



## Modeling growth of larval cod (*Gadus morhua*) in large-scale seasonal and latitudinal environmental gradients

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### ARTICLE INFO

#### Article history:

Accepted 12 November 2008

Available online 3 December 2008

#### Keywords:

Biophysical modeling  
Larval fish  
Northeast Arctic cod  
Latitudinal gradients  
Spawning strategies

### ABSTRACT

The spawning strategy of cod has evolved through natural selection to give larvae a good start in life. Therefore, larval drift, growth, and survival are key processes to understand spawning strategies. Spawning of Northeast Arctic (NA) cod stretches from late February to early May over 1500 km along the Norwegian coast. Hatching occurs from late March to late May, a period when the number of daylight hours increases from 11 to 17. Larval feeding opportunities are constrained by prey abundance and environmental variables such as light, while temperature determines the maximum growth potential. Here, we model seasonal and latitudinal constraints on larval cod growth by combining predictions from a bio-physically coupled model providing input on nauplii production and development (*Calanus finmarchicus*), a 3D physical model (ROMS) providing flow- and temperature-fields, and an individual-based model (IBM) of larval cod physiology and feeding processes. Our aim is to investigate the relative significance of temperature, turbulence, light, and prey density on growth of larval cod by integrative modeling. The models suggest that larval cod experience lower growth if hatched early in the season (prior to mid-April) when the foraging hours are few. Larval cod hatched in early May experience higher temperatures, better growth conditions, and are less susceptible to prey limitation due to increased day-length. We also suggest that increased prey abundance is more valuable early in the spawning season compared to later, when larvae have better feeding conditions. The model quantifies the strong relationship between larval feeding and growth in relation to day-length, time of the season, and water temperature, and the seasonal and spatial appearance of prey.

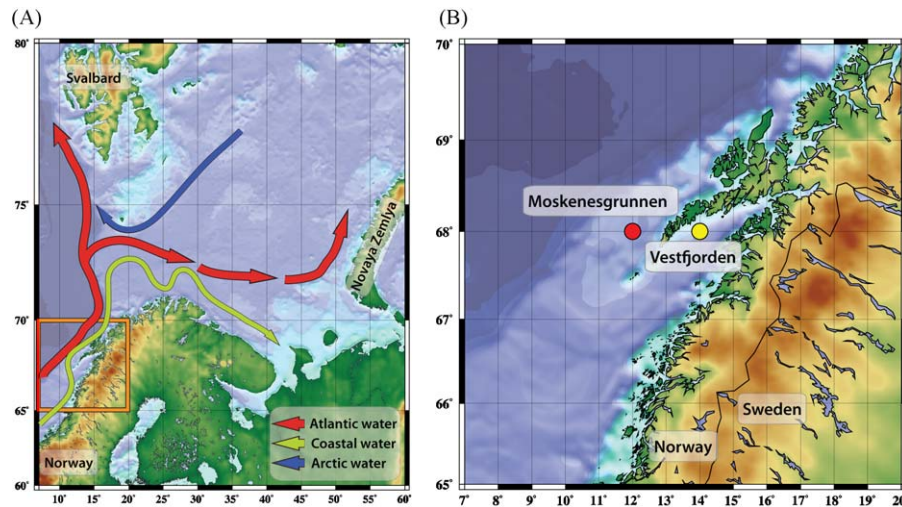
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### 1. Introduction

The spawning strategy of cod has been fine-tuned through generations to maximize offspring survival. Larval cod needs food to grow and survive and the combination and timing between larval hatching, geographical location, and the conditions of the environment they enter create boundaries for larval growth and survival (Jørgensen et al., 2008). Just after hatching, larval cod are able to sustain metabolic demands through their yolk-sac reserves, but after a few days (Fossum and Ellertsen, 1994) the larva needs to switch from endogenous to exogenous feeding. The transition from internal energy reserves to external feeding is regarded as a critical period for first-feeding larval survival (Hjort, 1914), and feeding success may continue to constrain survival throughout their pelagic phase (Cushing, 1990). First-feeding fish larvae are restricted to forage upon prey smaller

than their gape size (Puvanendran et al., 2004), and encounters between larvae and prey are strongly determined by light and turbulence (Fiksen et al., 1998). In addition, it is vital to the larvae to be placed in a favorable time-space location with regards to prey concentration. Along the coast of Norway it is important for larval cod to hatch during peak abundance of *Calanus finmarchicus* which is their main prey item (Sundby, 2000). However, the timing of the spring bloom and the peak in copepod nauplii availability along the Norwegian coast varies substantially between years (Ellertsen et al., 1989). This may be one reason why NA cod spawn over 2.5 months (at the population level) or 1.5–2 months for individual fish (Kjesbu et al., 1996), since it increases the likelihood that at least some larvae match the prey peak. This is a relatively long period in a spring-bloom marine ecosystem. Still, high prey abundance seems to be a requirement, but not sufficient condition to ensure rapid growth and high survival of larval cod (Buckley and Durbin, 2006), and abiotic factors such as temperature (Otterlei et al., 1999; Ottersen et al., 2001; Folkvord, 2005), turbulence (Sundby and Fossum, 1990; Sundby et al., 1994), and light conditions (Blaxter, 1986; Aksnes and Utne, 1997) modify physiological rates, feeding

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**Fig. 1.** (A) Map of the Lofoten area and the major current systems; the warm and saline Norwegian Atlantic Current (NAC, red), the less saline, cooler Norwegian Coastal Current (NCC, green). (B) Map of the Lofoten area with Moskenesgrunnen marked as red circle and Vestfjorden marked as yellow circle.

conditions, and the interaction between larval cod and their predators.

The NA cod stock spawns along a 1500 km coastline from southwestern parts of Norway ( $\sim 60^\circ\text{N}$ ) to the Finnmark coast ( $\sim 71^\circ\text{N}$ ) (Fig. 1) (Bergstad et al., 1987). The majority (60–70% for the period 1983–1985 (Ellertsen et al., 1989)) of spawned cod eggs are found in the Lofoten and Vesterålen areas ( $68\text{--}69^\circ\text{N}$ ) (Sundby and Bratland, 1987). Spawning starts at the end of February and lasts until early May. Based on egg samples collected using net hauls from 1968 to 1982 in the traditional spawning areas in Lofoten ( $\sim 68^\circ\text{N}$ ), Pedersen (1984) found mean peak spawning of NA cod to occur during transition from March to April. At the Møre spawning ground ( $\sim 62^\circ\text{N}$ ) peak spawning occurs at about the same time as in Lofoten (Godø and Sunnanå, 1985), while there is a progressive delay in peak spawning with increasing latitude from Lofoten. Hence, the spawning is about 2 weeks later at the Finnmark coast ( $\sim 71^\circ\text{N}$ ) than in Lofoten (Sundby and Bratland, 1987). Larger and older cod tend to have longer spawning periods (Kjesbu et al., 1996). An individual female cod spawns 15–20 batches of eggs over a period of 1.5–2 months. Mature, older cod tend to arrive earlier at the spawning sites than the younger ones (Solemdal and Sundby, 1981), however, the time of spawning may also be influenced by water temperature (Kjesbu, 1994). The developmental time of the egg into larva is typically 20–35 days (Pepin et al., 1997).

The number of daylight hours increases from 13 (April 1) to 17 (May 1) and 21 (June 1,  $68^\circ\text{N}$ ) (Fig. 2). This constrains the number of hours available to feeding for newly hatched larvae, and may influence growth and survival. The objective of this study is to investigate the significance of temperature, turbulence, light conditions, and prey density on growth of larval cod for different spawning strategies by integrative modeling. Our model of larval cod growth conditions is driven by output from two models; (i) a general circulation model (GCM) (Vikebø et al., 2005) and (ii) prey fields generated using a zooplankton model (Huse, 2005). The oceanographic conditions (i) and prey fields (ii) are used as forcing for an individual-based model (IBM) for larval cod (Kristiansen et al., 2007). The models allow us to explore the effects of day-length, prey abundance, water temperature, turbulence, and spawning ground on daily growth of larval and juvenile cod along the Northern coast of Norway. All simulations were repeated for two sizes (standard length, SL) of larval cod; 5 mm which is the

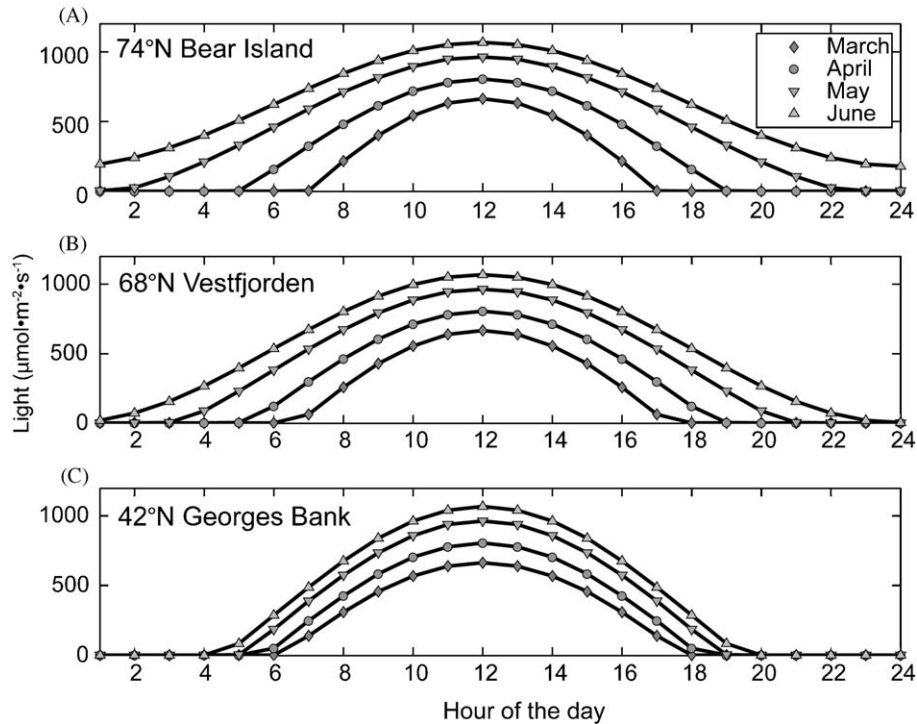
typical size of a larva after the yolk-sac stage (Ellertsen et al., 1989), and 7 mm. We then address the questions: How sensitive is larval growth to prey abundance at different times of the season? What is the prey requirement for maximum (or minimum) growth, and does it differ between spawning grounds? How could this influence the spawning strategies and recruitment variability of NA cod?

## 2. Models

Forcing an IBM with oceanographic conditions, seasonal and latitudinal irradiance, and the output from a zooplankton model covering the same domain allow us to integrate processes at different scales. Combined, these models provide an effective tool to study interactions that emerge between processes important for larval growth. The GCM provides information on the abiotic conditions at the location of each individual. However, only water temperature is utilized in this study. Turbulence is estimated as a function of the surface wind stress (MacKenzie and Leggett, 1993). Along with modeled values of irradiance (Skartveit and Olseth, 1988) these variables change with longitude, latitude, depth, and time of day. The IBM is comprised of a mechanistic feeding module and a bioenergetics module.

### 2.1. The ocean model

The regional circulation model used is ROMS (<http://www.myroms.org/>; Haidvogel et al., 2008), a 3D, free-surface, terrain-following, primitive equations ocean model. Lateral boundary conditions are taken from a monthly mean climatology (Engedahl et al., 1998), while atmospheric forcing are based on NCEP daily mean sea level pressure, wind stress, and heat flux (Kalnay, 1996) for the year 1995. The horizontal resolution increased from about 3.5 km at the southern boundary to about 8 km in the north. The vertical is represented by 25 terrain-following vertical levels (Haidvogel et al., 2008). Horizontal viscosity and diffusivity is parameterized by biharmonic mixing on geopotential surfaces (Haidvogel and Beckmann, 1999). Vertical viscosity and diffusivity is parameterized by generic length scale. However, the turbulence level of importance for the pelagic larvae is for simplicity estimated as a function of surface wind speed



**Fig. 2.** Relative amount of surface light as a function of time of the day for March 1, April 1, May 1, and June 1 for the geographical locations; 74°N (Bear Island), 68°N (Vestfjorden), and 42°N (Georges Bank, US).

according to MacKenzie and Leggett (1993):

$$\varepsilon = 5.82 \times 10^{-6} W^3 / z$$

where  $\varepsilon$  is the turbulence level ( $\text{W m}^{-3}$ ),  $W$  the wind speed ( $\text{m s}^{-1}$ ) and  $z$  the depth (m).

## 2.2. The larval IBM

The individual-based model of larval growth, prey encounter rate and capture success is adopted from Kristiansen et al. (2007). The encounter rate between predator and prey is a function of prey availability, with particular emphasis on how light regulates search efficiency in larval fish (Fiksen and MacKenzie, 2002; Kristiansen et al., 2007). Light varies with depth, day of the year, and hour of the day and strongly affects the visibility of prey in the water column (Fiksen et al., 1998). Larval growth is modeled from standard biological processes including digestion, metabolism, and growth, all allometric, temperature-dependent formulations that have been independently validated in laboratory studies and mesocosms (Fiksen and MacKenzie, 2002; Kristiansen et al., 2007). Here, we present immediate daily growth rates of larvae at different times and locations along the potential range of occurrence. In the following we define *maximum growth rate* as the growth rate achieved under food-satiated conditions, when temperature (and body size) is the only limiting factor (Folkvord, 2005). The modeling here does not address drift of the larvae, but focuses on how seasonal and latitudinal gradients in temperature, light and prey availability constrain larval growth opportunities. Drift and particle tracking for these larvae has been treated elsewhere (Fiksen et al., 2007; Vikebø et al., 2007).

## 2.3. The prey field

The nauplii fields were taken from a *C. finmarchicus* IBM for the Norwegian Sea (Huse, 2005). Attribute and strategy vectors

specify the states of the individuals and their behavioral and life history strategies, respectively (Chambers and Trippel, 1997; Huse et al., 1999, 2002). The attribute vector (Huse et al., 1999) of individuals consists of eight different states including their stage, internal number, weight, fat level, age, depth, position. The strategy vector (Huse et al., 1999) which is evolved, comprises six behavioral and life history traits. The life history traits include the date for ascent from overwintering to the surface, the day for initiating fat allocation in copepodite stage 5, fat/soma ratio needed before descending to overwintering depth, and two genes that determine the day-time depth of copepodites and adults outside of overwintering. The life history traits are initiated randomly and evolved over a hundred year period in a process that corresponds to spin up time in ocean circulation modeling. Even though the individual-based structure is appealing, it is impossible to simulate copepod population dynamics on a truly individual basis due to the great abundances involved, and the entire *C. finmarchicus* in the Norwegian Sea is therefore simulated using the super-individual approach (Scheffer et al., 1995). A super-individual represents many identical individuals and the number of such identical siblings is an attribute of the super-individual. Input data on light, temperature and phytoplankton biomass were taken from a model system involving the Regional Ocean Model System (ROMS) (Haidvogel et al., 2000) and the NORWECOM phytoplankton model (Aksnes et al., 1995). Three-day fields were interpolated linearly to daily values. Hourly surface light was generated from a model giving hourly sun height above the horizon (Skartveit and Olseth, 1988). The model domain is the Nordic Seas, with a 20 km horizontal resolution and a 1 m vertical resolution. The fields are interpolated to the GCM domain (see above). Presently, fields of all the *C. finmarchicus* nauplii stages combined were used as prey field for the cod larvae. However, the maximum and minimum concentrations of prey estimated from the model were scaled to 0–10 nauplii  $\text{L}^{-1}$  for simplification. Simulations of larval feeding did not feed back on the zooplankton prey abundance. In total, we performed 4 model

experiments. In experiments 1–3 we varied the nauplii concentration systematically between 0 and 10 nauplii  $L^{-1}$ . This allows us to disentangle effects of prey concentration and water temperature. In experiment 4 we used prey fields from the 3D model for the model year 1982.

#### 2.4. Model experiments

The first two experiments address growth of larval cod at two of the major spawning sites along the coast of Northern Norway, the Moskenesgrunnen and Vestfjorden (Fig. 1). Moskenesgrunnen (68°N, 12°E) is located near the shelf break at the border area between the Norwegian Atlantic Current (NAC) and the Norwegian Coastal Current (NCC), while the spawning areas in Vestfjorden (68°N, 14°E) are found in the cooler inner branch of the NCC. Moskenesgrunnen is exposed to the open ocean with high current speeds and strong mixing, while Vestfjorden is a somewhat more sheltered coastal location with lower advection. Growth rate is estimated as the relative increase in body weight per hour. Daily mean growth rates are estimated by averaging hourly growth rate over a 24-h period, and are computed for each day in the period March 1–May 1. Larvae are kept at fixed depths of either 10 or 30 m. To explore the relative importance of light, temperature, and prey abundance we split the simulations into two distinct experiments.

- *Experiment 1*: Growth as a function of prey density, depth, and time in the season (surface irradiance)—keeping temperature fixed.
  - *Experiment 2*: Growth as a function of prey density, depth, and time in the season (surface irradiance)—adding the seasonal temperature.
- Next, we focus on how growth rates vary in the entire model domain, which stretches from 63 to 80°N and –5 to 25°E, as the environmental conditions change during spring. We select two specific days, April 1 and May 1, and calculate daily growth rates (hourly growth rates integrated over 24 h) of larvae at fixed depth (10 m) over the entire model domain for 5 (86  $\mu$ g dry-weight) and 7 mm (285  $\mu$ g dry-weight) larvae with 30% gut fullness as a function of local irradiance, temperature, and prey density. We also do a simple sensitivity analysis of the effect of wind at surface (turbulence), and two levels of prey density (2 and 5 prey  $L^{-1}$ ).
- *Experiment 3*: Growth in the whole model domain at different dates (April 1 and May 1) for two fixed levels of prey concentration, turbulence and larval size.
  - *Experiment 4*: Growth in the whole model domain at different dates (April 1 and May 1) for two fixed levels of turbulence and larval size—with modeled distribution and abundance of nauplii prey.

### 3. Results

#### 3.1. Experiment 1

Simulations with constant temperature demonstrate the effect of day-length on growth rates for 5 and 7 mm larval cod (Fig. 3). The gut run empty at night during early spring due to the many dark-hours, resulting in negative larval growth during parts of the night and early morning. Maximum growth rates (which are higher for 7 than 5 mm larvae (see Folkvord, 2005) are therefore never achieved during March, even with prey abundance of 10 nauplii  $L^{-1}$ . Subsequently, larval growth during March and most of April are light-limited (Table 1). By the end of April, nights

are sufficiently short for larval growth to approach maximum growth for prey abundances above about 3–5 nauplii  $L^{-1}$  (Fig. 3). Moskenesgrunnen are typically characterized by higher sea-temperatures than at the inner spawning sites in Vestfjorden. In April temperature at Moskenesgrunnen is typically 2–3 °C warmer than at Vestfjorden (Sundby and Bratland, 1987). In May the temperature differences are smaller, typically 0–1.5 °C. The result is an increase in energy demand to sustain maximum growth rates at Moskenesgrunnen compared to Vestfjorden, but the growth potential is higher at Moskenesgrunnen (Fig. 3).

Inter-annual variation in temperature is observed in the Lofoten area, e.g. average surface temperature in 1981 reached a low of 1.6 °C, while in 1983 temperature was measured to 3.6 °C (Ellertsen et al., 1989). When we increased the temperature by 2 °C, the energy needed to sustain metabolism and potential growth increased slightly.

#### 3.2. Experiment 2

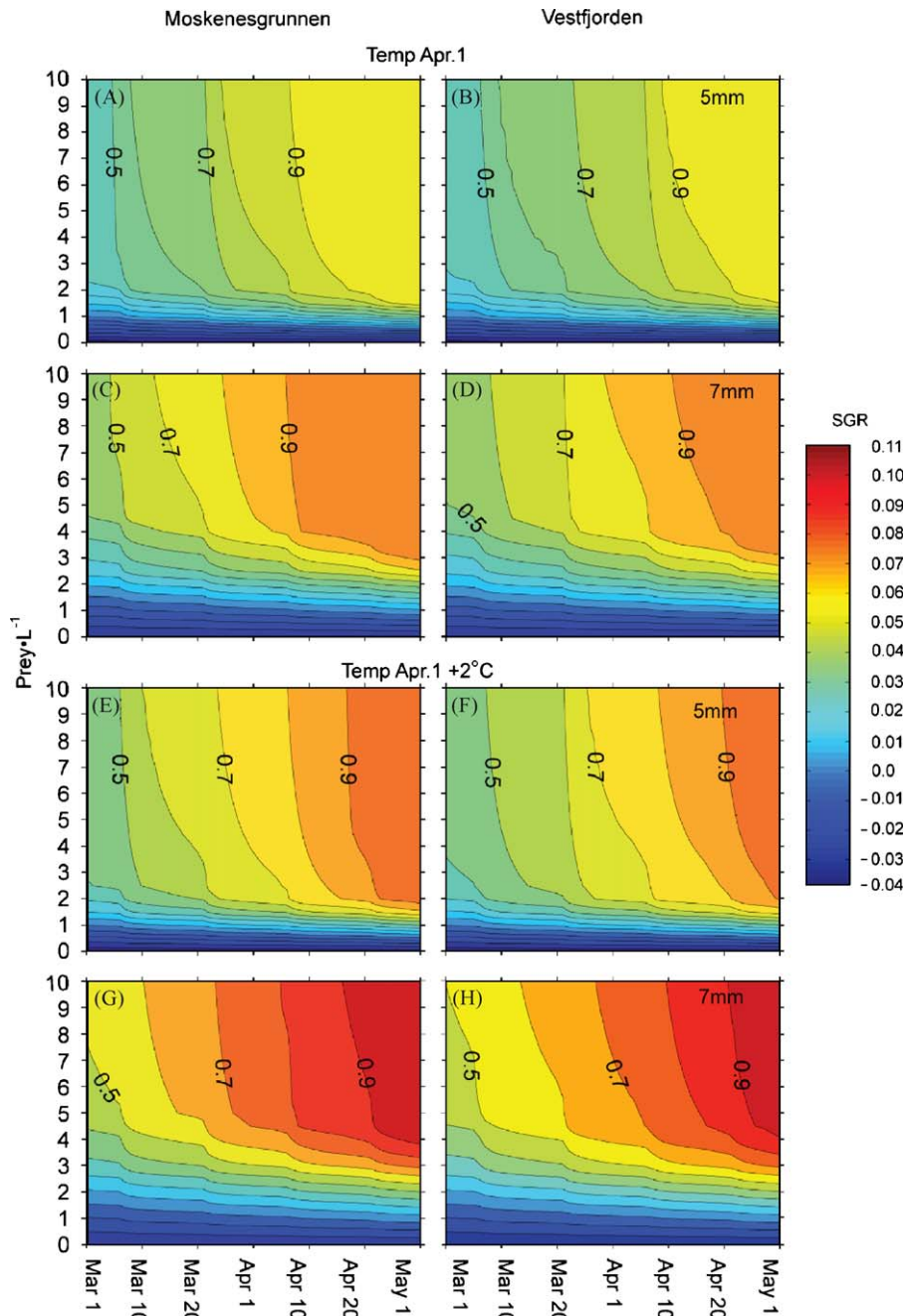
When we use daily temperatures predicted by the GCM, growth rates are driven by both the seasonal increase in temperature and day-length. The main pattern from Fig. 3 remains, indicating that light is the dominant driver for growth variations over temperature. The variation in temperature is relatively low during April and May for both Moskenesgrunnen and Vestfjorden (range 3–4.5 °C) relative to the increase in daylight hours. Light decreases exponentially with depth leading to reduced visibility and prey encounter rate at 30 m (Fig. 4E–H). This makes larval growth at this depth more dependent on prey concentration, especially for 7 mm long large larvae, which have the highest growth potential.

#### 3.3. Experiment 3

We next present growth rate of 5 and 7 mm larval cod at discrete, fixed points in the whole model domain matching the resolution of the GCM, repeating the simulations with 2 and 5 prey  $L^{-1}$ , with and without turbulence, for April 1 and May 1. Areas of high temperature-dependent growth rates (Figs. 5A and 6A) follow warm Atlantic Water masses, and decrease with increasing latitude. The number of hours available for larval feeding increases from 13 at April 1 to 17 at May 1 (68°N, Fig. 2). Growth rate is therefore less sensitive to increasing prey density or turbulence at this time of the year, since the long night limit growth (Fig. 5). Contrary, light is not limiting larval cod feeding in early May (Fig. 6). The potential growth rates increases from April to May with increasing sea-temperatures. In early May, the growth rate of a 5 mm larval cod reach its maximum growth when prey density exceeds about 2 nauplii  $L^{-1}$ . However, as physiological growth rates increase with the size, a prey density of 2 nauplii  $L^{-1}$  is not enough to sustain maximum growth rates of a 7 mm larva (Fig. 7B). The 7 mm larva needs prey density of about 5 nauplii  $L^{-1}$  (Fig. 7C). This may also be accomplished by introducing a favorable turbulence level, here induced by surface winds of 10  $m s^{-1}$  (Fig. 7D), increasing encounter rate between predator and prey 2–3-fold relative to calm conditions.

#### 3.4. Experiment 4

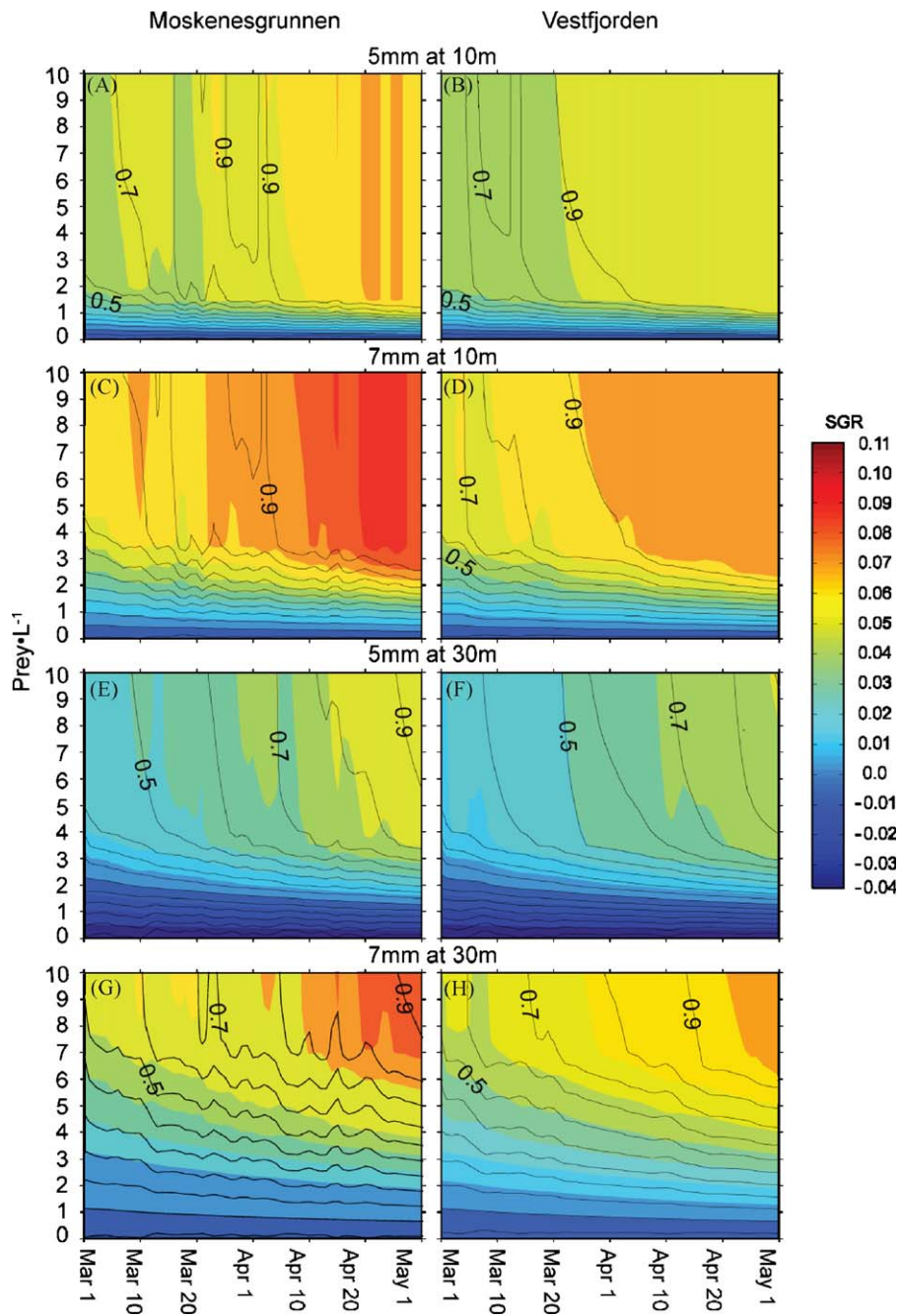
Experiments 1–3 used homogeneous prey fields, with no spatial or temporal variability. In the final experiment we add the prey fields predicted by the model of *C. finmarchicus* egg production, stage propagation, and spatial distribution (Fig. 8A, B).



**Fig. 3.** Colors indicate specific growth rates [ $g \cdot g^{-1} \cdot day^{-1}$ ] (same scale for all panels), while contour lines show the ratio between realized and maximum temperature-dependent growth rates at each date and prey density. Since temperature is the same at all times in this realization, absolute and relative rates reveal the same pattern. Growth rates are shown for 5 and 7 mm larvae fixed at 10 m depth at two locations; Moskenesgrunnen and Vestfjorden. Temperature is fixed to modeled value of April 1 at 10 m depth (upper four panels). The lower four panels show the effect of elevating the temperature by 2 °C.

**Table 1**  
Ratio of realized model growth rates to maximum growth rate of a larva size 5 mm.

Copepod ( $L^{-1}$ )	Temperature	Max growth ( $g \cdot g^{-1} \cdot day^{-1}$ )	Growth (% of maximum growth rate)				
			March 1	March 15	April 1	April 15	May 1
2	Normal	0.0607	33 (0.0204)	51 (0.0312)	69 (0.0419)	82 (0.0496)	100 (0.0606)
2	Normal+2 °C	0.0841	30 (0.0252)	46 (0.0383)	64 (0.0535)	75 (0.0631)	91 (0.0762)
5	Normal	0.0607	45 (0.0273)	60 (0.0365)	75 (0.0457)	90 (0.0549)	100 (0.0607)
5	Normal+2 °C	0.0841	44 (0.0367)	55 (0.0465)	71 (0.0593)	82 (0.0690)	100 (0.0841)
10	Normal	0.0607	45 (0.0274)	60 (0.0365)	75 (0.0458)	90 (0.0549)	100 (0.0607)
10	Normal+2 °C	0.0841	44 (0.0370)	57 (0.0481)	71 (0.0593)	84 (0.0705)	100 (0.0841)

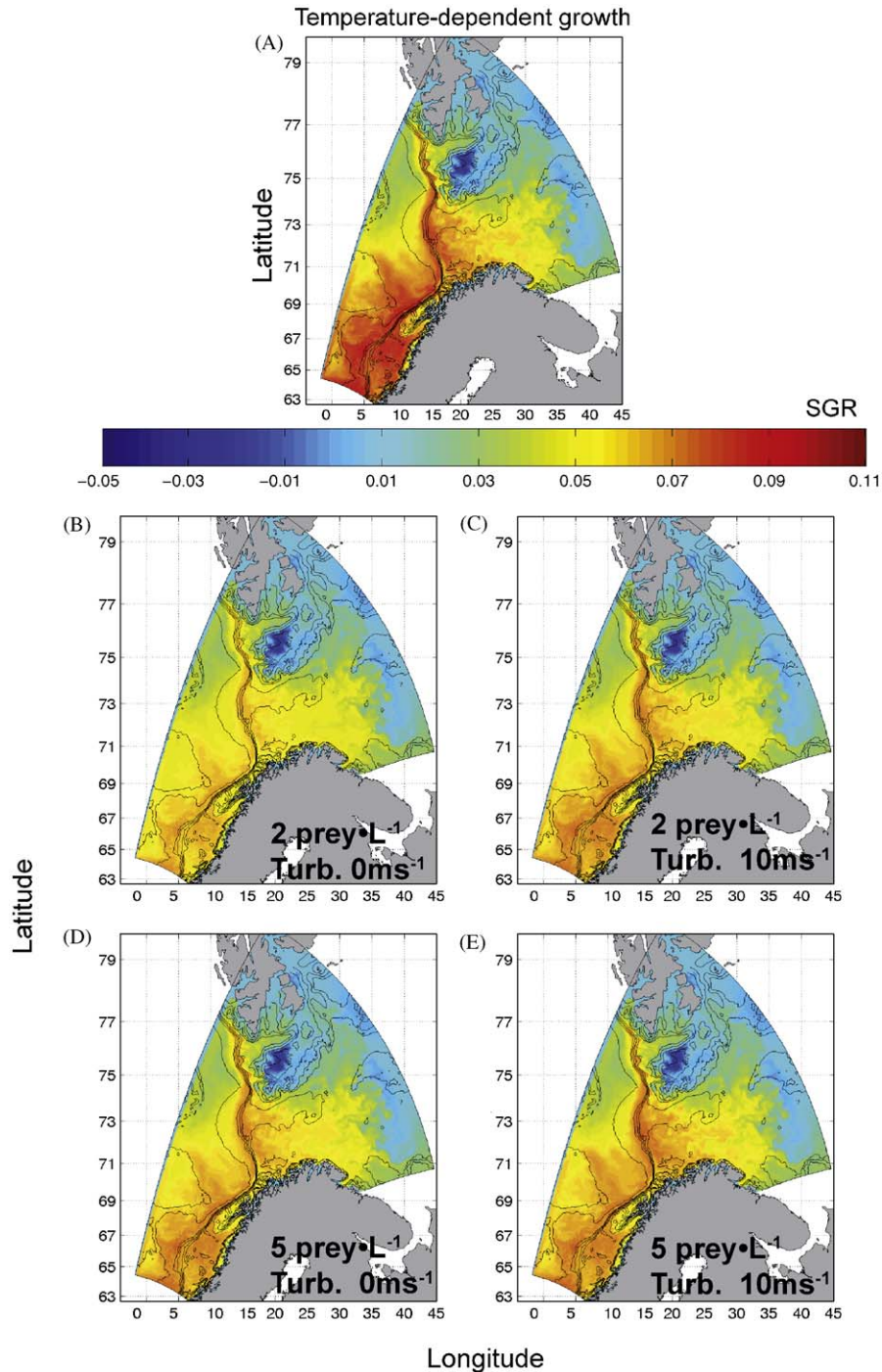


**Fig. 4.** As in Fig. 3, but now the temperature varies with day and depth. Consequently, the contour lines show growth relative to the potential growth at each day, while the color gradient remains the same for all panels. Growth rates are shown for 5 and 7 mm larvae fixed at 10 (upper 4 panels, A–D) and 30 m (lower 4 panels, E–H) depths at two locations; Moskenesgrunnen and Vestfjorden.

The modeled nauplii fields indicate areas where and when high concentrations of prey for first-feeding larva may be located, and as such, represents a high-resolution spatio-temporal matrix of when larvae should be present to match their prey availability. Large quantities of prey were supplied in the surface layer along the shelf break of Norway. The inflow to the northern part of the shelf is limiting to larval feeding and growth in early April (Fig. 8C,D), but a mixture of increasing prey abundance and environmental conditions (day-length) increased feeding rates to a non-limiting level by May. By May, growth seems very much determined by temperature.

#### 4. Discussion

The model presented here reveals that the shorter day-length in early spring, prior to mid-April, is the most important factor limiting growth of larval cod given other key variables like prey concentration and turbulence are suboptimal in that period. The mixture of light limitation and prey appearance may therefore be key factors constraining the timing of spawning in fish at high latitudes, like NA cod. Based on the observed spawning period and the temperature-dependent incubation time, the peak abundance of first-feeding larval cod would be expected to occur around



**Fig. 5.** (A) Maximum growth (temperature-dependent or food unlimited) rates for a 5 mm larva on April 1. (B) Prey abundance is fixed at 2 nauplii L<sup>-1</sup> and turbulence is zero. (C) Prey abundance is 2 nauplii L<sup>-1</sup> and turbulence is generated from a 10 m s<sup>-1</sup> wind stress at surface. (D) Prey is 5 nauplii L<sup>-1</sup> and turbulence is zero. (E) Prey abundance is 5 nauplii L<sup>-1</sup> and turbulence is generated from a 10 m s<sup>-1</sup> wind stress at surface.

April 20 in warm years and May 10 in cold years (Ellertsen et al., 1989). However, the peak abundance of the main prey varied considerably more with temperature, appearing around April 1 in warm years and May 20 in extreme cold years (Fig. 6 in Ellertsen et al., 1989). This indicates that years of average temperature would give better synchrony between first-feeding larvae and their prey than both the warm and cold years, and that high prey abundance is not the only variable that determines the year class

strength. During April, when light is a limiting factor, high prey abundance might partly compensate for the lack of light in the food encounter.

Suthers and Sundby (1993) analyzed the abundance and age distribution (based on otoliths) of pelagic juvenile cod from July 1988, a year of below-average recruitment. Compared to the observations on spawning frequency that same year and the hatch date distributions derived from the spawning observations, it was

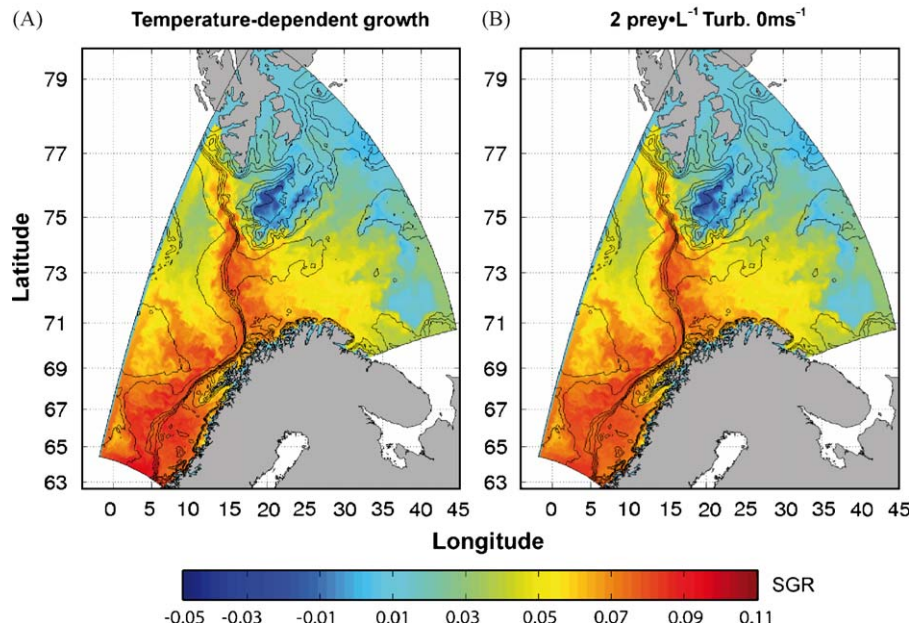


Fig. 6. Growth rate on May 1 for a 5 mm larva given (A) temperature-dependent growth (food-unlimited) and (B) prey is 2 nauplii  $L^{-1}$  and turbulence is zero.

shown that the major portion of the surviving juveniles on the average were hatched 10 days later than what would have been expected from a constant survival rate of the hatched larvae (Suthers and Sundby, 1993). Although, these data are from only one single year it does support predictions from the present model: under otherwise similar conditions, larvae hatched late will maintain their high growth rates at lower prey densities compared to those born earlier, when light is more limiting. In other words: increased prey abundance early in the season may contribute more to growth rates of larvae than a comparable increase later in the season.

Peak spawning in Lofoten occurs in late March or early April (Pedersen, 1984) and the surface temperature varies between 1.4 and 4.0 °C temperature (Ellertsen et al., 1989). This implies an egg developmental time of 20–35 days (Pepin et al., 1997), and the majority of hatching probably occurs by the end of April and early May when day-length is beneficial for survival. Suthers and Sundby (1996) concluded that day-length could partly explain the difference in observed growth rates between NA cod and southwest Nova Scotia cod stocks (4X) in Canada. NA cod experienced 48% more time available for foraging during May–July compared to 4X cod. Although the NA cod experienced significantly higher growth rates during the summer months, the 4X cod benefit from a longer productive season and shorter winter. Consequently, Suthers and Sundby (1996) found the weight of 4X cod at the age of 1 and 2 years to be higher than NA cod. Individuals of NA cod that experience high growth during summer have a higher probability of survival through the first winter compared to smaller individuals (Suthers and Sundby, 1996). Hence, the continuous daylight during summer of Northern Norway may compensate for the short season when prey abundance is high.

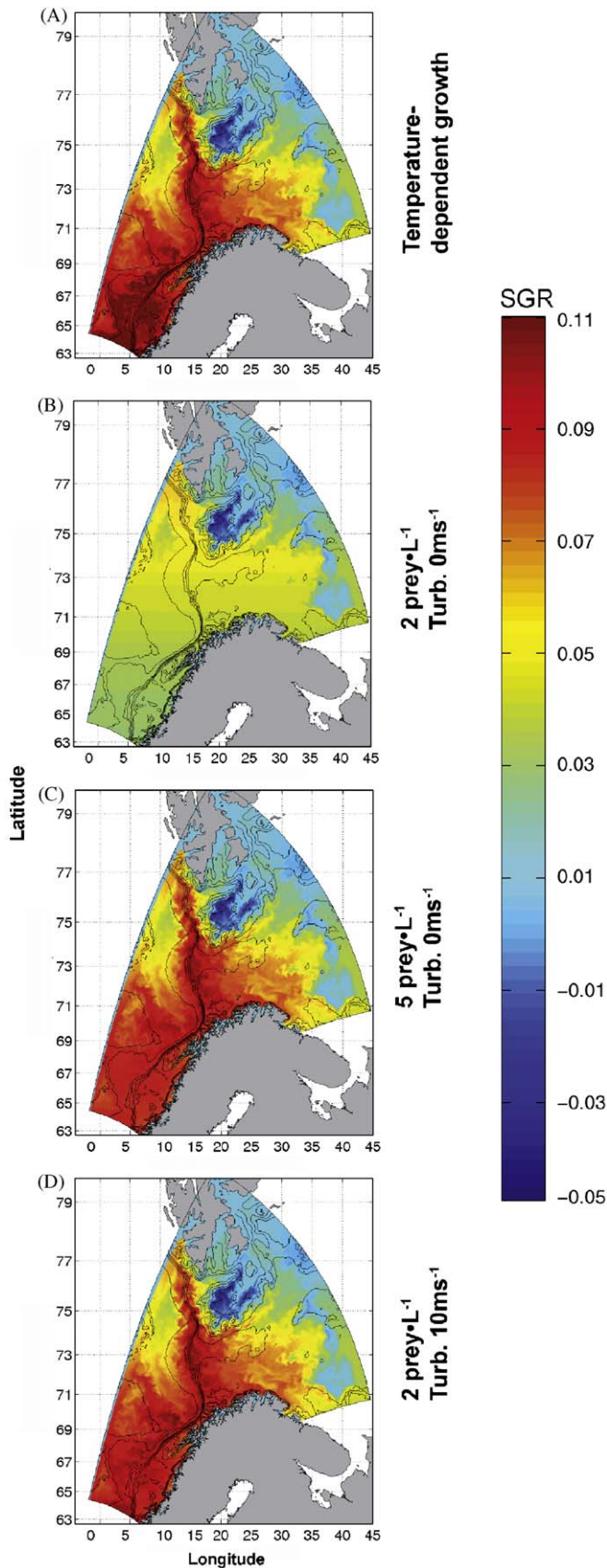
Under natural conditions, it is difficult to separate the effect of photoperiod from the concurrent changes in seasonal temperature (Imsland and Jonassen, 2001; Buckley et al., 2006). However, controlled experiments have revealed increased growth rates caused by an increased photoperiod for Atlantic cod (Folkvord and Otterå, 1993) and Atlantic salmon (Stefansson, 1989). The day-length increases with latitude during spring and summer (ca. 23 March–23 September), and in a macrocosm experiment at

70°N in Norway, Pedersen et al. (1989) observed high growth rates of larval cod which the authors attributed to the continuous light which allowed for extensive feeding. One mechanism of our model that should be explored experimentally is the premise that pulsed feeding, i.e. the lack of feeding during night has the effect on realized growth rates that our model suggests. Potentially, increased assimilation efficiency during lower feeding rates, higher foraging efforts at night, moonlight, prey patchiness or non-visual feeding abilities could reduce the effect of diurnal feeding proposed here.

Field observations by Sundby and Fossum (1990) and Sundby et al. (1994) suggested that feeding conditions of small larvae were good when prey concentration exceeded 1–5 nauplii  $L^{-1}$  depending on the turbulent intensity of the water masses. Our model results suggest that prey densities between 2 and 5 nauplii  $L^{-1}$  would be sufficient for larval cod to grow at physiological limits in some environmental settings. The prey density needed for satiation increased with larval size, but no change was evident above 10 nauplii  $L^{-1}$  at least for larvae size 7 mm or smaller. The modeled threshold values correspond to observations by Munk (1997) who found high growth rates in larval cod in environments with prey density below 10 nauplii  $L^{-1}$ . The prey availability and size composition in Lofoten during April and May varies spatially and temporally (Fossum and Ellertsen, 1994); e.g. sheltered areas often contain patches of high densities of nauplii (Tilseth and Ellertsen, 1984). Tilseth and Ellertsen (1984) found concentrations of 600 nauplii  $L^{-1}$  concentrated in such patches. Larval cod have been observed to be able to horizontally locate (Skreslet, 1989) and aggregate in these areas of high prey abundance (Tilseth and Ellertsen, 1984). However, it should be emphasized that such concentrations are rare and exceptional in this region and the normal values are below 10 nauplii  $L^{-1}$ .

The prey concentration in the main spawning areas along the coast of Northern Norway often exceeds 5 nauplii  $L^{-1}$  (Ellertsen et al., 1984; Solberg and Tilseth, 1984). During feeding, larval cod performs saltatory search (O'Brien et al., 1989). In addition to prey within their visual perception area, turbulence move prey into detection range of the larvae, thereby increasing the relative encounter rate between predator and prey. The effect of





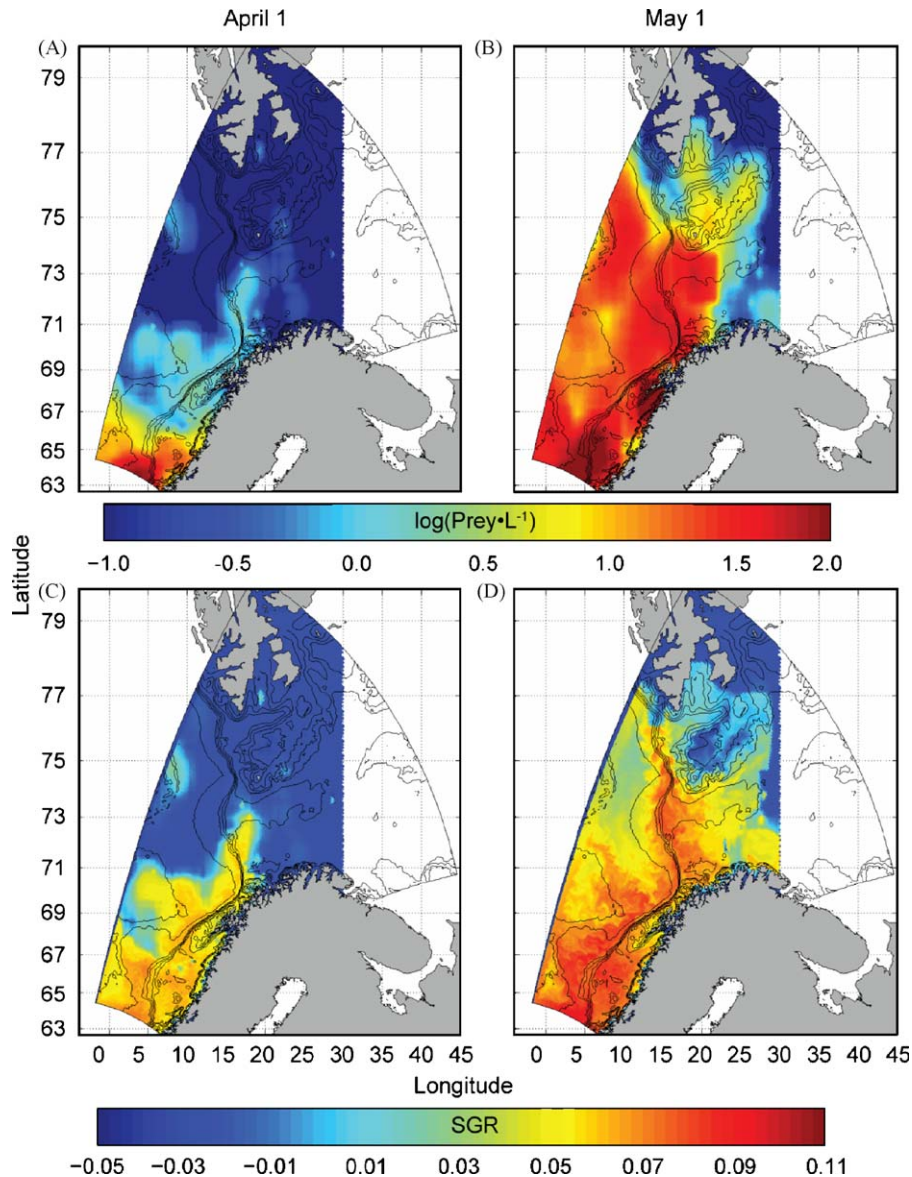
**Fig. 7.** Growth rate over 24 h for 7 mm larvae on May 1 under combinations of turbulence and prey concentrations: (A) temperature-dependent growth (food-unlimited), (B) 2 nauplii  $L^{-1}$  and zero turbulence, (C) 5 nauplii  $L^{-1}$  and zero turbulence, and (D) 2 nauplii  $L^{-1}$  and turbulence generated from  $10 \text{ m s}^{-1}$  wind stress at the surface.

turbulence on encounter rate and gut filling has been observed both in the field (Sundby and Fossum, 1990; Sundby et al., 1994; Sundby, 1995) and in laboratory studies (MacKenzie and Kjørboe, 1995). The level of beneficial turbulence changes with larval size and too strong turbulence may move the prey outside perception area of the larvae before a response is triggered (Fiksen and MacKenzie, 2002). Sundby et al. (1994) concluded that turbulence generated from surface winds reaching  $10 \text{ m s}^{-1}$  increases the feeding rate by a factor of seven. From our simulations we found that the effect of turbulence was strongest for 7 mm larvae in early May (Fig. 7), where growth rates in a habitat of 2 nauplii  $L^{-1}$  with turbulence corresponded to a habitat with prey density of 5 nauplii  $L^{-1}$  without turbulence. For a 5 mm larva, the effect of turbulence was masked by the effect of day-length in early April. Despite an increased encounter rate with prey during the day, the night hours depleted the larva for energy and growth were slow (Fig. 5).

The *Calanus* model recreates the main features of the *Calanus* population in the Norwegian Sea with most of the simulated population being confined to the Atlantic waters as is seen in the field (Melle et al., 2004). The maximum nauplia densities in the model corresponds well to maximum values near the Norwegian coast of around 150 000–250 000 nauplia  $m^{-2}$  (Ellertsen et al., 1989; Bjørke and Rey, 1991). In addition, the model predicts the south to north shift in timing of maximum nauplia concentration seen in these studies. Although there is substantial inter-annual variation, the peak in nauplia at Møre (lat. 62–63°N) occurs about 1 month earlier than in Lofoten (lat. 68°N). The model reproduces this pattern as seen in Fig. 8. The timing of peak reproduction of *C. finmarchicus* depends on the phytoplankton bloom along the Norwegian coast and in the Norwegian Sea, which is the core overwintering area of *Calanus*. The modeled fields represent this dependence of *Calanus* dynamics on the spring bloom and therefore provide a more realistic time-space description of the prey availability than assumptions about homogeneous prey fields. Fig. 8 illustrates that the assumption of a homogenous prey distribution is rather unreasonable early in April since the spring bloom is yet to take place in parts of the area. Consequently, there is a clear difference between Figs. 5 and 8 with regards to larval cod growth in the northern part of the area. Here the lack of prey in the *Calanus* model run (Fig. 8) limits growth while for the simulation with homogeneous prey distribution (Fig. 5), growth remains much more homogenous. This pattern is not seen in May when the nauplia in the *Calanus* model is more evenly distributed throughout the distribution area (Fig. 8B). A similar pattern in delay in nauplia abundance from south to north is seen in field samples from the Norwegian coast (Bjørke and Rey, 1991). Thus, even though we found physical properties such as light and turbulence to be important in determining the growth rate of larval cod, Experiment 4 shows that the role of prey limitation should not be ruled out, especially early in the spawning season.

## 5. Conclusion

Latitudinal constraints on larval fish growth were analyzed using coupled model systems. The results suggests that high growth rates are possible to achieve for larval cod even at low prey densities (2 nauplii  $L^{-1}$ ) if first feeding is initiated sometime during the latter part of April. The larvae seem inaccessible to reach potential growth earlier in the season due to the long nights allowing only a low feeding activity. The model suggests there are latitudinal and seasonal shifts in the importance of prey abundance for recruitment success.



**Fig. 8.** Nauplii distribution (log-scale) on April 1, 1982 (A) and May 1, 1982 as predicted from the coupled NP-*Calanus finmarchicus* model (B); and the corresponding specific growth rate of a 5 mm larva on April 1 (C) and May 1 predicted by the larval IBM (D).

## Acknowledgments

We are thankful for comments and suggestions on this manuscript from three anonymous reviewers and the guest editors. T. Kristiansen and F. Vikebø were supported by the Norwegian Research Council through the ECOBE Project (P. No. 155930/700).

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