Linking stage-resolved population models with field observations: an integrated approach on population dynamics of *Pseudocalanus elongatus* in the German Bight

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The population dynamics of *Pseudocalanus elongatus* have been investigated within the framework of the GLOBEC-Germany project to gain a better understanding of its life cycle and population dynamics and to estimate secondary production in the North Sea. During an intensive field study in the German Bight between February and October 2004, experiments on reproduction were performed and data on length of copepodids and abundance were collected to characterize the population in the southern North Sea. This data set was used to update the literature-based parameterization of a population model for *P. elongatus* to investigate the population dynamics, life history and production in the German Bight. The ability of data to improve population models is also discussed. *Pseudocalanus elongatus* was found to be a major contributor to carbon uptake contributing about one-third of copepod production. Though the spatial variability in field observations was not reflected by the model, the simulation matched data within one order of magnitude at most stations. The high-resolution field observations and experiments mainly improved the parameterization of the reproductive parameters. Mortality is found to be a critical parameter due to its influence on population size. Using constant rates, though based on observation-derived estimates, seems not to capture realistic variability. Our study confirms the need for experimental and field data to build a robust parameterization for concentration-based population models.

KEYWORDS: *Pseudocalanus elongatus*; Zooplankton sampling; reproduction; copepod population model; secondary production; German Bight; North Sea

INTRODUCTION

Within the marine food web, calanoid copepods represent an important link between primary production and higher trophic levels and are therefore an essential component of the structure and functioning of marine ecosystems. To understand and predict changes in copepod communities, detailed knowledge on species-specific reactions to the biotic and abiotic environment is required.

Pseudocalanus elongatus is a dominant copepod in the southern North Sea and its correct taxonomic classification was recently confirmed (Grabbert *et al.*, 2010). In the Dutch and German Wadden Seas, it is one of the most important copepod species (Fransz, 1975; Krause *et al.*, 1995) forming up to 46% of the zooplankton community abundance in late spring, following the phytoplankton spring bloom (Fransz *et al.*, 1991). It contributes significantly to the diet of larval herring (Hardy, 1924), sprat (Conway *et al.*, 1991; Voss *et al.*, 2009) and gadoid larvae such as pout or haddock (Economou, 1991). *Pseudocalanus elongatus* is among the most studied copepod species in the North Sea (Krause *et al.*, 2003). Its abundance is monitored in time-series studies, e.g. at Helgoland Roads (Greve *et al.*, 2004) or in the English Channel (Green *et al.*, 1993; Eloire *et al.*, 2010), the spatially resolved CPR survey (Batten *et al.*, 2003) as well as in short-term investigations, e.g. the ZISCH survey (Krause *et al.*, 1995).

Two life-history strategies have major influence on its population growth: the temperature relation of development results in adaptation to colder water (Thompson, 1982; Klein Breteler *et al.*, 1995), whereas the egg carrying strategy results in relatively low egg production rates (EPRs) compared with broadcasting species (Halsband and Hirche, 2001) along with lower egg mortality (Eiane and Ohman, 2004) as found from estimates based on data in the Fladen Ground (Krause and Trahms, 1983). Although many aspects of its life cycle are well studied in the laboratory, few studies have been made of the regional and seasonal development of field populations, as this requires large sampling efforts.

Numerical models describing the life cycle of *Pseudocalanus* species have been used to study demographic patterns on Georges Bank (McGillicuddy and Bucklin, 2002) and to examine the sensitivity of distinct processes in the North Sea (Stegert *et al.*, 2009), the Baltic Sea (Dzierzbicka-Glowacka, 2005; Neumann and Fennel, 2006) and the northwestern Atlantic Ocean (Ji *et al.*, 2009).

Stage-resolved copepod population models, coupled with ocean circulation models, are a useful tool for the mechanistic understanding and quantitative description of the influence of environmental conditions like the effects of advective transport, temperature and food availability on development and secondary production of a population (Carlotti *et al.*, 2000). Furthermore, they are capable of reflecting demographic effects and size-dependent processes (Rinke and Vijverberg, 2005). These models permit a detailed temporally and spatially resolved representation of the population structure for a certain species, while field sampling is often sparse compared with the space-time scales of planktonic organisms (Davis, 1987). However, stage-resolved models require a species-specific calibration of biological traits. To obtain robust parameter values for a realistic representation, usually data from laboratory experiments and field observations are combined (Carlotti and Sciandra, 1989; Carlotti and Nival, 1992; Heath *et al.*, 1997). This is a trade-off, which might explain some differences between model results and observations, as copepod behaviour is not necessarily the same under controlled conditions as it might be in the field. A key problem of linking data and models is the diversity of zooplankton population dynamics, the wide range of physiological and behavioural aspects as well as the complex interplay with hydrography (Krause *et al.*, 2003). In 2004, an extensive field study in the southern North Sea included seven cruises which carried out sampling and processes studies (Renz *et al.*, 2008). This data set is chosen to synthesise the *P. elongatus* life cycle from observations and by modelling.

A zero-dimensional, stage-resolving population model, based on Fennel (Fennel, 2001), was parameterized for *P. elongatus* in the North Sea by Stegert *et al.* (Stegert *et al.*, 2007) and embedded in the three-dimensional marine ecosystem model ECOHAM (Moll and Radach, 2003) to study the annual cycle under realistic weather and hydrographical conditions. A first comparison of simulated stage-resolved abundances with counts at several stations in the German Bight during the GLOBEC-Germany project was used as a basis for validation (Stegert *et al.*, 2009). While growth could be successfully calibrated based on stage duration estimations in the laboratory, reproduction and mortality, which strongly affect total abundance, could at that time only be parameterized from literature data or were calibrated to fit mean abundances from time-series (Table I). Now, spatially high-resolution measurements of reproduction and abundance from GLOBEC-Germany are available to more realistically parameterize reproductive success and mortality for *P. elongatus* in the German Bight.

The aim of this study was to (i) refine the process formulations of reproduction and mortality for *P. elongatus* with measurements from the field program in the North

Table I: Parameter values used in the population model (Stegert et al., *2007) along with the source the parameters have been calibrated to*

Stage	Unit/function	Source
Ingestion terms		
Max. ingestion rate	day^{-1}	
Half saturation	µg C L^{-1}, f(food)	
Power coefficient	n.d., f(food)	Calibrated to stage durations
Q10 parameter ingestion	n.d., f(T)	Klein Breteler *et al.* (1995)
Reference temperature Q10	°C, f(T)	
Loss terms		
Assimilation efficiency	n.d., f(ing)	
Active metabolism	n.d., f(ing)	Calibrated to stage durations
Basal metabolism	day^{-1}, f(T)	Klein Breteler *et al.* (1995)
Q10 parameter loss	n.d., f(T)	
Weight parameters		
Reference weight (start transfer)	µg C	
Critical moulting mass	µg C	Various literature
Critical ingestion mass	µg C	
Reproduction parameters		
Maximum invested matter	µg C female^{-1}	Calibrated to fit EPR
Slope factor	n.d.	Corkett and McLaren (1978)
Reproductive females	n.d.	
Mortality		
Mortality rate	day^{-1}	Calibrated to fit time series
Half saturation	ind. m^{-3}, f(#)	Data

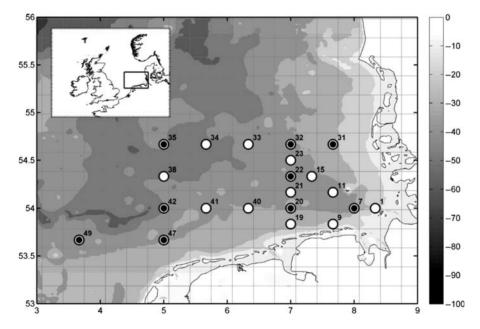The dependent variable and the unit are given if applicable (n.d., non-dimensional).

Fig. 1. Topography, model grid boxes (grey lines) and numbered stations of the field study in the German Bight; circles: stations with bongo samples; black dots: stations with multinet samples (focus stations); upper left box shows the model domain and the area of interest.

Sea in 2004 (Renz *et al.*, 2008) and to estimate the effect on the simulated population dynamics, (ii) identify key processes in the population dynamics by comparing simulated and observed distribution and development of *P. elongatus* in the German Bight and finally (iii) discuss its importance within this ecosystem in terms of production based on the integrated field-model approach.

METHOD

Field data

Zooplankton sampling
Sampling and experiments were performed on five cruises between February and October 2004 on a station grid in the German Bight, North Sea (Fig. 1).

On every station, oblique bongo net hauls (mouth opening 0.2 m², mesh size 150 μm, towing speed 3 knots) were taken from above the bottom to the surface. Furthermore on nine focus stations, sampling was performed using a multinet (Hydrobios, 0.25 m² mouth opening, 50 μm mesh size, towing speed 0.2 m s⁻¹) towed vertically with a 10-m resolution from the bottom to the surface. Bongo net hauls were used for determination of abundance and prosome length of copepodids I–V (CI–V) and adult stages (CVI), while the multinet was used to determine nauplii abundance. Additionally, at the focus stations, samples for experiments on reproduction and development were taken with a WP-2 net (UNESCO 1968, mouth opening 0.26 m², mesh size 200 μm, towing speed 0.2 m s⁻¹) towed vertically from above the bottom to the surface.

A general overview of the GLOBEC-Germany data sets is given in Schulz *et al.* (Schulz *et al.*, 2008). For detailed information regarding the preservation of zooplankton samples, identification of *P. elongatus*, length measurements of developmental stages and protocols for experiments on reproduction and development, see Renz *et al.* (Renz *et al.*, 2008).

Hydrography
Concurrent to the zooplankton sampling, vertical profiles of temperature were recorded using a CTD-probe (SBE 911þ, ME). As an index of food availability, the vertical distribution of phytoplankton was recorded using a Fluoroprobe (bbe Moldaenke, Kronshagen, Germany). This instrument is based on the measurement of chlorophyll fluorescence emission after excitation at five different wavelengths. Using normal spectra of different algal groups and the actual 5-point excitation spectrum of a water sample, an estimate of the respective chlorophyll concentration can be obtained.

Biomass and production
Carbon mass of nauplii and copepodids was calculated according to a length–weight relationship (Klein Breteler *et al.*, 1982), assuming 0.4 mg C mg⁻¹ dry mass (Parsons *et al.*, 1984).

Population egg production was calculated from data on abundance and egg production for the focus stations. Mean population stage structure, including eggs, was then described for all focus stations for stage groups: eggs-nauplii, CI–III, CIV–V and adults.

Secondary production ($P_i = g_i B_i$) was derived from carbon biomass B_i, abundances of a certain stage (Rigler and Downing, 1984) and growth rates g_i determined in moulting experiments (Renz *et al.*, 2008):

$$g_i = \ln\frac{W_{i+1}}{W_i} \times D^{-1},$$

where $W_{i,i+1}$ are the individual masses and D_i the stage duration. Spatial variability in population secondary production was exclusively due to variability in abundances of stages, as we did not account for spatial differences in growth rates or mass of single stages. Growth rates were highest in April (0.31 day⁻¹ for CI to 0.09 day⁻¹ for CV) and generally decreased afterwards, except for high CII growth in June (0.31 day⁻¹).

Mortality rates
Mortality rates were estimated using the vertical life table (VLT) approach (Aksnes and Ohman, 1996; Ohman *et al.*, 2002). Stage durations were calculated from the Belehrádek function with parameters from Klein Breteler *et al.* (Klein Breteler *et al.*, 1995) using temperatures at weighted mean depth (Bollens and Frost, 1989) for each stage. There was no difference between day and night distributions as vertical mixing was high in the water column and temperature differences between upper and deeper layers were usually below 1°C. We took abundances of copepodids from 8 to 21 stations on seven cruises and of nauplii from 4 to 7 stations on four cruises. Although the required number of nine stations for mortality calculation (Aksnes and Ohman, 1996) was not always available, we assume that the data provide a reasonable estimate of mortality rates for *P. elongatus* in the German Bight. The mortality rate was calculated for each successive pair of developmental stages according to the VLT. For nauplii, a mean mortality rate of all nauplii to stage CI was calculated, as nauplii stages were not distinguished in the counts. As adult mortality cannot be calculated by the VLT, it was assumed to equal mortality of older copepodids.

Population demographics
The number of generations was estimated from field observations using female length measurements and the predicted temperature-dependent generation time by Klein Breteler *et al.* (Klein Breteler *et al.*, 1995) for interpretation.

Model and simulation

Model outline
The stage-resolving population model for *P. elongatus* (Stegert *et al.*, 2007) adapted the generic stage-resolving population model by Fennel (Fennel, 2001). The model consists of 10 state variables, with biomass and abundance for each of five model stages: non-feeding stages (eggs-NII), nauplii (NIII–VI), young (CI–III) and old copepodids (CIV–V) and adults (CVI). According to Carlotti and Sciandra (Carlotti and Sciandra, 1989), the
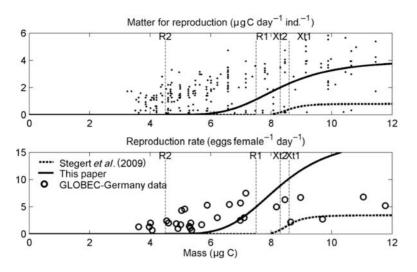
Fig. 2. Comparison of observed values (dots) and model function (line) of maximum invested matter (upper) and EPR (lower), where the parameterization of Stegert *et al.* (Stegert *et al.*, 2009) is given by dashed lines and for the present paper is given by solid lines. R1 and Xt1 are reference weight and critical weight from Stegert *et al.* (Stegert *et al.*, 2009) and R2 and Xt2 from this paper.

development of stages is defined by a constant critical weight, at which the transfer rate from one stage to the next increases by a sigmoidal function to describe a statistical scattering. The life cycle of the model copepod includes growth processes and the influence of the environment. Furthermore, physiological processes are implemented, which consist of two categories: (i) processes affecting the state variable abundance, i.e. reproduction, hatching and moulting (which are controlled by weight, Fig. 2) and mortality (described as a constant rate which decreases at low abundance) and (ii) processes affecting only biomass, i.e. ingestion, respiration and excretion, which are controlled by food and temperature. The population model was coupled to the 3D ecosystem model ECOHAM to simulate the annual cycle of *P. elongatus* during 2004 (Stegert *et al.*, 2009).

Estimation of number of generations and secondary production
From the 3D coupled model, the number of generations was identified counting the maxima of the simulated total abundance within one generation time, which was estimated by the Belehrádek function (Klein Breteler *et al.*, 1995). To exclude minor variation, only abundance peaks >15% of maximum abundance were used.

Simulated growth (G) was calculated by subtracting the carbon fluxes within losses [excreted (U), egested (E) and respiratory (R) carbon] from the ingested (I) carbon: $G = I - U - R - E$ (Corkett and McLaren, 1978). In the model, calculated total loss through physiological processes and mortality was divided into state variables for small (sinking at 0.16 m h^{-1}) and large (4 m h^{-1}) detritus. The latter was attributed to mortality, as the sinking

speed of dead *Pseudocalanus* particles was reported to be 1.1 mm s^{-1} (Mauchline, 1998), while flux into small detritus was attributed to physiological loss and only considered in the calculation of secondary production.

RESULTS

Field data for refinement of parameterization

Measurements during the 2004 field programme (Renz *et al.*, 2008) showed that several parameters in the life history of *P. elongatus* differed from the literature data used by Stegert *et al.* (Stegert *et al.*, 2009). These differences and the adaptations for the present study are described below.

Mass of developmental stages and transfer processes
As described by Renz *et al.* (Renz *et al.*, 2008), prosome lengths of copepodids are up to 25% larger in spring than in autumn (35% for females). Carbon mass calculated from length–weight relationships for copepodids collected during GLOBEC-Germany tended to be up to 30% lower than parameterized by Stegert *et al.* (Stegert *et al.*, 2009). Therefore, stage masses were replaced by mean field weights (Table II). Furthermore, the observations showed that females are able to start reproducing immediately after moulting from the CV stage, and the reference weight R of adults equals the critical weight Xt (CIV–V), when the transfer rate is 50%.

Reproduction
The mean EPR over the study area was 1.1 eggs female^{-1} day^{-1} in October and 5.3 eggs female^{-1}

Table II: Parameter values of the proportion of reproductive females, max. invested matter, hatching success, mortality, reference weights (R), critical weights (Xt) and the critical ingestion masses (Xg) for P. elongatus from Stegert et al. *(Stegert* et al*., 2009) and from this article based on new field observations*

Parameter	Stage	Observations	Stegert *et al.* (2009)	This article
Reproductive females (fem./ad.)	Adults	0.2	1.0	0.2
Max. invested matter (μg C day^{-1})	Adults	4.0	0.8	4.0
Hatching success (n.d.)	Eggs-NII	0.79 (std: 0.22)	0.6	0.8
Minimum weight for transfer into next stage, $R(i)$ (μg C)	Eggs-NII	n.d.	0.14	0.14
(using observed mean weight)	NIII–VI	n.d.	0.5	0.4
	CI–III	1.48 (CIII)	1.8	1.5
	CIV–V	3.37 (CV)	4.3	3.4
	Adults	5.32 (Fem.)	7.5	5.3
Critical weight transfer (transfer rate = 50%), $Xt(i)$ (μg C)	Eggs-NII	n.d.	0.1	0.1
(using 0.9 of observed maximum weight)	NIII–VI	n.d.	0.7	0.5
	CI–III	1.66 (CIII)	2.4	1.7
	CIV–V	4.48 (CV)	5.4	4.5
	Adults	8.32 (Fem.)	8.6	8.3
Critical weight ingestion (ingestion = 0), $Xg(i)$ (μg C)	Eggs-NII	n.d.	—	—
(using observed maximum weight)	NIII–VI	n.d.	0.8	0.6
	CI–III	1.84 (CIII)	2.7	1.8
	CIV–V	4.98 (CV)	6.0	5.0
	Adults	9.24 (Fem.)	9.6	9.2

Respective weights from GLOBEC-Germany field observations in 2004 are given.

day^{-1} in April with a mean clutch size of 25 eggs female^{-1}, which corresponds to 4 μg C invested biomass per female (Fig. 2) and is much higher than the 0.8 μg C female^{-1} used in Stegert *et al.* (Stegert *et al.,* 2009). Observed hatching success was highest during times of highest reproduction and varied around 80%. Due to the short life span of males, females usually dominate the adult population and the median ratio of females to males was ~2.8 (i.e. females comprise ~74% of total adults). The mean proportion of spawning females was 28% of all females (Renz *et al.*, 2008).

In the model, females provide a certain amount of biomass for reproduction, when reaching the maturation mass (R). While in Stegert *et al.* (Stegert *et al.,* 2009) only reproductive females were considered in the adult stage, we now considered all adults and allowed only the observed proportion of 20.1% which were reproductive, as the product of hatching success and sex ratio (Table II).

As field measurements of EPR, clutch size and proportion of spawning females, measured during the GLOBEC-Germany, were in good agreement with earlier field studies of *P. elongatus* in the German Bight by Halsband and Hirche (Halsband and Hirche, 2001), these values were used in the new model simulation (Fig. 2). At the weight Xg = 9.2 μg C (Table II) female ingestion equals zero, so females cannot get larger. This limits EPR at 12, which corresponds to the maximum observed rate (Renz *et al.*, 2008).

Table III: Mortality rates (d^{-1}) of P. elongatus derived from field observations in the German Bight in 2004 (annual mean over all stations), and reported by Eiane and Ohman (Eiane and Ohman, 2004), as well as parameter values used in Stegert et al. *(Stegert* et al*., 2009) and this article.*

Stage	Field study GLOBEC	Eiane and Ohman (2004)	Stegert *et al.* (2009)	This article
Eggs-NII			0.14	0.14
Nauplii-CI	0.08	0.0–0.11		
NIII–VI		0.0–0.03	0.17	0.08
CI/II	0.21	~0.1		
CII/III	0.13	0.0		
CIII/IV	0.07	0.0		
CI–III		0.0	0.16	0.14
CIV/V	0.14	0.0		
CV/adults	0.18	~0.5		
CIV–V			0.15	0.19
Adults			0.13	0.19

Mortality

Stegert *et al.* (Stegert *et al.,* 2009) used mortality values between 0.13 and 0.17, with lowest rates for adults and highest for older nauplii. In contrast, mortality rates from the field study were highest for stages CI/II and CV/adults (up to 0.21 day^{-1}, Table III), while CIII/IV showed lowest rates (0.07 day^{-1}). Hence, mortality rates of nauplii (0.08 day^{-1}) and young copepodids (0.07–
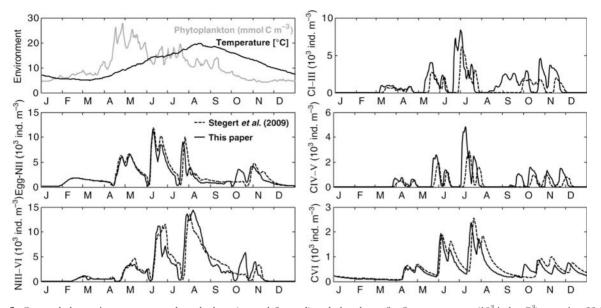
Fig. 3. Seasonal change in temperature, phytoplankton (upper left panel) and abundance for five-stage groups (10^3 ind. m^{-3}) at station 32 in 2004. Simulation with parameters after Stegert *et al.* (Stegert *et al.*, 2009) as dashed line versus parameters according to GLOBEC-Germany observations as a solid line.

0.21 day^{-1}) from field samples in the southern North Sea were higher than those reported by Eiane and Ohman (Eiane and Ohman, 2004) but lower than fitted in the model simulation by Stegert *et al.* (Stegert *et al.*, 2009). As in this study adults include male and female abundance, the mortality rate was increased to reflect high male mortality. The estimated mean values from the field were therefore taken for the new parameterization.

Effects of refined parameterization on simulated population dynamics

The adjustments described before resulted in earlier and higher abundances especially for CI–III and CIV–V during late spring and early summer (Fig. 3) than in the model by Stegert *et al.* (Stegert *et al.*, 2009). While the overall abundance of non-feeding stages eggs-NII and older nauplii stages NIII–VI was similar in the new simulations, the lower mortality of older nauplii and young copepodids resulted in higher copepodid abundances in the new simulation. The adjustment of reproduction parameters did not change the abundance of non-feeding stages, as the increase in the maximum invested matter and hatching success was counteracted by the decreased proportion of spawning females and higher mortality rates of adults. The lower weight of all stages led to an earlier transfer from nauplii into young copepodids and thus to a ca. 10 days earlier occurrence of copepodid cohorts as well as to the development of a CI–III cohort in late summer (around day 225). The latter developed into adults 50 days later. Despite this,

the refinement of the parameterization did not affect the abundances during winter.

Comparing simulation to observation at all stations for each month of field study, the new parameterization resulted in a better fit with a tendency to overestimation; 71% of values were within 1 order of magnitude with 20% being more than 10 times higher than observations (Fig. 4). In comparison, in the simulation of Stegert *et al.* (Stegert *et al.*, 2009), 66% of values were within 1 order of magnitude, while 16% were underestimated.

Integrated analysis of field data and refined model results: population dynamics and secondary production

Abundance

Observed and simulated distributions showed similar overall spatial variability in abundance with lowest numbers of NIII–VI in the northwestern part (stations #34–38) and of CI–III in the northeastern part (station #31/32) of the study area (Fig. 5). Largest peaks of older nauplii and copepodids were found in June in the model as well as field observations. However, simulated abundance of older nauplii as well as copepodids exceeded observations during summer, while simulated abundances of older copepodids were generally lower than observations. Differences between observation and simulation were mostly within 1 order of magnitude (Fig. 5) showing strong spatial differences. While total copepodite abundances were low and spatially
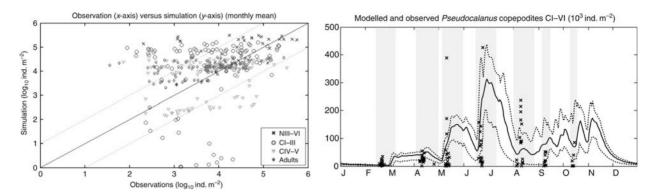
Fig. 4. (Left panel) Comparison between field observations (*x*-axis) and simulated abundances (*y*-axis) at 18 stations in the southern North Sea. Note: simulated abundances represent NIII–VI, while observed abundances represent all nauplii. (Right panel) Spatial variability in *P. elongatus* copepodites CI–VI abundance as observed (cross) during the GLOBEC-Germany cruises in 2004 (grey shaded) and simulated (mean of 18 stations as a solid line with minimum and maximum values as crossed lines). See online Supplementary data for a color version of this figure.
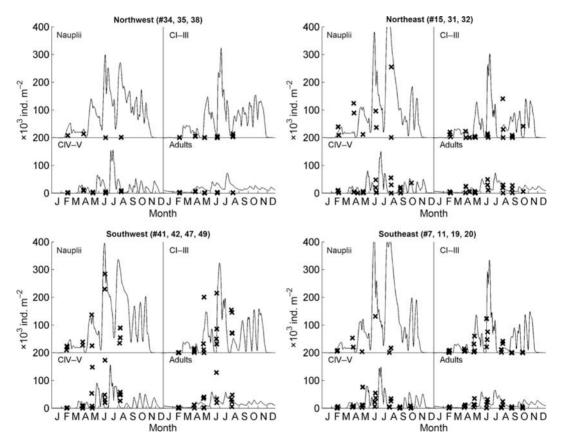

Fig. 5. Comparison of simulated (lines as mean over given stations) and observed (cross including all observations at those stations) abundance of developmental stages NIII–VI (upper left in each panel), CI–III (upper right), CIV–V (lower left) and adults (lower right) of *P. elongatus* in the southern North Sea in different parts of the GLOBEC-Germany station grid. Note: Nauplii were not counted at each station. Station by station plots of single model stages are given in Supplementary data for a clear spot.

homogeneous in spring in simulation and observation variability was high in summer. Observations indicated generally low abundances in autumn ($<100 \times 10^3$ ind. m^{-2}) and the model calculated a distinct increase until October (up to 180×10^3 ind. m^{-2}).

Stage structure

During the field study (Renz *et al.*, 2008), eggs and nauplii dominated the population between February and June (ca. 70% of all individuals) and decreased thereafter to 15% in October (Fig. 6). Younger

copepodids increased over the summer from 10% in June to 40% in October, while the proportion of older stages and adults doubled to 20%. Due to restricted sampling of nauplii during autumn, no information is available about the exact stage structure from August onwards. Considering only copepodids and adults, younger stages dominated while older copepodids and adults accounted for an equal proportion of ca. 25% each.
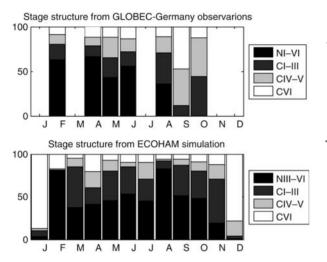

Fig. 6. Monthly mean observed (upper) and simulated (lower) stage structure in the study area as mean values over 18 stations and corresponding model grid cells in 2004.

The simulated population at station 32 showed a strong cyclic occurrence of stages with a pronounced cohort structure. At the end of January, adults started reproduction and the population consisted mostly of eggs and nauplii. Their percentage decreased to ∼60% by the end of March before increasing again with the next generation. With each following generation the percentage of eggs and nauplii decreased until a break-down of these stages in September. Most individuals remained in the adult stage at the end of the year.

Number of generations
In the field, 4−5 generations were identified by differences in prosome length of adult females (Fig. 7), with the first generation developing from overwintering CIV−V in April and generations 2 and 3 following in May and June (Renz *et al.*, 2008). The sampling gap in July made it difficult to identify the number of generations. However, the overlap in female prosome length from June onwards suggested that a maximum of two further generations followed until October.

The simulation showed a development of 5−6 generations of *P. elongatus* in the Wadden Sea and the southern German Bight and 7−8 generations in the Dogger Bank area outside the station grid (Fig. 7). Timing of occurrence of a new generation was mostly the same at different stations, with the first generation occurring around day 50 and the following generations developing around
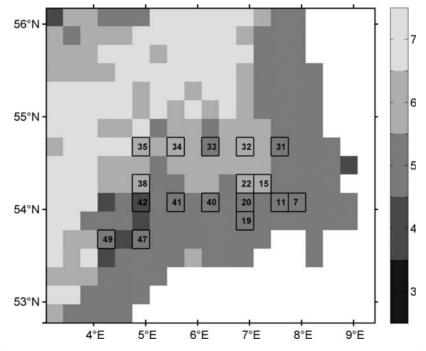

Fig. 7. Spatial variability in estimated number of generations of *P. elongatus* in the southern North Sea from simulation. Indicated are model grid cells including sampling stations from the field study.
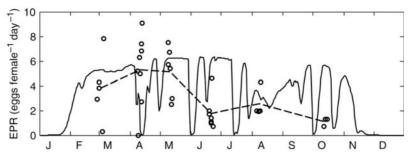
Fig. 8. Comparison between the simulated (line) seasonal EPR at station 32 and at all stations of the field study (dots) with the monthly median value as a dashed line as given in Renz et al. (Renz et al., 2008).

days 125, 160, 205 and 300. Depending on the occurrence of abundance peaks in autumn, an additional generation developed around day 280 at several stations.

Egg production

In the field, variability in egg production in the study area was large (Renz et al., 2008). High EPRs were already observed at the beginning of March (Fig. 8). They lasted until the beginning of May and dropped from a mean of ca. 5 to ca. 2 eggs female^{-1} day^{-1} in October.

The simulation showed a similar pattern for station 32 in the German Bight (Fig. 8) with rates matching the mean observed EPR until summer. In August, egg production ceased more or less except for a small peak in October, while field values were much higher during the rest of the year. Including the main factors of reproductive females, sex ratio and invested matter in the parameter values, simulated EPR matched the observations in number and seasonal course.

Secondary production

Secondary production of *P. elongatus* derived from observations was highest during early summer in the central and southern part of the study area (Fig. 9), with mean production of 26 mg C m^{-2} day^{-1} and maximum values of up to 142 mg C m^{-2} day^{-1} in June (Renz et al., 2008).

This general picture was also displayed by the simulation, however, with less spatial variability and a spatial shift of highest production to the east (Fig. 9). Simulated production was highest in the inner German Bight during May and June, reaching a maximum of up to 120 mg C m^{-2} day^{-1} in May in the inner German Bight and in the coastal region during June. A strong decrease in production after the summer peak during August, which is in contrast to field observations, was followed by an increase during September, while observed abundances remained low from August to October.

DISCUSSION

The current paper combines published data from an extensive field study in the German Bight in 2004 (Renz et al., 2008) with simulation results of a population model within a 3D ecosystem model for the same year. In the following discussion, we (i) identify important factors driving the population dynamics of *P. elongatus* in the German Bight, (ii) discuss its distribution and life cycle, (iii) evaluate its role in the ecosystem of the German Bight and (iv) finally, present conclusions with respect to the current status and future perspectives of the population model.

Implications for driving factors in population dynamics from observation and simulation

The adaptation of weight, reproductive parameters and mortality based on field observation resulted in an overall more specific model for the *P. elongatus* population in the southern North Sea. Discrepancies between (new) simulation and observation can be ascribed (i) to patchiness obscuring the field observations, (ii) to imprecision in the driving factors of the ecosystem model (i.e. temperature and food concentration) and (iii) to intrinsic and/or extrinsic factors driving population dynamics that are currently not implemented in the population model. Although the first two factors should not be underestimated, we here concentrate on the comparison between observations and simulations to identify factors driving population dynamics.

Temperature effects

Temperature is a key factor driving population dynamics of copepods (Huntley and Lopez, 1992). In the model, temperature impacts are realized by temperature-dependent physiological rates (ingestion, catabolism, anabolism), which determine growth rates, which in turn determine stage duration. However, laboratory data indicate a differential effect of temperature on the rates of
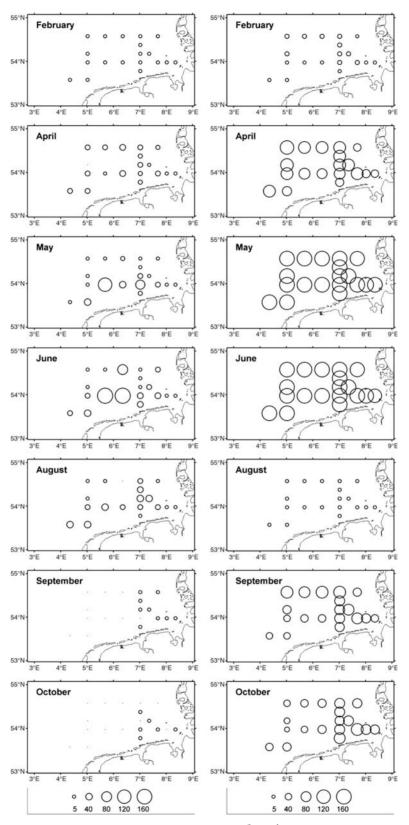
Fig. 9. Spatial distribution of the secondary production of *P. elongatus* (mg C m^{-2} day^{-1}) estimated from field data (re-drawn after Renz *et al.*, 2008) (left) and from model results (right).

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Table IV: Generation times of P. elongatus *at different mean* in situ *temperatures as derived from length-frequency data of females at six stations (left column) as given in Renz* et al. *(Renz et al., 2008), from simulations (middle) at station 32 and from data by Klein Breteler* et al. *(Klein Breteler et al., 1995) for laboratory reared* P. elongatus *at fixed temperature/food scenarios (right)*

| Month | Estimated generation time (days) | | |
	Field observation (6 stations)	Model simulation (station #32)	Klein Breteler *et al.* (1995) lab expts
February	59 (5°C, 75 µg C L^{-1})	66 (5°C, 87 µg C L^{-1})	71 (5°C, 77 µg C L^{-1})
April	26 (7°C, 100 µg C L^{-1})	44 (8°C, 225 µg C L^{-1})	33 (10°C, 91 µg C L^{-1})
June	33 (12°C, 225 µg C L^{-1})	31 (14°C, 176 µg C L^{-1})	31 (10°C, 363 µg C L^{-1})
August	37 (17°C, 75 µg C L^{-1})	41 (19°C, 142 µg C L^{-1})	32 (15°C, 59 µg C L^{-1})

growth and development (Vidal, 1980). Growth rates seem to become more temperature-independent with increasing body size of copepods, while development rates remain proportional to temperature. This means that copepodids, which grow at low temperatures, will experience greater weight increments between moulting periods, since stage duration is longer at low temperature. This is also reflected in the observed seasonal length variations for *P. elongatus* in the North Sea. An incorporation of a temperature-dependent dynamic length/mass variation would influence the stage durations, leading to longer generation times in the colder season, when mean masses are higher. This might adjust underestimated generation times at low temperatures in February (Table IV).

The slow simulated development at several stations in August was caused by metabolic losses resulting in longer stage durations at high temperatures. Such an inhibition of development was also observed in our field data. Klein Breteler *et al.* (Klein Breteler *et al.*, 1995) found that developmental times at 20°C did not proceed faster than at 15°C in laboratory experiments, which points towards physiological stress. Applying their temperature-dependent development to *P. elongatus* at the lower chlorophyll concentrations observed at that time also resulted in longer generation times comparable with those approximated by field data or derived from model simulations (Table IV).

Food effects
Copepod recruitment and its related parameters in the simulation (i.e. hatching success, number of spawning females, maximum invested matter) are influenced by a variety of factors. While some (e.g. food quantity, temperature) can be assessed well in the model, others are less well studied and their influence is not completely understood yet (age of females, food quality). These factors might temporally or spatially dominate recruitment patterns. Our methods to measure egg production and hatching success are widely used. The observed seasonal variability in EPR of *P. elongatus* in the field could partly be explained by

variation in the proportion of spawning females, which in turn was related to food concentration (Chl *a*; Renz *et al.*, 2008). In contrast, maximum invested matter or hatching success showed a large variability in space and time, probably caused by undetermined environmental conditions. Insufficient food quality or deleterious effects of diatoms, as reported for *P. newmani* by Lee *et al.* (Lee *et al.*, 1999) might influence hatching success but cannot be assessed in a model like the one presented here. In order to evaluate the importance of food quality on seasonal and regional changes in recruitment processes, more detailed studies and mechanistic understanding will be needed. However, while we found indications that these processes might play an important role regionally, they seem to be of less importance at the larger population scale.

Mortality
Observed total abundance as well as abundance of single stages was subject to a high spatial variability. This spatial variability was not always reflected in the simulation. According to the model, temperature and food conditions would have allowed for larger numbers of *P. elongatus* especially in the northwestern part. This might indicate a spatial variability in factors that can so far only be roughly approximated in the model parameterization, e.g. mortality. Mortality is a crucial factor controlling population dynamics (Uye *et al.*, 1992; Ohman and Wood, 1995; Ohman *et al.*, 1996; Hirst and Kiørboe, 2002) and is therefore an important measure to realistically simulate life-cycle dynamics in population models. However, there are only few studies that have investigated the variability in mortality in the field. Earlier field studies assumed mortality to increase with increasing length or stage (Miller and Tande, 1993), while studies found mortality to be bimodal within a population (Twombly, 1994; Ohman and Wood, 1996), density (Ohman and Hirche, 2001), food (Paffenhöfer, 1970), temperature (Tande, 1988; Ji *et al.*, 2009) or predator-dependent. The latter is considered a major contribution to mortality in copepods (Ohman, 1986; Hirst and Kiørboe, 2002). Thus, temporal and spatial variability in the distribution of

predators in the North Sea (e.g. schools of clupeid) might also explain the differences between high mean mortality derived from field data and low rates estimated by Eiane and Ohman (Eiane and Ohman, 2004). However, despite spatial discrepancies between simulated and observed abundances, their temporal variability in the seasonal cycle was quite similar in each grid box.

Life cycle characteristics of *P. elongatus* in the German Bight

While the overall simulation-derived number of generations (5−6 in the German Bight) resembled those interpreted from length-frequency data of females (4−5), the phenology of generations differed strongly. The overwintering parameterization together with the general definition of a generation in the simulation led to a fast development of the first generation at the beginning of the year and the first newly produced adults mid February. However, the onset of the main reproduction in February/March (Halsband and Hirche, 2001), low food concentration until March and slow development at low temperatures (Klein Breteler et al., 1995), suggests that the first generation occurred more likely in April as also indicated by the field data.

Secondary production and the role of *P. elongatus* in the food web

The estimation of copepod secondary production is one of the most important aims in marine ecology, elucidating the amount of energy, which is transferred within communities and ecosystems and provided for higher trophic levels. The secondary production of *Pseudocalanus* spp. plays a key role in the trophic ecology of northern temperate and subarctic waters (Corkett and McLaren, 1978). The estimated secondary production of *Pseudocalanus* sp. was $52 \, \mathrm{mg \, C \, m^{-3} \, year^{-1}}$ on Georges Bank (Davis, 1984) and $> 70 \, \mathrm{mg \, C \, m^{-3} \, year^{-1}}$ in the Gulf of Alaska (Napp et al., 2005) being comparable with the production of large copepods such as *Calanus finmarchicus* or *Neocalanus* sp., respectively.

Heath (Heath, 2005) calculated an average secondary production by omnivorous zooplankton in the North Sea of $35 \, \mathrm{g \, C \, m^{-2} \, year^{-1}}$ based on the temperature relationship of Huntley and Lopez (Huntley and Lopez, 1992), while annual copepod production in the southern North Sea was estimated to be at least $12 \, \mathrm{g \, C \, m^{-2} \, year^{-1}}$ in the Dutch coastal zone as opposed to $5−10 \, \mathrm{g \, C \, m^{-2} \, year^{-1}}$ in the offshore region (Fransz and Gieskes, 1984). Based on field and model data, we estimated for *P. elongatus* an annual production of ca $10 \, \mathrm{g \, C \, m^{-2}}$, which indicates a contribution of at least one-third to the copepod production in the southern North Sea. This as well as maximum values up to $120 \, \mathrm{mg \, C \, m^{-2} \, day^{-1}}$ in late spring and early summer implies that *P. elongatus* is a large contributor to the energy transport from lower to higher trophic levels. High abundances of *Para-/Pseudocalanus* as well as *Calanus* seem to co-occur with abundant cod and herring year-classes in the North Sea (Rothschild, 1998), suggesting both to be important items in the nutrition of commercially exploited fish.

Many zooplankton species in the North Sea have exhibited pronounced changes in abundance since the regime shift in the late 1980s (Reid and Edwards, 2001). Greve et al. (Greve et al., 1996) reported an initially increasing biomass of the *Para-/Pseudocalanus* group in the beginning of the 1980s followed by a decrease in this group between 1988 and 1994. Unfortunately, they did not distinguish between species and a direct effect on *P. elongatus* alone cannot be verified (Valdes et al., 2006). During our study, mean annual abundance of *P. elongatus* in bongo net hauls with a comparable mesh size was in the lower range of the observed mean annual abundances of the *Para-/Pseudocalanus* group at Helgoland Roads between 1988 and 1995 (Greve et al., 1996) but well in the range reported by previous studies in different locations of the North Sea (Lücke, 1912; Krause and Trahms, 1983; Krause et al., 1995).

Status and perspectives for population modelling

Validation

The comparison of simulation and observation revealed the deviation of the model. The question is: how good can and should a model capture observed data? We chose 1 order of magnitude as the targeted range as this is the range phytoplankton biomass is represented compared with climatological data in present state ecosystem models (Radach and Moll, 2006).

In the population model, we assume the functional response of vital rates to mainly depend on temperature and food abundance as used in other copepod models (Carlotti and Nival, 1992). However, there are numerous indications that population dynamics of copepods can be significantly influenced by often unknown environmental or internal triggers, e.g. reaching thresholds in temperature, light periodicity, food quantity or quality, energy reserves, which can happen temporarily on a small scale. As a result comparison becomes more difficult when narrowing any of the structural (functional unit to species to stage), the spatial

or the temporal scale on which the comparison is made. While 72% of all simulated single-stage data were within 1 order of the observations, >80% of simulation data were within this range when comparing the total copepodid abundance (sum of CI–VI) or comparing the sum over all stations for each stage. Further, model data show stronger fit when compared with climatological data, rather than to single years as found for a model validation in the Northwest Atlantic Ocean using the 30-year MARMAP data set (C. Stegert, personal communication). Thus, the description presented of the population model is capable of giving reasonable results for the whole region of the German Bight, while the capability to capture local variability is likely limited by the horizontal resolution of the ecosystem model. Though advection is assumed to influence local abundances, the large amount of secondary production indicates that local processes contribute significantly in shaping the population.

Key processes for future research
Mortality is found to be one major process, which needs elaborate investigation. In our model setup, we used a constant stage-specific rate as introduced in Carlotti *et al*. (2000), including reduced rates at low abundances. However, the strong variability indicates that this is not sufficient. Recent model studies (Ji *et al*., 2009; Plourde *et al*., 2009) have shown that the relation with temperature is capable of rendering the seasonal variability, assuming grazing rates of potential predators to increase with temperature. More data are needed to obtain confident estimates, which can be used in population models.

Another parameter recently discussed is overwintering and the choice of initial conditions (Daewel *et al*., 2008). Copepods of the genus *Pseudocalanus* are known to arrest development during autumn, and usually overwinter as CIII (Conover and Siferd, 1993; Lischka and Hagen, 2005), CIV and CV (Davis, 1976; McLaren *et al*., 1989; Norrbin *et al*., 1990; Renz *et al*., 2007). The parameterization of overwintering was realized in the model by limited reproduction in winter restricted by low food conditions and by preventing the dying off of the population by holding a lower threshold of 1000 ind. m^{-2}, so that individuals were summed in the model stage group for adults. As the field study was performed between February and October, only limited information about overwintering stages is available. Although in winter female *P. elongatus* are known to still reproduce in the North Sea (Halsband and Hirche, 2001) and the genus might be able to fuel reproduction at least partly from lipid reserves (Peters *et al*., 2006), the large numbers of

nauplii simulated in autumn are not realistic. Further consequences of this parameterization are most likely the lower number of younger copepodids in the simulations at the beginning of the year and the discrepancies between low simulated, but high observed, numbers of copepodids during summer. Though the simplified overwintering parameterization seems to have minor influence on the population development during summer the effect of initial distributions should be considered in further investigations.

CONCLUSION

Our study further corroborates the idea that stage-resolving population models have the potential to analyse population dynamics of copepods, to produce a quantitative, regional description and to assess variations in recruitment. The temporal resolution produced by such a model cannot be achieved by field observations, and thus the model provides a useful tool for the interpretation of population dynamics and a valuable supplement to field studies.

Recent publications show the reaction of some copepod species to environmental factors to be subject to intra-specific variability due to adaptive phenotypic plasticity (Avery, 2005). We found further improvement of the model by implementing population-specific process data from field experiments (i.e. parameterization of reproduction and mortality). This points towards the importance of species and area-specific parameterization of life cycle processes to simulate population dynamics of copepod species as accurately as possible. Further improvements should include a dynamic mortality term (e.g. due to fish predation) and a temperature-dependent length (and mass) variation over the season. However, much more detailed field studies will be needed to provide a more accurate and comprehensive *in situ* measurement of key processes and vital rates as well as a better understanding of species and genus-specific life-cycle characteristics (e.g. overwintering).

SUPPLEMENTARY DATA

Supplementary data can be found online at http://plankt.oxfordjournals.org.

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