	t1 vs. t2	t2 vs. t3
PLS_{annual}	0.6073	**0.0019**
Tav_{annual}	0.1850	**< 0.0001**
$Uav_{Jan–Apr}$	0.6263	**0.0001**
$ZOO_{Jan–Apr}$	0.6263	**0.0453**
NPP_{annual}	0.2340	0.6456
$NAO_{Dec–Mar}$	0.1167	0.0858
AMO_{annual}	**< 0.0001**	**0.0001**

single parameters for the estimated shift in PLS at the end of the 1980s. Therefore, long-term averages of all time series with correlations >0.5 and the NAO and the AMO were calculated for each of three 20 yr time periods (t1: 1949 to 1968; t2: 1969 to 1988; t3: 1989 to 2008). This is convenient, since t2 and t3 denote the time before and after the potential shift (Fig. 7). The results show a common average pattern during the first 2 time periods, with very little change between t1 and t2 for almost all parameters except the AMO. In contrast, many of the considered parameters show a clear change from t2 to t3. The significance test (Table 2) highlights that all included parameters (Tav, Uav, ZOO, AMO) except NPP and the NAO change significantly from t2 to t3, with the most pronounced changes for Tav and Uav.

The statistical analysis of the time series indicates that PLS variability is tightly linked to variations in Tav and Uav but also, to a lesser degree, to changes in the prey fields. The results could support a strong direct impact of temperature, such as via changes in physiological rates (Pörtner et al. 2001), while other observational-based studies highlight particularly the impact of the zooplankton biomass and composition on the survival of cod early life stages in the North Sea (Beaugrand & Kirby 2010). But as mentioned before, simple correlation analyses do not necessarily imply causal relationships. Following the findings derived from the 3 different years simulated in Daewel et al. (2011) and the present correlation analy-

Fig. 7. Twenty year averages for potential larval survival (PLS) and all parameters with correlation coefficients to PLS >0.5 (see Fig. 3) in addition to the climate indices Atlantic Multidecadal Oscillation (AMO) and North Atlantic Oscillation (NAO). Time periods are t1: 1949 to 1968; t2: 1969 to 1988; t3: 1989 to 2008. t2 and t3 represent 20 yr before and after a potential regime shift. Uav: average *U*-current velocity; Tav: average water temperature; ZOO: zooplankton biomass; NPP: annual net primary production

sis, we hypothesize that the following mechanisms are potentially relevant for variability in PLS:

(I) Direct temperature response (scenario Ia,b, see Table 1): Increased temperature enhances the development rates of cod early life stages. The effect for North Sea Atlantic cod is potentially negative. Since cod spawn prior to the spring bloom, an increased pre-feeding development would cause cod larvae to hatch before suitable prey is available (mismatch). A concomitant phenological shift in the spring bloom has neither been estimated by the model (Daewel et al. 2011) nor been found in long-term observations (Wiltshire & Manly 2004).

(II) Response to atmospheric forcing (scenario II a–c): Air temperature variations and changes in the wind field co-occur in the North Sea region (Pingree 2005), while the latter can impact early cod survival in 2 different ways. (1) Like temperature, it has a direct effect on the match–mismatch dynamics of first-feeding cod and their prey. The stronger the currents in the southern North Sea, the higher the risk that larvae are transported out of the nursery areas prior to first feeding (spatial mismatch). (2) Strong winds affect not only the currents but also the turbulence levels in the water column. The maximum turbulent dissipation rates that larvae in the North Sea are exposed to are in the range of >10^{-6} W kg^{-1} (Simpson et al. 1996). Under high-turbulence conditions, fish larvae experience a reduced capability to capture food (MacKenzie et al. 1994). We can assume that the wind-induced turbulence can be neglected in the shallow, highly turbulent, tidally influenced southern North Sea. That is likely the reason why we cannot find a statistically relevant correlation between the dispersion coefficient and PLS, but in the seasonally stratified regions of the central North Sea, wind-induced turbulence might play an important role for interannual variability in larval fish survival.

(III) Indirect response to atmospheric forcing (scenario IIIa–c): (1) Changes in the atmospheric temperature forcing would cause changes in ocean stratification and hence impact the magnitude and timing of the prey field. (2) The wind and subsequently the current velocity impact North Sea productivity by changing ocean stratification, mixing and by impacting the nutrient supply from the North Atlantic.

Spatial variability

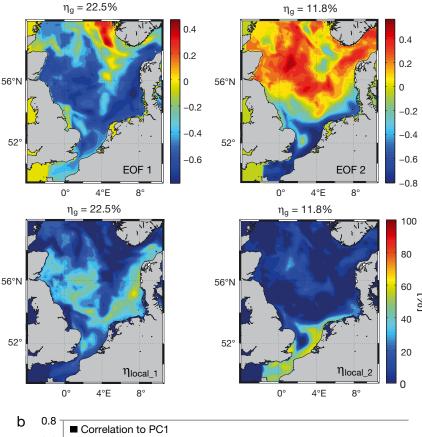The EOF analysis of the annually averaged PLS indicates 2 (EOF 1 and 2) main areas with different temporal dynamics (Fig. 8). The EOF patterns clearly show that potential spawning grounds alongshore and in the English Channel (EOF 2) would express different interannual variability in PLS than spawning grounds further offshore inside the frontal system (EOF 1). A third EOF (not shown) describes the variability along the northern English coast and northern boundary but appears to be of minor relevance for the presented configuration of the model and the analysis.

With respect to observed spawning grounds (see 'Introduction'), the first mode of the EOF analysis is more relevant for describing the variability in Atlantic cod early life stages in the North Sea than the second mode, as indicated by the pattern of the local explained variance. Consequently, the inherent variability from the second EOF mode is likely artificially introduced and to an unknown degree biased by the model setup not considering any restrictions to spawning grounds (e.g. avoidance of turbid coastal waters). This mode is therefore not considered further. A correlation analysis reveals that the dominant first mode co-varies with different environmental parameters and is strongly correlated with temperature, U-current velocity speed and the NAO but also to NPP and ZOO. This is coherent with the results presented in Fig. 6 and Table 2.

Scenarios

To distinguish the impacts of the 3 different mechanisms identified (see 'Interannual variability') on cod early larval development, growth and survival, we applied 3 different types of scenarios (Table 1). By doing so, we can identify the individual impact of the single processes undisturbed from non-linear interactions due to changes in stratification or in the prey fields as well as the combined effects. Since the spatial analysis revealed essential differences between potential spawning areas, we analysed the scenarios not only for the North Sea average but also for 3 subareas (spawning grounds between 30 and 60 m depth, beyond 30 m depth in the southwestern North Sea and beyond 30 m depth in the southeastern North Sea; note that there is an overlap between the areas).

Scenario experiments Ia,b: Both NFS and GR are highly impacted by direct changes in temperature (Fig. 9). When temperatures are increased by 1.2°C, NFS was shortened by over 4 d. In cases where the temperature increase is only applied to the non-feeding life stages (Ia), the growth rates (Fig. 9b) of feeding larvae decrease due to an exposure to colder water temperatures earlier in the year after a shorter
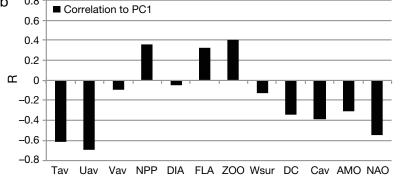
Fig. 8. (a) First 2 empirical orthogonal function (EOF) analyses of 60 yr estimated potential larval survival (PLS). Upper panels show η_g: global explained variance (overall explained variance by the associated pattern in %); lower panels show associated local explained variance. (b) Correlation between the associated time series of EOF 1 (principal component 1, PC1) and environmental parameters. Uav: average *U*-current velocity; Vav: average *V*-current velocity; Tav: average water temperature; ZOO: zooplankton biomass; NAO: North Atlantic Oscillation index; AMO: Atlantic Multidecadal Oscillation index; Cav: average mean current velocity; FLA: flagellate production; DIA: diatom production; NPP: net primary production; DC: dispersion coefficient; Wsur: vertical current velocity at the surface

non-feeding period (Fig. 9a). This effect is compensated for when the temperature increase is equally applied to feeding and non-feeding life stages (Ib). In terms of PLS (Fig. 10), the average response to single-effect changes in experiments in sets I and II lies in the range of 1 to 3% PLS, which is smaller than the

standard deviation of the reference run for the same time period (SD_{ref} = 4.13%). Our results indicate (Fig. 10) that an increase in temperature during early life stages reduces PLS potentially due to changes in the temporal match–mismatch dynamics (see Daewel et al. 2011). Additional consideration of a temperature increase on the early feeding larvae (Ib) in addition to non-feeding larvae (Ia) further reduces the PLS by a small percentage. A plausible explanation for the further reduced PLS in Expt Ib is that under increased temperatures, larval metabolism and prey requirements are enhanced, which leads to a strengthened mismatch situation when prey fields are kept constant. The spatial fields in PLS variability (Fig. 11b,c) indicate that the main changes occur in the southern North Sea and are linked to the areas of high PLS (Fig. 11a).

Scenario Expts IIa–c: In Expt IIa, we tested the impact of air temperature changes, and the results are comparable to those of Expt Ia,b but with a weaker impact on NFS (Fig. 9a), GR (Fig. 9b) and PLS, which is certainly because the change in resulting water temperatures is lower compared to the range tested in Expt Ia,b. In Expts IIb,c we tested the impact of wind speed changes. The results from these Expts indicate clear impacts of wind speed on NFS, GR (Fig. 9a,b) and PLS (Fig. 10). When wind speed was enhanced by 16% (IIb), NFS showed a slight increase, while GR and PLS were decreased; under reduced wind conditions (IIc), the results are reversed accordingly. This can be explained when we consider the changes in larval distribution at the time of the critical first-feeding period (Hjort 1914, Daewel et al. 2011) (Fig. 12a–d). The distribution clearly shows that the number of particles in the zooplankton-rich southern North Sea and particularly in the frontal areas is reduced when wind speed is increased (Fig. 12c). In contrast, when the wind speed is reduced, more larvae remain in the supportive areas of the southern North Sea (Fig. 12c). Since water temperature in
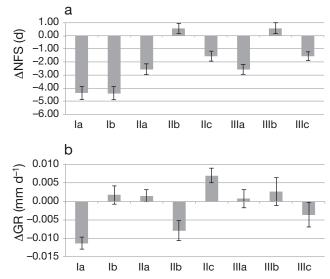
Fig. 9. Estimated change in annually averaged (a) non-feeding stage (NFS) development time and (b) growth rates (GR) simulated for Atlantic cod larvae and standard deviation for scenario experiments (see Table 1) (simulated time period 1949 to 1978)

spring increases more quickly in that region than water temperature in the northern North Sea, mean NFS is shorter and GR increases for the low-wind experiment (IIc). When considering only the surviving larvae in the distribution map as shown in Fig. 12e–k, it becomes clear that transport alone cannot explain the change in PLS. In Expt IIb, considerably less (Fig. 12g) (in Expt IIc, more [Fig. 12h]) of the first-feeding larvae in the central and northern North Sea survive to length 20 mm, although the general distribution after the non-feeding phase (Fig. 12c,d) does not indicate this change in PLS in those areas. A

possible explanatory mechanism in those regions could be the change in the turbulence level impacting the capture success of feeding larvae (see explanation in 'Interannual variability'). Since in Expt IIb,c larval transportation is impacted by wind field changes while prey transportation is not, another explanation might be a mismatch in larval vertical positioning with respect to the vertical distribution in plankton concentrations. The latter is caused by differences in the vertical turbulence profile and/or in stratification. The combination of these processes leads to clear changes in the PLS, which dominantly occur at the northern Danish coast and in the Dogger Bank area (Fig. 11e,f).

The results indicate that direct temperature effects on non-feeding life stages (Ia) and changes in the wind field (IIb,c) are more relevant for PLS than direct temperature effects on feeding life stages (Ib) or the hydrodynamic consequences of increased air temperature (IIa), such as earlier stratification, turbulence or the baroclinic current component (Otto et al. 1990).

Scenario Expts IIIa–c: The results from Expt IIIa are only slightly different than the estimates in Expt IIa. NFS (Fig. 9a) is alike in both experiments, while the change in growth rates was slightly smaller in Expt IIIa compared to IIa (Fig. 9b). There is a relatively small reduction in the prey biomass in most parts of the North Sea, likely induced by a strengthening of stratification in the more central parts of the North Sea under increased temperatures, which cause both reduced GR and PLS when compared to the experiment with reference prey fields, IIa. Changes in the wind field are highly relevant for changes in larval
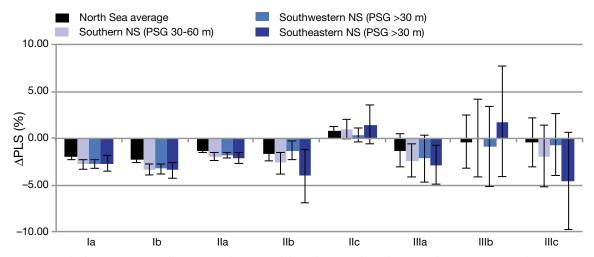

Fig. 10. Estimated change in annually averaged potential larval survival (PLS) (spatial averages over different potential spawning grounds [PSG] of the North Sea [NS], see Fig. 1) simulated for Atlantic cod and standard deviation for scenario experiments (see Table 1) (simulated time period 1949 to 1978)
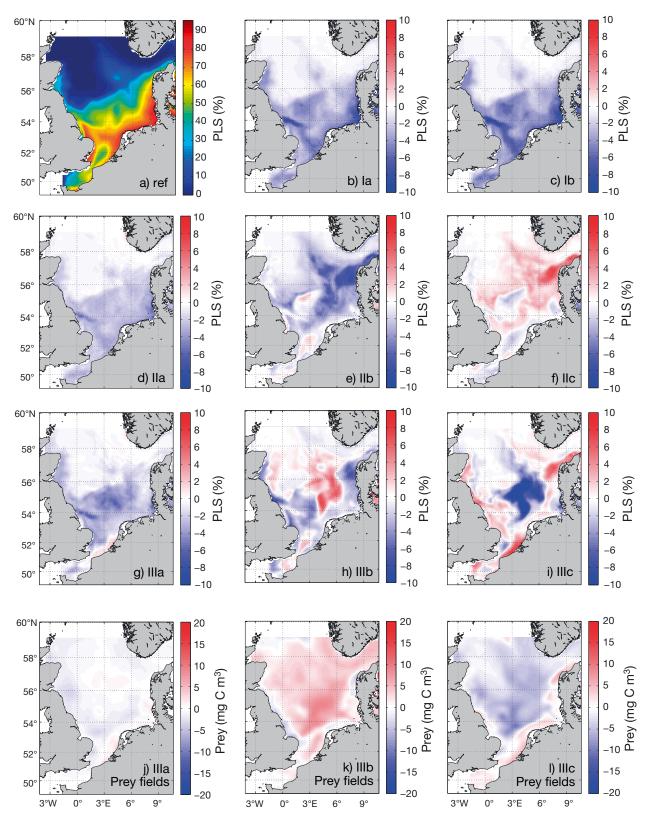
Fig. 11. Estimated spatial change in annual potential larval survival (PLS) simulated for Atlantic cod in the North Sea (averaged for the time period 1949 to 1978). (a) Spatial variability in PLS in the reference run; (b–i) difference between scenario simulations and reference simulation (for scenario description, see Table 1); (j–l) estimated change in prey fields under the respective scenarios (for reference prey distribution, see Fig. 4, top right panel)
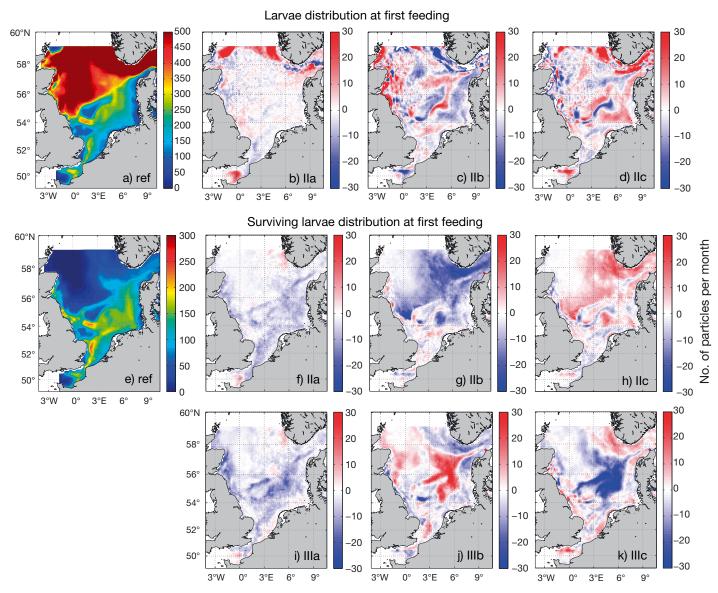
Fig. 12. (a–d) Spatial distribution of simulated Atlantic cod larvae at the time of first feeding (all individuals were considered independent of survival) in the (a) reference run (ref) and (b–d) differences from the reference for Expts II and IIIa–c. (e–k) Spatial distribution of simulated surviving Atlantic cod larvae only at the time of first feeding in the (e) reference run and (f–k) differences from the reference for Expts (f–h) IIa–c and (i–k) IIIa–c

drift routes and subsequently for the potential to meet supportive feeding conditions in time. By decoupling the larval drift from the prey field, we could assess the relevance of the former for PLS and found that larvae are more likely transported out of the supportive feeding grounds under increasing wind speed (Fig. 12c). Since the prey field itself can be expected to be highly variable under changing environmental conditions (Daewel & Schrum 2013), we conducted concomitant experiments using consistent forcing for the prey field dynamics and the spatially explicit IBM. The response of GR to changes

in the wind field (Expt IIIb,c) in these experiments (Fig. 9b) is reversed compared to the decoupled IIb,c, indicating the relevance of the spatial prey distribution for the growth and survival of early cod larvae. The average change in PLS for these scenario experiments is likewise in the range of 1 to 3 % (Fig. 10), but in contrast to the process-specific experiments, the standard deviation is much larger, highlighting the relevance of those secondary and non-linear impacts on prey fields for the estimated long-term dynamics of PLS. Similar to Expts I and II, the south-eastern North Sea exhibits the strongest response to

changes in forcing in terms of PLS. The spatial analysis of the response reveals inhomogeneity for all experiments except the pure temperature experiments (Fig. 11g–i). In Expt IIIb,c (Fig. 11h,i), more pronounced anomalies are found in the central parts of the southern North Sea. Contrasting the conclusion that increased wind will promote larval death by transporting the individuals into unsuitable feeding areas, these experiments show that the changed wind field will modulate the feeding grounds accordingly (Fig. 11k,l) through transport and local production of zooplankton and hence support larval survival for those specific areas. Increased wind increases mixing and subsequently the nutrient supply to the surface mixed layer, which increases primary and secondary production. The accumulated model response is in no way linear, and opposing spatially variable processes need to be considered when aiming to explain the simulated response of PLS to changes in environmental forcing.

Both temperature and wind speed are negatively correlated with changes in PLS, which supports the potentially relevant mechanisms (I–III) hypothesized in 'Interannual variability'. A decrease in wind speed would lead to retention of individuals in the nursery areas (Fig. 12d), while increased temperature causes temporal and spatial (due to shorter transport times) mismatch between first-feeding larvae and their prey (Fig. 12i). This can serve as an explanation for the observed negative temperature relationship of cod recruitment (Drinkwater 2005) as has already been documented in Daewel et al. (2011).

That increased temperature can potentially promote larval survival in the North Sea by prolonging the matching time period, as proposed by Kristiansen et al. (2011), cannot be confirmed by our model results. Since the latter authors exclude the non-feeding phase from their simulations, their model setup could not represent the potential mismatch, which we assume to be one major reason for the difference between their results and observations.

Relevance for recruitment

IBMs for early life stages are on the one hand useful tools to understand non-linear interactions that are difficult to deduce from observations directly. On the other hand, the models are rather restricted in the resolved processes and often lack (or insufficiently resolve) relevant processes for recruitment and population dynamics. This includes for our model primarily post-larval survival, predation mortality and intraguild competition. The reasons for excluding these are practical, concerning predominantly the lack of relevant and adequately resolved information. Nonetheless, our model setup allows for an improved assessment of the relevance of bottom-up effects on recruitment control. Although the comparison of our model results to observed recruitment cannot serve as model validation, it can inversely indicate the relevance of early larval survival for recruitment and long-term changes in the latter. Here, we used the first PC from the EOF analysis for the comparison to 2 measures for recruitment, (1) recruitment and (2) recruitment divided by the spawning stock biomass (recruitment/SSB) (Fig. 13a), since it contains the most relevant information about interannual variability and is particularly relevant in areas that can be expected to be important spawning grounds for cod in the North Sea. Data on cod recruitment and spawning stock biomass are available at www.ices.dk. Here, we utilized the time series published in Olsen et al. (2011). Both recruitment measures, recruitment and recruitment/SSB, give comparable results with respect to the correlation with PLS, indicating that the relationship between PLS and recruitment is only slightly influenced by changes in SSB. Although the time series do not correlate over the full time range, it is obvious that the time series exhibit similar variability over longer, clearly defined time periods. Applying a 5 yr running correlation (Fig. 13b) reveals time periods with substantially higher correlations in the 1960s and particularly in the 1990s, while the 2 time series were negatively correlated during the 1980s.

As already discussed, the model approach is a theoretical one excluding some processes and emphasizing bottom-up impacts. Based on these results, we conclude that the high correlations between PLS and recruitment time series during the 1960s and in the 1990s onwards provide a strong indication that Atlantic cod recruitment in the North Sea was mainly controlled by bottom-up processes during these periods. Low or negative correlations during other time periods point to alternative processes driving recruitment, which are not resolved by our modelling approach. These include both bottom-up controls on post larval life stages and top-down controls. One major process not captured by the model is the change in prey size and composition that has been observed associated with the regime shift in the late 1980s and which has been found to be highly relevant for cod recruitment (Beaugrand et al. 2003). Here, we assume that species composition in the North Sea is highly diverse (Krause et al. 2003) and
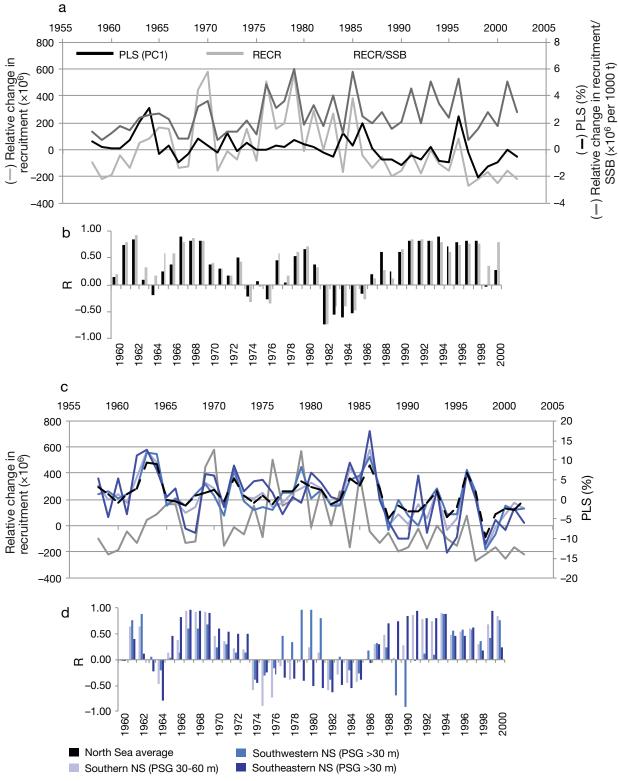
Fig. 13. (a) First principal component (PC1) of potential larval survival (PLS) (black), observed recruitment (RECR) (1 yr time lag, light gray) and observed recruitment divided by spawning stock biomass (RECR/SSB) (dark gray) of Atlantic cod in the North Sea. (b) Associated 5 yr running correlation between PLS (PC1) and recruitment (black), PLS (PC1) and recruitment/SSB (gray). (c) PLS time series from different potential spawning grounds (PSG, see Fig. 1) (color code is given in the legend) and observed recruitment (1 yr time lag, gray) and (d) associated 5 yr running correlation between the PLS time series and recruitment for different potential spawning grounds. NS: North Sea

that in the case of changing species composition, specific size classes are substituted by another species, leading to a more or less steady size composition over time (see Daewel et al. 2008b). Pronounced changes in North Sea zooplankton species composition are not addressed by this approach. Our results indicate, however, that major variations in recruitment success can be explained by variations in total productivity and physical environment.

Another important issue has been extensively reported in the recent literature, concerning the predation of planktivorous fish on cod early life stages. Some studies indicate that the recruitment success of cod in the North Sea is tightly linked to herring biomass. Both Hjermann et al. (2013) and Fauchald (2010) describe a negative correlation between herring stock biomass and cod recruitment. In the German Bight, where the majority of young cod in the North Sea are situated (Heessen 1993, Hjermann et al. 2013), Hjermann et al. (2013) found high cod recruitment being linked to low herring abundance, while herring recruitment was negatively correlated with the abundance of large cod. This indicates a negative feedback mechanism between those 2 species possibly initiated by overfishing of cod (Hjermann et al. 2013). The latter then supports the increase in herring stock, which, by preying on cod early life stages, potentially prevents the recovery of the North Sea cod stock (Fauchald 2010, Hjermann et al. 2013). The role of fishing pressure on the collapse of the cod stock in the late 1980s is still unclear. Beaugrand & Kirby (2010) suggest that in the North Sea, at the edge of the thermal ecological niche for cod, cod recruitment and the collapse of the cod stock might be triggered by climate forcing alone and fisheries would play an inferior role, a hypothesis that is supported by findings from Speirs et al. (2010). Our finding that PLS and recruitment are related in certain time periods, and particularly during the time of the stock collapse at the end of the 1980s, supports this hypothesis.

Independent of the role of fisheries, the herring stock seems to be tightly coupled to cod. Speirs et al. (2010) developed a partial ecosystem model that includes the potential food web interactions relevant for cod in the North Sea. In their model, one of the most relevant interactions is herring predation on cod early life stages. In a specific scenario experiment, they showed that the removal of predation mortality by herring would prevent or at least dampen the decrease of cod stock in the last decades (their Fig. 9a). But their results also show that herring predation is not equally important for the cod stock

biomass throughout their simulation period (1960 to 2006). During some periods, the results of the reference run with predation and the scenario run appear to be parallel, hence indicating no strong effect of herring predation. In contrast, during the occasions when herring predation impacted the cod stock, a rather large and sustainable effect on the latter was simulated. This occurred especially in the late 1960s, during the 1980 period and again in 2000, which at least partly (especially in the 1980s and in 2000) agrees with time periods of low (and/or negative) correlation between PLS and recruitment and hence could provide one possible explanation for the latter.

Additionally, we compared recruitment to the averaged PLS time series for restricted spawning areas (spawning grounds between 30 and 60 m depth, beyond 30 m depth in the western North Sea, beyond 30 m depth in the eastern North Sea; note that only surviving individuals are considered, which reduces the spawning grounds to the identified areas of PLS; see Fig. 11a) (Fig. 13c,d). Although all subregions exhibit the general pattern with decreasing PLS after 1990, it is clear that the eastern and western spawning areas show quite different interannual variability. This indicates that the high correlations between PLS and recruitment in the late 1960s and from the 1990s onwards are particularly valid for the eastern spawning sites, while in the early 1980s, the variability in the western spawning sites agreed better with recruitment (Fig. 13d). From 1995 onwards, both areas show similar positive correlations with recruitment. These results point to an alternation of the relevance of different spawning grounds in the southern North Sea for North Sea cod recruitment. This alternation might be due to different survival of cod offspring with respect to the environmental situation as our model suggests or regional alternation of Atlantic cod spawning activity in the North Sea. To our knowledge, there is no sufficient observational data available to compare our model results; however, previous studies show that the spatial distribution of Atlantic cod populations display large fluctuations among years (Blanchard et al. 2005, Brander et al. 2010).

CONCLUSIONS

Cod recruitment variability in the North Sea is not easily explained with a single process or predictor index. Prior to recruitment, young fish undergo a chain of multidimensional processes, leading to success or failure of a year class. The comparison be-

tween our model results and cod recruitment indicates that temperature (e.g. Drinkwater 2005), prey availability (e.g. Beaugrand & Kirby 2010) and connectivity or predation (Minto & Worm 2012) alone cannot be used to successfully describe or eventually predict cod recruitment. Additionally, we conclude that the relevance of single processes is not monotonic but highly variable in both time and space. In that way, the major questions concerning recruitment predictability are (1) Which processes drive cod recruitment? (2) Under what conditions are these processes relevant or more relevant than others?

The comparison between our IBM results and recruitment variability indicates that spatially explicit IBMs can serve to define indicators for larval survival and recruitment and that the model is a useful step to identify important missing processes. For the example of North Sea Atlantic cod, our results suggest that the knowledge about temperature and wind fields, together with knowledge about additional processes like herring stock biomass and/or zooplankton species composition, could provide a recruitment index that in future studies might be used for short-term predictions. The predictive power of such an index remains to be evaluated. Recruitment prediction is difficult to accomplish not only due to the complexity of the recruitment process itself but also because of the difficulties in predicting the environmental conditions and food web interactions correctly. Recently, some attempts were made to improve the predictive skill of global climate models (GCMs) on shorter time scales (years to decades) (Keenlyside et al. 2008, Yeager et al. 2012), such as by relaxing the GCM initial conditions to observed sea surface temperatures and using more accurate predictions of the external radiative forcing (Keenlyside et al. 2008). The results were especially promising in the North Atlantic region. This offers the unique possibility to combine those predictions with recruitment-relevant information derived from the spatially explicit IBM to estimate a future cod recruitment index on annual up to decadal time scales.

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Appendix. Model parallelization technical issues

To perform long-term simulations and allow for multiple sensitivity and scenario experiments with the ECOSMO–IBM efficiently, both ECOSMO and the IBM needed to be parallelized for use on multiple processors. For this task, MPI for distributed memory systems was applied to the model system. For the basic 3D ECOSMO, a 2D decomposition was performed (along plane surface), while the third dimension (depth) was not divided among processors. For computational efficiency, calculations are performed on interconnected wet grid cells only. The domain decomposition was chosen such that each subdomain has an approximately equal number of wet grid cells in total. However, this does not involve equal numbers of surface wet grid points. Load balancing for a semi-implicit numerical model with free surface and sea ice is therefore challenging. While hydrodynamics are solved for each grid cell in 3D, sea surface height is solved iteratively in the 2D domain, which makes optimization for both 2D and 3D calculations difficult. A decent vertical resolution and a computationally demanding advection scheme results in most computational resources demanded for the 3D simulations, and load balancing is therefore optimized accordingly.

In contrast to ECOSMO, the IBM was not spatially decomposed, but the particles were equally divided to an additional number of processors for better load balancing. Since development and spatial location of the particle is determined by the results from ECOSMO, the related variables are provided globally (for the entire grid) on all of the processors. Hence, the model can handle millions of particles with a good computational efficiency.

The parallelized model version is optimized for Cray XE6m-200. The model examined has approximately 680 000 grid cells, of which only 82 108 (ca. 12%) are wet grid cells. At the surface, 36 256 grid cells include only 8216 (ca. 23%) wet grid cells. A model version with the mentioned specification was executed on the CRAY machine with 21 (for ECOSMO) and 32 (for the IBM) MPI processors, which resulted in a 67 and 54% increase in efficiency, respectively. This means that the model can handle 25 times more particles than the sequential version in the same time.