

# Empirically modelling the potential effects of changes in temperature and prey availability on the growth of cod larvae in UK shelf seas

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It has been hypothesized that changes in zooplankton community structure over the past four decades led to reduced growth and survival of prerecruit Atlantic cod (*Gadus morhua*) and that this was a key factor underlying poor year classes, contributing to stock collapse, and inhibiting the recovery of stocks around the UK. To evaluate whether observed changes in plankton abundance, species composition and temperature could have led to periods of poorer growth of cod larvae, we explored the effect of prey availability and temperature on early larval growth using an empirical trophodynamic model. Prey availability was parameterized using species abundance data from the Continuous Plankton Recorder. Our model suggests that the observed changes in plankton community structure in the North Sea may have had less impact on cod larval growth, at least for the first 40 days following hatching, than previously suggested. At least in the short term, environmental and prey conditions should be able to sustain growth of cod larvae and environmental changes acting on this early life stage should not limit stock recovery.

**Keywords:** cod, Continuous Plankton Recorder, larval growth, prey fields, temperature, trophodynamic model, UK shelf.

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## Introduction

Historically, Atlantic cod (*Gadus morhua*) stocks supported some of the world's most important fisheries. However, during the past few decades, many of the North Atlantic stocks (e.g. North Sea and Irish Sea) have declined (Myers *et al.*, 1997), to the extent that the species is now classified as “vulnerable” in the IUCN Red List of Threatened Species ([www.iucnredlist.org](http://www.iucnredlist.org)). Several stocks around the UK are currently at, or close to, historically low levels, and are the subject of stock recovery programmes to prevent further stock decline (Cook *et al.*, 1997; Brander, 2005a). In the North Sea, cod is well below its safe level of spawning-stock biomass (SSB) and, as a result, ICES considers its productivity to be impaired. In the past few years, ICES has advised massive reduction in fishing mortality as part of a plan to rebuild a sustainable spawning stock rapidly, at least to the precautionary level (Horwood *et al.*, 2006). Although fishing mortality has a major impact on the size of commercial fish stocks (Myers *et al.*, 1997), it has become clear that environmental factors, including physical variables and plankton composition and/or abundance, have probably also contributed to the decline (Brander, 1997; Heath, 2007). Establishing a link between environmental variability and changes in fish populations is difficult because of the wide range and complexity of mechanisms involved. However, climate effects and cod recruitment have been linked in various ways, and the correlations have become increasingly stronger during the past few decades in the Barents Sea (Ottersen *et al.*, 2006), as well as in the North Sea (Brander, 2005b).

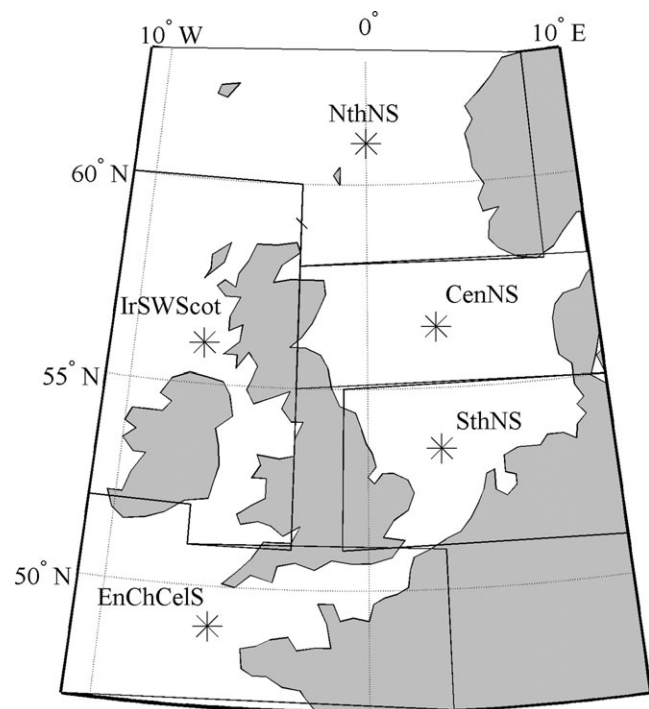
Several studies have linked environmental conditions during the egg, larva, and settlement stages with subsequent recruitment (at stock management scales). For cod around the UK, which are close to the southern geographic limit of the species, it has generally been concluded that strong recruitment is associated with cold winters and early summers (Planque and Fox, 1998; Planque and Frédou, 1999). Because there is little evidence that cod eggs and larvae are adversely affected by temperatures typical of those experienced in the wild, it has been concluded that interannual temperature variability acts as a proxy for other processes influencing survival (Brander and Mohn, 2004).

Another indirect influence of temperature on the recruitment processes is via trophic transfer. Sundby (2000) proposed that the recruitment–temperature relationship of Atlantic cod is a proxy for food abundance during early life stages, and that the inverse response of Atlantic cod recruitment to temperature change, in the upper and lower range of ambient temperatures, is likely to be the result of advection of zooplankton from core production regions. Most fish larvae feed primarily on zooplankton, so changes in food quantity and quality, as well as in seasonal timing, will affect their survival. Bottom–up control is thought to be a significant factor determining year-class strength (Bremigan and Stein, 1994).

In the North Sea, there have been significant changes to plankton composition associated with recent long-term climate change and temperature increases (Beaugrand *et al.*, 2002). Beaugrand *et al.* (2003a) suggested a mechanism involving the match/mismatch

hypothesis (Cushing, 1990) to link temperature variability with the long-term decline of cod recruitment in the North Sea via fluctuations in plankton. They reported that the ecological regime shift that started in the mid-1980s radically changed the food environment for cod larvae, concluding that rising temperature since then has resulted in reorganization of the plankton ecosystem that is unfavourable to the survival of cod larvae. Among the most obvious changes has been the decline in the abundance of the larger copepod *Calanus finmarchicus*, particularly in the northern North Sea. Research so far has mainly focused on *Calanus* spp. as the main prey. However, this cannot be the whole story. Historically, significant spawning took place around the southern edge of the Dogger Bank (Daan, 1978), and 1-year-old cod were caught predominantly in the central and southeastern North Sea (Blanchard *et al.*, 2005), areas where *Calanus* was never dominant. Moreover, as cod have been successful in many other areas where *C. finmarchicus* have not been dominant (e.g. the Baltic Sea, the English Channel, and the Celtic and Irish Seas), they can clearly survive on other prey (Planque and Fromentin, 1996).

The cases above demonstrate the plethora of direct and indirect effects climate variability may have on fish populations. This emphasizes the importance of furthering our understanding of the biological mechanisms through which climate changes affect the dynamics of fish stocks, to aid the design of realistic stock recovery plans, and to be able to evaluate claims that natural changes, in addition to fishing, are responsible for stock collapse (Beaugrand *et al.*, 2003a; Clark *et al.*, 2003; Schiermeier, 2004). The issue is particularly pressing because climate change models further anticipate that sea surface temperature (SST) will continue to rise in all waters around the UK coast; and fish stocks at low levels of biomass may be particularly sensitive to environmental change, perhaps compromising plans for recovery (Brander, 2005b). So far, results linking environmental changes and recruitment have been based on correlations, and significant correlations have been established for North Sea cod recruitment time-series and environmental factors such as temperature. It is important to understand the causes of long-term zooplankton variations in biomass and community composition, as well as how these changes affect higher trophic levels. We have adopted a modelling approach in the absence of data or samples that would allow us to estimate the growth of cod larvae over the past four decades directly. Individual-based models of larval fish trophodynamics have found increased application in understanding the complex processes affecting larval growth and survival (Letcher *et al.*, 1996; Fiksen and Folkvord, 1999; Leising and Franks, 1999; Lough *et al.*, 2005; Kristiansen *et al.*, 2007). However, the data demands of this approach are high and ideally use physical and prey fields derived from focused observational campaigns. For this reason, such studies have not been carried out over the time-scales necessary to identify climate-related effects. In the absence of long-term time-series of observations on absolute plankton abundance for UK Shelf Seas, we have used the only available source of data, the Continuous Plankton Recorder (CPR). The advantage of CPR data is that the whole period 1960–2002 and the whole UK shelf can be covered. Here, we explored the effect of prey availability from CPR zooplankton data and temperature variability on early larval (first 40 d) growth using a simple, deterministic, trophodynamic model of the growth of cod larvae. Our aim was to evaluate whether observed changes in plankton abundance, species composition, and temperature could have led to periods



**Figure 1.** The study area and the five subareas modelled. The asterisks indicate the coordinates at which sunrise and sunset were calculated for daylight: northern North Sea, NthNS ( $61^{\circ}\text{N } 0^{\circ}$ ); central North Sea, CenNS ( $56.3^{\circ}\text{N } 3^{\circ}\text{E}$ ); southern North Sea, SthNS ( $53.5^{\circ}\text{N } 3^{\circ}\text{E}$ ); English Channel and Celtic Sea, EnChCelS ( $49^{\circ}\text{N } 6^{\circ}\text{W}$ ); Irish Sea and west of Scotland, IrSWScot ( $56^{\circ}\text{N } 7^{\circ}\text{W}$ ).

of poorer growth of cod larvae (and by inference reduced survival).

## Material and methods

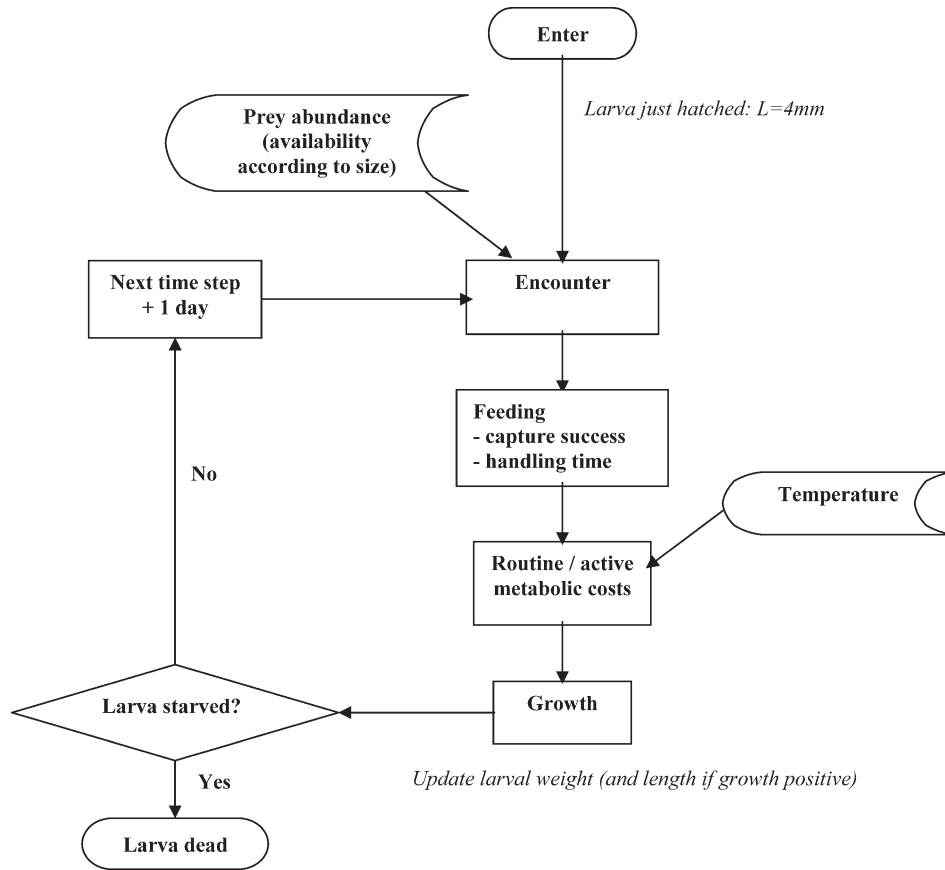
### Area of study and time frame

We limited our area of study to the Northeast Atlantic shelf delimited by latitudes  $45^{\circ}$ – $63^{\circ}\text{N}$  and longitudes  $15^{\circ}\text{W}$ – $10^{\circ}\text{E}$  over the period 1960–2002. CPR data are consistent over this time and, for most cod stocks, fisheries assessment data (North Sea, Irish Sea and west of Scotland, English Channel and Celtic Sea) are available. The area was divided into five subareas based on biogeography and the known spawning locations of cod (Brander, 2005a). Reasonably large sea areas were required to keep the number of missing CPR values in each box to a minimum (Figure 1).

### Structure of the trophodynamic model

Cod larval feeding and growth was implemented based on the approach developed by Letcher *et al.* (1996). The formulations are described fully in that reference, and only the main features of the subroutines and the differences in our application are presented here.

We assume that larvae hatch at a length of 4 mm at the start of January, February, March, and April, corresponding to the spawning season for cod stocks around the UK (Brander, 2005a). Following hatching, we model larval development in 24-h time-steps through the sequence shown in Figure 2. Throughout the model, we used a length (Len, mm)–weight (Wgt,  $\mu\text{g}$  dry weight)



**Figure 2.** Flow chart for the growth model computing daily growth of an individual larva. During daylight, the larva forages on prey of appropriate size. The prey items encountered are pursued and, if successfully captured, ingested by the larva until satiated. The metabolic costs are summed, and growth is either added or subtracted; if the weight of the larva falls below the “death barrier”, it is considered dead, and the model stops.

relationship following Finn *et al.* (2002):

$$DW_{gt} = \frac{a \times Len^b}{1000}, \quad (1)$$

where *a* and *b* were set according to the length of the larva:

for larval size *Len* within the 4–7 mm range: *a* = 4.12 × 10<sup>-4</sup>, *b* = 3.109;

for larval size *Len* within the 7–12 mm range: *a* = 6.40 × 10<sup>-5</sup>, *b* = 4.129;

for larval size *Len* within the 12–60 mm range: *a* = 3.59 × 10<sup>-4</sup>, *b* = 3.406.

During model runs, the larva could not lose length, but it could lose weight.

Prey availability was calculated as a subset of all potential prey based on larval size. As larvae grow in size, progressively larger prey items are taken in preference to smaller items (Kane, 1984; Economou, 1991; Pepin and Helbig, 1997). We used a predator–prey size ratio to estimate prey selectivity (Economou, 1991; Leising and Franks, 1999; Werner *et al.*, 2001). Prey sizes, measured as prosome length, were set between minima and maxima of 0.015 and 0.106 times larval length, respectively. Typical prey prosome lengths were extracted from the literature

(Sars, 1903; Rose, 1933; Massuti and Margalef, 1950) and ICES identification Leaflets for Plankton (<http://www.ices.dk/products/idleaflets.asp>), following Pitois and Fox (2006). Body size and species-specific behavioural and morphological characteristics are all key factors determining the prey preference of cod larvae (Heath, 2007). However, owing to the complexity of defining prey selection in the model according to prey behavioural patterns, we have taken just size into account.

We assumed that larvae are active during daylight. For each month and each of the five subareas, the proportion of the day during which there was sufficient light for feeding was estimated from sunset and sunrise times at the central location of each box (Figure 1, Table 1).

At each 24-h time-step, the mass of prey *i* (*I*) ingested by larva *l* was calculated as a function of encounter rate (*EC*<sub>*l,i*</sub>), prey mass (*m*<sub>*i*</sub>), capture success (*CS*<sub>*l,i*</sub>), handling time (*HT*<sub>*l,i*</sub>), and time interval  $\Delta t$ :

$$I = \frac{\sum_i m_i EC_{l,i} CS_{l,i}}{1 + \sum_i EC_{l,i} HT_{l,i}} \Delta t. \quad (2)$$

We chose to follow the method of Lough *et al.* (2005) to calculate metabolic cost, so as to include the effect of temperature on metabolism. Routine metabolic cost (*MC*, µg larval tissue individual<sup>-1</sup> h<sup>-1</sup>) was calculated at night, when larvae were not

**Table 1.** Portion of the day during which light was assumed to be sufficient for feeding, estimated from sunset and sunrise times for each month used in the larval growth model, and at the central location of each area (Figure 1).

Area	Portion of day sufficient for feeding (h)				
	January	February	March	April	May
1	6.66	8.33	11.33	14.75	16.30
2	7.75	9.30	12.24	14.25	15.75
3	8.25	9.66	11.80	13.66	15.25
4	8.80	10.25	12.00	13.66	14.80
5	7.75	9.33	11.66	14.33	15.75

feeding and were dependent on temperature ( $T$ , °C) and larva dry weight ( $Wgt$ ,  $\mu\text{g}$ ) at the current time-step:

$$MC = 0.00114 \times Wgt^{(1.02900 - 0.00774 \times \ln Wgt)} \times e^{[(0.10720 - 0.00320 \times \ln Wgt) \times T]} \quad (3)$$

During daylight, when the larva was active, it was possible to scale the routine metabolic cost to active cost, using a  $k$ -ratio ( $k$ ) of 1.4 for smaller larvae and 2.5 for larvae measuring at least 5.5 mm. Routine ( $RoutM$ ,  $\mu\text{g d}^{-1}$ ) and active costs ( $ActM$ ,  $\mu\text{g d}^{-1}$ ) during a 24-h time-step can be calculated from

$$RoutM = 24(1 - \text{Light}) \times MC, \quad (4)$$

$$ActM = k \times 24 \times \text{Light} \times MC, \quad (5)$$

where  $\text{Light}$  is the proportion of daylight calculated for a particular month (Table 1).

Larval daily growth ( $\mu\text{g d}^{-1}$ ) was calculated as the difference between the net energy input (i.e. the amount of food absorbed by the larva) and metabolic cost:

$$\text{Growth} = (I \times AE) - TC, \quad (6)$$

where the ingested prey mass ( $I$ ,  $\mu\text{g dry mass per 24-h time-step}$ ) was reduced by an assimilation efficiency ( $AE$ ). The total cost ( $TC$ ,  $\mu\text{g d}^{-1}$ ) was the sum of metabolism components and included routine and active metabolism, specific dynamic action ( $SDA$ ), and egestion ( $E$ ):

$$TC = RoutM + ActM + I(SDA + E), \quad (7)$$

where  $SDA$  and  $E$  were defined as a constant proportion of ingestion, and  $SDA + E = 0.30$ .

The model was run for 40 d, spanning the period under maximal potential growth conditions, when larvae start switching from copepods to larger prey such as euphausiids, appendicularians, and the larvae of other fish (Heath, 2007), prey items not present in our dataset. Larval weight at 40 d was taken as an indication of good, average, or poor growth for a cohort hatched in a particular year, month, and region.

If as a result of negative growth, larval weight fell below a minimum value or “death barrier” ( $Wgt_{\text{death}}$ ,  $\mu\text{g}$ ), then the larva died and the model stopped. We calculated the threshold minimum larval weight using a relationship based on the smallest

larva alive at a particular age during laboratory experiments (Werner *et al.*, 1996; Leising and Franks, 1999). This relationship depends on the age ( $\text{Age}$ , d) of the larva at the current time-step of the model:

$$Wgt_{\text{death}} = \text{HatchWgt} \times e^{0.0282 \times \text{Age}}. \quad (8)$$

### Prey and temperature data

Monthly average SST (°C) data for  $1^\circ \times 1^\circ$  (latitude  $\times$  longitude) subareas were obtained from the International Comprehensive Ocean–Atmosphere Data Set (ICOADS), the data being averaged in each of the model subareas (NOAA–CIRES Climate Diagnostics Center, Boulder, CO, USA, from their website at <http://www.cdc.noaa.gov/>). Temporal smoothing was applied to monthly data to derive daily values. Zooplankton abundance values (as accepted values of abundance) were obtained from the CPR dataset. The CPR survey has now been running for >70 years and is one of the longest and most extensive ecological time-series in the world, providing a unique source of long-term, large-scale information covering >300 species of zooplankton in the North Atlantic (Beare *et al.*, 2003; Reid *et al.*, 2003). The CPR is towed by ships of opportunity at speeds in the range 15–20 knots and at an approximate depth of 10 m. Water enters the recorder through an aperture of 1.62  $\text{cm}^2$ , and is filtered through a continuously moving band of silk with an average mesh size of 270  $\mu\text{m}$ . The plankton are covered by a second band of silk, and this double band is wound into a storage tank containing formalin. When returned to the laboratory for processing, the roll of silk is unwound and divided into sections representing 10 miles of tow, equivalent to  $\sim 3 \text{ m}^3$  of filtered seawater. Methods of counting and data processing are described by Colebrook (1975) and Batten *et al.* (2003). Information on the abundance of copepods and cladocerans (total 60 taxa) was extracted from the CPR database for the selected period (44 years of sampling), covering the UK shelf (Figure 1). Copepods and cladocerans were selected because they are important prey of many fish larvae, and identification is generally carried out to species or genus level (in other taxonomic groups, identification is limited to family or higher category). In all, 29 species, each contributing at least 0.1% of the total abundance in at least one of the five subareas, were retained for analysis. The 31 species excluded from the analysis made up <1% of total abundance (Table 2). The average monthly abundance of individual species was calculated for each subarea, taking into account diel variability of the CPR data (Beaugrand *et al.*, 2003b). Temporal smoothing was applied to monthly data to derive daily values. The CPR underestimates zooplankton abundance when compared with other datasets (Clark *et al.*, 2001; John *et al.*, 2001). To account for this, we corrected the data for undersampling by using WP-2/CPR ratios, as described in Pitois and Fox (2006). The CPR is inefficient at catching copepod nauplii, owing to its relatively large mesh size of 270  $\mu\text{m}$ , but these stages are important for first-feeding cod larvae (Fossum and Ellertsen, 1994). We used a production model to estimate nauplii abundance from adult abundance. Unfortunately, the CPR does not give adult numbers for any species of copepod, but rather combines C5 + C6 stages. We also assume here that females constitute 60% of the total adult population (Hirst and Lampitt, 1998). The model first calculates daily egg production estimated from fecundity values;

**Table 2.** List of species selected for our model in each area and their relative contribution to total abundance.

Species	Relative contribution to abundance (%)				
	Northern North Sea	Central North Sea	Southern North Sea	English Channel + Celtic Sea	Irish Sea + west of Scotland
<i>Calanus</i> 1–IV	4.1	2.6	0.7	1.7	1.9
<i>Pseudocalanus elongatus</i>	5.3	4.8	5.1	7.1	6.3
<i>Para-Pseudocalanus</i> spp.	22.8	24.8	26.1	37.9	26.1
<i>Temora longicornis</i>	11.6	11.1	23.7	6.9	5.4
<i>Acartia</i> spp.	20.3	13.6	15.6	12.2	26.6
<i>Centropages typicus</i>	0.3	0.5	0.4	1.5	0.5
<i>Centropages hamatus</i>	0.1	0.1	0.3	0.1	0.2
<i>Isias clavipes</i>	0	0	0.1	0	0.1
<i>Clausocalanus</i> spp.	0	0	0	1.7	0.4
<i>Oithona</i> spp.	20.6	26.4	14.7	21	21.5
<i>Corycaeus</i> spp.	0.1	1	1.6	2.4	0.4
<i>Podon</i> spp.	1.4	1.3	1.4	0.8	1
<i>Evadne</i> spp.	11.8	12.9	9.8	4.2	6.7
<i>Calanus finmarchicus</i>	0.7	0.3	0.1	0.1	0.2
<i>Calanus helgolandicus</i>	0.1	0.1	0.1	0.4	0.3
<i>Calanus hyperboreus</i>	0	0	0	0	0.1
<i>Calanoides carinatus</i>	0	0	0	0	0.1
<i>Eucalanus crassus</i>	0	0	0	0	0.1
<i>Euchirella rostrata</i>	0	0	0	0	0.1
<i>Euchaeta norvegica</i>	0	0	0	0	0.1
<i>Euchaeta acuta</i>	0	0	0	0	0.1
<i>Euchaeta hebes</i>	0	0	0	0.1	0.1
<i>Metridia lucens</i>	0.4	0.1	0.1	0.7	0.7
<i>Pleuromamma robusta</i>	0	0	0	0	0.1
<i>Candacia armata</i>	0	0	0	0.1	0.1
<i>Penilia</i> spp.	0	0.3	0.3	0.1	0.1
<i>Candacia</i> 1–IV	0	0	0	0.1	0.2
<i>Metridia</i> 1–IV	0.2	0.1	0.1	0.5	0.4
<i>Undeuchaeta plumosa</i>	0	0	0	0	0.1

fecundity values are defined here as the biomass of eggs produced per day by the biomass of females. Egg mortality was then calculated before the abundance of nauplii was estimated.

For adult broadcast-spawning zooplankton, fecundity rates are dependent on body weight, but independent of temperature, and for the egg-sac spawning zooplankton, fecundity rates are independent of body weight, but temperature-dependent. Fecundity was calculated for broadcast spawners ( $f_{bs}$ ,  $d^{-1}$ ) and egg-sac carriers ( $f_{sc}$ ,  $d^{-1}$ ) as follows:

$$\log_{10}(f_{bs}) = -0.6516 - 0.5244(\log_{10}BW), \quad (9)$$

$$\log_{10}(f_{sc}) = -1.7726 + 0.0385(T), \quad (10)$$

where  $T$  is the temperature ( $^{\circ}C$ ) and  $BW$  the adult female body weight ( $\mu g$  C ind. $^{-1}$ ), which is assumed to be equivalent to 40% of individual dry weight (Hirst and Lampitt, 1998). Individual species dry weights were converted from biovolumes calculated from published measurements (Pitois and Fox, 2006). Fecundity values were used to estimate egg biomass ( $\mu g$  C  $m^{-3}$ ) produced

per species per day and were then converted to egg abundance (eggs  $m^{-3}$ ) produced per species per day, by dividing the egg biomass by the carbon content ( $\mu g$  C egg $^{-1}$ ) of species-specific eggs (Kiørboe and Saiz, 1995). Egg carbon content data were extracted from the relationship between adult carbon weight and egg carbon weight:

$$\log_{10}(\text{EggCWeight}) = 0.674 \times (\text{AdultCWeight}) - 1.77. \quad (11)$$

Daily egg mortality rates for broadcast spawners ( $M_{bs}$ ,  $d^{-1}$ ) and egg-sac carriers ( $M_{sc}$ ,  $d^{-1}$ ) were calculated using the formulation of Hirst and Kiørboe (2002):

$$\log_e(M_{bs}) = 0.0730 \times T - 1.150, \quad (12)$$

$$\log_e(M_{sc}) = 0.0627 \times T - 3.040, \quad (13)$$

where  $T$  is the temperature ( $^{\circ}C$ ).

Nauplii abundances were converted to biomass using species-specific dry weights. Species-specific naupliar lengths

were estimated from the ICES identification Leaflets for Plankton (<http://www.ices.dk/products/ideaflets.asp>). For species where data on nauplii were missing, naupliar lengths were extrapolated from the relationship

$$\log_{10}(\text{Nlen}) = 0.77 \times \log_{10}(\text{Alen}) - 0.75, \quad (14)$$

where Alen ( $\mu\text{m}$ ) is the zooplankton adult length and Nlen ( $\mu\text{m}$ ) is the length of the corresponding naupliar stage.

We then used species-specific relationships between nauplii dry weight (NWgt,  $\mu\text{g}$ ) and length (Nlen,  $\mu\text{m}$ ) from the literature (Mauchline, 1998), to calculate as many values of nauplii species-specific dry weights as possible; otherwise, the following general relationship was used:

$$\log_{10}(\text{NWgt}) = 1.57 \times \log_{10}(\text{Nlen}) - 4.16. \quad (15)$$

### Sensitivity analysis

To test the functional responses over the range of prey, temperature, and light conditions used in the model, we performed simulation runs in which only one of the input variables was allowed to vary, keeping the others to their long-term average. We chose to distinguish between nauplii abundances calculated from the production model, and adult and juvenile zooplankton extracted from the CPR, resulting in a total of four parameters for the simulation runs. We also elected to vary the abundance of nauplii and other prey by  $\pm 20\%$  from the long-term average, down to 0 and up to twice the average value. Temperature and the proportion of daylight in the day were varied from their minimum value (i.e.  $1.5^\circ\text{C}$  and  $7/24$ , respectively) to their maximum value (i.e.  $14^\circ\text{C}$  and  $15/24$ , respectively) with  $1^\circ\text{C}$  and  $2/24$  increments, respectively.

## Results

### Sensitivity analysis

The sensitivity analysis shows that the best growth obtained from running the model is achieved under conditions of higher prey biomass and daylight proportion (i.e. the number of hours of daylight per day), and lower temperature (Figure 3). Very poor growth was obtained when the model was run with the biomass of nauplii fixed to its long-term average, regardless of other parameters (Figure 3a, c, and e). A relatively high biomass of the smallest prey is therefore essential for larvae to start feeding after hatching, because other zooplankton are too large to be selected by first-feeding cod larvae. This is well illustrated by the results obtained when the model was run under conditions of fixed light proportion (i.e. 11 h of daylight per day) and temperature (i.e.  $8.02^\circ\text{C}$ ; Figure 3b). Only when the larvae are large enough will juvenile and adult zooplankton become a more important part of their diet than nauplii. In contrast to nauplii, the biomass of adult and juvenile zooplankton is not required to be higher than its long-term mean to support good larval growth (Figure 3d and f).

### Temperature

Temperature patterns were consistent in all five areas: temperatures decreased from January to March and warmed in April through May (Figure 4a). Sea temperatures were highest in the English Channel and Celtic Sea, ranging from  $8.1^\circ\text{C}$  to  $13.3^\circ\text{C}$

throughout the entire period of study. The southern North Sea had the greatest intra-annual fluctuations, from a minimum of  $1.8^\circ\text{C}$  to a maximum of  $8.4^\circ\text{C}$  over the period of study. Cooler periods are evident in all regions during the early 1960s and 1975 and 1985, followed by warming from the late 1980s to the early 1990s. This feature is apparent in all regions, but particularly during April and May in the central and southern North Sea.

### Prey fields, size of prey, and biomass

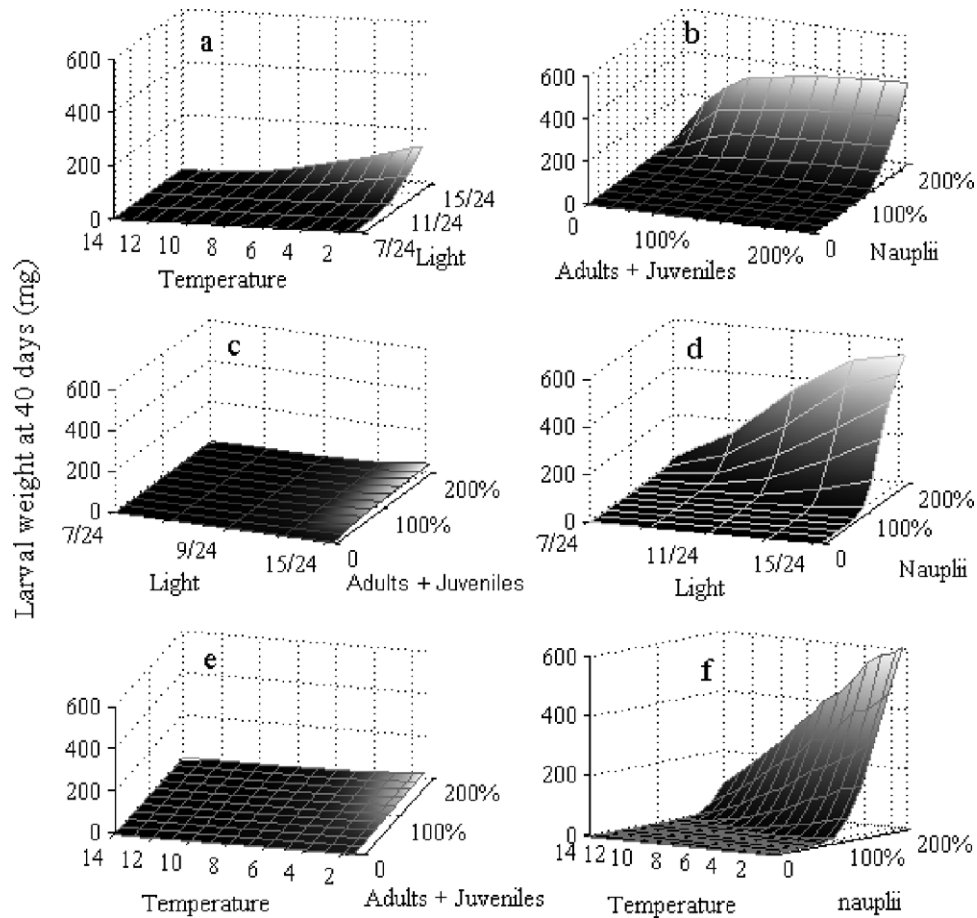
Total potential prey biomass was usually at its lowest in February (Figure 4b–d), coincident with the lowest temperatures. The biomass of adult/juvenile zooplankton and nauplii stages remained low from January to March, but increased during April and May. Only the months warm enough to sustain a substantial adult population exhibited good nauplii production, because nauplii production was calculated as a function of temperature and adult copepod biomass.

Throughout the period 1960–2002, there was quite high inter-annual variability in total zooplankton biomass for all months. Since the 1990s, zooplankton biomass appears to have decreased, particularly in the Irish Sea and the central North Sea, but such declines are not so obvious in other regions. Unfortunately missing CPR data for the southern North Sea for the period 1978–1986 meant that no estimate was possible for that period (Figure 4b–d). Overall, the highest levels of total biomass were in the southern North Sea, the English Channel and Celtic Sea, followed by the central North Sea. Total zooplankton biomass tended to be lowest in the northern North Sea, and in the Irish Sea and west of Scotland.

In all regions, prey mean dry weight was highest in February, coinciding with the lowest levels of nauplii production (Figure 4e). The lowest levels of adult and total biomass (i.e. adults + juveniles + nauplii) in the early 1980s were accompanied by higher mean dry weights, likely a consequence of temperatures being too low for substantial zooplankton production. Prey mean weight was usually higher in the northern North Sea than elsewhere. There was a general pattern of density-dependent prey growth, with high total prey biomass accompanied by low prey mean weight, and vice versa. This arises because lower prey biomass coincides with lower temperature and phytoplankton production, and consequently a very low concentration of nauplii. The relative contribution of adults and nauplii to total potential prey biomass is not constant in all subareas and across time. In January, nauplii and adults contribute roughly the same amount to total biomass in the northern and central North Sea, and nauplii contribute more in the southern North Sea, and in the English Channel and Celtic Sea. In February, adults always contribute most to total biomass. In March and April, nauplii contribute equally or more to total biomass. In the northern North Sea in March and April, adult prey generally contribute more to total biomass up to the early 1980s, whereupon the situation reverses, with nauplii contributing more to total biomass.

### Modelled growth of cod larvae

Larvae hatched in January either died or exhibited little growth (Figure 4f). In a few years, some growth was obtained in the southern North Sea in January 1992 and 2002, but larvae did not exceed 2.5 mg after 40 d. Positive growth was obtained for larvae hatched at the start of March in all but the two most northern areas (northern North Sea, and the Irish Sea and west of Scotland), but final weights were highly variable between regions.



**Figure 3.** Larval weight predicted from the model with the following simulation runs: (a) all species-specific prey abundances fixed to their long-term average values. (b) Temperature fixed to  $8.02^{\circ}\text{C}$ , daylight proportion fixed to 11/24. (c) Nauplii abundance kept to its long-term average, temperature =  $8.02^{\circ}\text{C}$ . (d) Adult + juvenile abundance kept to their long-term average, temperature =  $8.02^{\circ}\text{C}$ . (e) Nauplii abundance kept to its long-term average, daylight proportion fixed to 11/24. (f) Adult + juvenile abundance kept to their long-term average, daylight proportion fixed to 11/24.

In the central North Sea, growth was seen in 1998 only. In the southern North Sea, there was growth in a few years, in the early 1960s, in 1975 and from 1989 to 1996. The number of years per decade with good predicted larval growth in this region appears to have increased since the 1990s. In the English Channel and Celtic Sea, there was growth only in 1965.

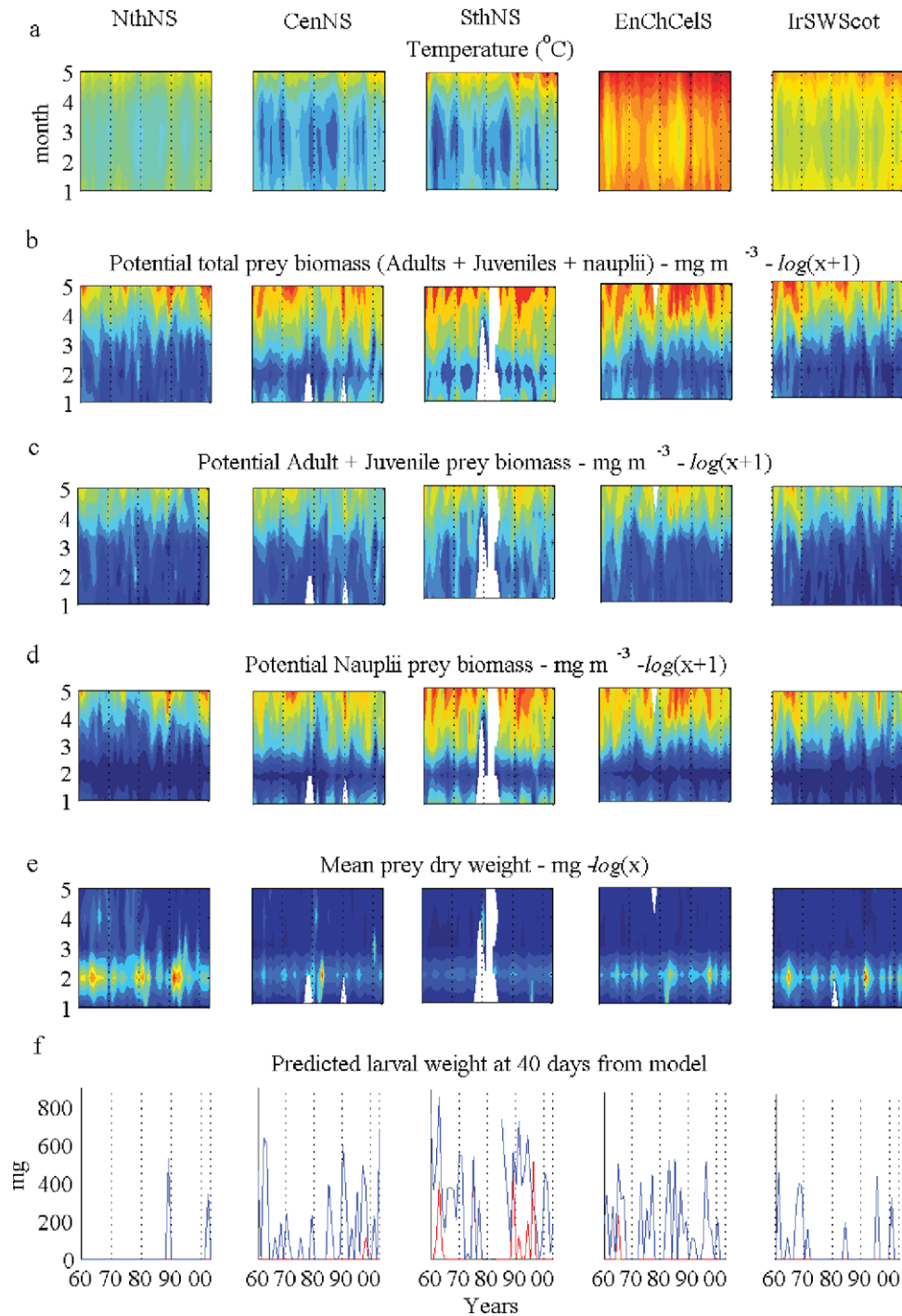
For larvae hatched at the start of April, better growth was predicted for all regions, the larvae often exceeding a weight of 400 mg after 40 d in the following subareas: central and southern North Sea, English Channel and Celtic Sea, and Irish Sea and west of Scotland. The northern North Sea was the only area with just two years of good predicted growth (1989 and 2002).

In all areas where growth was detected, the signal was irregular. In the North Sea subareas, there was a big drop in growth in the late 1970s and early 1980s, followed by a recovery in the late 1980s. This period of poor growth coincided with cooler temperatures and lower total prey biomass. Growth recovery in the three regions from the late 1980s was associated with increasing temperature and biomass. Although no growth was predicted, there was no obvious slowing of growth in the early 1980s in the Irish Sea and west of Scotland, just a succession of good and bad years. The trend in the English Channel and Celtic Sea was of

generally good growth for larvae hatched in April, with occasional poor years, including the period 1978–1981.

Data obtained from ICES assessment working groups (ICES, 2006a) indicate that recruitment and SSB has been in decline since the 1980s in the areas covering the North Sea, Skagerrak, Irish Sea, and west of Scotland (Figure 5). No significant relationship could be detected, from simple correlation analysis, between the results of predicted larval growth from the model in April and the number of recruits per year (northern North Sea:  $\rho = -0.16$ ,  $p = 0.33$ ; central North Sea:  $\rho = -0.10$ ,  $p = 0.55$ ; southern North Sea:  $\rho = -0.11$ ,  $p = 0.51$ ; English Channel and Celtic Sea:  $\rho = -0.11$ ,  $p = 0.56$ ; Irish Sea and west of Scotland:  $\rho = -0.25$ ,  $p = 0.22$ ; Figure 6).

Overall, the trophodynamic model predicted very poor conditions for the growth of cod larvae hatched in January and February in all areas. Larval growth was predicted to improve from March, with increasing prey availability. Modelled growth of cod larvae was strongly influenced by the biomass of prey available and by temperature acting via the rates of metabolic processes. Overall, the most consistent growth for the first 40 d of larval cod life (and hence survival) was predicted in April in the southern North Sea, and English Channel and



**Figure 4.** (a)–(e): Hovmoller diagrams of model variables at the time of running the model for the period 1960–2003 and months January–April/May. Colour varies from blue (low) to red (high), and no scale is indicated because interest is only in the variability. (f) Larval weight (mg) output from model after a 40-d run; the red line indicates the results obtained when the model run started on 1 March, and the blue line when the model run started on 1 April. Growth obtained when the model started in January and February was too weak to be seen on the plots.

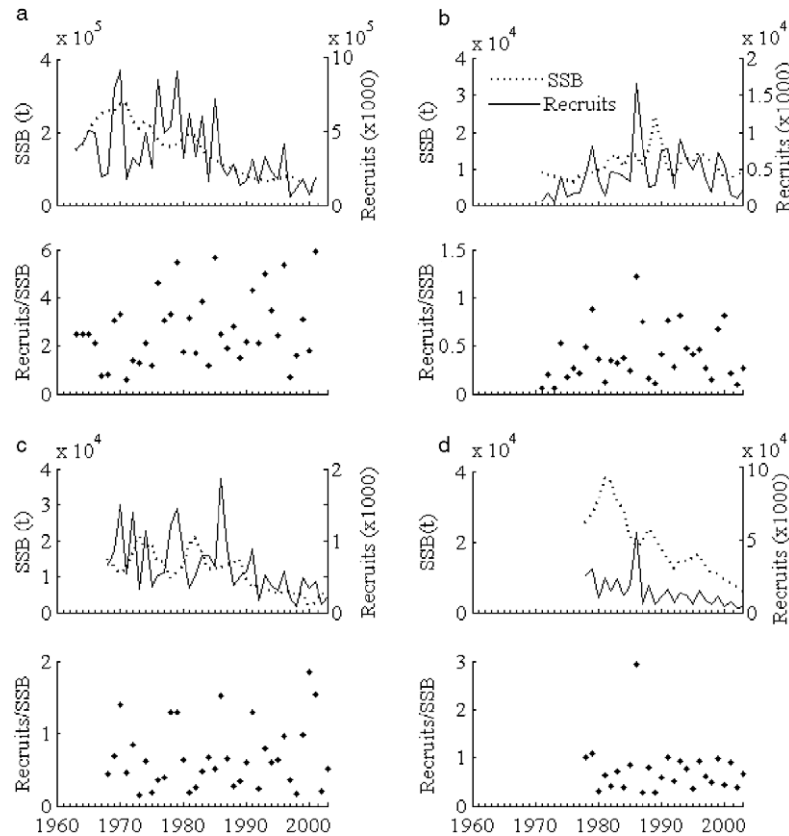
Celtic Sea subareas. On the one hand, lower temperatures tend to be beneficial to larval growth, but such conditions are usually associated with lesser abundance of prey, such as in winter. On the other hand, higher temperatures, which tend to be detrimental to larval growth through increased rates of metabolism, are usually associated with higher prey biomass.

There is therefore a trade-off between metabolic rate and prey availability.

### Discussion

Many studies have suggested that changes in the environment have either contributed to stock collapse or inhibited stock recovery



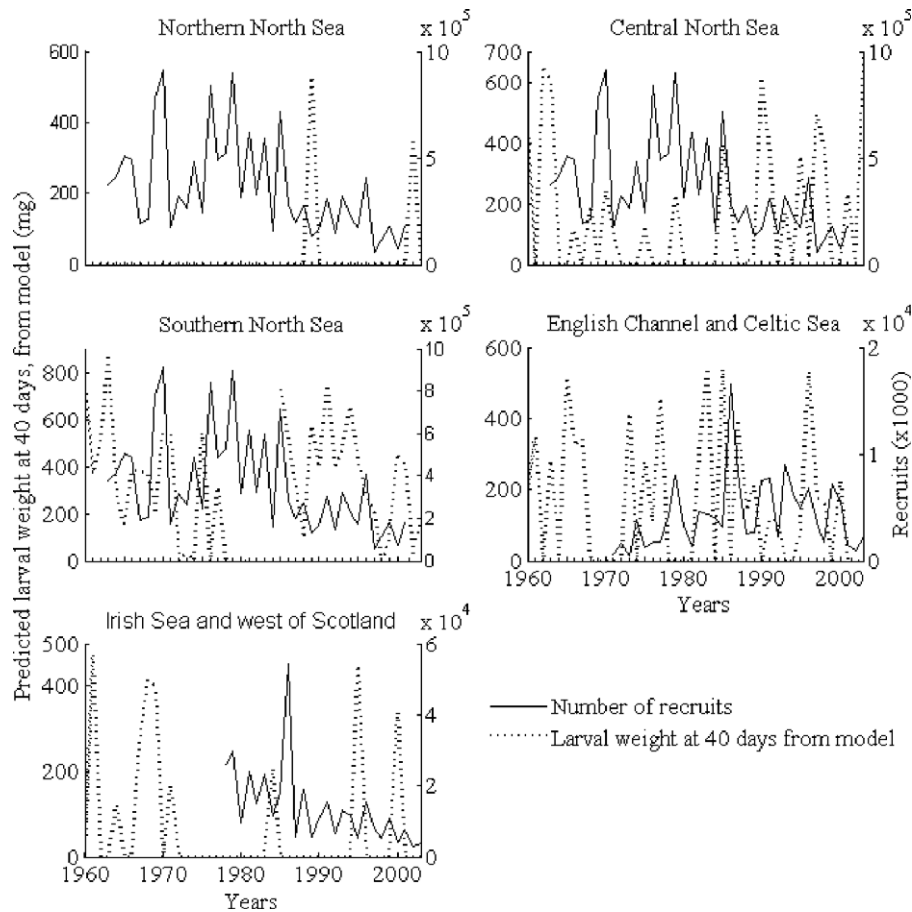


**Figure 5.** Data on spawning-stock biomass (SSB, t) and number of recruits aged 0 obtained from ICES (2006a, b, c) and plotted on the top panel of each of a–d. The bottom graph of each double panel of a–d is a scatterplot of the ratio of the number of recruits to SSB. (a) ICES Areas IIIa (Skagerrak), IV (North Sea), and VIId (Eastern Channel); (b) ICES Areas VIIe–k (Western Channel and south of Ireland); (c) ICES Area VIIa (Irish Sea); (d) ICES Area VIa (west of Scotland).

(Brander, 1997; Hutchings, 2000; Schiermeier, 2004). Changes in average recruit survival (recruits per spawner) can have a great impact on stock sustainability, and the influence of the environment on the survival of fish eggs, larvae, and juveniles remains a key theme in fisheries biology. Cod recruitment has been correlated with environmental factors for various stocks (Planque and Frédou, 1999; Brander and Mohn, 2004). Increased temperatures during the first 6 months of the year seem favourable for cod stocks at higher latitudes but detrimental to stocks at the southern limit (Planque and Frédou, 1999; O'Brien *et al.*, 2000; Sundby, 2000). In our model, the analysis with perturbation of parameters clearly shows that increased temperature is detrimental to growth of cod larvae (Figure 3). This is because temperature acts through the rates of metabolism only, and these increased with increasing temperature. However, temperature also acts on secondary production, higher temperatures leading to increased production of nauplii. The presence of these small prey items in concentrations greater than the long-term average is critical for first-feeding larvae to grow successfully. This trade-off between the direct detrimental effects and the indirect beneficial effects of temperature on larval growth is not seen in the sensitivity analysis.

Other more complex links between temperature and recruitment include trophodynamics, changes in foodwebs (Litzow *et al.*, 2006), shifts in the advection of eggs and larvae (Rindorf and Lewy, 2006), predation rates (Köster *et al.*, 2005), and disease (Harvell *et al.*, 2002). Of these, changes in prey availability

and factors affecting larval feeding success should be the easiest to test. This is indeed what we have attempted to do here. Many authors have reported a general decline in abundance of key species of zooplankton over the European Shelf in the period 1958–2002 based on data from the CPR (Lindley *et al.*, 1995; Reid and Edwards, 2001). However, except the Irish Sea and west of Scotland, such declines, based on observations (corrected for undersampling) from the CPR data, and therefore not including the estimated biomass of nauplii, are most significant for the warmer months of the year (June–October). This is particularly true for the North Sea, where the trend of such biomass throughout the study period remained roughly constant until August (Figure 7). When the biomass of nauplii estimated from the production model used here is added to the biomass measured from the CPR, declines can be significant from April/May to October. As the peak of cod spawning is thought to be in February in the southern areas and up to late March in the northern North Sea (Brander, 1994), conditions between March and June will be most relevant to larval growth and survival. When comparing the levels of available prey biomass for the period January–April (Figure 3b–d), there does not seem to have been any noticeable decline, except the Irish Sea and west of Scotland. We ran the model only for the four months stretching into May, so a general decline in biomass that affects the months from June to October would not have any detrimental effect on our larvae, except the Irish Sea and west of Scotland.

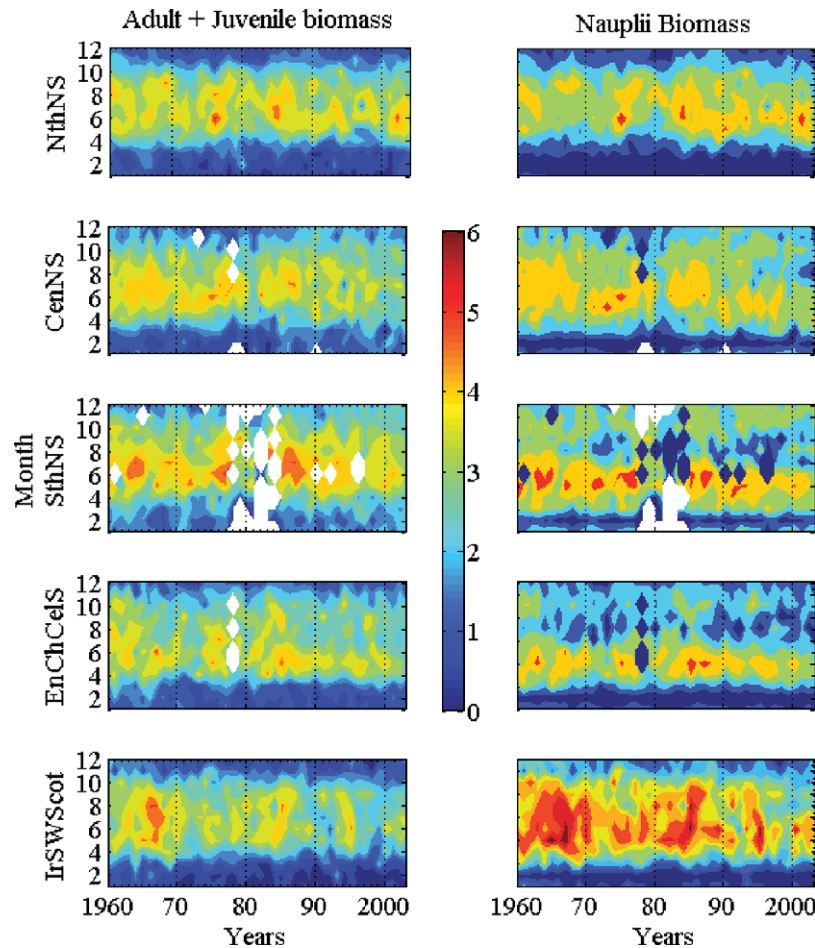


**Figure 6.** Larval weight (mg) predicted from the model and the number of recruits aged 0 as obtained from ICES (2006a, b, c).

Our model suggests that cod larvae grew poorly in the early 1980s in all areas, but in particular in the North Sea. This period was associated with both lower biomass of potential prey for the larvae and lower temperatures; this was particularly noticeable from as early as March/April (Figure 4). This was also a period of generally lower production of nauplii resulting in higher mean prey size, which would disadvantage first-feeding larvae. The 1980s and early 1990s were associated with many dramatic changes in abundance and composition of plankton and fish that were of a sufficiently large scale to be referred to as a regime shift (Reid *et al.*, 2001; Beaugrand, 2004b), and the period reflected a shift in the ecosystem towards a warmer dynamic equilibrium (Reid and Edwards, 2001; Beaugrand *et al.*, 2002; Beaugrand, 2004a; Beaugrand and Ibañez, 2004). Analysis by Pitois and Fox (2006) suggests that the decrease in the early 1980s, followed by the subsequent partial recovery, affected most species. The results show reorganization within zooplankton communities through changes in mean size. In particular, mean zooplankton size peaked in the early 1980s, coinciding with the cold episodic event, followed by a sudden drop in the late 1980s and early 1990s, coinciding with the warm episodic event, and a steady recovery thereafter. Indeed, in the northern areas of the North Sea, prey dry weight displayed a generally decreasing trend from 1960 to 2002 (Figure 3e). A decrease in prey size would be beneficial to smaller larvae, so helping the earlier

stages to feed and grow, and compensating for the increase in temperature. Beaugrand *et al.* (2003a) reported that the regime shift that started in the mid-1980s radically changed the food environment for larval cod, and this is reflected in North Sea cod year-class strength. They concluded that rising temperatures since the mid-1980s modified the plankton ecosystem in a way that reduced the survival of young cod. Our results do not show a decrease of predicted larval growth after the 1980s, and if anything, it seems that larvae grew better after the 1980s in the central North Sea (Figure 4f). At first sight, our results seem to contradict those of Beaugrand *et al.* (2003a). However, our model is only applicable to the very first stages of larval growth, whereas the results of Beaugrand *et al.* (2003a), which included calanoid copepods and euphausiids but not the earliest stages of zooplankton, could apply more to later stages of larval growth.

This period of poor predicted growth in the early 1980s coincides with the recruitment of several very good year classes of cod (Figure 6). This is an unexpected result because we would expect years of good growth to coincide with years of large number of recruits aged 0. This paradoxical result highlights the complexity of untangling the mechanisms behind the biology of first-feeding larvae. In this specific case, it is clear that the larvae seem able to cope and survive well in an environment that seems to be poor in terms of prey biomass. It could be that the larvae can switch to other types of food not taken into account



**Figure 7.** Hovmöller diagrams of monthly potential prey biomass for the period 1960–2003 in each of the five model subareas. Biomass values are in  $\text{mg m}^{-3}$  and transformed to  $\log_{10}(x + 1)$ .

in this model. Alternatively, perhaps natural predators of cod larvae may have been affected by poor conditions, reducing predatory pressure on the larvae.

Although growth was predicted to recover from the early 1990s on, at least in the central and southern North Sea, and in the English Channel and Celtic Sea, this coincided with a continuing decreasing trend in the number of age-0 recruits in all areas (Figures 5 and 6), and no positive correlation between years of good growth and years of good recruitment. In this case, we might be able to suggest that although the larvae grow well for the first 40 d, the model gives us no idea about what happens after 40 d, when the larvae start to switch to prey types not included in our study. This result suggests that the stages not covered here may also be critical in promoting good or poor recruitment of cod. Calculating and plotting the ratio of the number of recruits to SSB indicates that this value has undergone a constant (Irish Sea and west of Scotland) or even rising trend (North Sea, Skagerrak, English Channel and Celtic Sea; Figure 5). This rising recruitment/SSB ratio indicates that SSB has been falling relatively quicker than the number of recruits produced, possibly as a result of removal of adult fish by fishing.

The results from our model do not demonstrate any obvious adverse effect of combined changes in temperature and prey environment on the growth of cod larvae. Although rising temperatures are directly detrimental to larval growth via increased

metabolic rates, this is compensated for by increased production of nauplii and a generally decreasing prey weight, which is beneficial to the growth of the earliest larval stages. This, combined with the trend in recruitment/SSB ratio throughout the period of study, suggests that changes in prey availability and temperature within the range seen over the UK shelf during the past 50 years seem to have had little overall negative effect on North Sea cod recovery, at least in the short term. Recovery seems therefore to be dependent upon conserving the year classes recruited and allowing cod to survive to a reproductive age, rather than on larval survival *per se*. Cardinale and Svedäng (2004) further demonstrated that it was fishing pressure and not variable environment via recruitment that was the pivotal variable explaining the dynamics of the Skagerrak–Kattegat (North Sea) cod stock. They concluded that collapse and extinction of marine commercial fish populations is not attributable to the environment via recruitment, but to unsustainable fishing pressure.

#### Limitations of the model

The model was run assuming that each subarea was homogeneous in term of environmental conditions on both horizontal and vertical scales. In addition, we assumed that cod larvae and their prey remain at a depth of 10 m, which is the sampling depth of the CPR. In natural conditions, zooplankton are distributed heterogeneously, and both prey and predators undertake vertical

migration (Mackas *et al.*, 1985; Solow and Steele, 1995; Brentnall *et al.*, 2003; Frank *et al.*, 2005). Processes that drive patchiness may be physical (e.g. turbulence) and biological (e.g. diel vertical migration, predator avoidance, hunting for food, mating) (Folt and Burns, 1999). A model for patch and prey encounters was presented by Pitchford and Brindley (2001), and it led to the conclusion that prey patchiness increases individual variance in predator–prey encounter rates. In low-food environments, increased stochasticity resulting from the effect of prey patchiness on encounter rates was beneficial to recruitment, but the effect was reversed in environments richer in food. Patchiness does seem to have an important influence, and should indeed be taken into account in predator–prey encounter rates. In particular, predicted larval growth during the cooler months might improve if prey patchiness was taken into account.

The model was run for the first 40 d of larval life only, after which the larvae start to feed on other larger prey, such as euphausiids. In future work, larger prey should be included, so as to extend the duration of the model.

Clearly, the bioenergetic model and the production model lack adequate data for validation purposes, and substantial parameterization would need to be undertaken, to reduce the number of assumptions and deterministic relationships. Both would require monitoring surveys and laboratory experimentation. It is obvious that current observational data are inadequate for the type of work we have attempted here, and Heath and Lough (2007), in their re-assessment of the predation loading on zooplankton by fish in the North Sea, concluded that a fresh look at estimating North Sea zooplankton production was required. Our results support this contention.

## Conclusions

Modelled growth of cod larvae was heavily influenced by the biomass of prey available and temperature, and in particular the biomass of the smallest prey available (i.e. nauplii) was critical for the growth of the earliest stages of cod larvae. We were forced to model the production of nauplii, and this production was also strongly affected by temperature. Warmer years within a region tended to generate enhanced production and prey biomass, particularly in April and May. Although temperature had a direct detrimental effect on the growth of larvae, through increased metabolic rates, good growth rates of cod larvae tended to be associated with warmer periods, as a result of higher prey biomass in general and higher nauplii production and biomass in particular.

We were unable to find any correlation between years of good predicted growth from our model and good years for cod recruitment. Similarly, we failed to find a correlation between years of poor predicted growth and low recruitment, highlighting the complexity of the mechanisms involved in the biology of first-feeding cod larvae. Although there has been a general decline in zooplankton biomass in the Northeast Atlantic over the past two decades, we were unable to show that this would have had a consistently detrimental effect on the growth of cod larvae hatched at the peak of spawning. Growth and survival of cod larvae hatched before March may be highly dependent on small-scale patchiness in prey and environment. If, as our model suggests, cod larvae can survive well in the present environment, reductions in fishing effort combined with technical measures that reduce the overall mortality of cod would promote stock recovery.

In light of the weaknesses associated with our modelling approach, explained above, and the many assumptions we have had to make to allow this model to run, one has to be cautious when interpreting the results. We did not aim to make predictions of larval growth on a small scale, but rather attempted to evaluate the better general conditions for first-feeding cod larvae and compare them over the UK shelf for the past 50 years. Our aim was to detect whether food conditions and temperature may have had a detrimental effect on the survival of first-feeding cod larvae, because this has been shown in the literature using correlations between CPR data and fish recruitment (Beaugrand *et al.*, 2003a). Our approach is novel, but it does show that there is no simple link between cod recruitment and climate effects via changes in the plankton.

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