

Bio-energetics underpins the spatial response of North Sea plaice (*Pleuronectes platessa* L.) and sole (*Solea solea* L.) to climate change

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Abstract

Climate change is currently one of the main driving forces behind changes in species distributions, and understanding the mechanisms that underpin macroecological patterns is necessary for a more predictive science. Warming sea water temperatures are expected to drive changes in ectothermic marine species ranges due to their thermal tolerance levels. Here, we develop a mechanistic tool to predict size- and season-specific distributions based on the physiology of the species and the temperature and food conditions in the sea. The effects of climate conditions on physiological-based habitat utilization was then examined for different size-classes of two commercially important fish species in the North Sea, plaice, *Pleuronectes platessa*, and sole, *Solea solea*. The two species provide an attractive comparison as they differ in their physiology (e.g. preferred temperature range). Combining dynamic energy budget (DEB) models with the temperature and food conditions estimated by an ecosystem model (ERSEM), allowed spatial differences in potential growth (as a proxy for habitat quality) to be estimated for 2 years with contrasting temperature and food conditions. The resulting habitat quality maps were in broad agreement with observed ontogenetic and seasonal changes in distribution as well as with the recent changes in distribution which could be attributed to an increase in coastal temperatures. Our physiological-based model provides a powerful tool to explore the effect of climate change on the spatio-temporal fish dynamics, predict effects of local or broad-scale environmental changes and provide a physiological basis for observed changes in species distributions.

Keywords: connectivity, DEB, eco-physiology, ERSEM, flatfish, spatial dynamics, thermal tolerance

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Introduction

Climate change is currently one of the main driving forces behind changes in species distribution and abundance (Parmesan, 2006) and significant effects have already been observed across a variety of ecosystems (Parmesan & Yohe, 2003; Thomas *et al.*, 2004; Perry *et al.*, 2005). As taxa will differ in their response to climate change, ecological communities can also be affected by changes in local species composition, diversity and phenology (Freitas *et al.*, 2007; Cheung *et al.*, 2009). Whilst statistical analysis of time-series data have shown correlations between species distributions and abundances in relation to the environment (Hiddink & Ter Hofstede, 2008; Van Hal *et al.*, 2010), it is necessary to understand the general ecological mechanisms and processes that underpin macroecological patterns at coarse spatio-temporal scales in order for a more

predictive science to evolve (Rijnsdorp *et al.*, 2009; Kearney *et al.*, 2011).

The 'niche concept', which describes the specializations and limitations of species to a range of biotic and abiotic environmental factors (Hutchinson, 1957; Pörtner *et al.*, 2010), has been widely applied in this context. Changes in abiotic variables can affect the geographical distribution of an organism's 'fundamental niche', the potential space an organism can occupy in the absence of competition and predation, and as conditions shift in space (and time), species ranges tend to follow (e.g. Röckmann *et al.*, 2011). Within the oceans, a rise in sea temperatures is expected to drive changes in species ranges due to the ectothermic nature of marine organisms and the physiological processes which limit their thermal tolerance and consequently their geographical distribution (Beaugrand *et al.*, 2002; Perry *et al.*, 2005; Dulvy *et al.*, 2008). Life cycles of marine organisms show several distinct life-history stages (egg, larvae, juvenile, adult) and each of these stages can differ in its habitat requirements due to ontogenetic changes in the thermal tolerance window (Rijnsdorp

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et al., 2009; Pörtner & Peck, 2010). It is therefore important to consider the spatial shifts in fundamental niche space of different life stages, the connectivity between suitable habitats and the effects on successful life cycle closures to determine the full impact on a population. Species-specific physiological changes at the molecular-, cellular- and organismal level, which determine a species' performance, will ultimately govern the impacts of climate change at the organismal, population and ecosystem level (Pörtner, 2001; Rijnsdorp *et al.*, 2009; Pörtner & Peck, 2010). A physiological approach is therefore valuable in trying to gain a mechanistic understanding of the potential impacts of climate change on marine communities.

Predicting the physiological response of a species to changes in the environment requires a generic framework to link abiotic factors with measures of physiological performance, such as growth and reproduction. Using a framework that can be applied across taxa allows community effects to be tested based on comparable species-specific responses. Dynamic energy budget (DEB) models describe the flow of energy through an organism in a systematic way, taking into account the variability of environmental conditions (Van Der Meer, 2006; Kooijman, 2010). Interspecific differences in physiological traits are reflected in species-specific parameters, but underlying processes are the same. Combining DEB models with ecosystem models, which provide information on temperature and food availability, provides a powerful tool to explore the performance of organisms in terms of their growth potentials in space and time (Kearney & Porter, 2009; Kearney *et al.*, 2011).

Plaice (*Pleuronectes platessa*) and sole (*Solea solea*) are two important commercial flatfish species in the North Sea and understanding their spatio-temporal dynamics in relation to the variation in habitat quality under uncertain environmental futures is key to implementing successful management measures (Rijnsdorp & Pastoors, 1995). For example, the 'plaice box', an area closed to fishing for large vessels (Pastoors *et al.*, 2000), was established in 1989 based on knowledge of the spatial segregation between juvenile and adult fish. The aim was to help reduce the catch of undersized plaice along the coast of the southern North Sea. In the 1990's, however, an offshore shift in the distribution of juvenile plaice to outside of the plaice box was observed, which reduced the effectiveness of the closed area as a management tool (Van Keeken *et al.*, 2007). Fish can be directed away from particular areas due to adverse environmental conditions such as extreme temperatures or low oxygen (Beverton & Holt, 1957; Gibson, 1994, 1997) and it was hypothesized that coastal water temperatures may have either exceeded

the tolerance range of the juvenile plaice, or lead to an increase in food requirements beyond availability (Van Keeken *et al.*, 2007). Such observations highlight the importance of understanding the drivers of spatial dynamics when designing management and conservation tools.

The aim of this study was to couple a physiological model (DEB) with an ecosystem model (GETM-ERSEM) to examine the physiological-based habitat utilization of plaice and sole under different climate conditions in the North Sea with a focus on the summer period when growth rates are high and temperatures may reach their seasonal maximum (Rijnsdorp, 1990; Teal *et al.*, 2008). Maximum potential growth rates are used as a measure of physiological performance and a proxy for habitat quality. Species-specific size-, temperature- and food-dependant growth rates are calculated with DEB models using input from a North Sea ecosystem model (GETM-ERSEM, see http://www.nioz.nl/northsea_model). To validate the models, hind casts were made of 2 years (1989 and 2002) with contrasting environmental conditions and known differences in species distributions. The size-specific nature of the DEB models allowed bio-energetics to be tested as a mechanism underpinning the different ontogenetic movement patterns of both species. In addition, it was possible to test whether recent changes in spatial distributions could be related entirely to temperature or whether these were in fact caused by food limitation (due to increased metabolic rates at higher temperatures). Temperature effects can be disentangled from effects of food limitation by setting feeding rates to a maximum and comparing to outcomes where feeding rates are dependent on the productivity given by ERSEM. It is argued that bio-energetics provides a valid mechanistic explanation of the size-dependant movement patterns of both fish species as well as the potential spatial shifts caused by a warming sea. Due to the generic and mechanistic nature of the DEB models, the combination of these with an ecosystem model is seen as a valuable tool for exploring spatial dynamics across marine and terrestrial taxa, whilst enhancing the predictive power of climate impact studies.

Materials and methods

Environmental data

High spatial (10 × 10 km) and temporal (daily) resolution of environmental data (temperature, benthic productivity) was acquired through predictions from the coupled hydrodynamical and ecosystem model GETM-ERSEM (General Estuarine Transport Model – European Regional Seas Ecosystem

Model; Baretta *et al.*, 1995). GETM is a 3D hydrodynamical model that uses the General Ocean Turbulence Model (GOTM) for the vertical turbulence structure. The biological model in ERSEM-BFM is a further development of BFM and ERSEM III (European Regional Seas Ecosystem Model; Baretta *et al.*, 1995; Vichi *et al.*, 2004).

ERSEM-BFM describes the dynamics of the biogeochemistry in the water column and the sediment. To make it applicable for temperate shelf seas, additional processes were included in the pelagic model over the oceanic version presented by Vichi *et al.* (2007): (1) a better parameterization of diatoms to allow growth in spring and account for the excretion of transparent extracellular polysaccharides (TEP) which affect particle stickiness, sinking rates and therefore benthic food supply (Engel, 2000), (2) a *Phaeocystis* functional group for improved simulation of primary production in coastal areas (Peperzak *et al.*, 1998) and (3) a suspended particulate matter (SPM) resuspension module that responds to surface waves for improved simulation of the underwater light climate. Cycles of carbon, oxygen and the macronutrients N, P and Si are simulated allowing for variable internal nutrient ratios inside organisms, based on external availability and physiological status of the organisms. ERSEM-BFM (Fig. 1) uses a functional group approach and contains 6 phytoplankton, 4 zooplankton (Baretta-Bekker *et al.*, 1995) and 5 benthic (Meio-benthos, deposit-feeding macrobenthos, filter-feeding macrobenthos, benthic predators and epibenthic fauna such as shrimp) functional groups (Ebenhoeh *et al.*, 1995; Blackford, 1997). Simulation data are used on a daily basis to provide temperatures near the sediment and to calculate the amount of benthic productivity which is available for top-consumers, such as fish. As fish and higher trophic levels are not included within ERSEM-BFM, the energy flow within the model is

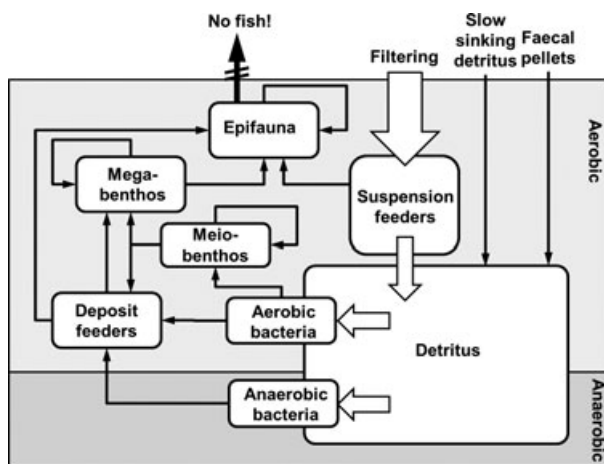


Fig. 1 Schematic diagram of the benthic component of the ERSEM-BFM model, showing the input from the pelagic zone and the various benthic functional group compartments. The arrow circulating epifauna to epifauna represents the closure of the model by an imposed density-dependant mortality of epifauna, which is the production assumed to otherwise be available as food for fish.

‘closed’ by allowing a density-dependant mortality of the top-grazers in the benthic module (Fig. 1). Based on the assumption that in reality this mortality must be caused by higher trophic levels feeding on benthos, benthic production lost through the density-dependant mortality is assumed to be available as food for fish. A small proportion of this [x_{ed} ; see Eqn (3)] is calculated as being available food for plaice and sole.

The years 1989 and 2002 were selected to compare summer habitats between an average year with high productivity in the coastal areas (1989) and a year with high local (particularly coastal) temperatures coupled with low productivity in coastal areas (2002).

Growth

In the standard DEB model, the ingestion rate of an organism is proportional to the organism’s surface area. Assimilated energy is then converted into reserves with a constant efficiency. A fixed fraction κ (Kappa rule) of reserve is mobilized and allocated to growth plus somatic maintenance, whilst the remainder fraction $(1-\kappa)$ is allocated to maturity maintenance and development or reproduction. Somatic maintenance has priority over growth, thus growth ceases if reserve density becomes too low. The energy costs of maintenance (both somatic and maturity) are proportional to the volume of the structure. At constant food densities, the reserve density also becomes constant and consequently growth of structural volume represents a weighted difference between surface area and volume and can be represented as:

$$\frac{dV}{dt} = \frac{(\kappa f \{p_{Am}\})V^{2/3} - [p_M]V}{\kappa f [E_m] + [E_G]} \quad (1)$$

which is mathematically equivalent to the von Bertalanffy growth model, but with a special relationship between ultimate length and the von Bertalanffy growth rate (Van Der Meer, 2006; Kooijman, 2010). The scaled functional response f is described below and all other parameters and associated units are described in Table 1, along with parameter values for plaice and sole which were obtained from the peer-reviewed literature.

Food dependency

In the standard DEB model, food conditions in the environment are described in the form of a scaled type II functional response f , whereby 0 reflects starvation and 1 indicates *ad libitum* food conditions. f is calculated using the Michaelis-Menton form:

$$f(X) = \frac{X}{K + X} \quad (2)$$

where X is the resource density and K is the resource density at which ingestion is half its maximum (i.e. $p_A = p_{Am}/2$). Based on the assumption that handling time (duration of digestion) and search rates are similar between fish species, K was set to $6.9 \times 10^{-5} \text{ J cm}^{-2}$ (Persson *et al.*, 1998).

Table 1 Estimates of parameters of the dynamic energy budget (DEB) model for female plaice, *Pleuronectes platessa* (from Van Der Veer *et al.*, 2009), and sole, *Solea solea* (from Freitas *et al.*, 2011; T_L and T_H from Fonds, 1975). T_{ref} plaice = 10 °C, T_{ref} sole = 20 °C

Symbol	Dimension	Interpretation	Plaice	Sole
$\{p_{Am}\}$	$J\ cm^{-2}\ d^{-1}$	Maximum surface area-specific assimilation rate	390	864
$[p_M]$	$J\ cm^{-3}\ d^{-1}$	Volume-specific maintenance costs	19.4	54.1
$[E_M]$	$J\ cm^{-3}$	Maximum storage density	2500	1986
$[E_G]$	$J\ cm^{-3}$	Volume-specific costs of structure	5600	5600
κ	-	Fraction of utilized energy spent on maintenance plus growth	0.85	0.9
δ_m	-	Shape coefficient	0.219	0.192
T_A	K	Arrhenius temperature	7000	8500
T_L	K	Lower boundary of tolerance range	277	282
T_H	K	Upper boundary of tolerance range	297	305
T_{AL}	K	Rate of decrease at lower boundary	50 000	50 000
T_{AH}	K	Rate of decrease at upper boundary	100 000	100 000

Because ingestion by flatfishes is known not only to relate to food availability but also to behavioural changes (e.g. reduced feeding during winter or during spawning), the choice not to feed even when food is available was taken into account. f_B was introduced to describe a seasonal feeding pattern expected to capture feeding behaviour during spawning. f_B describes the percentage of fish assumed to be feeding for each day of the year and takes on a value between 0 (no fish feeding) and 1 (all fish feeding). f_B was derived from North Sea stomach data (plaice: Rijnsdorp & Vingerhoed, 2001; Todd, 1914; $n = 31$; sole: Molinero & Flos, 1992; Redeke & Van Breemen, 1907; Rijnsdorp & Vingerhoed, 2001; $n = 20$). A binomial generalized additive model (GAM; Wood, 2006) was used to model the percentage of fish feeding (fish with food in stomach) as a smoother function of Julian day. A cyclic smoother function was used to ensure day 365, and day one acquired the same value. Daily values for f_B were then predicted and used in the calculation of the scaled functional response f (Eqn 3).

As not all of the benthic production output by ERSEM is available as food for plaice and sole, due to the species- and size-specific selection of prey items, an adjustment was made: Benthic production, or resource density X (in Eqn 2), was multiplied by the proportion x_{ed} of the total production estimated to be edible for plaice and sole. The estimated edible proportion x_{ed} was derived by calculating the DEB predicted length increments of 2- to 3-year olds within an area of the North Sea (10×15 ERSEM cells = 100×150 km) where these size-classes are known to occur, and then calibrating these predicted length increments with known length increments from surveys (plaice) or back-calculated growths based on otolith measurements (sole). The estimated edible proportion x_{ed} was then adjusted until the growth increments matched those of the field data. Taking into account these adjustments, the scaled functional response f was calculated by:

$$f(X) = \frac{(46 \times x_{ed} \times X)}{X_h + (46 \times x_{ed} \times X)} \times f_B \quad (3)$$

where X is the resource density (from ERSEM). Because units of Joules were required for the growth model, benthic

productivity data was converted from mg C to J using a conversion factor of $\times 46$ (Salonen *et al.*, 1976).

Temperature effects

Temperature affects all physiological rates and in DEB theory, the Arrhenius relationship is used to scale all rates to specific temperatures:

$$\dot{k}(T) = \dot{k}(T_{ref}) \times \exp\left(\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right) \quad (4)$$

where \dot{k} is the respective rate, T the absolute temperature to which the rate is to be scaled to, T_{ref} the reference temperature at which the rate is known and T_A the Arrhenius temperature (all in Kelvin). Using equation Eqn (4), the temperature-dependant parameters $\{p_{Am}\}$ and $[p_M]$ are scaled to the temperature output of ERSEM. In addition, the specific assimilation rate, $\{p_{Am}\}$, is affected by the temperature tolerance range of the organism, which is defined as the range of temperatures where body growth is positive. Within this tolerance range, the optimum temperature is defined as the temperature that results in maximum growth of the organism (Willmer *et al.*, 2000). For temperatures below the optimal temperature, a steady increase in metabolism with temperature is observed. Conversely, for temperatures above the optimum, a stabilization or decline in growth rates is observed. Sharpe & Demichele (1977) proposed a quantitative formulation for the reduction in rates at low and high temperatures, based on the idea that the rate is controlled by an enzyme that has an inactive configuration at low and high temperatures. Temperature tolerance ranges can thus be incorporated into the DEB growth model by multiplying reaction rates (i.e. p_{Am}) by the enzyme fraction that is in its active state (Kooijman, 2010). The fraction Fr is calculated as:

$$Fr = \exp\left(\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right) \times \left(\frac{1 + \exp\left\{\frac{T_{AL}}{T_{ref}} - \frac{T_{AL}}{T}\right\} + \exp\left\{\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T_{ref}}\right\}}{1 + \exp\left\{\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right\} + \exp\left\{\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T}\right\}} \right) \quad (5)$$

Incorporating both food density and temperature dependence into the growth model results in:

$$\frac{dV}{dt} = \frac{(\kappa f\{\dot{p}_{Am}\}Fr)V^{2/3} - [p_M] \times \exp\left(\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right)V}{\kappa f[E_m] + [E_G]} \quad (6)$$

The DEB models for plaice and sole (Van Der Veer *et al.*, 2009; Freitas *et al.*, 2011) have been validated in accordance with most up to date estimation methods (Lika *et al.*, 2011a,b). All parameters are described in Table 1.

Growth and ERSEM

The DEB equations combine with the ERSEM temperature and benthic food productivity estimates to allow daily calculations of size-, food density- and temperature-dependent growth rates for each ERSEM grid cell. To determine the habitat quality of each cell, the growth potential was calculated across the growing season for separate starting lengths of plaice and sole, reflecting separate size/age classes. As continuous processes are assumed, average growth of individuals living in that specific cell was calculated, rather than realized growth of any one individual. The 0-group was given a starting length reflecting the size at settlement in the nursery grounds (plaice, 1.5 cm; sole, 1.2 cm; Russell, 1976). The first day of the growing season was adjusted for the separate years and species based on predictions of Teal *et al.* (2008). The other size-classes were run from day 1 and started at 20 cm and 40 cm for both species.

Growth increments for day *n* were calculated using length of day *n*-1, and temperature and benthic productivity on day *n* as input for the DEB model. In this way the daily growth

rates remained size dependant throughout the season and the length reflected the achievable length on a given day taking into account the environmental conditions.

The model output was validated using annual trawl survey data (Dutch Beam Trawl survey, data available from <http://datras.ices.dk>) from which abundance estimates of plaice and sole in the North Sea were obtained. The validation addressed two points, (1) the ontogenetic shifts in space of both species and (2) the interannual variability in distribution in relation to environmental change. Broad-scale patterns in distribution linked to ontogenetic habitat shifts were visualized using maps of survey data. Due to the rough spatial resolution of the trawl data (one to four hauls per ICES statistical rectangle, which has a resolution of 0.5° latitude by 1° longitude) in comparison to the model output, the data were aggregated over the period 1990–2010. Distribution maps were drawn on a grid using linear interpolation between stations to aid visual comparison with model output.

Statistical comparisons were then carried out between presence/absence data from the trawl survey and the predicted growth potential on day 236 (August) of the DEB-ERSEM model using a binomial generalized linear model (GLM). The presence/absence data were extracted from the survey data for 1989 and 2002 and for the three length ranges (<15 cm, 19–25 cm, >35 cm) separately to match up with the modelled growth data. Due to the differences in spatial resolution, survey data and modelled growth data were averaged per ICES rectangle. GLMs were run on all combinations of year and size-classes (Table 2) to test whether the output of a given model per year and size-class also predicted the presence/absence data of the same year and size-class better than any other year or size-class combination. Model performance was

Table 2 Summary table of the results from the binomial GLM models of presence/absence data from trawl survey data (species, year and size-class given down the left side) on the modelled potential growth rates (year and size-class shown across top) from the dynamic energy budget (DEB)-ERSEM model. The numbers indicate % deviance explained by the model and, in brackets, the significance of the modelled growth rates in explaining presence/absence data. Cells printed in bold show a significant correlation and cells with grey text indicate where the correlation is negative. Grey shaded cells show which models are expected to perform best as they are comparing same species, year and size-class

				Modelled potential growth rates (August)					
				1989			2002		
Species	Year	Size		small	med	large	small	med	large
Trawl survey data	Plaice	1989	small	17.34 (0.041)	4.08 (0.202)	4.26 (0.183)	9.26 (0.121)	43.81 (0.003)	35.37 (0.005)
		med	6.28 (0.159)	18.68 (0.035)	1.71 (0.459)	1.14 (0.546)	3.36 (0.358)	2.15 (0.429)	
		large	10.91 (0.232)	0.32 (0.806)	9.85 (0.135)	18.99 (0.175)	4.04 (0.314)	13.80 (0.105)	
	2002	small	15.58 (0.020)	39.09 (0.003)	2.38 (0.332)	33.81 (<0.001)	12.45 (0.001)	2.28 (0.105)	
		med	11.51 (0.521)	0.012 (0.974)	7.75 (0.420)	27.12 (<0.001)	24.73 (<0.001)	2.65 (0.079)	
		large	14.94 (0.022)	2.49 (0.302)	10.95 (0.048)	2.69 (0.067)	0.039 (0.816)	5.20 (0.013)	
Sole	1989	small	28.47 (0.056)	28.08 (0.056)	30.11 (0.056)	43.35 (0.014)	17.00 (0.92)	9.15 (0.172)	
		med	61.39 (0.003)	57.58 (0.003)	35.95 (0.004)	9.15 (0.126)	57.76 (0.019)	46.76 (0.016)	
		large	20.71 (0.012)	17.75 (0.018)	8.22 (0.090)	6.89 (0.185)	29.53 (0.011)	24.19 (0.016)	
	2002	small	42.42 (0.021)	38.67 (0.025)	26.52 (0.150)	8.04 (0.055)	50.80 (0.004)	46.20 (0.005)	
		med	64.57 (0.012)	62.75 (0.009)	42.16 (0.010)	32.07 (<0.001)	69.62 (<0.001)	67.43 (<0.001)	
		large	6.81 (0.103)	5.59 (0.138)	2.22 (0.341)	27.95 (<0.001)	36.45 (<0.001)	36.02 (<0.001)	

compared on the basis of the *P*-value associated with the explanatory variable (potential growth) and the deviance explained by the model.

The sensitivity of the growth estimates to errors in ERSEM was explored by plotting the relationship between August growth rates and lengths in both years for four individually selected cells across the North Sea (representing the Dogger Bank, Southern Bight, German Bight and off the Danish coast). The temperature was then varied by $\pm 5\%$ and the benthic production estimates by $\pm 50\%$ and the new relationships compared with the original estimates.

Results

Environmental conditions

Temperature and food conditions were predicted to differ between the years 1989 and 2002 (Fig. 2). 1989 is considered a warm year in relation to the last 35-year time series, resulting from warmer temperatures across the North Sea. Although 2002 does not stand out as a warm year within this time period, it is characterized by particularly warm local temperatures along the coast of the southern North Sea, where August temperatures were predicted to reach $\sim 24^\circ\text{C}$ (Fig. 2b).

In 1989, the highest benthic production is concentrated along the southern coast, whereas in 2002, a peak

of productivity is found in the Southern Bight just off the English Coast and low benthic productivity is evident along the southern coast. In both years a band of high productivity runs along the northern Dogger Bank (Fig. 2c and d).

Dynamic energy budget predictions

Dynamic energy budget model predictions of growth rates, based on the parameters given in Table 1, show a decrease in growth rate as fish size increases (Fig. 3a and d) and as food uptake decreases (Fig. 3b and e), as well as an increase in growth rate to a given optimum temperature, after which growth rate declines rapidly (Fig. 3c and f). The temperature tolerance range (range of temperatures where growth is positive) is larger for smaller size-classes. Furthermore, the optimum temperature is food dependant, i.e. where food conditions are good, higher temperatures give higher growth rates, but where feeding is poor, lower temperatures become preferable to higher temperatures (Fig. 3b and d). Size-, food and temperature dependency interact with each other. Although the patterns are similar between plaice (Fig. 3, top row) and sole (Fig. 3, bottom row), the differences seen can be related directly to the species-specific parameters of the DEB model describing the

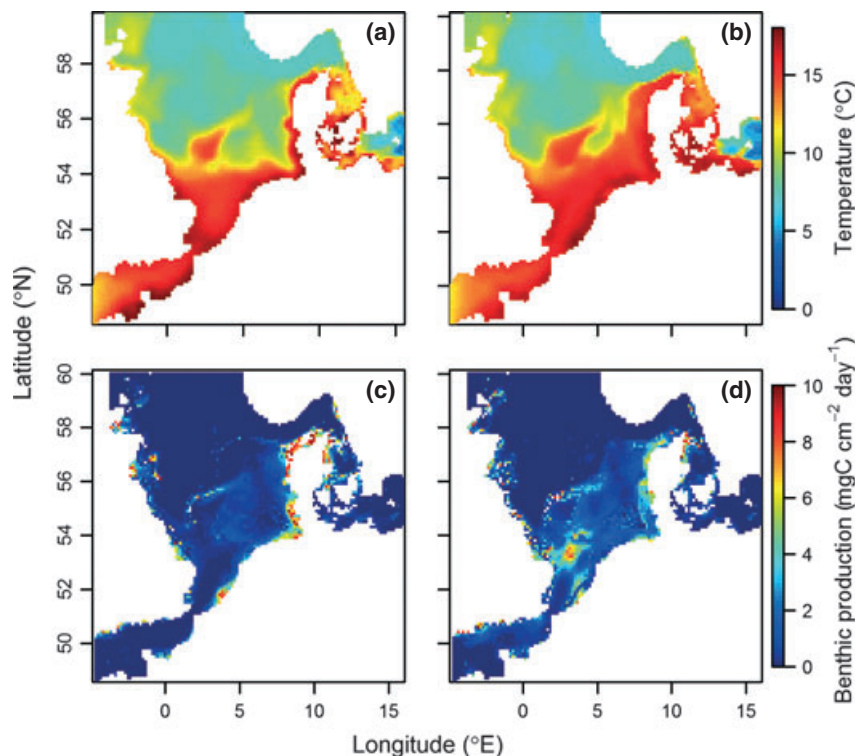


Fig. 2 Average annual temperature (a, b; colour scale, $^\circ\text{C}$) and benthic production (c, d; colour scale, $\text{mg C m}^{-2} \text{ day}^{-1}$) estimated by ERSEM for 1989 (a, c) and 2002 (b, d).

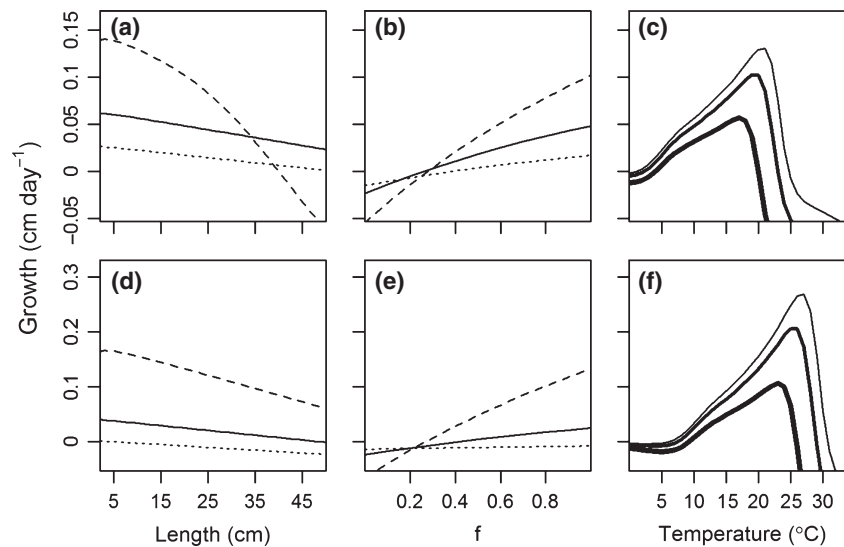


Fig. 3 Relation between dynamic energy budget (DEB) predicted growth rates and length (a, d), food ingestion rates (scaled; b, e) and temperature (c, f) for plaice (top panels) and sole (bottom panels). In panels a, b, d and e, the dotted line represents growth where temperature = 5 °C, the solid line = 10 °C and the dashed line = 20 °C. In panels c and f, the thin line represents lengths of 10 cm, the medium line = 20 cm and the thick line = 40 cm. In panels a, c, d and f, scaled food ingestion is set to 1 (*ad lib*) and in panels b and e, length is set to 20 cm.

specific physiological traits of the organism. Sole have a higher optimum temperature than plaice for any given size-class (Fig. 3c and f), and this is reflected in the differences in length-dependant growth rates at high temperatures, where larger sole are still able to grow but larger plaice are not (Fig. 3a and d).

Estimation of f

The stomach data indicated strong differences between seasonal feeding patterns of plaice and sole (Fig. 4). The percentage of empty stomachs of plaice was high (~90%) during the winter months and low (~10%) from spring to autumn with little variability observed. Percentage of empty stomachs of sole remained high and varied only slightly between 55% in the winter to 40% in the summer. Large variability was present, resulting in large confidence bands around the predicted smoother. Due to the nocturnal feeding habits of sole, inconsistencies in the data can result from the different times of the day when sampling was conducted, which may add to the observed variability and make it difficult to detect seasonal feeding patterns.

The calibrations of the DEB predicted growth rates with observed growth rates gave an estimated percentage of benthic productivity edible, x_{ed} , of 0.00075% for both species (Fig. 5). Taking into account f_B , the seasonal feeding pattern expected from the stomach data, this results in an annual mean value for f of 0.370 (1989) and 0.385 (2002) for plaice, and an annual mean f of 0.325 (1989) and 0.334 (2002) for sole.

Growth rates

There are two ways to present the results of the growth calculations, either to look at the total length increment possible over the growing season or to consider potential growth each day. The first option of considering lengths reached at the end of the growing season is a good indicator of average habitat quality. However, it can be expected that the movements/migrations of a species are driven on the short term by evasive behaviour in response to unfavourable environmental conditions. In this case, considering local and temporal peaks in environmental conditions and therefore daily growth rate potentials will be more meaningful than seasonal averages. Thus, to examine the impact of differences in coastal temperatures between 1989 and 2002, model-derived growth estimates for August were examined.

Plaice. Clear differences in the distribution of the highest quality habitat (highest growth potential) were projected between years and for the different size-classes of plaice (Fig. 6). The length dependency of growth is reflected in the lower growth potential achievable for the larger size-classes (<0.04 cm day⁻¹). Differences between years occur due to temperature and food conditions. In 1989, highest growth rates of 0-group plaice can be achieved along the southern coasts and around the coast of East Anglia (England), whereas in 2002, the band of highest growth rates is shown to be just offshore, also connecting to the east Anglian coast across the Southern Bight (Fig. 6b). The 20 cm size-class can

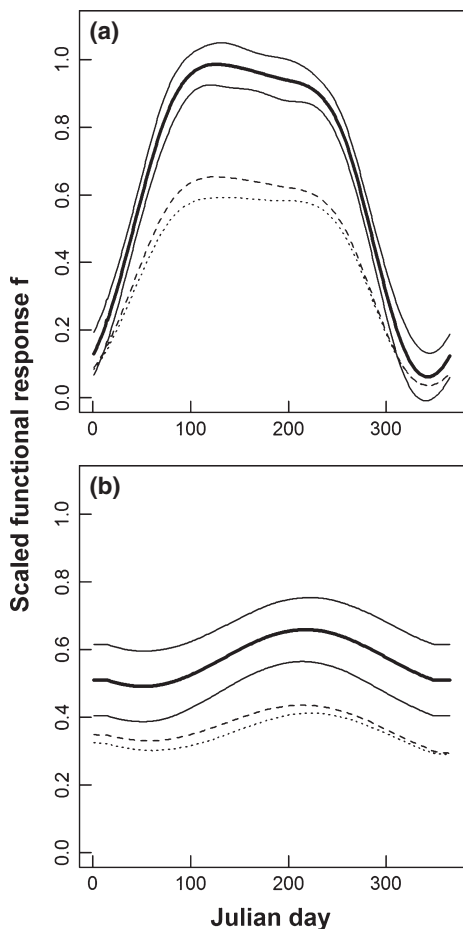


Fig. 4 Seasonal variability in feeding parameters of plaice (a) and sole (b). Thick solid lines represent predictions of the GAM smoothers fitted to the stomach data ($=f_B$) and the associated standard errors (thin solid lines). Dotted (year = 1989) and dashed (year = 2002) lines represent the mean daily scaled functional response f [see equation Eqn (3)] based on f_B and ERSEM benthic production output for a selected area of the North Sea inhabited by both species (between 52.6–53.6°N and 2.0–5.3°E).

achieve highest growth across a larger area stretching further offshore than that of the 0-group plaice. In 1989, an area of low growth is visible in the Southern Bight and in 2002, the stretch along the southern coast shows negative growth rates for this time period. The largest size-class considered, 40 cm, is no longer able to achieve positive growth rates in the areas south of $\sim 53^\circ$ N, which matches a thermal boundary of ~ 18 – 19° C (Fig. 6e). The same effect is seen in 2002, but with lower growth rates (down to -0.08 cm day $^{-1}$) in the southern areas, as well as low growth (~ 0 cm day $^{-1}$) on the shallow area of the Dogger Bank (Fig. 6f).

Sole. As with plaice, length dependency of growth is reflected in the lower growth potential achievable for the larger size-classes (<0.03 cm day $^{-1}$; Fig. 7). Differences

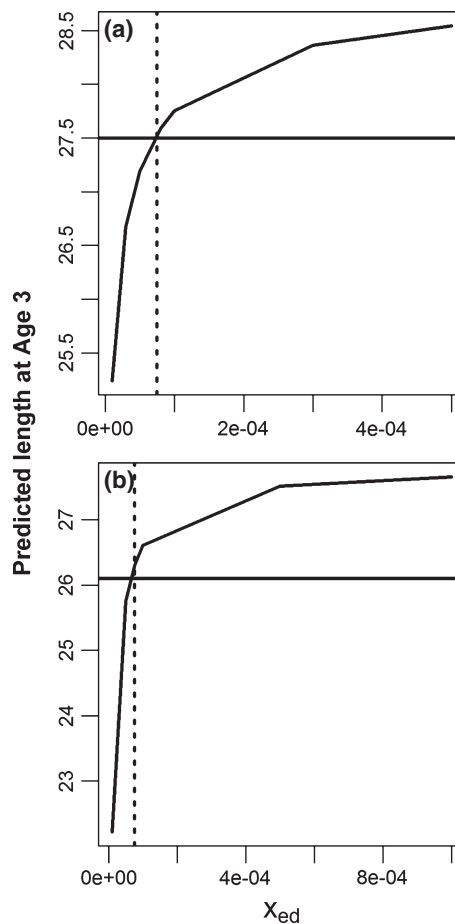


Fig. 5 Calibration results of the proportion of benthic production edible for the fish (x_{ed}) showing mean length increment of two to three group plaice (a) and sole (b) predicted by dynamic energy budget (DEB) calculations vs. a range of chosen x_{ed} values for a selected area of the North Sea (between 54.1–55.6°N and 4.5–7.0°E) where these size-classes occur. The horizontal line shows the mean length increment observed in survey data (plaice) or back calculated otolith data (sole). The vertical line shows where x_{ed} is set to calibrate the DEB results with the observed data.

between years are also present but more subtle than those seen for plaice. In 1989, 0-group sole achieve highest growth rates in a small area on the southern coast near the entrance to the English Channel (Fig. 7a). In 2002, the area of highest growth rates is expanded, stretching all the way up the coast of the southern North Sea, into the German Bight and up the coast of Denmark, as well as in the west around the coast of East Anglia (England) (Fig. 7b). Similarly to plaice, the best areas for growth stretch further offshore as size increases (Fig. 7c and d). The area of low growth in the Southern Bight in 1989 is larger and more prominent for sole (Fig. 7c) than plaice (Fig. 6c), whilst in contrast to plaice (Fig. 6d), the coastal areas remain good areas for growth in 2002 (Fig. 7d). The

largest size-class of sole show low growth rates in general, but the areas of highest growth remain in the southern North Sea and coastal areas (Fig. 7e and f), with the area of low growth in the Southern Bight again standing out in 1989. Whilst the 40 cm of plaice is found to achieve positive growth only north of the 53°N boundary, the same size-class of sole shows the opposite and best growth is achieved south of the 54–55°N boundary.

Validation. Maps of potential growth rates, used as a proxy for habitat quality, were validated against

observations of plaice and sole distribution derived from annual trawl survey data (Fig. 8). The survey period (August/September) matches closely with the days selected from the model. Comparison of Fig. 8 with Figs 6 and 7 shows a strong consistency between patterns in growth rates (habitat quality) and long-term averages of broad-scale distributions of the separate size-classes of both species. For plaice (Figs 6 and 8 left panels) it can be seen that the smallest size-class inhabits the coastal areas of the southern North Sea, gradually moving offshore as size increases. In the medium

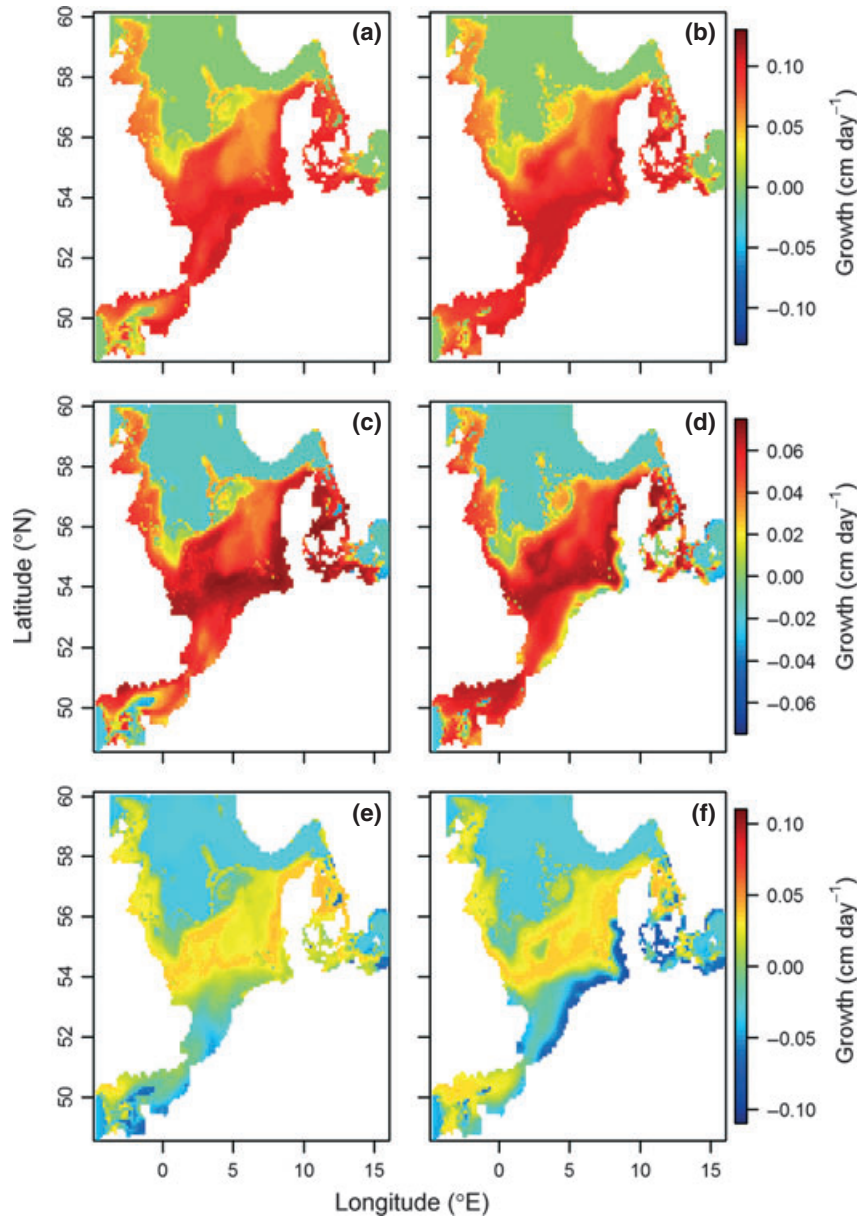


Fig. 6 Maximum potential daily growth rates (colour scale; cm day^{-1}) of plaice in August (day 236) based on dynamic energy budget (DEB) predictions and input from ERSEM (temperature and benthic production), using starting lengths of 1.5 cm (a, b), 20 cm (c, d) and 40 cm (e, f), for years 1989 (a, c, e) and 2002 (b, d, f).

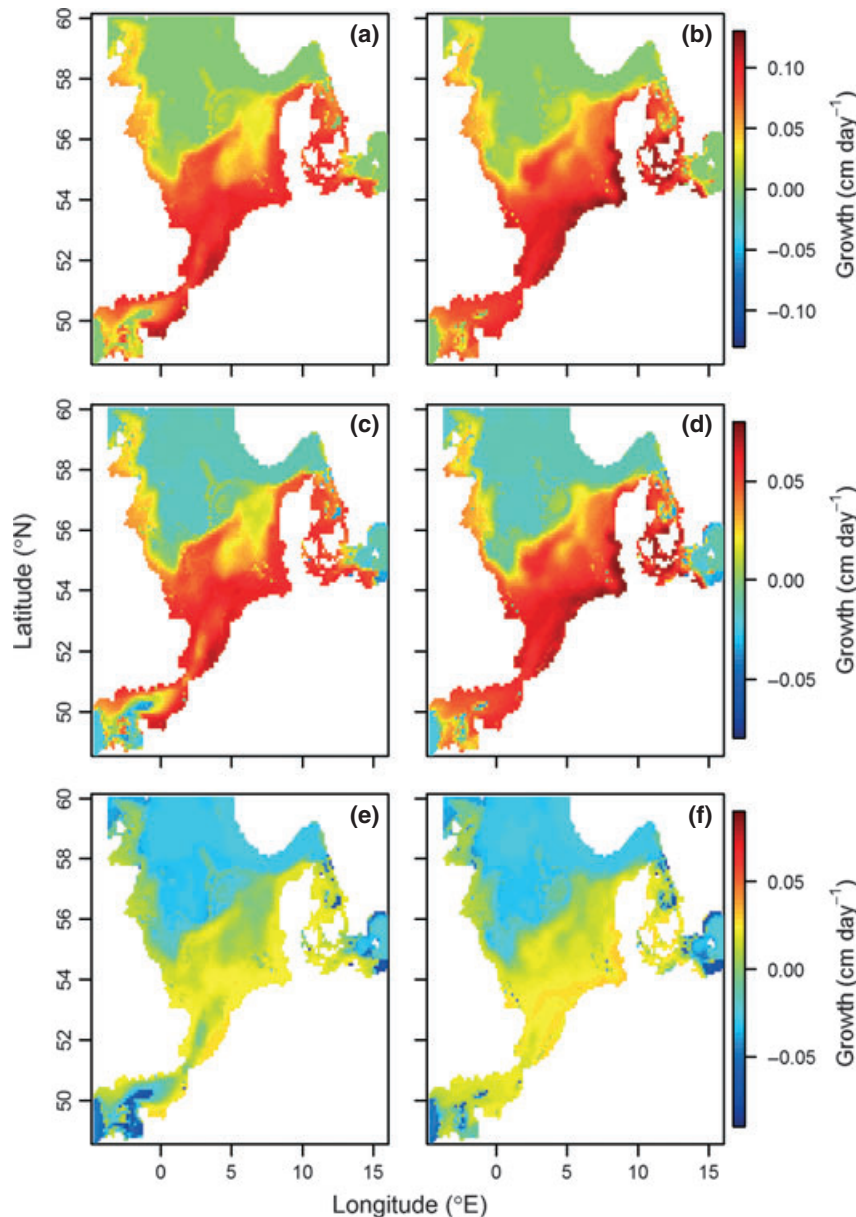


Fig. 7 Maximum potential daily growth rates (colour scale; cm day^{-1}) of sole in August (day 236) based on dynamic energy budget (DEB) predictions and input from ERSEM (temperature and benthic production), using starting lengths of 1.2 cm (a, b), 20 cm (c, d) and 40 cm (e, f), for years 1989 (a, c, e) and 2002 (b, d, f).

size-class (Fig. 8c), a decrease in abundance in the inshore areas is evident, matching closely with DEB predictions of an offshore shift in 2002 (Fig. 6d). Sole also spread further offshore as they grow (Fig. 8, right panels) and, as predicted by DEB (Fig. 7e and f), the adults continue to inhabit the southern area of the North Sea.

The statistical comparison between the trawl data of the 2 years investigated and the modelled potential growth rates showed that the DEB-ERSEM predicted habitats could be well matched with presence/absence

of the different size-classes of plaice in the 2 years observed in trawl survey data (Table 2). In general, the GLMs performed on the data combinations where year and size-class of the two data sets matched up performed better (higher deviance explained and/or smaller P -value; see grey cells in Table 2). Exceptions are found in 2002 where the presence/absence of the smallest size-class in the survey data matches with both small and medium DEB-ERSEM projections for both years (Table 2). One explanation for this could be that these smaller plaice are already spreading further offshore, as

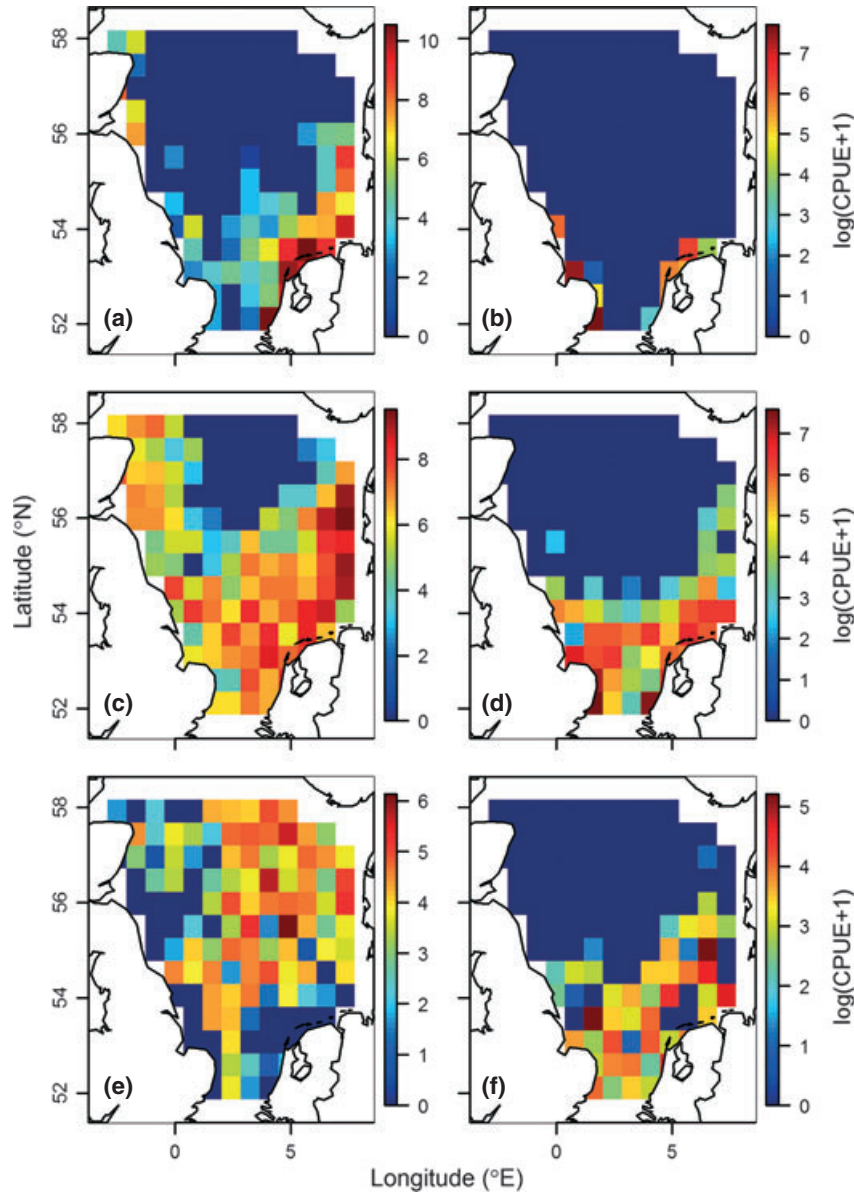


Fig. 8 Average abundances of plaice (left panels) and sole (right panels) calculated from the Dutch beam trawl survey data in August over the time period 1990–2010 for three size ranges, 9–15 cm (a, b), 19–25 cm (c, d) and >35 cm (e, f). Maps are drawn using linear interpolation between survey stations. Catch per unit effort (CPUE) is in numbers per km^{-2} and log-transformed to aid visualization.

is seen in the medium size-class, and therefore they can be matched with both projections. The comparison of data is less clear in sole, where the GLMs did not necessarily perform ‘best’ where year and size-class combinations are matched up. Although generally a positive relationship is found which is stronger within the same year, there is no clear pattern with size-class.

The sensitivity of the calculated potential growth rates to errors in temperature estimates used as input for the DEB model is shown to depend on how close the temperature estimate is to the optimum/upper tolerance of a given size-class. Where the temperature

is close to these values small variations will have larger effects and the DEB output for larger size-classes will generally be affected more due to the smaller temperature tolerance range of this size-class (Supporting Information Figures S1–S4). In a similar way, variability in benthic production estimates will have a larger effect in areas where growth is shown to be limited by food intake. In areas where food limitations does not occur, variability will have no effect (Supporting Information Figures S1–S4). The largest combined effect of variability in temperature and benthic production estimates on growth calculations can therefore be expected where

temperatures near the upper tolerance and food falls low enough to decrease ingestion rates.

Temperature versus food effects

To explore whether the patterns observed in growth rates were related to temperature effects or local differences in food availability, model runs were repeated with ingestion rates either set to a maximum to mimic *ad lib* feeding conditions (i.e. $f = 1$) or governed only by the behavioural seasonal feeding pattern imposed ($f = f_B$). The main patterns considered were the unsuitability of the coastal areas and southern North Sea for the larger size-classes of plaice and the low growth rates of sole in the Southern Bight. The results of runs where food is available *ad lib* show that high temperatures in the coastal areas in 2002 are enough to make this area unsuitable for growth of plaice and are also responsible for the unsuitability of the southern North Sea for large plaice. For sole, both feeding *ad lib* or with feeding governed only by seasonal behavioural changes showed good conditions for growth in the Southern Bight in 1989. Including the benthic production estimates from ERSEM into the feeding lead to reduced growth in this area, indicating that, given the model assumptions of food productivity and ingestion rates, food limitation may have occurred for sole in specific areas of the North Sea.

Discussion

Dynamic energy budget models assume that metabolic processes within an organism are organized in the same way across taxa. Species differences are described by species-specific traits (values of model parameters) that determine the relative amounts of energy directed to different processes as well as the tolerance levels to environmental factors (Kooijman, 2000, 2010; Freitas *et al.*, 2011). The effects of a changing environment on species with different physiological traits can therefore be assessed within a general framework (Kearney & Porter, 2009; Kearney *et al.*, 2011). In some cases, where the standard DEB model does not perform well, an extension to the model may be necessary to parameterize specific traits, such as nonisomorphic growth, presence of exoskeletons, long migration movements etc. (Kooijman, 2010). Using physiological performance as a measure of habitat quality and considering the physiology-based interactive effects of temperature and food availability on the organism, potential impacts of environmental change are explored mechanistically.

Experimental work has shown that larger fish can have a lower optimum temperature for growth as well

as a narrower temperature tolerance range (Rijnsdorp *et al.*, 2009; Pörtner & Peck, 2010). These size-specific differences are implicit in the DEB model and reflected in the results for plaice, showing that the best quality summer habitat in terms of the highest physiological performance (growth potential) moves steadily offshore and further north as size increases. Such spatial changes in habitat quality closely reflect the known ontogenetic shift of plaice distribution, also evident in survey data: Plaice spawn in the southern North Sea and eggs and larvae drift towards the coasts, where they settle and metamorphose (Van Der Veer, 1986; Bolle *et al.*, 2009). Juveniles are found predominantly along the coast, but the distribution shifts further offshore as size increases (Rijnsdorp & Beek, 1991). Adult plaice are found in deeper offshore waters of the central and northern North Sea and undergo seasonal migrations between feeding grounds in the north during the summer and spawning grounds in the south during the winter (Hunter *et al.*, 2003; Bolle *et al.*, 2005). Results presented here indicate that these migrations could largely be an effect of plaice moving to maximize their physiological performance during the growing season in summer (Rijnsdorp, 1990). In winter the adult distribution is determined by the spawning habitats that allow larvae to survive and be transported to suitable nursery grounds (Bolle *et al.*, 2009). As changing the food availability in the model to a maximum made little difference to the broad patterns observed, it can be hypothesized that these size-specific migrations are driven by temperature gradients. Evidence for such a thermal response may be found in Berghahn *et al.* (1993), where observations were made of a mass exodus of 0-group plaice from the tidal flats of the German Wadden Sea into the tidal channels on warm and windless days. The gradual offshore shift of juvenile plaice, which has been observed particularly since the late 1990s, when 1-group juvenile plaice completely left the Wadden Sea (Van Keeken *et al.*, 2007), can also be explained by a potential avoidance of warmer waters in the coastal areas. Peak water temperatures in August 2002 lie at (small size-class) or above (medium to large size-class) the temperature tolerance range of plaice. Due to the differential effect of temperature on different size-classes, as well as the variability in the extent of warming of the different parts of the North Sea, it can be expected that habitat quality of different life stages does not shift consistently. Plaice, as many marine species, rely on different areas to provide suitable habitats for the different stages in the life cycle. If the connectivity of these habitats is affected due to such differential effects then the impact of climate change on the physiology of the individual may translate up to population level changes (Rijnsdorp *et al.*, 2009).

Sole differ to plaice in their physiological traits and have a higher optimal growth temperature and upper thermal tolerance. As for plaice, the areas indicated as high-quality habitat for the different size-classes matches survey data, as well as results available from tagging experiments (ICES, 1965). Sole remain in the southern North Sea throughout their life cycle with the juveniles inhabiting mainly the coastal areas and the adults (>30 cm) spreading out offshore. In contrast to plaice, the increase in the coastal temperatures of the North Sea between 1989 and 2002 has not yet exceeded the optimal temperature of sole and is shown to have a positive effect on growth rates as well as providing a larger area of good quality habitat. Food limitation is indicated in the Southern Bight in 1989, which is not evident in 2002. Although shifts in the spatial distribution of summer habitat quality are less obvious in sole than for plaice, a southerly shift, opposite to that of plaice, in the centre of distribution (mean latitude of occurrence) of North Sea sole has been observed (Perry *et al.*, 2005; Engelhard *et al.*, 2011). This may be due to improving food conditions in the south, but there has been speculation that this could be related to the emergence of the Thames estuary as a major sole nursery ground following its clean-up (Perry *et al.*, 2005). A particularly strong effect of fishing on sole distributions has also been suggested (Engelhard *et al.*, 2011). These factors, in combination with the patchiness of catch rates, can also contribute to the fact that predicted habitat quality does not match as closely to survey data as is seen for plaice. Furthermore, due to the later spawning in comparison to plaice, the summer distribution of sole may still reflect suitable spawning areas which generally occur in coastal waters.

Whilst DEB is producing theoretical predictions of potential growth rates, similar contrasting effects of increasing water temperatures on growth rates of 0-group plaice and sole have also been observed in previous empirical studies using survey data (Teal *et al.*, 2008). As in our study, growth rates of 0-group sole measured in the field have been shown to be below growth rates obtained for *ad libitum* feeding fish in the laboratory (Teal *et al.*, 2008). Observed growth of 0-group plaice matched closely to predicted growth rates at the beginning of the growing season, but from July–August onwards growth is shown to be submaximum according to both theoretical DEB predictions (Van Der Veer *et al.*, 2009) and an RNA based growth index (Ciotti *et al.*, 2010). Temporal dynamics in observed growth rates and when growth begins to show food limitation are also shown to be site- (Ciotti *et al.*, 2010) and sex-specific (Van Der Veer *et al.*, 2009).

Considering that both plaice and sole show seasonal migrations and that both summer and winter

distributions can be limited by temperatures at the upper and lower end of a species tolerance range shows how important it is to consider the local and temporal peaks in environmental conditions, as opposed to average trends over a large spatial or temporal scale. Analysing long term trends using annual means may lead to surprising results, such as a time lag in the response to warming seas, which can be difficult to explain. These time lags may be an artefact of using mean temperatures as opposed to looking at specific locations during peak environmental conditions. Both our physiological modelling approach and survey data (Van Keeken *et al.*, 2007) suggest that plaice avoid warming coastal areas during the summer peaks. Sole, on the other hand, are more likely to respond to warmer winter temperatures increasing the suitability of coastal areas.

Whilst the DEB approach shows the areas suitable for high physiological performance, the realized habitats and shifts in distribution can also be affected by other factors, such as fisheries pressure (Engelhard *et al.*, 2011), changes in prey resources and/or overall system productivity and changes in precipitation and run-off patterns (Salen-Picard *et al.*, 2002; Le Pape *et al.*, 2003). The input used from ERSEM does not take into account possible changes to secondary production that may occur in relation to fishing pressure. The combined effect of climate and fisheries on food availability and habitat quality can only be addressed once the effect of fishing pressure on benthic production can be parameterized in the ecosystem model. Furthermore, although potential growth rates, as used here, are a valid first approximation of habitat suitability, life history theory predicts there will be a trade-off between growth and mortality (Stearns, 1992). Fish may not move to maximize their growth rate because an increase in feeding activity and food intake will increase the exposure to predators and parasites. Other species may undergo long periods of migration during which feeding ceases. Movement typically accounts for 5–10% of somatic maintenance costs, but may increase during such migration periods and should be addressed in an extension of the DEB model (Kooijman, 2010). Such effects must be taken into account when interpreting the differences between predicted and realized distributions. Nevertheless, the approach presented here offers some benefits over statistical habitat modelling, for example general additive modelling (GAM), where presence/absence of a species, or densities, are modelled as a function of different variables (e.g. Loots *et al.*, 2010). Statistical approaches suffer from the inability to make predictions outside the range of available data, and therefore require data across a wide range of environmental situations. A statistically significant correlation

does not necessarily indicate a cause–effect relationship or address underlying mechanisms. Understanding the principal processes is necessary, however, to enhance the predictive power of species distribution studies. The approach presented here is directly applicable across systems and taxa where input data are available, and provides a valuable mechanistic tool to explore species' spatio-temporal dynamics, predict effects of local or broad-scale environmental changes and provide a physiological basis for observed changes in species distributions.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Sensitivity analysis showing growth rates of plaice relative to lengths for four different areas of the North Sea: (a) Dogger Bank, (b) the Danish coast, (c) the Southern Bight and (d) the German Bight. Black lines show growth rates based on 1989 data as projected by ERSEM (temperatures and benthic production estimates used shown in plots). Red lines show growth rates where temperature was either increased (solid line) or decreased (dashed line) by 5%. Green lines show where benthic production was increased (solid line) or decreased (dashed line) by 50%.

Figure S2. Sensitivity analysis showing growth rates of plaice relative to lengths for four different areas of the North Sea: (a) Dogger Bank, (b) the Danish coast, (c) the Southern Bight and (d) the German Bight. Black lines show growth rates based on 2002 data as projected by ERSEM (temperatures and benthic production estimates used shown in plots). Red lines show growth rates where temperature was either increased (solid line) or decreased (dashed line) by 5%. Green lines show where benthic production was increased (solid line) or decreased (dashed line) by 50%.

Figure S3. Sensitivity analysis showing growth rates of sole relative to lengths for four different areas of the North Sea: (a) Dogger Bank, (b) the Danish coast, (c) the Southern Bight and (d) the German Bight. Black lines show growth rates based on 1989 data as projected by ERSEM (temperatures and benthic production estimates used shown in plots). Red lines show growth rates where temperature was either increased (solid line) or decreased (dashed line) by 5%. Green lines show where benthic production was increased (solid line) or decreased (dashed line) by 50%.

Figure S4. Sensitivity analysis showing growth rates of sole relative to lengths for four different areas of the North Sea: (a) Dogger Bank, (b) the Danish coast, (c) the Southern Bight and (d) the German Bight. Black lines show growth rates based on 2002 data as projected by ERSEM (temperatures and benthic production estimates used shown in plots). Red lines show growth rates where temperature was either increased (solid line) or decreased (dashed line) by 5%. Green lines show where benthic production was increased (solid line) or decreased (dashed line) by 50%.

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