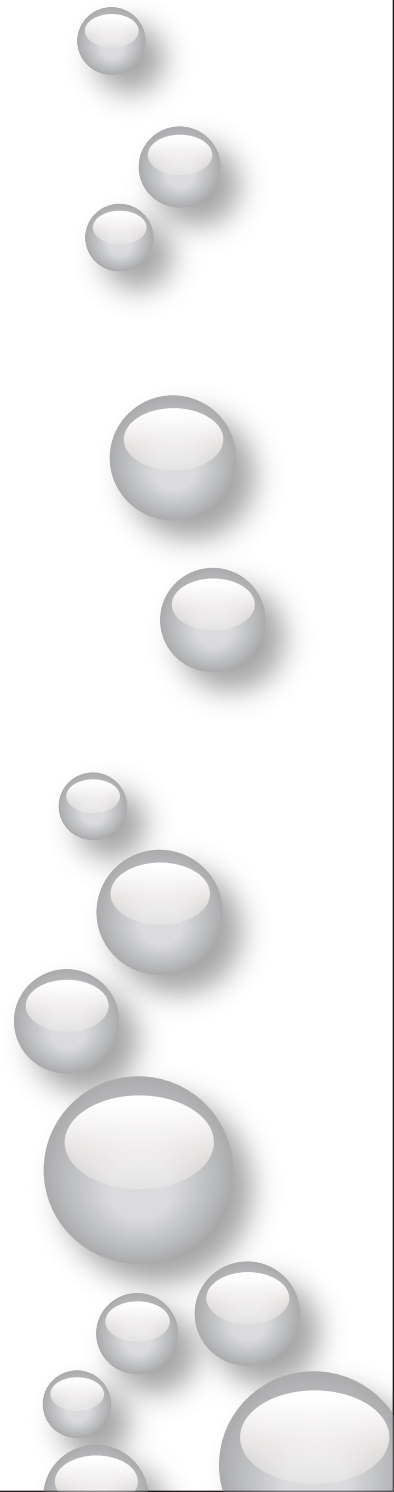# Paper 6

Growth and feeding of larval cod (*Gadus morhua*) in large-scale latitudinal environmental gradients

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Abstract

The spawning strategy of cod is tuned to give larvae a good start in life. Therefore, larval drift, growth and survival are key processes to understanding spawning strategies. Spawning of Northeast Arctic (NA) cod stretches from late February to early May over 1500 km along the Norwegian coast and the hatching stretches from late March to late May. During the latter period the number of daylight hours increases from 12 to 21. Larval feeding opportunities are constrained by availability of prey abundance, while temperature determines the maximum growth potential. Feeding of larval cod that hatches early in the season is limited by the low number of daily foraging hours, and this makes them particularly susceptible to food limitation. Here, we study constraints on larval cod growth by combining a bio-physically coupled model (NPZ-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 feeding ecology and physiology. Our aim is to better understand spatio-temporal constraints of larval ecology on the spawning strategy of adults. Results show that larval cod have low chance of survival if hatched early in the season (prior to mid-April) when the foraging hours are few. Larval cod hatched in early May experience good growth conditions due to the increased day-length, and the given temperature range. These results quantify the strong relationship between larval feeding and growth in relation to day-length, time of the season, and water temperature, while the importance of prey density is of second order when abundance > 5 nauplii$\cdot$L^{-1}. Peak spawning appears well timed to the seasonal variation in light, and we propose that the light-availability modify the importance of prey availability to larval success.

Keywords: biophysical modeling, larval fish, Northeast Arctic cod, latitudinal gradients, spawning strategies

Introduction

Just after hatching, larval cod are able to sustain metabolic demands through their yolk-sac reserves, but after a few days (4 days, Fossum & 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), while their poor swimming abilities (Hunter 1981, Peck et al. 2006) makes encounters between larvae and prey strongly determined by the prey density and turbulence (Fiksen et al. 1998). Consequently it is vital to the larvae to be placed in a favorable time-space location with regards to prey concentration. The timing of the spring bloom and the peak in nauplii availability along the Norwegian coast varies substantially between years (Ellertsen et al. 1989). The NA cod has adapted to this great environmental variability by having a spawning period spanning about 2,5 and 1,5-2 months for individual fish (Kjesbu et al. 1996) months, which increases the likelihood that at least some larvae match the prey peak. Compared to other marine ecosystems, e.g. upwelling ecosystems, where plankton production and fish spawning extend through most of the year, 2.5 months is a relatively long period of time in a spring-bloom marine ecosystem where the plankton production is confined to a limited period of time. However, high prey abundance is not sufficient to ensure survival of larval cod. Abiotic factors such as temperature (Otterlei et al. 1999, Ottersen et al. 2001, Folkvord 2005), turbulence (Sundby & Fossum 1990, Sundby et al. 1994), predation (Øiestad 1985, Bailey & Houde 1989), and light conditions (Blaxter 1986, Aksnes & Utne 1997) modify the physiological rates, the feeding ecology of the larva, and the interaction between larval cod and their predators.

The Northeast Arctic cod stock spawns along a 1500 km coast line from western Norway (~60 $^{\circ}$N) to the Finnmark coast (~71°N) (Fig. 1). The majority (60-70%) of spawned cod eggs are found in the Lofoten and Vesterålen areas (~68 $^{\circ}$N) (Sundby &

Bratland 1987). Spawning starts at the end of February and lasts until the first week of May. Based on egg samples collected using net hauls from 1968-1982 in the traditional spawning areas in Lofoten (~68 ^{o}N), Pedersen (1984) found mean peak spawning of Northeast Arctic cod to occur during transition from March to April (Julian date 90). At the Møre spawning ground (~62°N) peak spawning occurs at about the same time as in Lofoten (Godø & Sunnanå 1985), while there is an increasing delay in the peak spawning with increasing latitude at the spawning areas to the north of Lofoten. Hence, the peak spawning at the Finnmark coast (~71°N) is about 2 weeks later than in Lofoten (Sundby & Bratland 1987). Experimental work by Kjesbu et al. (1996) shows that larger and older cod tend to have longer spawning periods. An individual female cod spawns 15 – 20 batches of eggs over a period of 1,5 –2 months. The total spawning period of the whole population is less than one month longer than the spawning period of the most active spawners. As the larval period progresses, the number of daylight hours increases from 13 (April 1), to 17 (May 1), to 21 (June 1, 68˚N) (Fig. 2). This may constrain the feeding opportunities for newly hatched larvae, and influence growth and survival. Mature, older cod tend to arrive earlier at the spawning sites than the younger ones (Solemdal & Sundby 1981). However, the time of spawning does not seem to be significantly different between the older repeat spawners and the younger first time spawners (Kjesbu 1994).

The objective of this study is to investigate the significance of temperature, turbulence, light conditions, prey density on growth of larval cod at different spatial locations by integrative modeling. The work we present here, combine three models; (*i*) a general circulation model (GCM) (Vikebø et al. 2005), (*ii*) an individual based model (IBM) for larval cod (Kristiansen et al. in press), and (*iii*) prey fields generated using a zooplankton model (Huse 2005, Huse et al. in prep.). These models allow us to integrate effects of day-length, prey abundance (and size), water temperature, turbulence, and spawning ground over short-time growth of larval and juvenile cod drifting along the Northern coast of Norway. Simulations were repeated for two sizes of larval cod; 5mm which is the typical size of a larva after the yolk-sac stage

(Ellertsen et al. 1989), and 7mm; for comparison. This allowed for a comparative study of the significance of separate processes on larval cod. E.g. how well do first-feeding larval cod cope with a changing prey field when hatched at various dates throughout the season? What is the prey requirement for maximum (or minimum) growth, and does it change with spawning grounds and time of season?

Models

Coupled GCM and IBM integrate processes at scales from hundreds of kilometers (oceanic gyres) to millimeters. Combined, they provide an effective tool to study interactions that emerge between processes we know affect success of larval cod.

The IBM sequentially calculates processes of larval encounter, pursuit, and capture of prey items, and the succeeding ingestion, digestion, stomach fullness, metabolism and growth (Fiksen & MacKenzie 2002, Kristiansen et al. in press), and requires information of the local prey abundance, light level, turbulence estimated from surface wind (Mackenzie & Leggett 1993), and water temperature at a given position (depth, longitude, and latitude) as input. The GCM provides information on the biotic conditions at the location of each individual. Foraging of larvae did not feed back on the zooplankton prey abundance. Larval cod are kept at fixed depth (10 and 30 m) and monitored through 24 hours. This enabled calculations of the larval state variables; body mass and stomach fullness.

The properties of the GCM (Vikebø 2005, Vikebø et al. 2005), and the IBM (Fiksen & MacKenzie 2002, Kristiansen et al. in press) have been described extensively elsewhere, and we only provide a brief summary of the models here.

The prey model

The nauplii fields were taken from a *Calanus finmarchicus* IBM for the Norwegian Sea (Huse 2005, Huse et al. in prep.). This model represents the entire Norwegian Sea *C. finmarchicus* population using super individuals. The resolution of the model

is 20 km and the fields are interpolated to the GCM domain (see above). Presently, fields of all the nauplii stages combined were used as prey field for the cod larvae.

Simulation experiments

How does growth rate of larval cod depend on food concentration at different dates and locations along the Norwegian coast? To answer this question, we performed four different numerical experiments:

Larval daily growth at two important spawning locations

First, we explored diel growth rates of individual 5 and 7 mm larval cod, fixed at two well-known spawning grounds/sites, Moskenesgrunnen and Vestfjorden, for each day during the period March 1 - May 1 1985. Moskenesgrunnen (68° 20' N, 12° E) is located near the shelf break at the border area between the Atlantic Currents and the Coastal Current while the spawning areas in Vestfjorden (68° 00' N, 14° E) is located in the cooler inner branch of the Coastal Current. Moskenesgrunnen is exposed to the open ocean with high currents speeds and strong mixing, while Vestfjorden is a somewhat more sheltered coastal location with lower advection (Fig. 1). For these simulations, we varied the prey abundance systematically at each date, with fixed and variable temperature:

- **Experiment 1:** Varying prey availability each day at two locations, letting day-length change with date, but keeping temperature fixed.

- **Experiment 2:** Varying prey availability each day at two locations, letting day-length and temperature (derived from the GCM) change with date.

Larval daily growth in the whole model domain at fixed days

Then, we extracted the daily growth rates of larvae in fixed depths and locations over the whole model domain as a function of the environmental conditions at each position at a particular date. Each larva was initiated at either 5mm (86 µg) or 7mm (285 µg) with 30% stomach fullness at 10 m depth, and exposed to the local ambient

light, turbulence, temperature and prey density over the day. We performed two experiments:

- **Experiment 3:** Keeping prey abundance fixed (two levels) across the whole domain, we combine two levels of surface wind (turbulence), two larval sizes and two dates (1st of April and 1st of May) on daily growth rates.

- **Experiment 4:** In the final experiment, we fed values on abundance of *Calanus finmarchicus* nauplii at each grid point at two days (April 1 and May 1) into the larval IBM. The nauplii abundance was generated by the coupled zooplankton model described above, and were used as forcing for the larval growth (including the feeding) rates.

Results

Experiment 1. Simulations with the same temperature at all days isolated the effect of day-length on growth rates for 5 and 7mm larval cod (Fig.3). Stomach contents provide energy reserves during hours of no feeding to sustain growth and metabolic demands. However, the energy stored in the stomach proved to be insufficient during early spring due to the many dark-hours, resulting in negative larval growth during night. Pure temperature-dependent growth rates were therefore never achieved during March, even when prey abundance are as high as 10 nauplii·L^{-1}. Thus, modeled larval growth during March and most of April were food-limited in the sense that the potential growth rates could never be reached due to light limitation. By the end of April the day-length were sufficient (or rather, the nights were short enough) for high larval growth (Fig. 3). The water masses at Moskenesgrunnen are characterized by higher temperatures than at the inner spawning sites in Vestfjorden. In April temperature at Moskenesgrunnen is typical 2 – 3 ^{o}C higher than in Vestfjorden (Sundby & Bratland 1987). In May the temperature differences are smaller, typically 0 – 1, 5 ^{o}C. The result is an increased energy demand to grow at potential rates for larval cod at Moskenesgrunnen compared to those in Vestfjorden.

We further increased the surface temperature of the water column by 2°C to explore the effect on the growth rates (Fig. 3e-h). Such variation in temperature may occur between years in the Lofoten area; 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). The energy needed to sustain metabolism increased and growth rates were close to satiation when prey density exceeded 3 nauplii·L^{-1} for a 5 mm larva, and 5 for a 7 mm larva (7 mm larva has a higher inherent growth potential). Absolute growth rates increase, but potential growth rate is achieved later in the season compared to if temperature was 2°C lower.

Experiment 2. When we allowed temperature to change daily as predicted by the GCM, the growth rates will be driven by both the seasonal increase in temperature and day length. The pattern from Fig. 3 remains, indicating that temperature is relatively constant during April and May for both Moskenesgrunnen and Vestfjorden (range 3-4.5°C). Light decreases exponentially with depth leading to reduced visibility and encounter rate between predator and prey at 30 m relative to 10 m. Generally, Figs. 3 and 4 suggest that growth is not affected by variability when prey abundance exceeds 5 nauplii·L^{-1}.

Experiment 3. The results so far suggest that day-length prior to mid-April restricted growth of larval cod. To analyze this further, we modeled growth of 5 and 7 mm larval cod in all grid cells of the model domain (grid resolution is 4-6 km) at 10 m depth. We repeated the simulations with 2 and 5 prey·L^{-1}, with and without turbulence, for early April and May. Areas of high temperature dependent growth rates (Fig. 5a, 6a) followed Atlantic Water masses (Fig. 5), and decrease with increasing latitude. Hours available to feeding ranged from 13 on April 1st to 17 on May 1st (68°N, Fig. 2). This resulted in food-limited growth for larval cod in April, when prey density was below 5 nauplii·L^{-1}, even at high turbulence (Fig.5). The situation changed drastically when larval cod started feeding in early May (Fig. 6). The potential growth rates increased between April and May because of 1°C temperature increase of the water temperature. A 5 mm larval cod is close to

maximum growth rates when prey density exceeded 2 nauplii·L^{-1} by early May. Higher physiological growth rates imply an increased need for prey and 2 nauplii·L^{-1} is not enough (Fig. 7) for a 7mm larva. However, the 7mm larvae experienced temperature-restricted growth when prey density exceeded 5 nauplii·L^{-1}, or if turbulence were present, at 2 nauplii·L^{-1} (Fig. 7). In the model, the wind-generated turbulence (surface winds 10 m·s^{-1}) increase encounter between predator and prey 2-3 fold relative to calm conditions.

Experiment 4. The modeled nauplii fields indicated areas where high concentrations of prey for first-feeding larva may be located (Fig. 8). Large quantities of prey were distributed in the surface layer along the shelf break along the coast of Norway, probably distributed by the topographically steered Norwegian Atlantic Current. The inflow to northern part of the shelf seems limited by early April, but the mixing onto the shelf had increased by May, when prey concentrations exceeded 2 nauplii·L^{-1} in Vestfjorden. The estimated growth rate of a 5mm larva in a realistically modeled prey field resulted in low growth potential in early April, except along the shelf slope. By early May, the situation changed and both along the coast and along the shelf slope, high growth rates were achieved by a 5mm larva.

Discussion

Models present a theoretical framework for studying a simplified version of the properties of an ecosystem and its inhabitants. Short day-length in early spring may limit the survival probability of larval cod hatched prior to mid-April. 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 20 April in extreme warm years and 10 May in extreme cold years (Figure 7 in Ellertsen et al. (1989)). However, the peak abundance of the main prey varied considerable more with temperature, appearing around 1 April in extreme warm years and around 20 May in extreme cold years (Figure 6 in Ellertsen et al. (1989)). This would indicate that years of average temperature would give better synchrony between first-feeding larvae and their prey than both the extreme warm and extreme cold years. However,

warm years have been observed to be a necessary condition for producing strong year classes and that only poor year classes were produced in cold years (Ellertsen et al. (1989)). This indicates 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 and stronger turbulence might partly compensate for the lack of light in the food encounter. This means that in warm years the larval survival can be extended to occur also in April compared to in cold years when survival is only possible in May. This draws the attention to a different and novel view of the match-mismatch concept: Rather than focusing on the survival conditions for those larvae associated with peak abundance in time we focus on probabilities of survival during the entire integrated period of time. In other words: extending the period of possible larval survival contributes much more to the resulting year-class strength than increasing the probability of larval survival during the rather limited period of time of during peak abundance. This becomes even clearer when we consider a high temperature is not only beneficial for high abundance of the prey *Calanus finmarchicus* but also contributes to an extended period of prey production (Sakshaug et al. 1994, Sundby 2000).

Suthers and Sundby (1996) concluded that day-length could partly explain the difference in observed growth rates between Northeast Arctic (NA) cod and south-west Nova cod stocks (4X). 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 experienced high growth during summer have a higher probability of survival through the first winter compared to smaller individuals (Suthers & Sundby 1996). Hence, the continuous day-light during summer of Northern Norway may compensate for the short season when prey abundance is high.

Peak spawning in Lofoten occurs in late March or early April (Pedersen 1984), and the surface temperature varies between 3-5.5ºC 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 occur by the end of April, and early May when day-length is beneficial for survival. Under natural conditions, it is difficult to separate the effect of photoperiod from the concurrent changes in seasonal temperature (Imsland & Jonassen 2001). However, controlled experiments has revealed increased growth rates caused by an increased photoperiod for Atlantic cod (Folkvord & Otterå 1993), and Atlantic salmon (Stefansson 1989). The day-length increases with latitude, and in a macrocosm experiment at 70ºN 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.

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. In our model, prey densities between 2-5 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}. 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 & Ellertsen 1994). Sheltered areas often contain patches of high densities of nauplii (Tilseth & 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 & Ellertsen 1984). However, it should be emphasized that such concentrations are rare and exceptional in this region. The normal values are typically below 10 nauplii·L^{-1}. Patches may benefit the larvae through reduced swimming efforts, saved energy, and the reduced

vulnerability to predation as predators often react to movements (Bailey & Houde 1989, Utne-Palm 2000, Connell 2002).

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 & Tilseth 1984). During feeding, larval cod moves in a saltatory behavior (O'Brien et al. 1989). In addition to the prey within their visual perception area, turbulence may move prey into the view range of the larvae, thereby increasing the relative encounter rate between predator and prey. The effect of turbulence on encounter rate and gut filling has been observed both in the field (Sundby & Fossum 1990, Sundby et al. 1994, Sundby 1995), and in laboratory studies (MacKenzie & Kiørboe 1995). The level of beneficial turbulence changes with larval size as too strong turbulence may move the prey outside perception area of the larvae before a response is triggered (Fiksen & MacKenzie 2002). Sundby et al. (1994) did find turbulence generated from the surface wind up to 10m·s^{-1} to increase the feeding rate of larval cod, and a 7 fold increase in feeding rate when surface wind increased from 2 to 10 m·s^{-1}. The modeled encounter rate between larval cod and their prey increased, corresponding to a factor of 2-3 increase in prey density. 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).

Conclusion

We have coupled models of physical oceanography and latitudinal factors, prey supply and a model of feeding and physiology of larval cod to understand constraints of larval cod growth. We have seen that high growth rates are possible to achieve even at low prey densities, if first feeding is initiated sometime during the latter part of April. In the early phase, however, the temperature-limited growth seems inaccessible, due to the long nights with low feeding activity. The model suggests

there are latitudinal and seasonal shifts in the importance of prey abundance for recruitment success.

Acknowledgement

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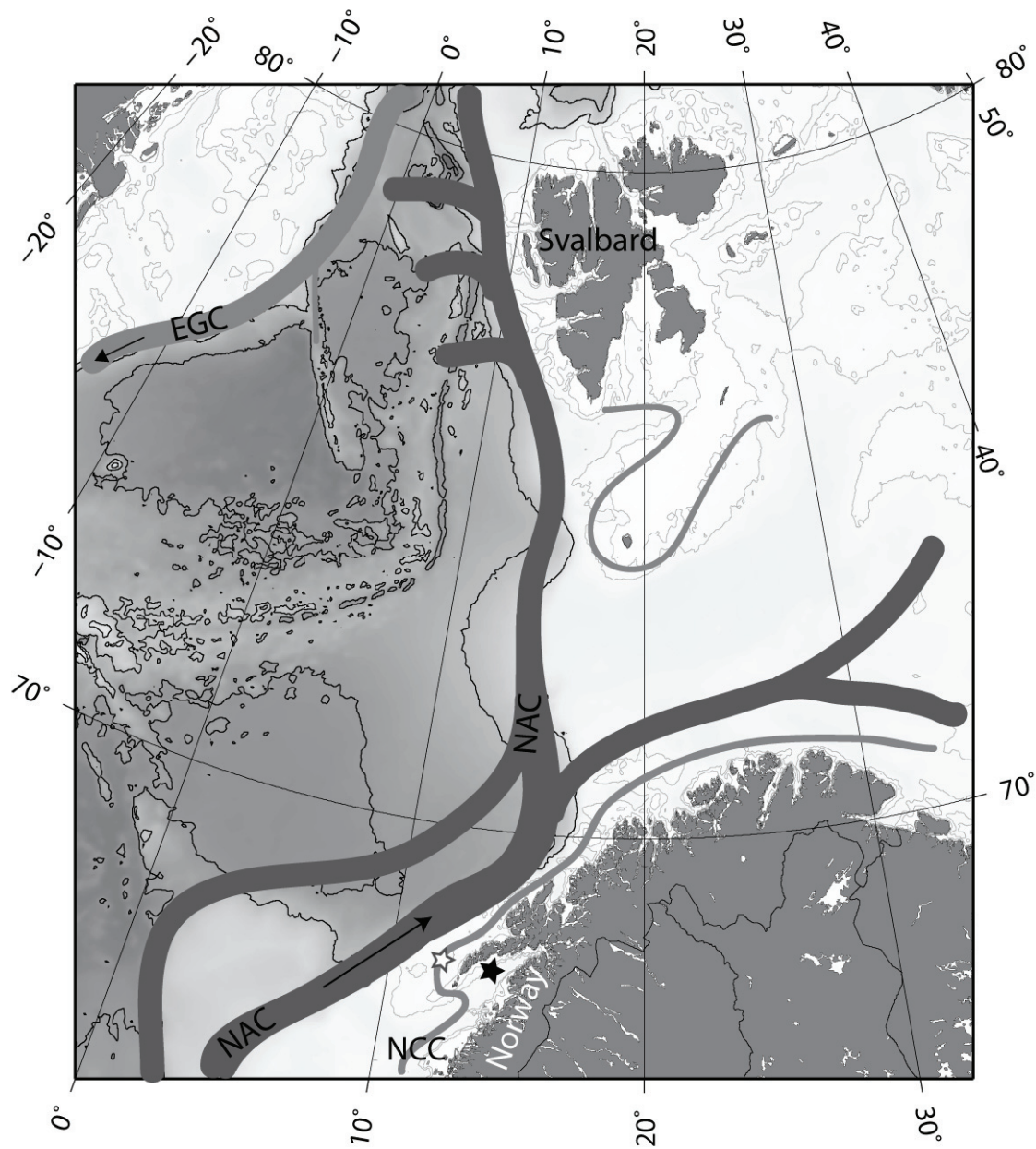
Figure 1 Map of the Lofoten area and the major current systems; the warm and saline Norwegian Atlantic Current (NAC), the less saline, cooler Norwegian Coastal Current (NCC). The location of Moskenesgrunnen is displayed with a white star and Vestfjorden with a black star.
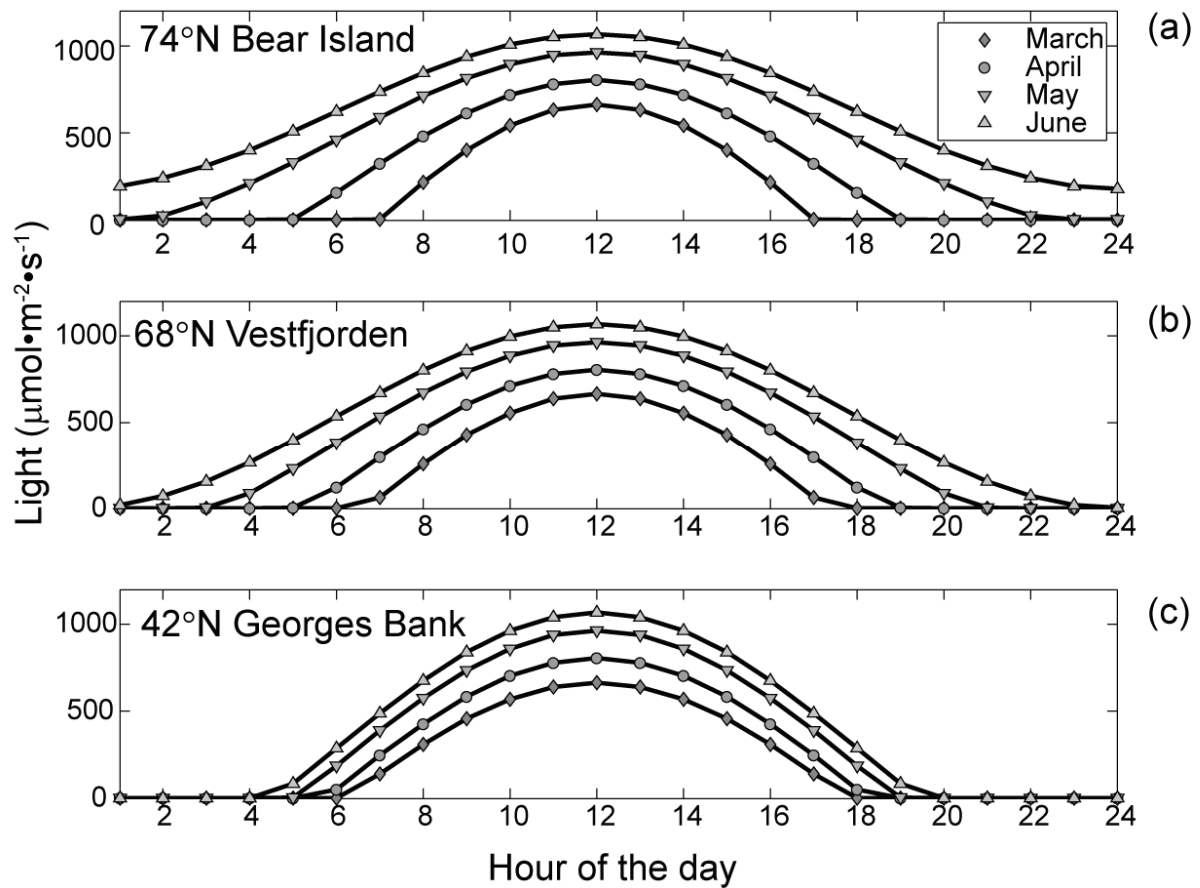
Figure 2 Relative amount of light at the surface as a function of time of the day for March 1, April 1, May 1, and June 1 for the geographical locations; 74°N (Bear Island), 68°N (Vestfjorden), and 42°N (Georges Bank, US).
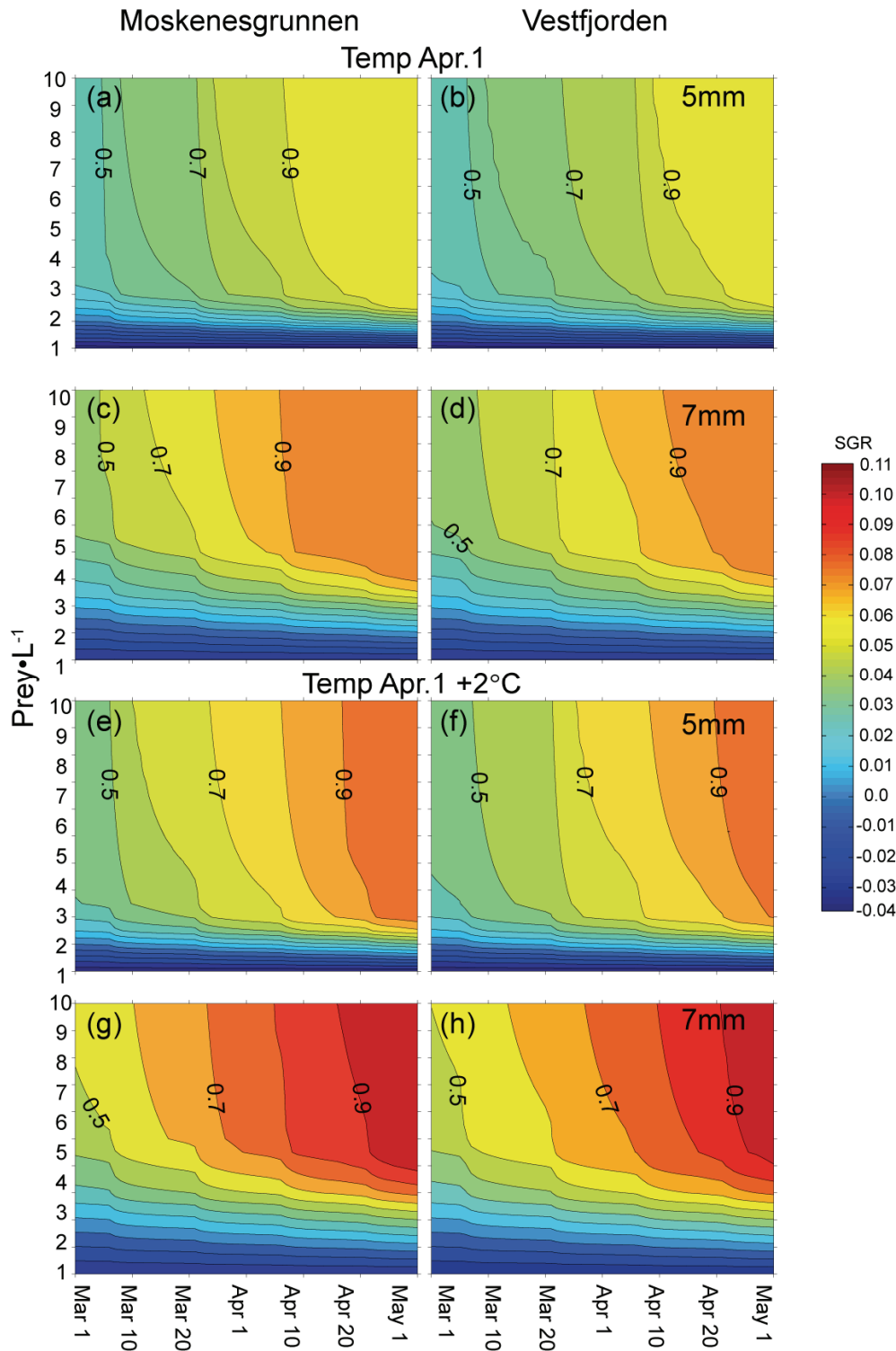
Figure 3 Colors indicate specific growth rates [g g^{-1} day^{-1}] (same scale for all panels), while contour lines show the ratio between realized and maximum temperature dependent growth rates at each date and prey density. Since temperature is the same at all times in this realization, absolute and 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 1st at 10 m depth (upper four panels). The lower four panels show the effect of elevating the temperature by 2ºC.
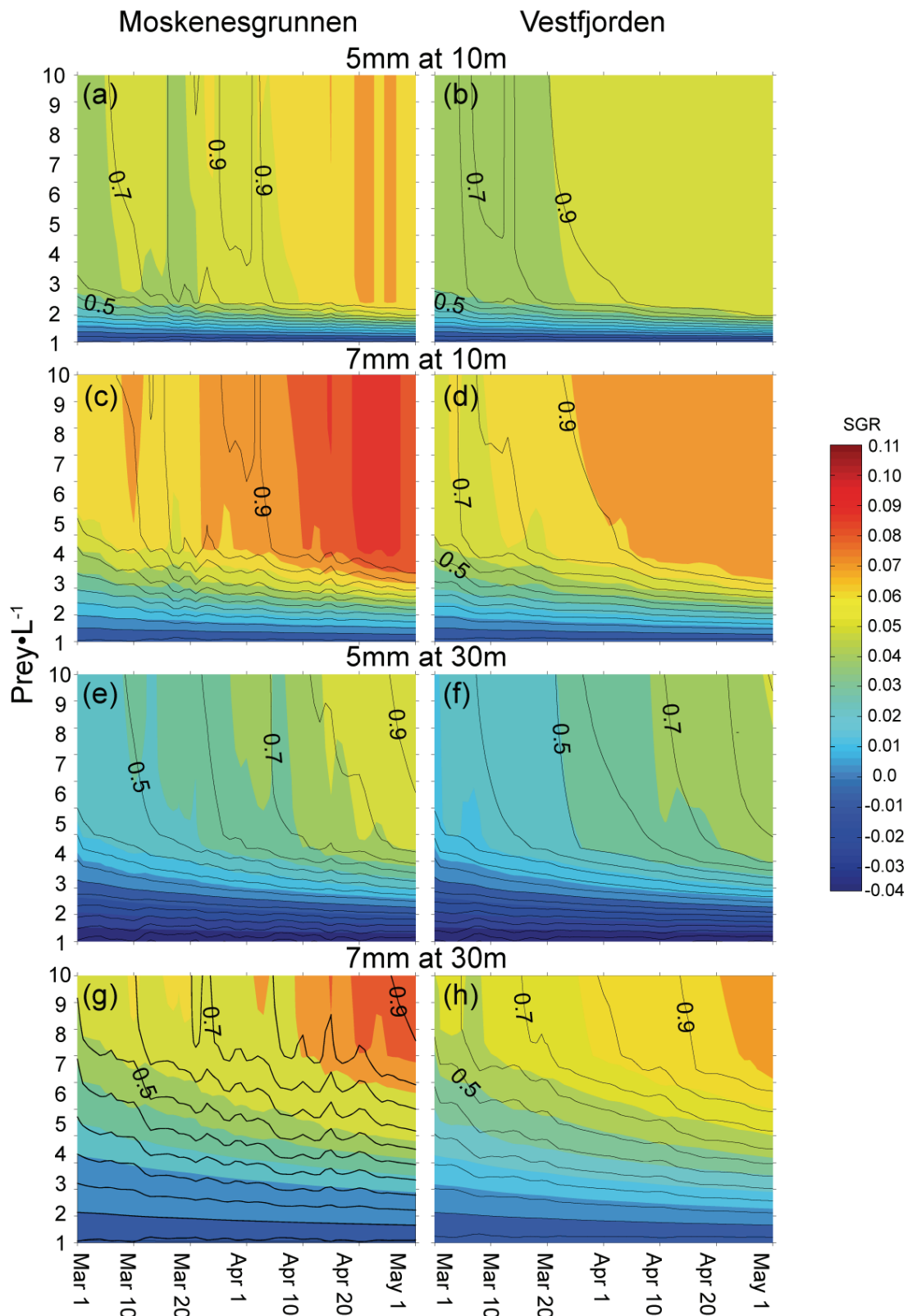
Figure 4 As in Fig 3, but now the temperature varies with day and depth. Consequently, the contour lines show growth relative to the potential growth at each day, while the color gradient remains the same for all panels. Growth rates are shown for 5 and 7mm larvae fixed at 10 (upper 4 panels, a-d) and 30m (lower 4 panels, e-h) depths at two locations; Moskenesgrunnen and Vestfjorden.
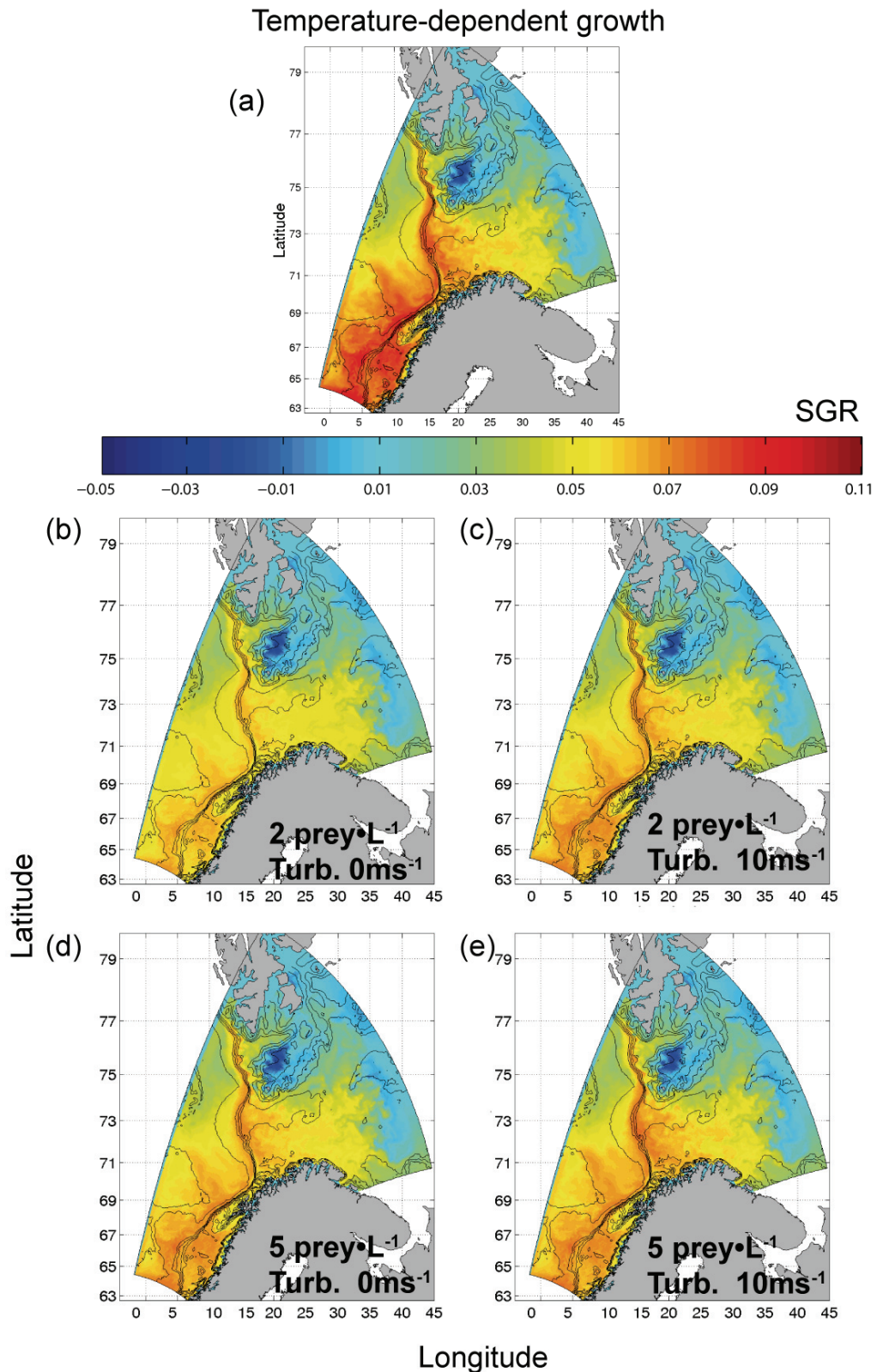
Temperature-dependent growth

Figure 5 a) Maximum growth (temperature-dependent or food unlimited) rates for a 5mm larva on April 1st. b) Prey abundance is fixed at 2 nauplii·L^{-1} and turbulence is zero. c) Prey abundance is 2 nauplii·L^{-1} and turbulence is generated from a 10 m·s^{-1} wind stress at surface. d) Prey is 5 nauplii·L^{-1} and turbulence is zero. e) Prey abundance is 5 nauplii·L^{-1} and turbulence is generated from a 10 m·s^{-1} wind stress at surface.
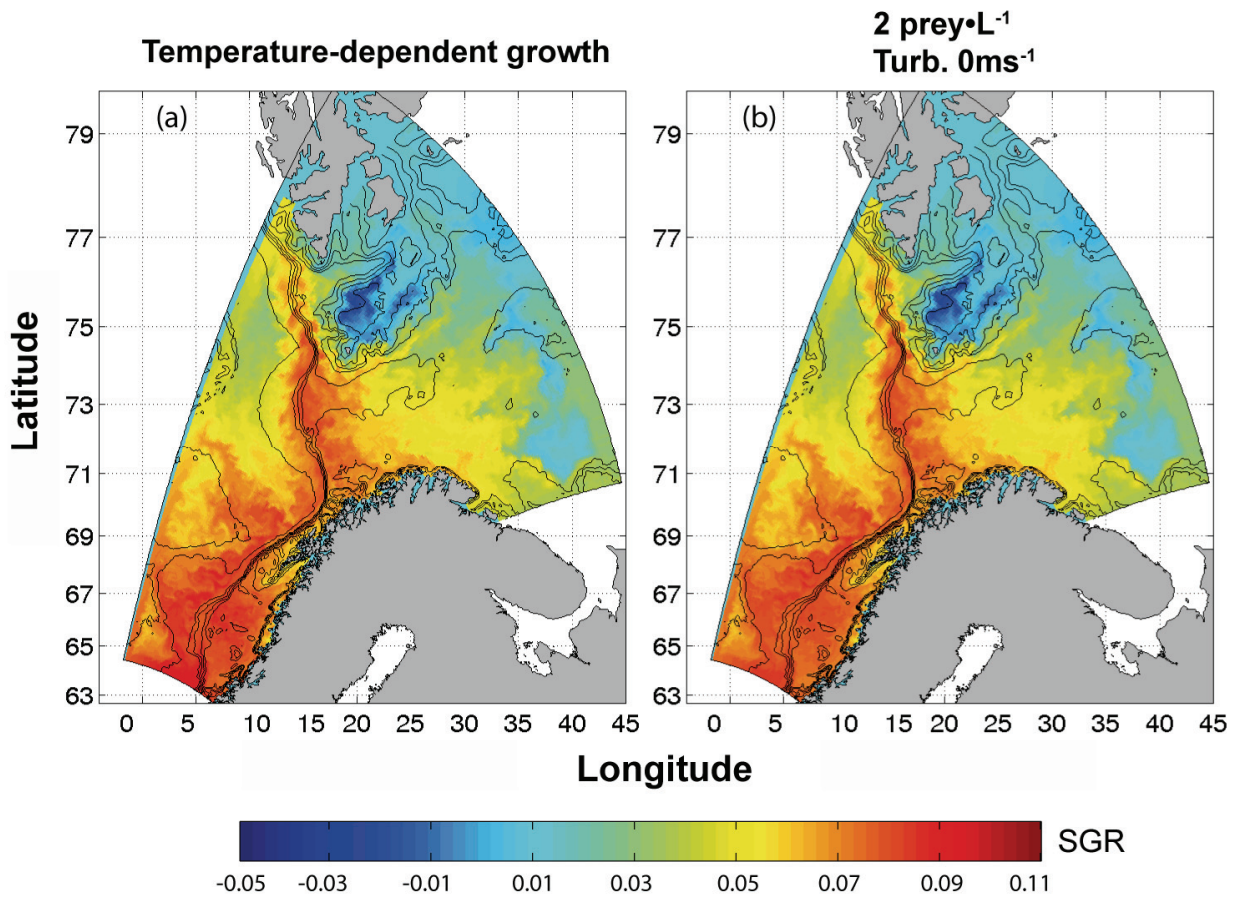
Figure 6 Growth rate on May 1st for a 5mm larva given (a) temperature-dependent growth (food-unlimited), and (b) prey is 2 nauplii·L^{-1} and turbulence is zero.
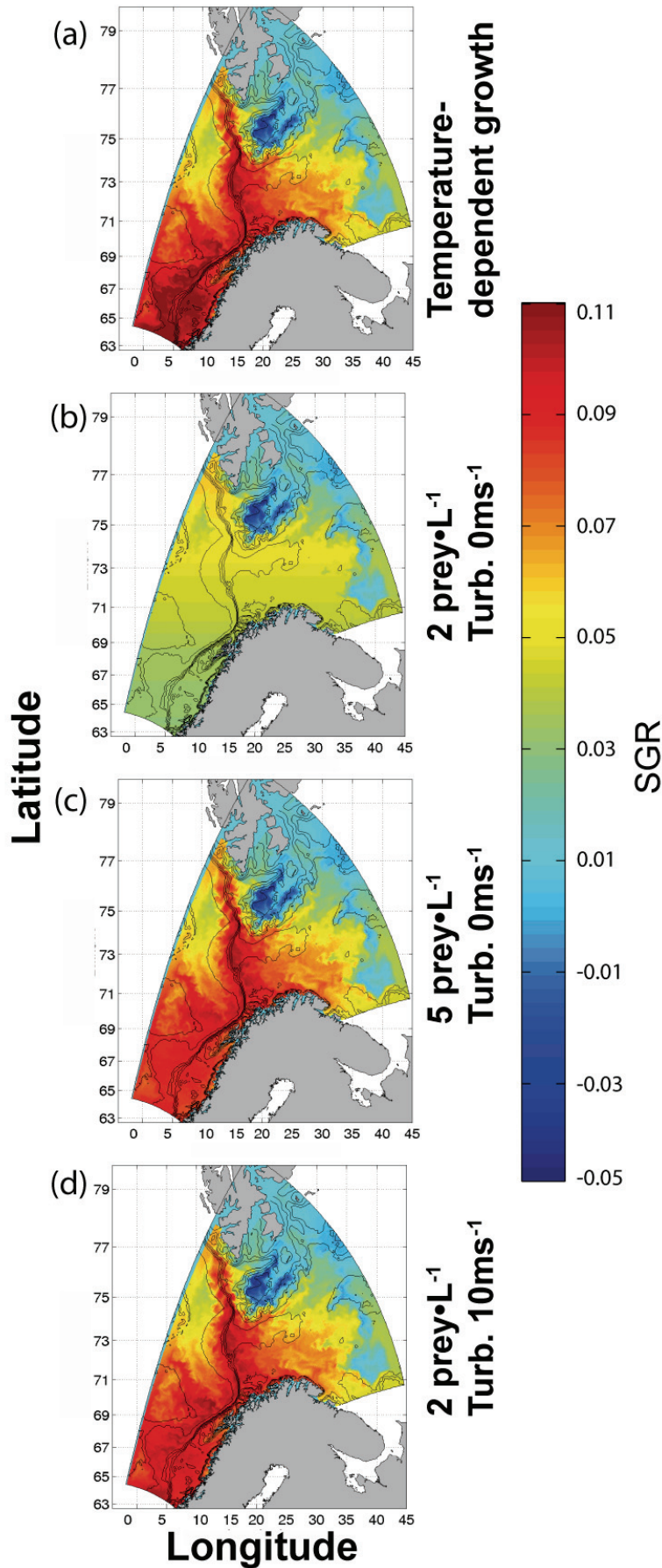
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Figure 7 Growth rate over 24 h for 7mm larvae on May 1st under combinations of turbulence and prey concentrations;

(a) temperature-dependent growth (food-unlimited).

(b) 2 nauplii·L^{-1} and zero turbulence.

(c) 5 nauplii·L^{-1} and zero turbulence.

(d) 5 nauplii·L^{-1} and turbulence generated from 10 m·s^{-1} wind stress at the surface.
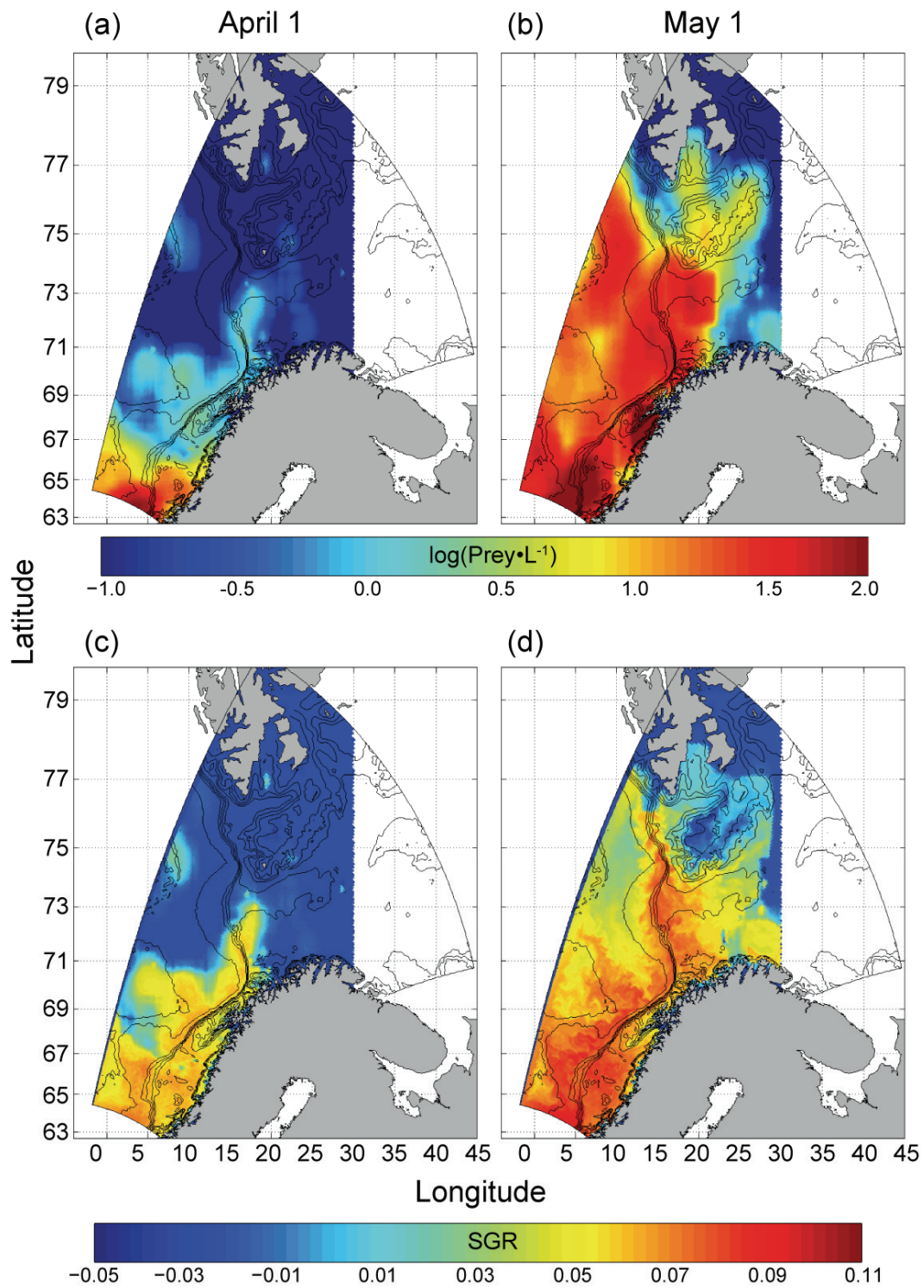
Figure 8 Modeled nauplii distribution (log-scale) on April 1st 1982 (a) and May 1st 1982 (b), and the corresponding modeled specific growth rate of a 5mm larva on April 1 (c) and May 1 (d).