Impact of prey field variability on early cod larval survival: a sensitivity study of a Baltic cod Individual-based Model*

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Abstract

Existing coupled biophysical models for Baltic larval cod drift, growth and survival use idealised constructed mean prey fields of nauplius distributions. These simulations revealed the best feeding conditions for Baltic cod larvae longer than 6 mm. For shorter, first feeding larvae (between 4.5 and 6 mm) pronounced differences in growth and survival were observed, which depend on food availability and to a lesser degree on ambient temperature. We performed runs with an Individual-based Model (IBM) for Baltic cod larvae in order to demonstrate how natural variability in prey abundance influences the survival success of first feeding larvae. In the Baltic, this larval stage lives mainly between 20 and 40 m depth and feeds exclusively on the nauplii of different calanoid copepods (*Acartia* spp., *Pseudocalanus acuspes*, *Temora longicornis* and *Centropages hamatus*). Prey data

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obtained from vertically stratified samples in the Bornholm Basin (Baltic Sea) in 2001 and 2002 indicate a strong variability at spatial and temporal scales. We calculated larval survival and growth in relation to natural variation of prey fields, i.e. species-specific nauplius abundance. The results of the model runs yielded larval survival rates from 60 to 100% if the mean size of nauplii species was taken and lower survival if prey consisted of early nauplius stages only.

1. Introduction

With regard to fish development, Hjort (1914) hypothesised that recruitment is affected by a critical period, one that is often stated as being the first feeding stage of fish larvae when these shift from endogenous to exogenous feeding (Hewitt et al. 1985, Houde 1989). Opinions differ as to whether this susceptibility is due to high levels of starvation or of predation (Leggett & Deblois 1994). However, as Bailey & Houde (1989) stated, whether starvation or predation is the primary cause of mortality could depend on the species, the area, the year and which developmental stage is mostly affected. For Baltic cod, predation by sprat and herring substantially affect the egg stage, whereas predation on larvae is negligible, because there is no spatial overlap with predators (Köster & Schnack 1994).

Different authors have set up various hypotheses covering different temporal and spatial scales regarding the causes of starvation in the early life stages of fish (Cushing 1990). The main reason is a temporal (seasonal; Cushing 1974, Pope et al. 1994) or a spatial (dispersion or retention; Parrish et al. 1981) mismatch between larvae and their prey. Laboratory experiments have demonstrated the importance of the patchiness of prey organisms to larval fish in their search for food (Gamble et al. 1981). A tool increasingly being used to study fish larval growth and survival are individual-based models (Hinckley et al. 1996, Letcher et al. 1996, Hinrichsen et al. 2002, Lough et al. 2005). They can be embedded within realistically simulated flow fields in order to explore the roles of growth, starvation, mortality and advective losses. Coupled hydrodynamic/trophodynamic modelling studies on the growth and survival of Baltic larval cod have highlighted the dependence of feeding and survival success on the availability of calanoid copepod nauplii (Hinrichsen et al. 2002). Using idealised constructed mean prey fields with a relatively coarse horizontal resolution, Hinrichsen et al. (2002) postulated the necessity for the co-occurrence of peak prey and larval abundance and oceanographic conditions favourable to high larval survival rates. All simulations revealed optimal feeding conditions for larger larvae, but for small, first feeding larvae, preying exclusively on copepod nauplii (Voss et al. 2003), there were pronounced differences in growth and survival that depend on food availability as well as on ambient temperature. However, even though

Hinrichsen et al. (2002) and others (Werner et al. 1996, Lough et al. 2005, Lough & Broughton 2007) were aware of the patchiness of larval prey, prey fields were averaged over large scales. In this paper we investigated the influence of prey field variability on cod larval survival in the Bornholm Basin (Baltic Sea) with field data obtained from a small spatial and temporal sampling in 2001 and from a basin-wide (mesoscale) monthly sampling in 2002. Further, we compared model outputs obtained from literature-based sizes of nauplii with a measured size distribution from samples obtained in the Baltic Sea in June 2001.

2. Material and methods

Zooplankton sampling

Copepod nauplii were sampled on cruises in June 2001 and in April, May and July 2002. In June 2001, six profiles were taken at one station covering day and night in a 48 h period (Figure 1). In 2002, sampling was performed at nine stations (Figure 1), the net being deployed only once at each station. In 2002, in parallel with the zooplankton sampling, hydrographic parameters (temperature and salinity) were recorded at each station using an ADM-CTD (Analoge und Digitale Meßsysteme GmbH). In 2001 this data was not recorded (see below).
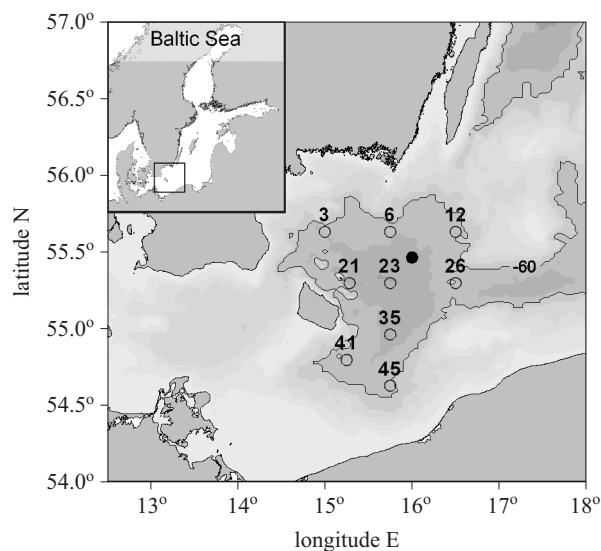

Figure 1. The Bornholm Basin study area in the Baltic Sea (overview in the upper left corner); the black dot shows the station sampled in June 2001; the open circles show the stations sampled in April, May and July 2002

Table 1. Length [mm] and weight [μm] of the different stages of the different species, and of sibling species where data for the original species was not available (*Pseudocalanus minutus*, *Centropages typicus*, *Acartia clausi*) taken from Ogilvie (1953); also the length-weight relationship given by Culver et al. (1985) for nauplius dry weight = a $\times$ length^b (where a = 3.009 and b = 1.706)

Species	N_1		N_2		N_3		N_4		N_5		N_6		Mean	
	length	weight	length	weight	length	weight	length	weight	length	weight	length	weight	length	weight
P. minutus	0.176	0.155	0.187	0.172	0.26	0.302	0.33	0.454	0.38	0.577	0.44	0.742	0.295	0.400
C. typicus	0.106	0.065	0.15	0.118	0.18	0.161	0.19	0.177	0.22	0.227	0.29	0.364	0.189	0.185
T. longicornis	0.112	0.072	0.16	0.132	0.21	0.210	0.26	0.302	0.32	0.431	0.38	0.577	0.240	0.287
A. clausi	0.12	0.081	0.14	0.105	0.16	0.132	0.19	0.177	0.23	0.245	0.28	0.343	0.187	0.181

Zooplankton samples were collected with a 0.25 m^2 multi opening/closing net system (Multinet, Hydro-Bios Kiel). The Multinet was equipped with five nets of 50 μm mesh size. The gear was applied vertically with a down- and upward speed of 0.2 m s^{-1}, resolving the water column into 10 m intervals from the bottom up to the surface, and filtering approximately 2.5 m^3 of water. Clogging, with the corresponding change in filtering efficiency, was not observed. Nauplii were preserved in 4% borax buffered formalin seawater solution and sorted in the laboratory under a binocular microscope. All nauplii except *Acartia* spp. were identified to the species level. The abundance was calculated as the number per cubic metre for each species. The biomass was calculated as the dry weight, using the length for each nauplius stage taken from Ogilvie (1953) as the basis for the growth term in the model (Culver et al. 1985) (Table 1). In June 2001 the length of *Pseudocalanus acuspes* nauplii was additionally measured, irrespective of stage, in order to obtain real size distributions. The measurements were done using ImageJ software (2003) with a precision of $\pm\,5$ μm. For our model calculations, only the nauplius abundances in the 20–30 m and 30–40 m depth layers were taken into consideration: these are the layers where first feeding cod larvae mainly live.

Model description and design of simulations

The individual-based model (IBM) used in this study was developed by Hinrichsen et al. (2002) using the generalised model described by Letcher et al. (1996) (Figure 2). This IBM tracks individual cod larvae through all larval phases including first feeding (4.5–6 mm). In the IBM, prey encounter rate, foraging, growth, survival and nutritional condition in terms of weight per length of larvae is simulated by specific sub-models in 6-h time steps.

The basis of this IBM is the standard bioenergetic supply-demand function (Beyer & Laurence 1980, Carlotti & Hirche 1997), where growth is represented as the difference between the amount of food ingested by a larva and the metabolic costs of its daily activities. To fill gaps in the data for Baltic cod, length-weight relationships from Otterlei et al. (1999) were applied to compute the expected weight under superabundant prey concentrations. Deviations of the simulated weight from the bioenergetic model and the maximum weight per length were used to run the starvation model. Larvae were defined as dying from starvation if the final weight per a specific length fell below specific threshold values, i.e. 75% of the maximum weight per length of larvae (Letcher et al. 1996).

Larval prey conditions were taken from in situ zooplankton measurements as described above. Each sample was assumed to be a 'potential prey field' that individual larva experienced during their first feeding phase.
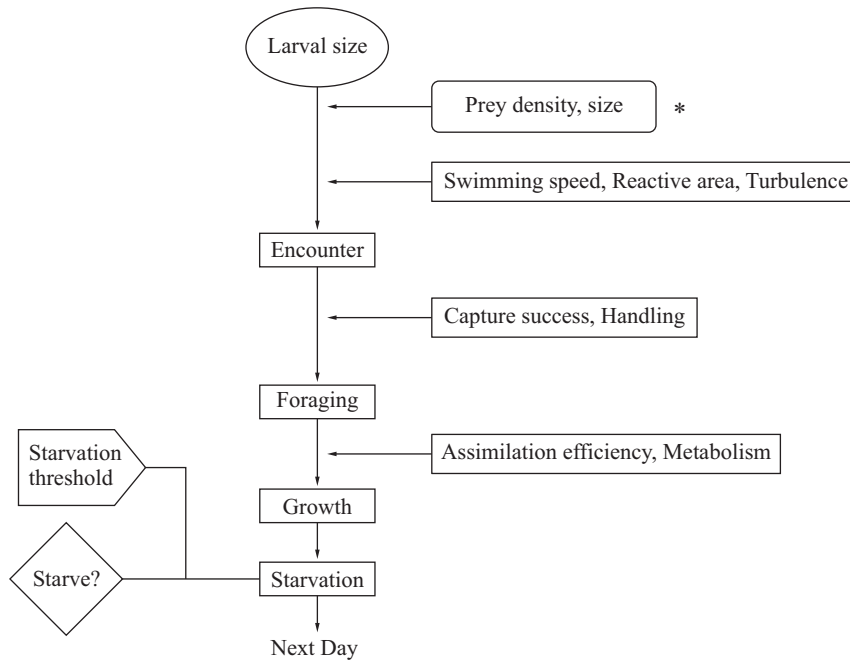
Figure 2. A scheme of the individual-based model (IBM) used in this study; the investigated parameter is marked with an asterisk. Modified after Letcher et al. (1996)

For June 2001 six profiles times two depth bins resulted in 12 'potential prey fields', and for 2002 nine profiles each month times two depth strata resulted in 18 'potential prey fields'.

To calculate the survival of the larvae experiencing the prey fields taken in June 2001, the IBM was coupled to the circulation model described in Hinrichsen et al. (2002). This was done primarily to obtain an estimate of the small-scale temperature variability the larvae experienced in this investigation period (Table 2). In the simulation, a cohort of larvae was

Table 2. Minimum and maximum temperature during the investigation periods at 20–40 m depths. The temperature in 2002 was measured in situ; the temperature in June 2001 was derived from the circulation model

Investigation period	Temperature [°C]
June 2001	5.8 − 7.9
April 2002	2.7 − 3.9
May 2002	3.2 − 6.9
July 2002	4.5 − 17.2

released and tracked for a period of 15 days. This time span approximately covers the first feeding period of larvae at June temperatures (Hinrichsen et al. 2002). 550 larval drifters were released at depths where first feeding larvae mainly live (26, 28, 30, 32 and 34 m) on a regularly spaced grid with a horizontal resolution of 500 m. To enable comparison of the model results with different prey field compositions, at the start of the model run (6 June) all larvae were defined as being of equal length and weight (4.5 mm). The larvae experienced specific temperature conditions along the drift trajectories within the coupled model. Only a one-dimensional version of the IBM was performed during all the investigation periods in 2002; larval drift was not taken into account. The temperature variability obtained from basin-wide measurements from each sampling period within the depth range of 20–40 m (Table 2) was split into 0.1°C steps for the model. One model run was performed for each 'prey field' and each temperature category. We assumed that with respect to the temporal development of nauplii, their abundances and sizes remained constant for the whole duration of the simulation periods, which were between 12 and 14 days, depending exclusively on the ambient temperature conditions. The sizes of the different copepod stages for each species were obtained from the literature (Ogilvie 1953). Where data for a species was not available we used data for a sibling species (Table 1).

Another set of model runs was performed using the abundances of *Pseudocalanus acuspes* in the 2001 samples with the real size distribution obtained from measurements and with the average size for *P. acuspes* taken from the literature (Ogilvie 1953). Two threshold values for nauplius abundance were calculated: (i) to ensure larval survival, and (ii) to gain maximum weight-at-age for the size range of 4.5 mm to 6 mm. To obtain some idea of the behaviour of the model, the prey density for a given prey weight needed for a larva with a given length at 5°C to survive one model step was calculated, assuming that the larva enters the model with maximum weight per length.

3. Results

Prey fields

In June 2001, *Pseudocalanus acuspes* nauplii were the most abundant of the four species within the 20–40 m depth stratum. Differences in abundance between samples were more than tenfold, from 369 to 5358 individuals per cubic metre (Figure 3). Peak abundance of the other species was only 120 individuals for *Temora longicornis*, 200 for *Centropages hamatus* and 80 for *Acartia* spp.
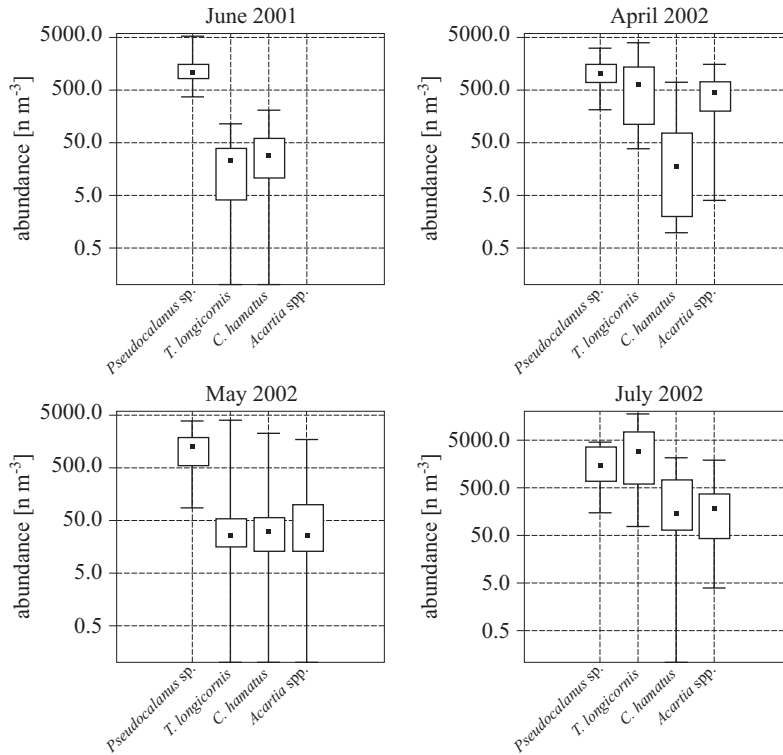
Figure 3. Abundances of the four copepod species estimated from multinet samples on a logarithmic scale; ■ – median, box – 25 and 75 percentiles, ⊥ – minimum, T – maximum; note the different scaling
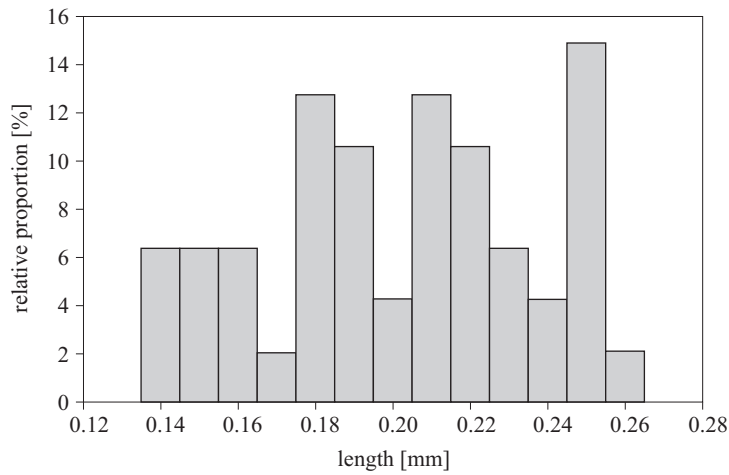

Figure 4. Size distribution of *Pseudocalanus acuspes* nauplii in samples from June 2001 (n = 47); lengths were measured accurate to ± 5 μm

In 2002 *P. acuspes* was the dominant species in April and May. The abundance of *P. acuspes* was almost constant in April, May and July. *T. longicornis* was also dominant in April, present in only very small numbers in May, but again the dominant species in July. *Acartia* spp. was found in high numbers only in April. *C. hamatus* was the least abundant species in all the sampling periods. Figure 4b shows the size distribution of 47 *P. acuspes* nauplii measured in June 2001. The length varied between 0.14 mm and 0.26 mm.

Results of the model runs

The first set of model runs revealed the influence of the variability in the density of nauplii as well as the influence of prey size; survival was strongly related to the latter. In general, the larger the prey was assumed to be in the model, the higher the survival probability of the larvae. Survival
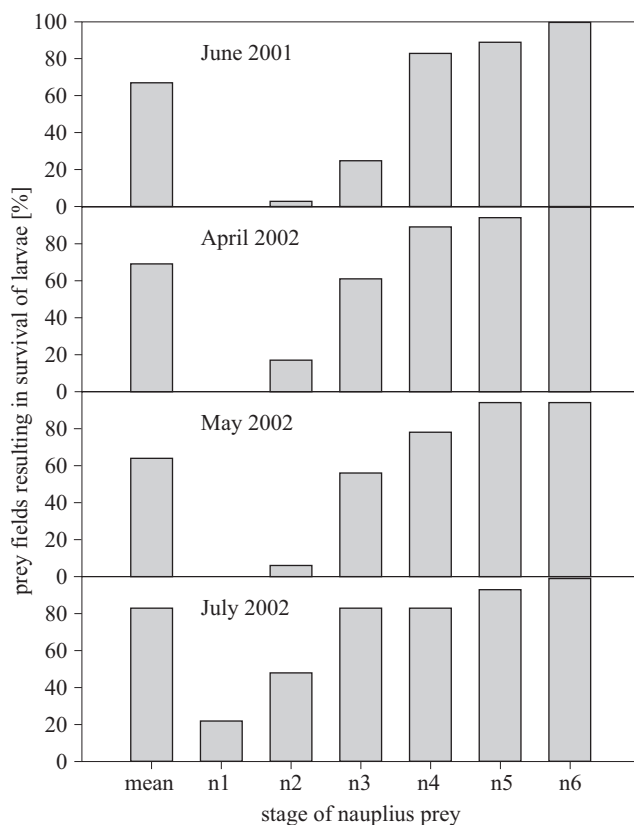

Figure 5. Percentage of model runs resulting in the survival of larva calculated by the model for the four periods sampled; 'mean' represents the results using the average size of nauplius stages 1 to 6 of each species gleaned from literature data

was highest in July 2002 (Figure 5), with large numbers of *P. acuspes* and *T. longicornis* present in the prey fields (Figure 3). Survival was lowest in June 2001 and in May 2002 (Figure 5), both months displaying a comparable prey field composition consisting mainly of *P. acuspes* (Figure 3). Taking all the sampling periods together, larval survival in the model runs was on average 65%, assuming an average size of the nauplius prey. If it was assumed that only stage 1 nauplii were present in the prey field, only the prey density in July 2002 was sufficient to guarantee survival of the larva in at least 20% of the model runs (Figure 5).

In the second set of model runs, the size distribution of the prey field was taken from the measured size distribution and was assumed equal for all prey fields in 2001, taking only *P. acuspes* as prey. Another set of model runs was performed with the literature average size of *P. acuspes* nauplii. For both sets of models, a threshold was calculated for survival and for maximum weight in 6 mm-long cod larvae. Figure 6 shows the minimum numbers of *P. acuspes* nauplii necessary for survival and for reaching the maximum weight at 6 mm length for these model runs, and for comparison,
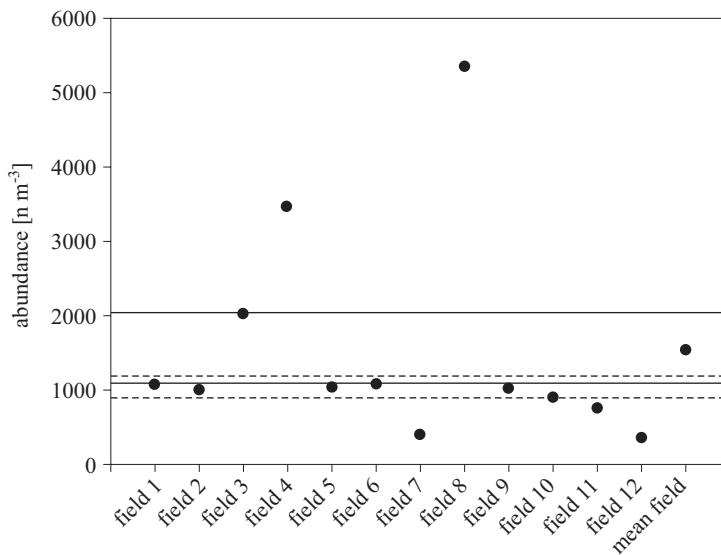

Figure 6. Abundance of *Pseudocalanus acuspes* nauplii in samples from June 2001; each point represents one sample (six stations, samples from 20–30 m and 30–40 m); the mean field represents the average of all 12 prey fields; dotted lines mark the survival threshold (lower line) and the threshold for maximum weight for length 6 mm (upper line) using the average size of nauplii taken from the literature (Ogilvie 1953); the solid lines mark the same using the real size distribution (shown in Figure 4) for each prey field (the lower line indicates the survival threshold, the upper line the maximum weight for length 6 mm)
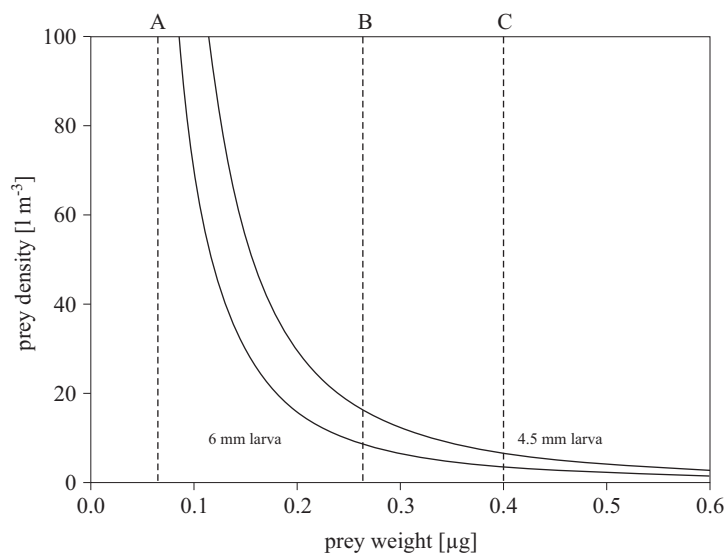
Figure 7. Number of nauplii with a given weight needed for a cod larva of 4.5 mm
and 6 mm length to survive one model step (6 h) at a given temperature of 5°C
(a larva survives if its weight at a given length exceeds 75% of the maximum weight
for the given length); A – minimum prey weight (*C. typicus* N1), B – average prey
weight (average of all species and stages), C – maximum prey weight (*P. minutus*
N6)

the numbers of average-sized prey items. The figure shows that for the latter
prey nine potential prey fields were above the survival threshold. Four of the
12 prey fields allowed the larvae to reach maximum weight at 6 mm length.
If the real size distribution was used, however, only five prey fields permitted
survival and only three prey fields were sufficiently abundant in nauplii to
enable larvae to reach their maximum weight. The calculated mean prey
field led to survival in both cases (mean size and real size), but maximum
weight was only attained if the mean size taken from the literature (Ogilvie
1953) was assumed.

In the model the smallest larvae were the most vulnerable to starvation
because they needed the highest density of prey in the field (Figure 7). Thus,
larger larvae are more competitive than smaller ones, because in a given
time period they are capable of searching for larger volumes of prey than
smaller larvae. Also, the required number of prey items rose dramatically
with decreasing prey size (Figure 7).

4. Discussion

Model results from a recent study (Hinrichsen et al. 2002) revealed the
importance of combined advective and trophodynamic processes on the

growth and survival of Baltic larval cod populations. An analysis in the above model study showed the encounter rate submodel (search volume, reactive distance etc.) to be the most sensitive to parameter changes, so in our most recent modelling approach such an analysis was deemed unnecessary. Because of the sensitivity of the prey encounter model to larval survival probability, we were interested mainly in the effect of the natural small-scale prey availability representing larval search volumes larger than the foraging range of a larva. Generally, this kind of modelling approach (Hinrichsen et al. 2002) has to cope with sparse temporal and spatial resolutions of zooplankton prey fields (Hermann et al. 1996, Werner et al. 1996). However, sensitivity studies like the present one demonstrate that the model is able to show the impact of natural perturbations of the number of encountered and ingested prey on growth and survival. Consideration of the development of zooplankton species and stages at scales with different temporal and spatial resolutions is highly recommendable, because the spatial and temporal variability of zooplankton is not merely noise but an essential feature of food web dynamics (Carlotti 2001); it is therefore crucial to link larval fish trophodynamics to different patch sizes and dynamic distributions of prey. This study does not directly address the patchiness of larval prey but attempts to analyse larval survival success in relation to natural variability in larval prey fields derived from a point sampling in 2001 and a basin-wide sampling in 2002. The point sampling in the central Bornholm Basin in June 2001 illustrates that the differences in prey concentration, and eventually in larval growth and survival, could be high on a small temporal and spatial scale, in fact nearly as high as the basin-wide variability during a comparable period (Figure 3).

For most of the analysed observation periods, idealised constructed mean prey abundance values based on long-term observations (Hinrichsen et al. 2002) led to high growth rates, optimum nutritional conditions, and, consequently, to high estimated rates of larval survival. Overestimation of survival and nutritional condition can be prevented by taking into account the natural variability of the prey fields obtained from spatially resolved zooplankton abundance measurements as well as by considering observed compositions the different species and stages of prey. The model results also stress the necessity to use in situ measurements of nauplius sizes instead of literature values. Although this study did not address the real stage-specific length of nauplii, taking size spectra from the North Sea or the Atlantic Ocean could lead to overestimation of larval survival and nutritional condition. The low salinity in brackish water systems like the Baltic may affect the growth and maximum size of marine organisms (Gunter 1961). The length distribution for *Pseudocalanus acuspes* measured

in this study was comparable with that of the three youngest nauplius stages taken from the literature (Figure 4 and Table 1). Neglecting realistic information on the stage composition, size and abundance of prey modifies the results of the bioenergetic supply-demand function used to describe the growth of Baltic cod larvae. It could substantially alter the amount of food ingested by a larva and, hence, could lead to inaccurate daily larval growth rates and subsequently to erroneous calculation of larval survival. The considerable variability in prey size and density affects mainly the survival of the youngest larvae, as these require the highest densities of prey of a given prey size. Although they need less food to maintain their metabolism and to grow, they are limited in their swimming and visual capabilities. This causes a reduction in their reactive area and lower contact rates as given by the individual-based model (Hinrichsen et al. 2002). The field-observed variability in temperature generally has a strong impact on larval growth conditions as well as on the survival of larval cod and may thus have contributed to the observed year-to-year differences in Baltic cod recruitment. In general, the higher temperature in the third quarter of the year than in the second quarter requires a higher prey abundance; the differences are small if the prey consists mainly of late nauplius stages, but could be significant if the prey is smaller.

A topic not investigated in this study was how behavioural changes, e.g. the swimming speed of larvae (Ruzicka & Gallager 2006) or predator avoidance of prey (Titelman & Kiørboe 2003), influence the rate of encounter between larvae and their prey. It was reported by Munk & Kiørboe (1985) that herring larvae alter their swimming speed after coming across a prey patch, thus increasing the probability of remaining within such a patch. Furthermore, although the small-scale variability on feeding success and survival was analysed, patch dynamics, e.g. turbulence or the behavioural adaptations of zooplankton to predation in terms of vertical migration, were not considered. Studies of predator and prey patch dynamics are envisaged for the future: models with a high spatial resolution may increase our knowledge of these processes in nature. This study dealt only with prey size and prey density, although the sensitivity analysis in Hinrichsen et al. (2002) showed that besides the parameterisation of the prey encounter rate, metabolism and the starvation threshold had a major influence on the output of the model (Hinrichsen et al. 2002). The metabolic costs may have been too high compared to other studies (Lough et al. 2005), but were not altered in this study, so that the impact of prey size and density compared to the study of Hinrichsen et al. (2002) could be demonstrated.

Acknowledgements

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