Bio-energetics underpins spatio-temporal dynamics in North Sea plaice (*Pleuronectes platessa* L.)

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Knowledge on the spatio-temporal dynamics of fish species and which biotic and abiotic factors act as drivers is key to identifying essential fish habitat and exploring the change in habitat quality under uncertain environmental futures. Plaice are an important commercial species in the North Sea, with a strong size and season-dependant spatial distribution. Because growth rates are influenced by the environment, and are closely linked to reproductive potential, one approach to assessing habitat quality is to derive spatially-explicit models of growth potentials. Using dynamic energy budget models to calculate size-, temperature-, and food density- dependant growth rates we assess the spatial differences in growth potentials for varying size classes of plaice under different temperature and food conditions. The resulting maps of growth potential are compared to known plaice distributions to identify the extent to which bio-energetics underpin their migrations. The models presented may be used as tool to explore spatio-temporal fish dynamics, predict effects of local or broad-scale environmental changes and provide a physiological basis for observed changes in species distributions.

Introduction

Fisheries management is evolving within the framework of the Ecosystem Approach to Fisheries (EAF) to address specific issues related to the impact of fisheries on the environment (including biodiversity and habitat), and the impact of the environment on fisheries (including natural variability and climate change; (Garcia & Cochrane 2005). Knowledge on the spatio-temporal dynamics of fish is necessary in identifying essential fish habitat (EFH). Furthermore, knowing which factors (biotic, abiotic) act as drivers in determining the quality of habitats helps in understanding how the environment influences the productivity of a fish stock.

Many processes play a role in a population's spatial distribution, both environmental drivers and internal controls. Environmental control finds its ecological basis through the ecological niche theory of (Hutchinson 1957), where a number of environmental factors that limit species survival, growth and/or reproduction combine to delineate suitable habitat. Internal controls are related mostly to the size and

demography of the population. As migration distances are related to the size of fish, for example, the distribution pattern of the population will depend on the demography of the population (Rijnsdorp and Pastoors 1995). Population size can further influence the spatial distribution through density-dependence, following the concept of ideal free distribution (Sutherland 1983, MacCall 1990).

One approach considered to compare habitat quality across different areas is the examination of fish growth rates (e.g. Necaise et al. 2005, Gilliers et al. 2006, Searcy et al. 2007). Because temperature influences metabolic rates within an organism, growth is directly affected by environmental conditions as well as food availability (Kooijman 1988, 2000). Growth rates are also closely linked to reproductive potential (larger individuals are known to produce more and larger eggs; Solemdal 1997). The ability of a fish to achieve its maximum growth potential is, therefore, a relative measure of a fish's well-being and ultimate survival, as well as its potential contribution to the population (Brandt & Kirsch 1993, Mason & Brandt 1996). If the quality of a habitat can be defined by a fish's growth potential, spatially-explicit models of fish growth rates under different temperature and food scenarios can provide an eco-physiological approach to understanding spatio-temporal changes in habitat quality.

Plaice (*Pleuronectes platessa*) are an important commercial species in the North Sea (Rijnsdorp & Millner 1996) and understanding their spatio-temporal dynamics is key to implementing successful management measures (Rijnsdorp & Pastoors 1995). Their distribution within the North Sea varies between age-classes as well as between seasons within particular age-classes. Juvenile plaice prefer shallow coastal waters along the southern North Sea coasts, where they settle and grow (Rijnsdorp & Beek 1991). As plaice increase in size, they are found progressively further offshore and further north (Wimpenny 1953). Adult plaice undergo further seasonal migrations along a north-south axis between feeding and spawning grounds (De Veen 1978, Hunter et al. 2003). The distribution pattern of plaice is therefore a combination of migratory behaviour to spawning grounds, when plaice becomes sexually mature (De Veen 1978, Rijnsdorp 1989, Hunter et al. 2003), and of small-scale random or directed movements. These may result from foraging behaviour (Beverton & Holt 1957), from tidal migration (Kuipers 1973) or as a result of evasive behaviour. 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). The autumn offshore migration from shallow inshore waters and the spring inshore migration may reflect such a response to temperature and feeding conditions (De Veen 1978). A mass exodus of 0-group plaice from tidal flats in response to temperature has also been recorded (Berghahn et al. 1993).

In the 1990's, an offshore shift in the distribution of juvenile plaice was observed, which was proposed to be a response to water temperatures, although other factors may be involved as well (Van Keeken et al. 2007). Higher water temperatures can either exceed the maximum tolerance range or increase food requirements beyond the available resources. The change in distribution of juveniles reduced the effectiveness of the "Plaice Box" as a management tool (ICES 1994, 1999) and highlighted the importance of understanding the drivers of spatial dynamics. As optimal temperatures decrease with fish size, it can be expected that habitat choice is at least partly related to the available temperature field (Van Keeken et al. 2007). Temperature will in turn determine food requirements and thus interact with food availability to determine ultimate growth potential (Teal et al. 2008).

The aim of this study was therefore to explore the interaction between temperature and food availability in determining potential growth rates as a proxy for habitat quality in space and in time. Using a spatially-explicit model of growth potentials, the extent to which bio-energetics underpins the spatio-temporal dynamics of fish will be identified. North Sea plaice is used as a case study to test the effectiveness of such a framework in detecting and interpreting age specific distributions as well as longer term changes, such as the offshore movement of juvenile plaice (Van Keeken et al. 2007). The specific objectives were to 1) use dynamic energy budget (DEB) models to calculate size-, temperature-, and food dependant growth rates, 2) use environmental data from a North Sea hydrodynamic model to model DEB growth in space and time, 3) determine the effectiveness of modeling habitat quality of different length classes of plaice based on growth in describing their size-specific spatio-temporal distributions, and 4) determine the effects of different temperature conditions and food availability on habitat quality and how these may explain longer term changes in spatio-temporal distribution of plaice.

Methods

Growth

Growth calculations were based on the dynamic energy budget (DEB) theory (Kooijman 1988, 2000), which describes energy flows through an animal under conditions in which food densities and temperatures vary. The DEB distinguishes between three life-stages (embryos, do not feed or reproduce; juveniles, feed but do not reproduce; adults, feed and reproduce) and three main body components (structural biovolume or somatic tissue, stored energy reserves, gonads and/or stored energy reserves allocated to reproduction). The contribution of each of the three body components to the total bio-volume changes over time.

Food uptake is assumed to follow a functional response relationship with food density (type II response, Holling 1959) and is proportional to the organism's surface area. Ingested food is converted into reserves with a constant efficiency. Stored energy is utilized from these reserves and is allocated to growth, maintenance and reproduction. A fixed fraction κ (Kappa rule) of reserve is allocated to growth plus somatic maintenance, whilst the remainder fraction (1 - κ) is allocated to maturity maintenance and development or reproduction. Maintenance has priority over growth, thus growth ceases if food densities become too low. The energy costs of maintenance are proportional to the volume of the structure. At constant food densities, the reserves are in equilibrium with the environment and consequently growth of structural biovolume represents a weighted difference between surface area and volume and can be represented as:

$$\frac{dV}{dt} = \frac{\left(\kappa f\{P_{Am}\}\right)V^{2/3} - \left[P_M\right]V}{\kappa f\left[E_M\right] + \left[E_G\right]} \tag{E1}$$

which is mathematically equivalent to the Von Bertalanffy growth model (Kooijman 2000, van der Meer 2006). All parameters are described in Table 1. Using this size-dependent starting equation for growth, the model was extended to incorporate temperature and food density dependence.

Food dependency: In DEB models, food conditions in the environment are described in the form of a scaled type II functional response f, whereby 0 reflects starvation and 1 optimal food conditions (feeding *ad libitum*). f can be derived from the traditional form of the type II functional response:

$$f = \frac{aX}{1 + aT_h X}$$ **(E2)**

where a is the search rate and T_h the handling time and X the resource density.. The term $aT_h X$ reflects the average number of food items which could have been encountered during the time T_h spent handling a prey item. This reflects the assumption that prey items are encountered following a Poisson (Ruxton & Gurney 1994), that the search rate is constant and that prey are uniformly randomly distributed in space. By substituting:

$$P_{Xm} \equiv \frac{1}{T_h}$$ **(E3)**

And

$$X_h \equiv \frac{1}{aT_h}$$ **(E4)**

into E2, the Michaelis-Menten form can be derived:

$$f(X) = \frac{P_{Xm} X}{X_h + X}$$ **(E5)**

P_{Xm} is now the maximum intake rate when resource density is so high that search time is zero and is thus determined only by the handling time T_h. X_h is the resource density at which the intake is half the maximum (i.e. $0.5 \times P_{Xm}$). Based on the assumption that handling time (time of digestion) and search rates can be similar between fish species, X_h was set at 6.9×10^{-5} J cm^{-2} following Persson et al. (1998). It is assumed that 20% of the ingested energy is lost from the body (Brett & Groves 1979) and P_{Xm} is thus replaced by the maximum surface area-specific assimilation rate P_{Am}.

Temperature tolerance: The temperature tolerance range of an organism is defined as the range of temperatures where body growth is positive. Within this tolerance range, the optimum temperature is defined where growth is maximal (Willmer et al. 2000). Where temperatures are below the optimal temperature, a steady increase in metabolism with temperature is observed, and where temperatures are above the optimum, a stabilisation or decline in ingestion rate is observed, which is thought to be due to temperature specific changes in enzymes (Sharpe & DeMichele 1977). In order to incorporate these temperature tolerance ranges into the DEB growth

model, reaction rates (i.e. P_{Am}, P_M) are multiplied by the enzyme fraction that is in its active state. The fraction Fr is calculated as:

$$Fr = \exp\left(\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right) \times \left(\frac{1 + \exp\left\{\frac{T_{AL}}{T_{ref}} - \frac{T_{AL}}{T_L}\right\} + \exp\left\{\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T_{ref}}\right\}}{1 + \exp\left\{\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right\} + \exp\left\{\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T}\right\}}\right)$$ **(E6)**

All parameters are described in Table 1. Incorporating both food density and temperature dependence into the growth model results in:

$$\frac{dV}{dt} = \frac{\left(\kappa\{P_{Am}\}\left(\frac{X}{X_h + X}\right)Fr\right)V^{2/3} - [P_M] \times \exp\left(\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right)V}{\kappa f[E_M] + [E_G]}$$ **(E7)**

Table 1: Estimates of parameters of the DEB model for female plaice *Pleuronectes platessa* at 10°C (from (Van der Veer et al. 2009).

Symbol	Dimension	Interpretation	Female Plaice (10°C)
$\{P_{Xm}\}$	J cm^{-2} d^{-1}	Maximum surface area-specific ingestion rate	487
$\{P_{Am}\}$	J cm^{-2} d^{-1}	Maximum surface area-specific assimilation rate	390
$[P_M]$	J cm^{-3} d^{-1}	Volume-specific maintenance costs	19.4
$[E_M]$	J cm^{-3}	Maximum storage density	2500
$[E_G]$	J cm^{-3}	Volume-specific costs of structure	5600
$[E_S]$	J cm^{-3}	Volume-specific structural energy content	4000
κ	-	Fraction of utilised energy spent on maintenance plus growth	0.85
δ$_m$	-	Shape coefficient	0.219
T_A	K	Arrhenius temperature	7000
T_L	K	Lower boundary of tolerance range	277
T_H	K	Upper boundary of tolerance range	297
T_{AL}	K	Rate of decrease at lower boundary	50000
T_{AH}	K	Rate of decrease at upper boundary	100000

Environmental Data

To achieve the required spatial and temporal resolution of environmental data (temperature and benthic food availability) for the growth models, predictions from the hydrodynamic ERSEM (European Regional Seas Ecosystem Model) model (www.nioz.nl/northsea_model) were used. ERSEM has been linked with a new and

extended version of BFM (Biogeochemical Flux Model) and has been coupled to the General Estuarine Transport model (GETM) in order to integrate benthic-pelagic processes. The model predicts a number of abiotic variables for the entire North Sea on a horizontal resolution of 10 km. Estimates are available on a daily basis and were used to provide daily temperature (°C) and benthic food productivity (mg C m^{-2} d^{-1}) data. Data was available for the years 1989 and 2002, which provided a warm year with high productivity in the coastal areas (1989) and a year with locally high temperatures coupled with low productivity in coastal areas (2002). These two years could therefore be used to evaluate the approach.

Growth model

The DEB equations combine with the ERSEM temperature and benthic food productivity predictions to allow calculation of size-, food density- and temperature-dependent daily growth rates for each North Sea grid cell (10km resolution) described in the ERSEM model. In order to determine the habitat quality of each cell, the growth potential was calculated across the growing season for three separate starting lengths (1 cm, 20 cm and 40 cm) of plaice (reflecting three separate size/age-classes). Length of plaice on day $n + 1$ was calculated as length at day n plus the growth increment calculated using the DEB model, the temperature and food conditions on day n and length on day n. In this way the daily growth rates remained truly size-dependant and the length reflected the achievable length on a given day taking into account the environmental conditions.

Model validation

The model was validated by comparing calculated growth rates with growth rates obtained from back-calculation of otolith measurements (Fig. 1; Rijnsdorp et al. 1990). Annual growth rates were converted to growth rates per day, assuming that the growth was realised over a time period of 180 days. Although a crude assumption, this growth period corresponds to the seasonal growth observed in the monthly recaptures of tagged plaice (Rijnsdorp and Visser 1987).
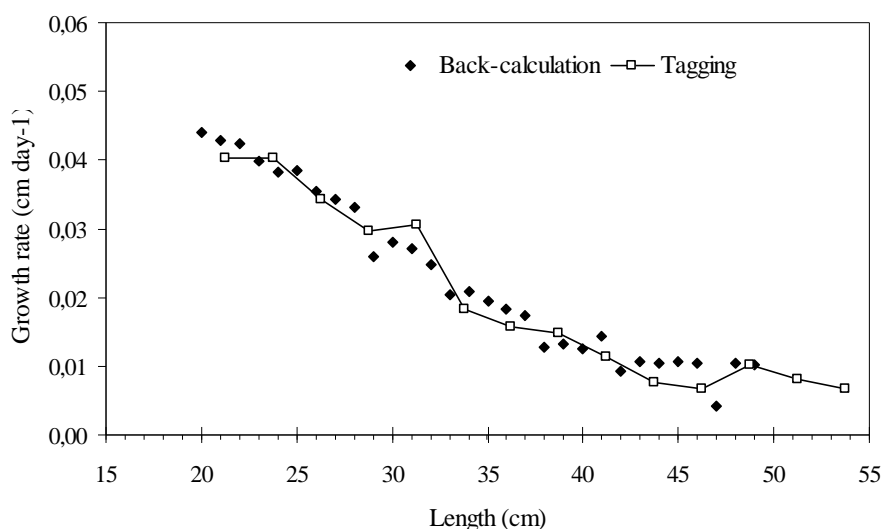
Fig. 1: Comparison of the back-calculated annual length increments in relation to body length at the start of the growing period with the annual length increment of tagged females (from Rijnsdorp et al. 1990)

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Results

Growth rates predicted by the DEB model (using parameters in Table 1) provided realistic estimates compared observed growth rate as obtained by back-calculation of otoliths and by tagging experiments (Fig. 1, Fig. 2a).

Growth rates are shown to decrease with length, although the shape of the relationship depends on temperature, with food availability influencing mainly the intercept (Fig. a). The type II functional response is reflected in the results with the intercept depending on size and the slope depending on the temperature (Fig. 2b). The optimum temperature for growth rates decreases with an increase in length, whilst food availability affects the potential growth rates at a given temperature (Fig. 2c).

Environmental conditions

Both temperature and food conditions differed between the years 1989 and 2002 (Fig. 3). August is selected as an interesting month to study due to the potential for temperatures to rise above the optimum for certain size-classes of plaice. Although 1989 is a warm year on average (van Hal, pers. comm), highest local temperatures are found in 2002 (Fig. 3 a and b), where coastal areas show August temperatures up to ~24°C (Fig. 3b). Food conditions between the two years differ distinctly, with food concentrated along the southern coast in 1989 (Fig. 3c). In 2002, very little benthic productivity is evident along the coasts and instead a peak of productivity is found in the southern Bight just off the English Coast (Fig. 3d). In both years a band of higher productivity is evident running along the northern Dogger Bank.

Growth increment

Differences in the spatial distribution of growth potential are evident between different length classes as well as between the two years, 1989 and 2002 (Fig. 4). In the 0-group class (starting length 1cm), the coastal areas show the highest growth potentials in both years, although the maximum potential length reached is higher in 2002 (Fig. 4 a and b). The area of habitat where the largest lengths are achievable also extends out further into the German Bight in 2002 compared to 1989.

For juvenile plaice (starting length 20cm), the coastal areas remain areas of highest growth potential, although the offshore areas also become more suitable (Fig.. 4 c and d). In 2002 maximum growth potentials are found further offshore, forming a narrow band along the Danish, German and Dutch coasts and as with the 0-group size class, the best areas extend further into the German Bight (Fig. 4d) compared to 1989 (Fig. 4c).

Areas of highest growth potentials of adult plaice (starting length 40cm) are less restricted to the coastal zones and become more homogenous throughout the North Sea up to a very defined northern boundary (Fig. 4 e and f). A northwards shift in comparison to the smaller size-classes is detectable with growth potentials in the southern bight decreasing. In 2002, the Dutch, German and Danish coasts as well as the tops of the Dogger Bank also become less suitable and the maximum growth is found in a band running just south of the Dogger Bank across to northern Denmark (Fig. 4f). The size-dependence of the DEB model is also reflected in the growth potential maps where the maximum increase in length is smallest for the largest size class.
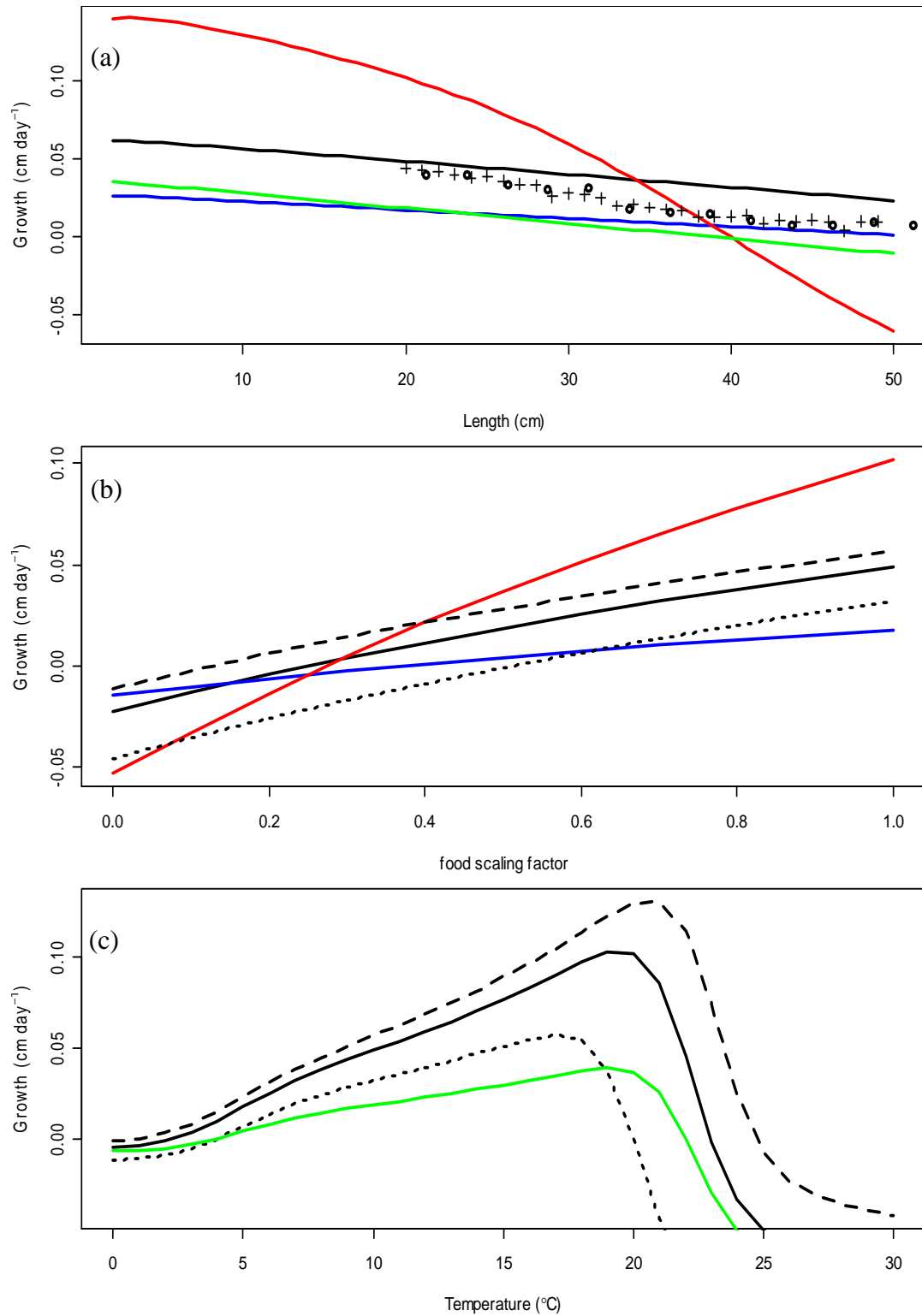
Fig. 2: Growth curves predicted using DEB model and parameters provided in Table 1. Relation between growth rates and a) length, b) food density and c) temperature are shown. The solid black line shows growth rates with *ad lib* food availability and temperature = 10 °C, and in panels b and c, for length = 25 cm. Dashed lines represent these same conditions for a length of 10 cm, dotted lines for a length of 40 cm. Red lines represent these conditions but at a temperatures of 20 °C, blue lines temperatures of 5 °C. The green line represents these conditions with a food scaling factor of 0.5. The crosses and circles in panel a) represent the growth data depicted in Figure 1.
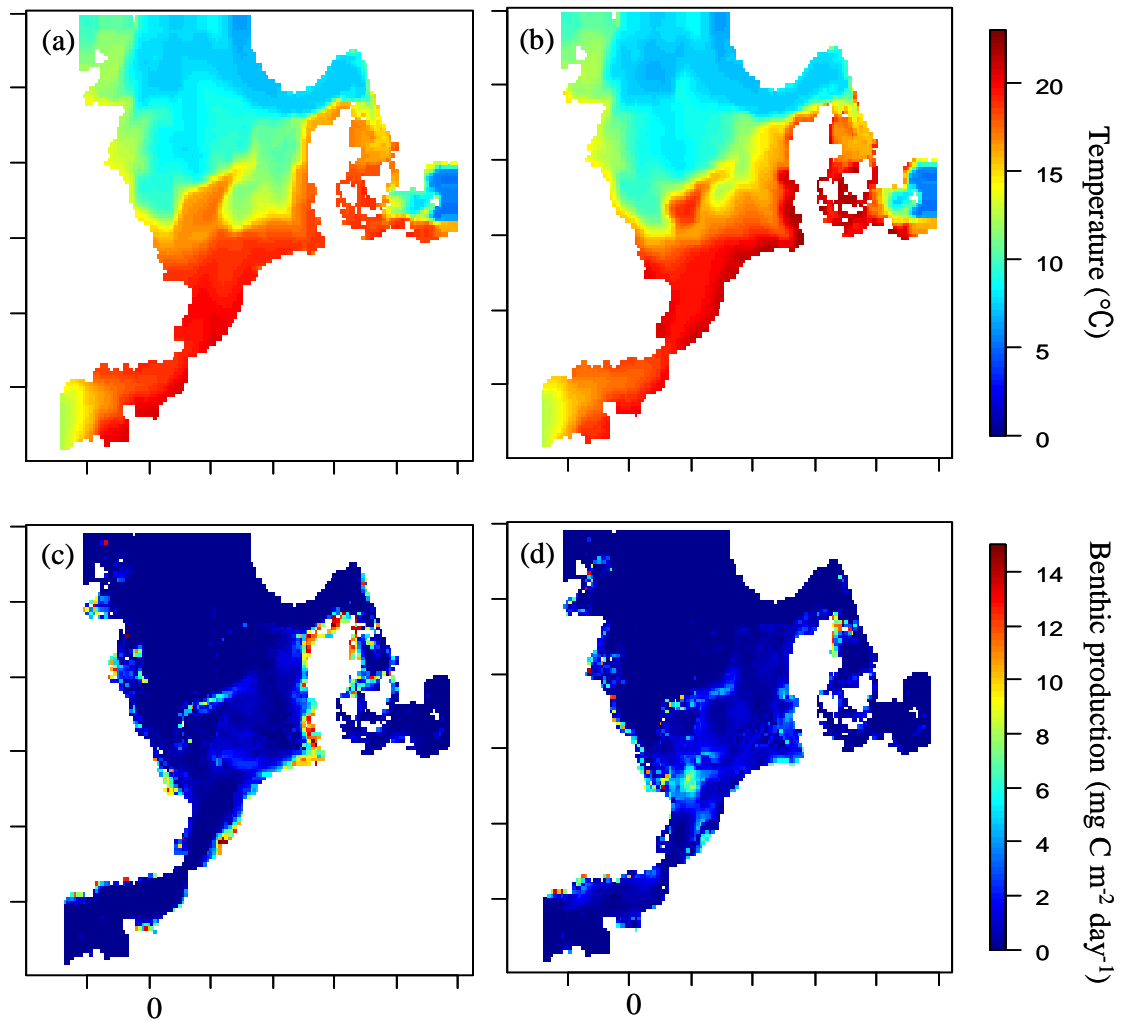
Fig. 3: August (day 200) sea temperatures (a and b) and benthic productivity (c and d) for the years 1989 (a and c) and 2002 (b and d).

Growth rates

Whilst potential increase in lengths reached at the end of the growing season is a good indicator of average habitat quality, it can be expected that movements of plaice are driven by evasive behaviour in response to unfavourable environmental conditions (i.e. high temperatures). In this case local and temporal peaks in environmental conditions will be more meaningful than seasonal averages. August growth rates were therefore considered to look at the effect of high coastal temperatures. Already in the smallest size-class (starting length 1cm) it is evident that highest growth rates are achieved slightly further offshore in 2002 compared to 1989 (Fig. 5 a and b). Reasons for this can be two-fold: Either the August temperatures have increased above the optimum for this size-class in the shallow coastal areas, or the lack of food in these areas in 2002 (Fig. 3d), coupled with higher temperatures, means that the increased food requirement at the higher temperatures cannot be met. As the size-classes increase, and therefore also the optimum temperature decreases (Fig. 2c), this effect becomes more evident (Fig. 5 c - f) and the coastal areas even become detrimental (negative growth rates). Remaining in these areas for any length of time and would thus ultimately result in death.
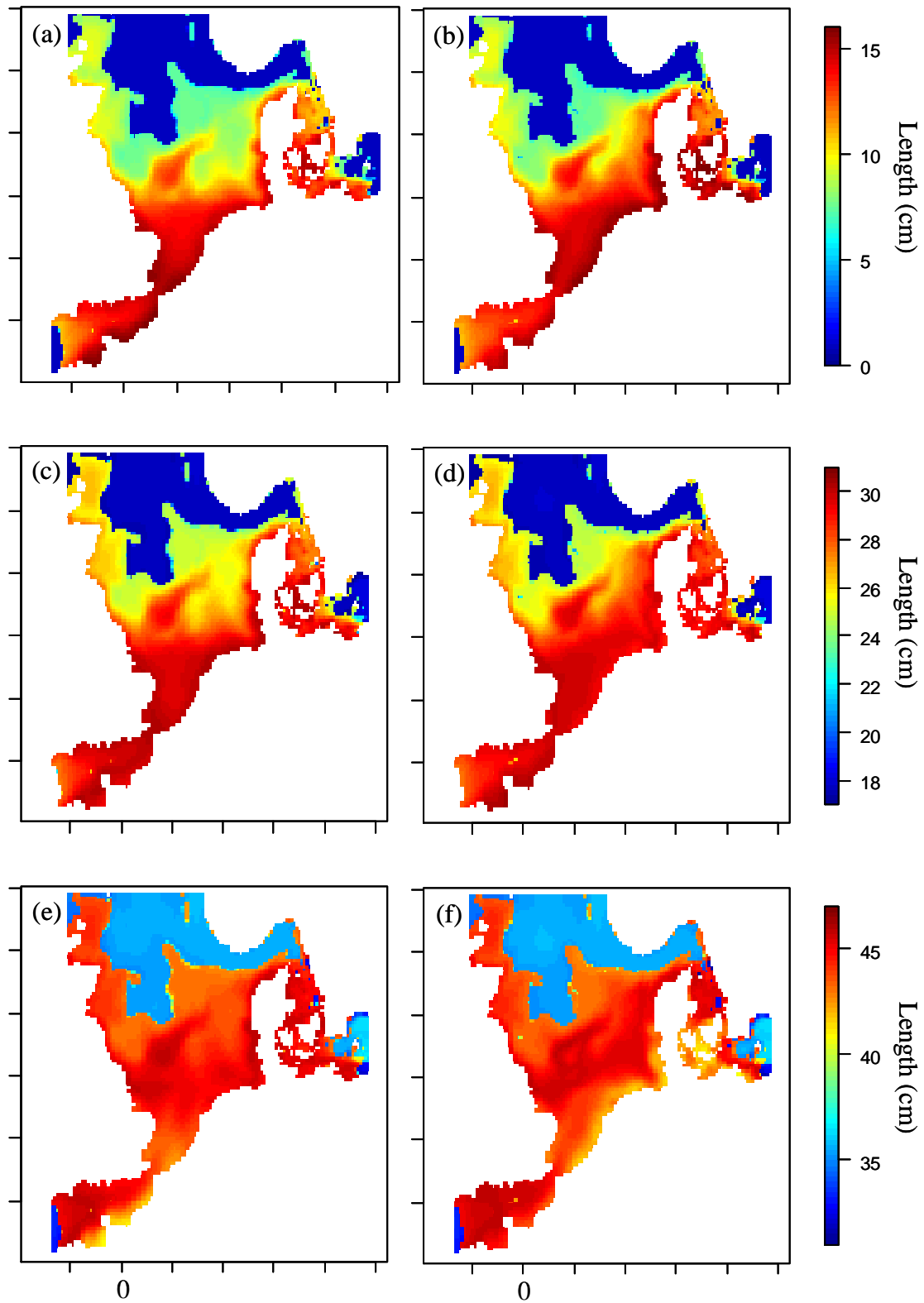
Fig. 4: Potential September lengths for a starting length of 1cm (a and b), 20cm (c and d) and 40 cm (e and f), for years 1989 (a, c, e) and 2002 (b, d, f).
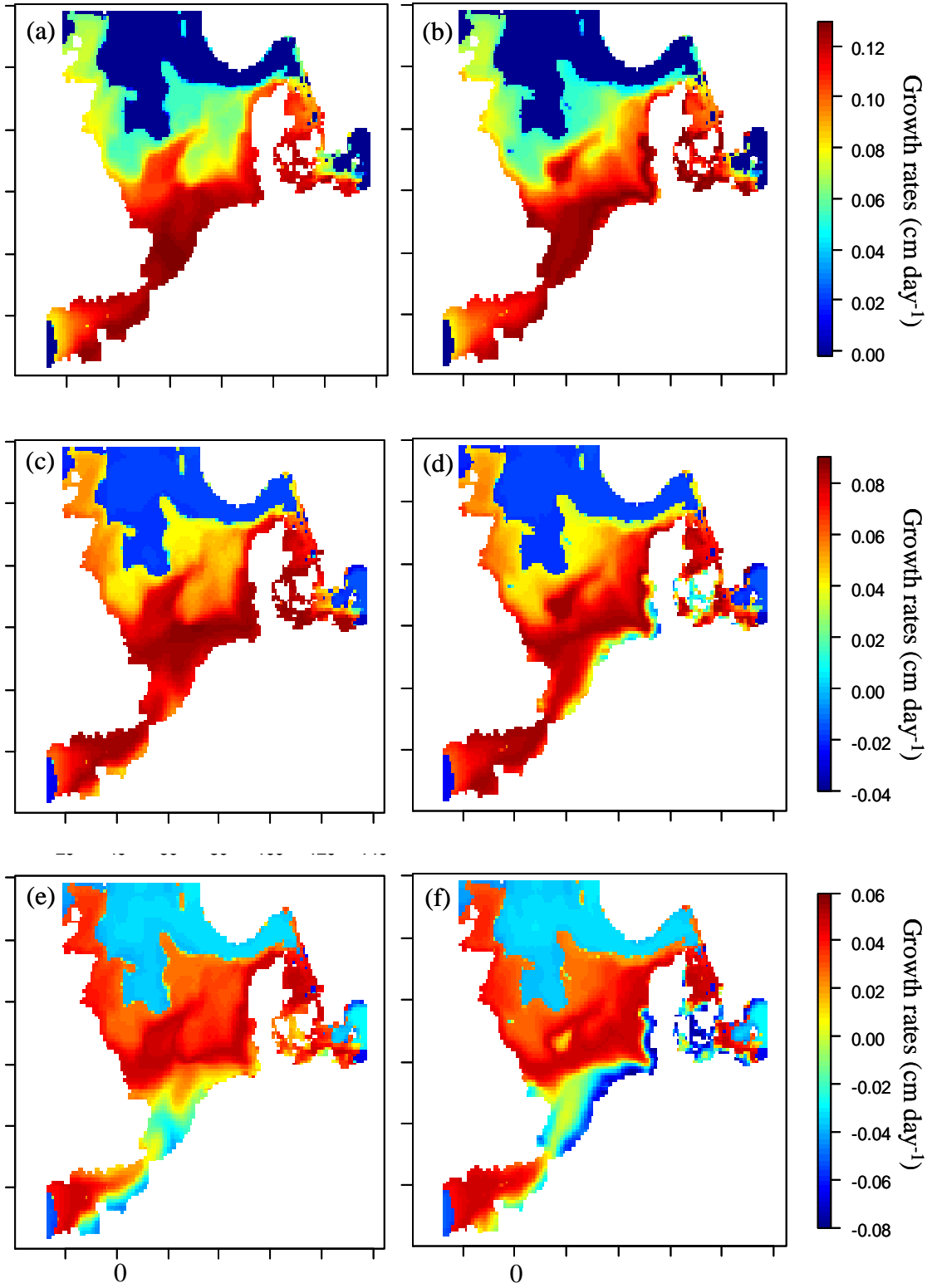
Fig. 5: Daily growth rates in August (day 236) using starting lengths of 1cm (a and b), 20cm (c and d) and 40 cm (e and f), for years 1989 (a, c, e) and 2002 (b, d, f).

Whilst August growth rates of the juveniles (starting length 20cm) still show better conditions in the southern North Sea (south of, or on, the Dogger Bank), the adult plaice (starting length 40cm) have a much wider suitable area to choose from, where potential growth rates remain consistent (Fig. 5 e and f). In contrast, the southern North Sea becomes unsuitable for this size class to grow during August, an effect that is even stronger in 2002. The top of the Dogger Bank also decreases in quality (based on achievable growth rates) in August between 1989 and 2002, which can be considered a temperature affect, as benthic productivity in this area remains similar between the two years. Although growth increment can therefore be seen as fairly homogenous throughout the North Sea (Fig. 4 e and f), it is the local and temporal peaks in temperature and food that are more likely to underpin the movement patterns of the adults.
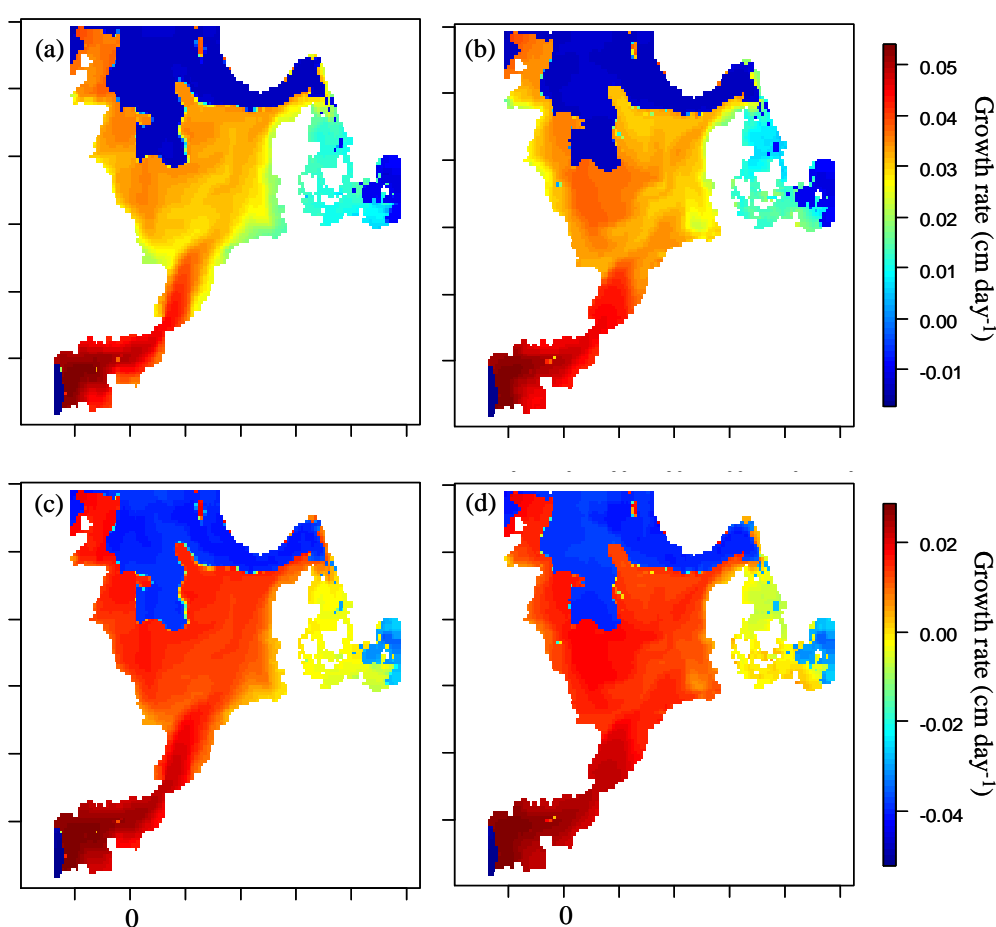

Fig. 6: Daily growth rates in February (day 45) using starting lengths of 15cm (a and b), 45cm (c and d) for years 1989 (a, c) and 2002 (b, d).

Winter conditions are also interesting to consider as this is the time period when juveniles are often observed to move slightly offshore and adult plaice begin their migrations to spawning grounds in the southern bight. Indeed, during winter (February), growth rates show a different pattern to summer conditions. For smaller fish, the coastal areas no longer optimal and areas slightly offshore or further south show better potential for growth (Fig. 6 a and b). In 2002, the coastal areas remain

reasonable for growth, although areas further south still show the highest growth potentials (Fig. 6b). As the food conditions within these coastal habitats do not differ distinctly between the two years, the change in habitat quality can be contributed mainly to warmer winter temperatures in 2002 (Fig. 7).

Habitat quality for larger plaice during February is shown to be highest in the southern Bight area, although conditions across the wider North Sea appear mostly homogenous with low growth rates (< 0.02 cm day^{-1}, Fig. 6 c and d). In 1989 the coastal areas appear less favorable compared to 2002, again most likely due to the slightly warmer temperatures in the latter year (Fig. 7).
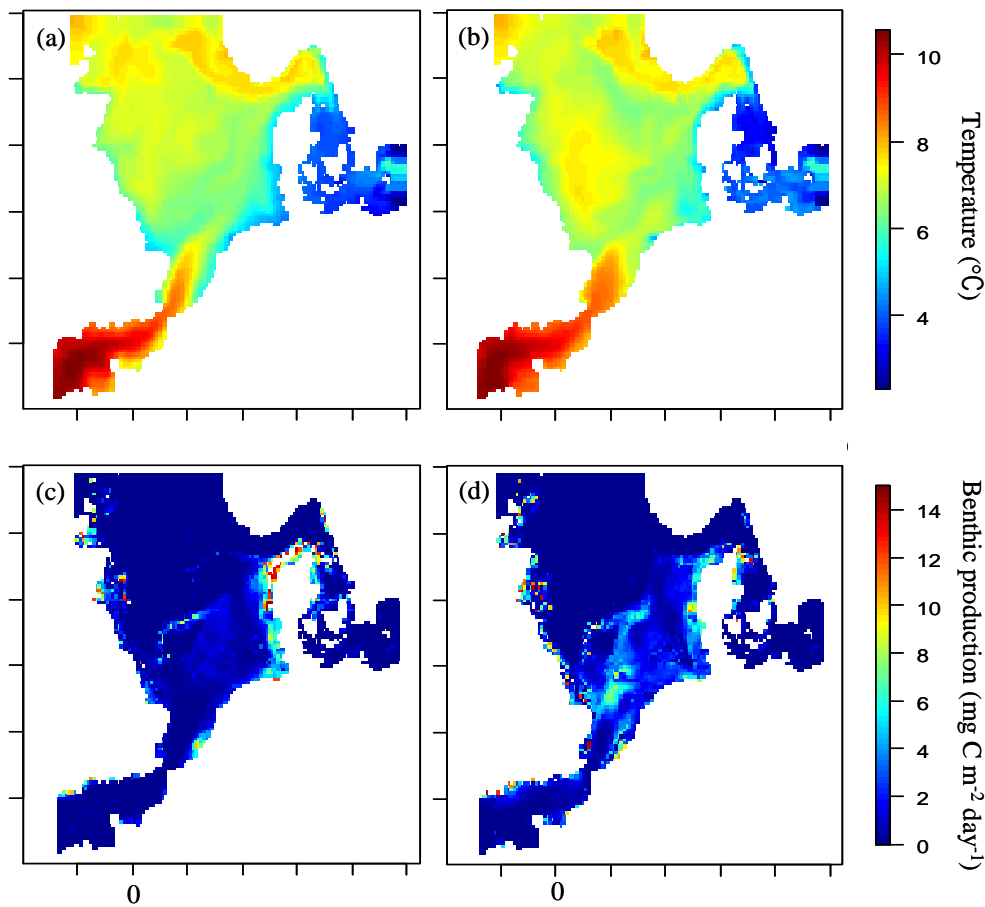
Fig. 7: February (day 45) sea temperatures (a and b) and benthic productivity (c and d) for the years 1989 (a and c) and 2002 (b and d).

Discussion

Spatially-explicit models of fish growth rates under different temperature and food scenarios are shown here to be a useful framework for interpreting spatio-temporal dynamics of fish and consequently may be used as a proxy for mapping habitat quality. Growth rates modelled here by means of dynamic energy budget (DEB) models closely match those observed in the field. Although the similarity between observed and calculated values adds confidence to the modelled values, estimated growth rates are dependent on the parameter estimates (Table 1) used, as

well as the environmental data input from the hydrodynamic model (ERSEM), both of which contain some uncertainties.

The majority of the DEB parameters used are species-specific to plaice and are largely obtained from observational data derived from tank experiments on 0-group plaice at different temperatures and *ad lib* food (Van der Veer et al. 2009). These parameters can therefore be considered to be reasonably well established for plaice and the DEB growth rates calculated previously using these parameters have also shown a close correspondence to observed growth rates in the field (van der Veer et al. 2001, Van der Veer et al. 2009). Larger uncertainty is involved in the parameters describing the size effect on the temperature tolerance range as well as in the parameter X_h that scales the functional response of plaice to the food levels predicted by the ERSEM model.

Although substantial evidence exists in a number of fish species that small (juvenile) fish grow well in, and will select for, a larger range of temperatures than larger (older) fish (e.g. Fonds et al. 1992, Portner & Farrell 2008), the evidence of the underlying mechanisms is not clear. The size-dependant temperature tolerance range used in the DEB model is based on the assumption that the decrease in optimal temperature is approximately 1°C per 10 cm increase in fish size (Van der Veer et al. 2009), but based on Fonds pers. comm.). With a lack of growth experiments on larger size plaice, however, this remains an area of uncertainty in the model.

The saturation coefficient, X_h, was based on the parameter determined for Swedish perch (Persson et al. 1998) and the assumption that handling times and search rates do not differ significantly between fish species. Again, as the value used returned reasonable results, it was accepted as a best approximation for the saturation coefficient in plaice. A species-specific estimate, however, would undoubtedly improve the model output.

Whilst some uncertainties remain in the parameters of the model, the model output is also affected by the accuracy of environmental data input. Obtaining reliable estimates for benthic food availability is particularly complex, as plaice feed on a selected number of benthic invertebrates and their preference changes with body size (Rijnsdorp & Vingerhoed 2001). Indeed, Jennings et al. (2001, 2002) showed that the trophic level utilised by plaice decreased with body size. Their feeding behaviour also varies with season, with juveniles continuing to feed at a reduced rate during winter and adults ceasing to feed whilst spawning but resuming feeding once spent (Rijnsdorp 1989). Tagging experiments of sub-adults have shown that plaice stop growing during November and April (Rijnsdorp and Visser 1987) and their energy content decreases (Rijnsdorp and Ibelings 1989). Hence, sub-adults are unable to even maintain their body condition during winter, most likely due to the lack of suitable food items. In addition to differences in plaice feeding behaviour, availability of invertebrate biomass may also change seasonally depending on benthic behaviour, e.g. burrowing behaviour of invertebrates during periods of low productivity (winter). ERSEM does not account for this as the model predicts benthic productivity in terms of carbon produced per day. However, not all of this carbon will be available to plaice through their preferred food items. The values used from ERSEM are therefore likely to be an overestimate of what is actually available for plaice to ingest and the values used in this study are a necessary crude estimate.

Despite these uncertainties in absolute values, the model provides useful results in gaining a better understanding of spatial dynamics and the relative quality of habitat in terms of growth potential of different size-classes. If plaice aim to maximise

growth rates, as well as reproduce successfully, they will need to migrate between the locations of maximum habitat quality (as juveniles) and between the best areas for growth in summer and spawning grounds in winter (as adults). The model shows that during summer, habitat quality of small plaice is highest in the warmer coastal areas, and for larger plaice, which have a lower optimum temperature, it is spread out over the cooler offshore waters. Furthermore, the locations of highest habitat quality change between seasons. During winter, juveniles may find better quality areas (to maximise growth) slightly offshore or further south. This observation is supported by (De Veen 1978) who documented an offshore migration of juveniles during winter. Larger (adult) plaice, are known to migrate south in autumn towards spawning grounds in the southern and south-eastern North Sea (Harding et al. 1978). Their potential growth rates during autumn and winter remain low throughout most of the North Sea.

The known seasonal movements of different size-classes of plaice thus appear to be consistent with the seasonal pattern in habitat quality (expressed as potential growth rate) for different size classes. Whether or not plaice will be able to utilise the highest quality habitats, however, will depend on the distances between the habitats and the cost of movement. If plaice do distribute themselves according to bio-energetics then long-term changes in distribution patterns in relation to climate change may be predicted. Indeed, the offshore movement of juvenile plaice (van Keeken et al. 2007), which has been speculated to be related to an increase in coastal water temperatures, can be linked to changes in habitat quality based on growth potentials. Although it is unclear from the results presented here whether the mechanism underpinning the offshore shift is due to temperatures rising above the optimum, or due to food limitation occurring at the higher temperatures, the offshore shift can be linked to bio-energetics and thus a physiological response. Consequently, impacts of potential future climates on spatial distributions and habitat quality may be explored using a bio-energetics approach.

Acknowledgements

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